

A COMPARISON OF PHENOTYPIC VARIATION AND COVARIATION PATTERNS AND THE ROLE OF PHYLOGENY, ECOLOGY, AND ONTOGENY DURING CRANIAL EVOLUTION OF NEW WORLD MONKEYS

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Abstract.—Similarity of genetic and phenotypic variation patterns among populations is important for making quantitative inferences about past evolutionary forces acting to differentiate populations and for evaluating the evolution of relationships among traits in response to new functional and developmental relationships. Here, phenotypic covariance and correlation structure is compared among Platyrrhine Neotropical primates. Comparisons range from among species within a genus to the superfamily level. Matrix correlation followed by Mantel's test and vector correlation among responses to random natural selection vectors (random skewers) were used to compare correlation and variance/covariance matrices of 39 skull traits. Sampling errors involved in matrix estimates were taken into account in comparisons using matrix repeatability to set upper limits for each pairwise comparison.

Results indicate that covariance structure is not strictly constant but that the amount of variance pattern divergence observed among taxa is generally low and not associated with taxonomic distance. Specific instances of divergence are identified. There is no correlation between the amount of divergence in covariance patterns among the 16 genera and their phylogenetic distance derived from a conjoint analysis of four already published nuclear gene datasets. In contrast, there is a significant correlation between phylogenetic distance and morphological distance (Mahalanobis distance among genus centroids). This result indicates that while the phenotypic means were evolving during the last 30 millions years of New World monkey evolution, phenotypic covariance structures of Neotropical primate skulls have remained relatively consistent.

Neotropical primates can be divided into four major groups based on their feeding habits (fruit-leaves, seed-fruits, insect-fruits, and gum-insect-fruits). Differences in phenotypic covariance structure are correlated with differences in feeding habits, indicating that to some extent changes in interrelationships among skull traits are associated with changes in feeding habits. Finally, common patterns and levels of morphological integration are found among Platyrrhine primates, suggesting that functional/developmental integration could be one major factor keeping covariance structure relatively stable during evolutionary diversification of South American monkeys.

Key words.—Cranial morphology, developmental modularity, morphological integration, phenotypic covariance structure, phylogeny, Platyrrhini, quantitative genetics.

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Patterns of correlation and/or variance-covariance (V/CV) among traits play a critical role in evolutionary processes with implications for quantitative genetics, systematics, phylogenetic analysis, and population genetics (Thompson 1961; Wright 1968; Stearns 1992; Price et al. 1993; Roff 1996a; Lynch and Walsh 1998). For example, when attempting to establish phylogenetic relationships among any group of taxa or studying geographic variation patterns, one should be aware of correlation between morphological characters (Emerson and Hastings 1998). Thus, if the particular suite of chosen traits is highly correlated, common or congruent patterns of variation could reflect some smaller number of underlying factors that produce the covariance structure. Covariance or correlation structure as used here refers to the patterns of covariation among traits as well as to the level (magnitude) of variation or correlation among traits. Any correlation or V/CV matrix, with nonuniform elements, variances, covariances, or correlations, presents a pattern. These

patterns are thought to represent the morphological integration of related trait complexes.

Morphological integration refers to the relationships and connections among morphological elements (Waddington 1957; Olson and Miller 1958; Chernoff and Magwene 1999). Three forms of morphological integration have been recognized: functional/developmental, genetic, and evolutionary integration (Cheverud 1996a). Functional/developmental integration refers to the interaction of morphological elements in the performance of some function or developmental process. Genetic integration, represented by the genetic V/CV matrix, refers to the common inheritance of traits arising from linkage disequilibrium or pleiotropy. Evolutionary integration refers to the coordinate evolution of elements contained within functional complexes. These three forms of morphological integration are linked (Cheverud 1996a). Quantitative genetic models (Lande 1980; Cheverud 1984; Wagner 1996) predict that the coordinate selection of traits involved in a common function or developmental process will lead to coinheritance of these traits, whereas functionally/developmentally unrelated traits will be relatively uncorrelated (Cheverud 1996a). The patterns of genetic variation and covariation produced by pleiotropic mutations and stabilizing (canalizing)

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selection (Waddington 1957) for functionally and developmentally interacting traits results in their specific coinherence relative to other traits. This coinherence leads to their coordinated response to selection. Therefore, functional and developmental integration at the individual level leads to genetic integration at the population level, which, in turn, leads to evolutionary integration (Cheverud 1996a). Of course, the genetically based developmental system could evolve (Raff 1996), making a final link between the evolutionary and functional/developmental integration and filling a circle interconnecting the three morphological integration types. We are concerned here not so much with the evolution of cranial morphology in the New World monkeys as with the potential evolution of the relationships between traits. If such evolution has occurred, it has profound implications for morphological evolution in divergent clades because the same selection pressures will lead to diverse coordinated morphological responses.

The evolutionary response of a set of quantitative traits is described by the equation $\Delta\bar{z} = G\beta$, where $\Delta\bar{z}$ is the vector of differences in means between generations, β is the selection gradient vector, and G is the additive genetic V/CV matrix (Lande 1979). Rearranging the evolutionary response equation, the pattern of selection responsible for species differences can be reconstructed from observed mean differences using the following relationship $\beta = G^{-1}(\bar{z}_i - \bar{z}_j)$, where β is the cumulative differential selection gradient summed over generations, G^{-1} is the inverse of the average within-species genetic V/CV matrix, and $(\bar{z}_i - \bar{z}_j)$ is the difference in means between species i and j (Lande 1979; Lofsvold 1988; Cheverud 1996b). This relationship is identical to that for a two-group linear discriminant function (Blackith and Reymont 1971), and therefore the selection gradient coefficients of Lande's (1979) model are genetic linear discriminant function coefficients. Although this equation was first developed for application to microevolutionary time scales (typically a few generations), it could be extended to macroevolutionary time scales under some conditions. In particular, selection reconstruction analysis, like any discriminant analysis, assumes homogeneity of within-group V/CV patterns. The within-group additive genetic V/CV matrix (G) should remain constant, or at least proportionally constant, whereas the mean phenotype evolves (Lande 1979; Turelli 1988a). It is unclear the extent to which this assumption can be relaxed in practice. For discriminant function analysis, moderate deviations from homogeneity do not have serious consequences (Klecka 1980). Blackith and Reymont (1971, p. 50) stated, "Providing the heterogeneity [among V/CV matrices] is not grotesquely manifested, little harm is done in performing the calculations in the usual way." According to Manly (1986, p. 29), "A moderate difference between population covariance matrices is . . . not too important" in a discriminant function analysis.

Substantial efforts have been devoted to evaluating the relative constancy of G during evolution (Arnold 1981; Lofsvold 1986; Cheverud 1988; Kohn and Atchley 1988; Wilkinson et al. 1990; Shaw et al. 1995; Roff 1996a,b). However, a generalization remains difficult because these studies differ in experimental and statistical approaches (Shaw et al. 1995).

Unfortunately, although theoretical models referring to the maintenance of inherited variation in continuous traits have been developed (Kimura 1965; Lande 1976, 1980; Turelli 1984, 1985), the expected constancy or proportionality of additive genetic matrices (G) remains unclear because the expected outcome differs according to the untested assumptions underlying the models. Some of these models suggest that a mutation-stabilizing selection balance could maintain additive genetic V/CV patterns at equilibrium (Lande 1979, 1980), whereas other models (Turelli 1984, 1988a,b; Barton and Turelli 1989) suggest that patterns of genetic variation and covariation should be quite labile. The question of stability or disparity in V/CV patterns remains an empirical one that should be addressed by broad-scale empirical comparisons of patterns (Turelli 1988a,b; Arnold 1992; Steppan 1997).

Accurate measures of G for sets of morphological traits are often difficult or impossible to obtain, making judgments about their consistency over evolutionary time difficult. In contrast, phenotypic (P) matrices can be estimated with far more confidence. When G is unavailable, the phenotypic V/CV matrix may be confidently substituted for its genetic counterpart if P is similar or at least proportional to its genetic counterpart. If this latter assumption holds, selection reconstruction analyses are greatly simplified, because P matrices are much easier to obtain and estimated with far more confidence than G matrices (Cheverud 1988, 1996b; Roff 1995, 1996a). Studies evaluating the constancy or proportionality of genetic and phenotypic correlation matrices for morphological traits suggest that phenotypic patterns are generally a good estimate of their genetic counterparts (Arnold 1981; Atchley et al. 1981; Cheverud 1988, 1995, 1996b; Kohn and Atchley 1988; Venable and Búrquez 1990; Roff 1995, 1996b; Arnold and Phillips 1999). However, significant dissimilarity in specific correlations or differences in levels and patterns of genetic variance across taxa have also been pointed out by some authors (Arnold 1981; Atchley et al. 1981; Lofsvold 1986; Willis et al. 1991; Paulsen 1996). Because the G matrix is the result of gene frequencies and allelic effects at all loci influencing the characters, at some point during evolutionary divergence additive genetic patterns should change, at least to some extent. The question is at what points during this process of change the P matrix remains a reasonable guide to the G matrix?

It seems likely that comparisons of P among taxa can stand in for comparisons of G , especially for morphological traits. Assuming additive and independent sets of genetic and environmental factors, the phenotypic covariance between characters is equal to the sum of their genetic and environmental covariances. Therefore, constancy of phenotypic covariance is unlikely without constancy of genetic covariation if the latter is a substantial component of the former (Lande 1979), as usually is the case for morphological characters. If phenotypic patterns are found to be relatively stable among species or even higher taxa (genera or families), the most probable explanation is that genetic covariance matrices are also stable. The alternative explanation is that environmental effects react to genetic patterns to compensate and mask changes in the genetic system, producing the observed relative stability of the phenotypic patterns. Such compensation

seems unlikely. Arnold and Phillips (1999) found diversity in genetic but not environmental covariance matrices for garter snake meristic traits, indicating a lack of compensation in their study. Patterns of phenotypic correlation have been compared across populations and species in studies for which genetic comparisons were unavailable. The usual finding is that phenotypic correlation structures are stable (Riska 1985; Cheverud 1989, 1996b; Wagner 1990; Voss et al. 1990; Zelditch et al. 1990; Voss and Marcus 1992; Steppan 1997; Ackermann and Cheverud 2000), even though some variability in correlation patterns has also been noted (Zelditch et al. 1990; Voss and Marcus 1992; Steppan 1997; Ackermann and Cheverud 2000).

Given variation in V/CV patterns among taxa, we may consider which factors are responsible for changes in covariance structure and how might these factors influence the stability of genetic and phenotypic correlation patterns. Specifically, it is possible that phylogenetic, ecological, and developmental factors affect patterns of variation. This study thoroughly samples the evolutionary history of the New World monkeys and compares phenotypic correlation and variance/covariance patterns among 40 species within nine different genera and among 16 genera, six subfamilies, four families, and two superfamilies within the infraorder Platyrrhini. New World monkeys form a distinct group, Platyrrhini ('flat nose'), that differ in many features from the Old World monkeys, the Catarrhini. These two infraorders combine to form the suborder Haplorrhini of the order Primates.

Platyrrhines are primarily diurnal (except the night monkeys, *Aotus*, with nocturnal habits) and arboreal, living in tropical and subtropical forests ranging from Mexico to Argentina. Despite being primarily forest inhabitants, New World monkeys live in a vast range of forest types (from flooded forests in the Amazon to secondary-growth forests and mountain forests in eastern Brazil), feed on several types of animal and vegetal items, and have complex and distinctive mating systems (Norconk et al. 1996; Kinsey 1997). These differences in habitats and habits are reflected in their distinct morphologies, with changes in size and shape of the body and in particular in the cranium (see Hershkovitz 1977).

The smallest adult Platyrrhine, the pygmy marmoset (*Cebuella*), is only 150 mm long (head and body) and weighs 150 g, whereas the largest (muriqi or woolly spider monkey) is 630 mm long and weighs 100 times more (around 15 kg). Food types consumed and their relative proportions in Neotropical primate diets are relatively well established for all living genera (Coimbra-Filho and Mittermeier 1981; Mittermeier et al. 1988; Norconk et al. 1996; Kinsey 1997), although detailed species-specific dietary studies are still needed and dozens of species' diets remain unknown. Neotropical primates are extremely diversified and share a complex biogeographical history (Marroig and Cerqueira 1997). Their diet comprises all sorts of food items, from fruits, seeds, insects, and small vertebrates to gums, flowers, and leaves. Some are specialized to eat seeds (the Pitheciines), whereas others primarily eat fruits and leaves (the Atelides). Available dietary information allows this ecological factor to be considered relative to V/CV matrix variability.

Evolutionary relationships among the New World monkeys are relatively well established, at least at the genus level (see

Schneider et al. 1993, 1996; Schneider and Rosenberger 1996; Barroso et al. 1997) and molecular data are available to represent their phylogenetic pattern. Although different datasets are not totally congruent and some disagreement about details of the Platyrrhine tree exists, there is an emerging consensus about their major phylogenetic groups (Schneider and Rosenberger 1996). Five complete or nearly complete gene datasets with all genera represented have been analyzed in recent years (Schneider et al. 1993, 1996; Canavez et al. 1999; Horovitz 1999; von Dornum and Ruvolo 1999). With the exception of the 16S rRNA analyses that was based on only 12 of the 16 genera, the other four analyses support three major Platyrrhine clades: a Pitheciini clade (with *Cacajao*, *Pithecia*, and *Chiropotes*), an Atelini clade (with *Brachyteles*, *Lagothrix*, *Ateles*, and *Alouatta*) and a Callitrichinae clade (with *Callithrix*, *Cebuella*, *Callimico*, *Leontopithecus*, and *Saguinus*). These analyses disagree on the branching order between these three major clades and that within the ateline and callitrichine clades (von Dornum and Ruvolo 1999; Schneider 2000). The placement of four genera (*Cebus*, *Saimiri*, *Aotus*, and *Callicebus*) is also variable across these analyses.

Another potential source of stability/dissimilarity in covariance structure is functional/developmental relationships among traits. The cranium is a particularly useful region to consider morphological integration because of the complexity of its growth and the several functions served by the various organs of the head. Although these several functions, such as olfaction, vision, respiration, mastication, and deglutition, may be generally distinct, they are served by a series of interconnected or even common organ systems necessitating integration of otherwise disparate parts. A common result from previous studies is that morphological integration of the cranium relates, in part, to functional and developmental process (Cheverud 1982, 1989, 1995, 1996b; Zelditch and Carmichael 1989; Zelditch et al. 1990; Chernoff and Magwene 1999; Ackermann and Cheverud 2000). One possible approach to understanding how ontogeny shapes cranial covariance patterns is a comparative analysis of empirical patterns of growth in several related organisms (Garber and Leigh 1997). Another approach is to consider information relative to cranial development and pattern of growth to predict observed patterns of integration. Cheverud (1995) reviewed information related to general development patterns in Eutherian skulls (see also Smith 1996, 1997) in terms of hormonal influence, embryonic origin, tissue interactions, and modes of ossification. These data were used to predict interrelationships among 39 skull measurements, the same characters used in this study, translating developmental information into theoretical connectivity matrices among traits. These predicted patterns of association were then compared to observed correlation matrices to test the hypothesis that functional/developmental integration contributes to morphological integration. Here we follow the same approach, comparing predicted patterns of correlation among skull traits to observed ones to determine whether shared developmental patterns are a source of morphological integration and covariance stability across species and genera of Platyrrhini.

In this study, we report on a broad-scale comparison of correlation and V/CV patterns among New World monkey

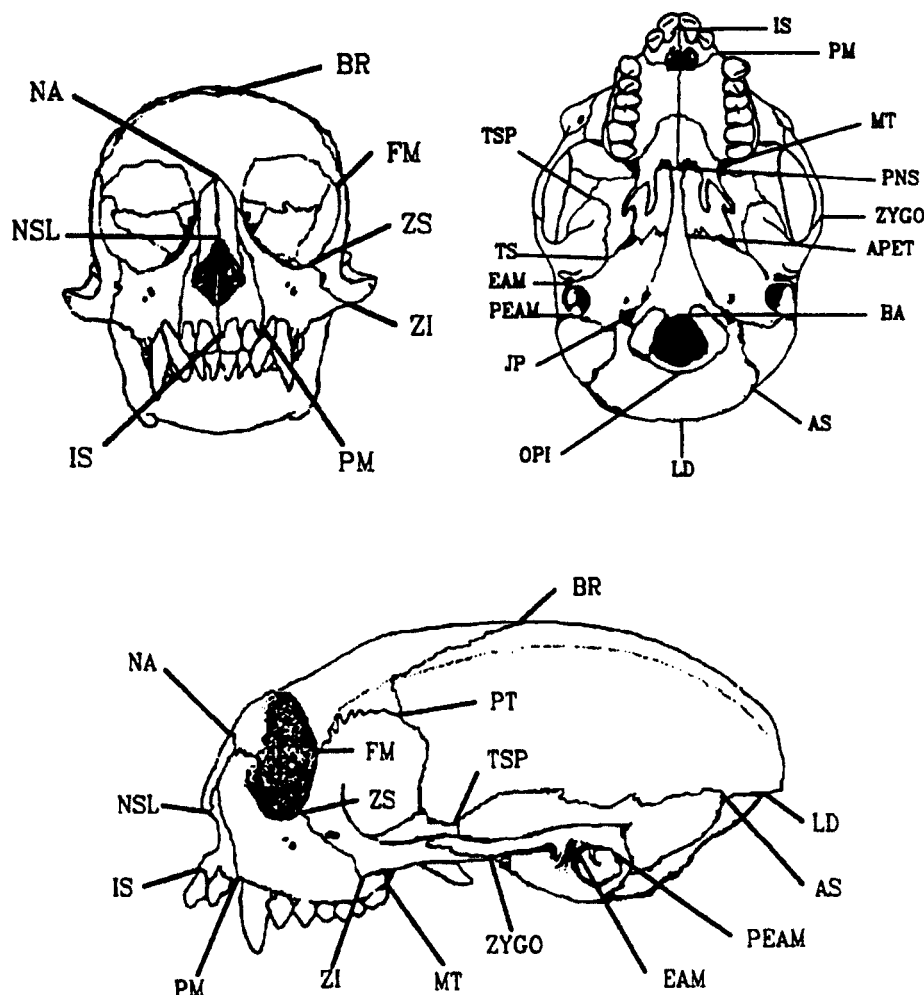


FIG. 1. Craniofacial landmarks recorded from New World monkeys skulls using three-dimensional digitizer. Refer to Table 1 for description of landmarks.

(Platyrrhini) crania. Patterns of correlation and covariance are compared at several taxonomic levels, from species within genus to superfamilies, and the roles played by the history (phylogeny), ecology (diet), and shared developmental basis (functional/developmental integration) on the evolution of these patterns are examined.

MATERIALS AND METHODS

Sample, Measurements, and Repeatability

More than 10,000 specimens of Platyrrhini were examined, and measurements obtained from 5222 crania deposited at the following institutions: American Museum of Natural History (AMNH); British Museum of Natural History (BMNH); Field Museum of Natural History (FMNH); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional do Rio de Janeiro (MNRJ); Museu Paranaense Emílio Goeldi (MPEG); National Museum of Natural History (USNM); and University of Tennessee, derived from the Marmoset Research Center, Oak Ridge Associated Universities' colonies (ORAU). A complete list of examined specimens may be obtained from the authors upon request. The Appen-

dix presents the taxonomic arrangement employed and sample sizes for each taxon. Only adult crania were used in the subsequent analyses. Specimens were considered adult when they had totally erupted and functional dentition as well as closed or fused sphenoccipital and/or sphenothmoid sutures.

Three-dimensional coordinates were recorded for 36 landmarks (Fig. 1) using a Polhemus 3Draw digitizer (Colchester, VT.) The general procedure for measuring specimens follows Cheverud (1995). A set of 70 linear measurements describing cranial morphology was calculated from the coordinate values. This set was reduced to a 39 measurement set, averaging the measurements present on both sides of the skull (Tables 1, 2). Whenever one of the skull sides was damaged, preventing us from taking any particular measurement, the other side is used as the average. All measurements are presented in millimeters. These 39 measurements are classified in functional/developmental groups (Table 2) following Cheverud (1995).

A subsample of about 25% of the specimens was measured twice. Most of these specimens were from the genus *Saguinus* but an additional 225 specimens from other genera were also

TABLE 1. Landmarks recorded in Neotropical primates skulls using a three-dimensional digitizer. The designation A (anterior) or P (posterior) after the landmark name indicates which position(s) the landmark was recorded in. Landmarks are also identified in Figure 1.

Landmark	Description	Position(s)
IS	intradentale superior, A	midline
PM	premaxillary suture at the alveolus, A	right, left
NSL	nasale, A	midline
NA	nasion, A	midline
BR	bregma, AP	midline
PT	pterion, AP	right, left
FM	fronto-malare, A	right, left
ZS	zygomaxillare superior, A	right, left
ZI	zygomaxillare inferior, A	right, left
MT	maxillary tuberosity, A	right, left
PNS	posterior nasal spine, A	midline
APET	anterior petrous temporal, A	midline
BA	basion, AP	midline
OPI	opisthion, AP	midline
EAM	anterior external auditory meatus, A	right, left
PEAM	posterior external auditory meatus, A	right, left
ZYGO	inferior zyo-temporal suture, A	right, left
TSP	temporo-spheno-parietal junction, A	right, left
TS	temporo-sphenoidal junction at the petrous, AP	right, left
JP	jugular process, AP	right, left
LD	lambda, P	midline
AS	asterion, P	right, left

measured in duplicate. Because each cranium was measured twice in this subsample, repeatability, the proportion of the total variance due to individual differences rather than measurement error (Falconer 1989), was estimated. The average of repeated measures was used for further analysis. Repeatabilities for *Saguinus* were reported elsewhere (Cheverud 1995, 1996b; Ackerman and Cheverud 2000), and therefore we report these results only for the other Platyrrhine genera.

Taxonomy

The Appendix presents the taxonomic arrangement used for Platyrrhini and species recognized in this study (Fooden 1963; Hershkovitz 1977, 1983, 1984, 1985, 1987a,b, 1990; Froehlich et al. 1991; Vivo 1991). Although this arrangement is still open to dispute, particularly in relation to higher taxa and some genera need taxonomic review, the arrangement is an attempt to translate the evolutionary history of the group in to a phylogenetically informed classification (see Horovitz 1999). We recognize that *Cebuella* should be considered as another species (or group of species) inside the genus *Callithrix*, as suggested by Barroso et al. (1997), but because pygmy marmosets represent a unique morphology within the Platyrrhini and an important evolutionary event in its history, we prefer to maintain it as a separate taxon in this study and identify it by its traditional designation. The objective of keeping *Cebuella* separate from *Callithrix* is to study the possible changes in covariance structure resulting from the reduced size of *Cebuella*.

Correlation and Covariance Patterns and Levels

Pooled within-group phenotypic correlation and variance/covariance matrices (below referred to as correlation or co-

TABLE 2. 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 1 shows their locations in a generalized Platyrrhini skull.

Measurement	Functional/developmental group(s)	Region
IS-PM	oral	face
IS-NSL	nasal	face
IS-PNS	oral, nasal	face
PM-ZS	oral	face
PM-ZI	oral	face
PM-MT	oral	face
NSL-NA	nasal	face
NSL-ZS	nasal	face
NSL-ZI	oral, nasal	face
NA-BR	cranial vault	neurocranium
NA-FM	orbit	neurocranium
NA-PNS	nasal	face
BR-PT	cranial vault	neurocranium
BR-APET	cranial vault	neurocranium
PT-FM	orbit	neurocranium
PT-APET	cranial vault	neurocranium
PT-BA	cranial vault	neurocranium
PT-EAM	cranial vault	neurocranium
PT-ZYGO	zygomatic	face
PT-TSP	cranial vault, zygomatic	neurocranium, face
FM-ZS	orbit	neurocranium
FM-MT	zygomatic	face
ZS-ZI	oral	face
ZI-MT	oral	face
ZI-ZYGO	zygomatic	face
ZI-TSP	zygomatic	face
MT-PNS	oral	face
PNS-APET	cranial base	neurocranium
APET-BA	cranial base	neurocranium
APET-TS	cranial base	neurocranium
BA-EAM	cranial base	neurocranium
EAM-ZYGO	zygomatic	face
ZYGO-TSP	zygomatic	face
LD-AS	cranial vault	neurocranium
BR-LD	cranial vault	neurocranium
OPI-LD	cranial vault	neurocranium
PT-AS	cranial vault	neurocranium
JP-AS	cranial base	neurocranium
BA-OPI	cranial base	neurocranium

variance matrices, for simplicity) were estimated for each genus using the general linear model SYSTAT 7.0 (SPSS, Inc., Chicago, IL.) routine to control for sexual dimorphism and species differences whenever appropriate. The same procedure was used to calculate residual Pearson product moment correlation/covariance matrices for each species with a large enough sample size (at least 40 specimens) and to control for sexual or subspecific variation.

Patterns of correlation and covariation were compared using matrix correlations and a random skewers method, respectively. Statistical significance of matrix and vector correlation was evaluated using randomization tests. Correlation-pattern similarity among matrices at the same taxonomic level was measured by a matrix correlation with a Mantel's test for statistical significance. The matrix correlation is a measure of the strength of association among matrices varying from -1.0 to $+1.0$. A matrix correlation of $+1.0$ indicates identity of correlation pattern between the matrices, although overall magnitude of correlation may still differ. A matrix correlation of zero indicates no structural

similarity among the matrices, and a matrix correlation of -1.0 specifies matrices that are mirror images. The significance test is performed by comparing the observed matrix correlation to an empirically derived distribution of 10,000 matrix correlations produced by randomly reordering the rows (and associated columns where appropriate) of one matrix and correlating the randomized matrix with the reference matrix (Cheverud et al. 1989). If the observed correlation exceeds 95% of the random correlations, the patterns are considered significantly similar. Shaw (1991, 1992) suggested that the permutation test could not be done with correlation matrices because the traits were not commensurate identities that could be shuffled at random. However, under the null hypothesis of no structure similarity, traits are commensurable identities with regard to their relationships with one another. Correlation magnitude in each matrix is measured as the average of the squared Pearson product moment correlation coefficients (r^2).

Variance/covariance matrices are compared using a modification of a random skewers method in which the simulated evolutionary responses of each of a pair of matrices to random selection vectors are compared (Pielou 1984; Manly 1991; Willis et al. 1991; Cheverud 1996b). In this procedure, a random selection gradient vector, to be used as a skewer, is generated and normalized to a length of one. This vector is then applied to each of the covariance matrices being compared using the multivariate response to selection equation to obtain expected evolutionary response vectors for comparison. The directions of evolution specified by each covariance matrix in response to the random selection vectors are compared using the vector correlation between the paired expected responses. Because each multivariate dimension specified by a given selection differential could produce different results, the procedure is repeated to randomly sample the dimensions of multivariate morphometric space. The average vector correlation between responses to 1000 random selection vectors is used here as a measure of the similarity among the matrices. This analysis provides a measure of the degree of similarity among covariance matrix patterns. Vector correlations will be 1.0 when matrices are identical or proportional and will decrease to zero when matrices lack a common structure. This is a measure of association, not a significance test. The statistical significance of this vector correlation is determined by the distribution of correlations among random vectors. For 39 element vectors, as used here, vector correlations greater than 0.35 are significantly greater than zero.

The significance tests performed here consider the null model of no similarity among matrices. Others have preferred to test the null hypothesis of equality because, formally, that is the assumption made in evolutionary systematic comparative studies (Shaw 1991, 1992; Phillips and Arnold 1999). However, we believe that more emphasis should be placed on the measures of association than on the tests of significance for null hypotheses of no similarity or identity. From the perspective of quantitative genetic theory, we expect covariance matrices to change whenever allele frequencies change or diverge from one population to another. In nature, covariance matrices will not be identical from one population to the next because of stochastic differences in allele fre-

quencies and the possibility of different stabilizing selection regimes in different populations. Thus, we think that the null hypothesis of identity, while formally appropriate, is not very informative because all real populations are different. Furthermore, statistical tests of the null hypothesis of identity will quite naturally be strongly affected by the statistical power of analysis. A test that fails to reject the null hypothesis of identity is likely one in which inadequate sample sizes were used. One can assure a failure to reject identity by using inadequate sample sizes. Thus, we test the null hypothesis of no similarity because if we fail to reject this hypothesis we really cannot make statements concerning relative degrees of similarity. With this null hypothesis, inadequate samples lead to a lack of statements about matrix similarity.

Anderson (1958) developed a maximum-likelihood test for covariance matrix equality. This test is very sensitive to the assumption of multivariate normality (Morrison 1976). Recently, common principal component (CPC) analysis has been introduced as a potentially useful tool for comparisons of covariance matrices (Cowley and Atchley 1992; Stepan 1997; Arnold and Phillips 1999; Phillips and Arnold 1999), but we have not reported the results of these analyses here. The CPC method generalizes the maximum-likelihood test of identity to a series of nested hierarchical tests of multivariate similarity. Stepan (1997) applied CPC analyses to broad-scale comparisons of covariance structure across taxa and noticed some discrepancy between CPC and matrix correlation results (Arnold and Phillips 1999; Phillips and Arnold 1999; Ackermann and Cheverud 2000). Ackermann and Cheverud (2000) also reported some discrepancy between CPC and matrix correlation results among tamarins. In both studies CPC results suggest no shared covariance structure among taxa, whereas matrix correlation results point to a high degree of similarity. These results do not really conflict with one another because with adequate sample sizes and complexity of covariance pattern very minor differences in covariance matrices can be statistically significant. For example, Stepan (1997) noted that increasing the number of traits in the covariance matrices compared by CPC increases the likelihood of rejecting a common structure with CPC analysis when indeed there is strong similarity among covariance structures. We found that CPC results for comparisons of Platyrrhine genera were very strongly affected by sample size. With the large sample sizes used here, failure to reject common structure was strongly associated with relatively small sample sizes. Taken at face value these results indicate that taxa that are relatively poorly represented in our sample have more similar covariance structures. A matrix correlation followed by Mantel's test between the geometric mean of the sample sizes and CPC results (limited to the first seven principal components) produces a correlation of -0.404 ($P = 0.0028$), indicating that pairwise comparisons with larger sample sizes tend to reject common structure more frequently than comparisons with smaller sample sizes, as expected. Phillips and Arnold (1999) suggest that looking at the reconstructed covariance matrices at each step in the CPC hierarchy and evaluating how well these matrices reproduce the original matrices provides an insight into the biological meaning of the CPC results. We compared original pairs of matrices for which the CPC significance tests had rejected

any common structure (unrelated structure) with the matrices reconstructed and constrained by the CPC model. We found that the reconstructed matrices were nearly identical to the original ones at all steps in the hierarchy (from unrelated matrix structure to equality the random skewers vector correlations were all > 0.97). This indicates that the matrices were actually very similar, although not identical or proportional. Given the lack of biologically relevant insight gained from these analyses, we do not report these results.

Matrix Repeatability and Adjusted Matrix Correlation

Phenotypic patterns of interrelationships among any set of quantitative traits described by correlation or V/CV matrices are estimated with some degree of error (Cheverud 1988, 1996b). In terms of matrix comparisons, this measurement error is due to error in the estimates of individual matrix elements, limiting the maximum observable correlation between estimated matrices. In judging any measure of matrix similarity (like matrix correlation or vector correlation) one should be aware that the maximum observable correlation between estimated matrices is not one, but a value R_{\max} corresponding to $(t_A t_B)^{0.5}$, where t_A and t_B denote the repeatabilities of matrices A and B respectively (see Cheverud 1996b). The theoretical maximum matrix correlation between two matrices, R_{\max} , can be used to calculate adjusted matrix correlations, which account for the effects of sampling error on matrix correlation magnitude. Adjusted matrix correlations are the observed correlation (R_{obs}) between the two matrices divided by the maximum matrix correlation (R_{\max}) calculated for that pairwise comparison.

Pairwise comparisons of covariance matrices using the random skewers method also suffer from a downward bias due to estimation error. But another procedure needs to be used to estimate (R_{\max}) in this case by the same reason one could not use a matrix correlation followed by Mantel's test to compare similarity in any pair of covariance matrices. Patterns of covariance are measured on a different scale for each row (and associated column) of the V/CV matrices and are therefore not suitable for randomization tests of matrix similarity (Turelli 1988a; Cheverud 1989, 1996b;). V/CV matrix repeatability is evaluated using a resampling procedure of self-correlation. Because samples used to estimate pooled within-group V/CV matrices have a structure, which controls for variation associated with sex and taxonomic differences, a bootstrap procedure is difficult to apply. Instead we used a Monte Carlo approach by generating m datasets, each composed of n individuals with 39 measurements randomly drawn from a population having the observed V/CV structure, where n stands for the number of specimens in the sample. The V/CV matrix specified by each of these m datasets is calculated and then compared to the observed V/CV matrix using the average vector correlation between simulated selection responses. The V/CV matrix repeatability is the average vector correlation between simulated responses of the original and resampled matrices. Observed vector correlations were adjusted for repeatability as described above.

Integration

Following the approach described in Cheverud (1995, 1996b), theoretical matrices based on shared development/

function among characters are used to assess morphological integration. Two major cranial regions are distinguished on the basis of growth pattern, the neurocranium and the face. The neurocranial region is subdivided into the cranial vault, cranial base, and the orbit, whereas the facial subregion is grouped into oral, nasal, and zygomatic subregions. Morphological integration is assessed within these two major regions, neurocranium and face as well as within six cranial subregions: cranial vault, cranial base, orbit, oral, zygomatic, and nasal (Table 2). Additionally, a connectivity matrix was also formed linking all neural traits and all facial traits. This neural-somatic integration matrix tests for the general effect of neural (early) versus somatic (later) growth pattern. These matrices are derived independent of the observed correlation matrices and are constructed in the following manner: When two traits belong to the same development/functional set, a value of one is entered in the integration matrix; otherwise, a value of zero is entered. Finally, a single total integration connectivity matrix combines all six separate cranial subregion matrices for an overall test of morphological integration. This matrix is obtained as the sum of the six subregion matrices with any entries greater than one being reduced to one.

Correlation was assessed between these morphological integration matrices and observed correlation matrices using the Mantel's procedure to test for statistical significance. The overall mean of the observed Pearson's correlation coefficients for traits with zero (negative) or one (positive) in each of the 10 integration matrices described above were also calculated. This mean is informative because the average difference between integrated traits and nonintegrated traits gives an idea of how much the shared developmental/functional basis influences the integration process.

Phylogeny, Ecology, and Morphological Distance

A DNA-based phylogenetic distance matrix was used to compare matrix similarity results with the phylogenetic history of the South American primates and investigate if this history influenced Platyrrhine morphological integration. Sequences obtained from GENBANK included data on four nuclear genes: IRBP (Schneider et al. 1996), ϵ -globin (Schneider et al. 1993), β 2m microglobulin (Canavez et al. 1999), and G6PD (von Dornum and Ruvolo 1999). These datasets were chosen because the 16 genera of Platyrrhini are represented, except for the G6PD data, which does not include *Cebuella*. Phylogeny is a crucial starting point for comparisons of covariance patterns among Platyrrhini. Given the current uncertainty about phylogenetic relationships among New World monkey genera, we also report here on the resulting phylogeny obtained using the pooled dataset of these four genes (IRBP, ϵ -globin, β 2m, and G6PD). The Jukes-Cantor model was used to calculate a phylogenetic pairwise distance matrix for Platyrrhini using a dataset with all four genes in tandem spanning nearly 6700 bp. The Platyrrhine phylogenetic tree was reconstructed using the neighbor-joining method (Saitou and Nei 1987) available in the program MEGA (Kumar et al. 1993), and the bootstrap confidence

level (BCL) was calculated for each node based on 5000 replications. Topological reliability of the tree was also evaluated using the confidence probability (CP) obtained from the standard error test of the neighbor-joining branch lengths (Rzhetsky and Nei 1992, 1993). Like the bootstrap confidence level, values above 0.95 or 0.99 for CP indicate significant branches.

Correlation between Jukes-Cantor genetic distance matrix and the matrix similarity results (obtained from the random skewers and the matrix correlation test) was calculated using a matrix correlation and Mantel's test. The observed Pearson correlation and the associated r^2 between the matrix similarity results and the phylogenetic distance measure the extent to which matrix similarity is phylogenetically structured. Because phylogeny is represented by a dissimilarity matrix and covariance structure by similarity matrices, a negative correlation is expected if phylogeny structures phenotypic correlation patterns.

To study ecological influences on changes in covariance structure, we construct an ecological matrix based on the proportion of diet shared among genera (Kinsey 1997). For each of five categories (fruits, leaves, insects, seeds, and plant exudate), we attribute a value for each genus corresponding to the percentage of the total diet each item contributes. For example, *Brachyteles* is considered primarily a leave-eater, with fruits being a minor part of the diet. In this case, a value of 0.75 is entered for leaves and a value of 0.25 is entered for fruits. The amount of shared diet between each pair of genera is calculated as the sum across the five categories, where each category had a value corresponding to the square root of the product of paired genus-specific values in the same category. Therefore, values in the diet matrix range from zero to one. This diet matrix was correlated with the correlation and covariance matrix similarity results, as well as with the phylogeny matrix, using matrix correlation followed by a Mantel's test for significance. Because closely related genera could be more similar in diet than distantly related ones, correlation between phylogenetic distance and dietary similarity was removed by regressing dietary similarity on phylogenetic distance and using the residual values as a new residual dietary similarity matrix, which represents variation in diet independent of phylogenetic history. Given that diet is a similarity matrix, a positive correlation between diet or diet residual matrices and phenotypic correlation or covariance similarity is expected.

We also use an extension of Mantel's strategy to three matrices (Dow and Cheverud 1985) that allows a formal test of which of two matrices best fits a third matrix. In this three-matrix test, two matrices, B and C, are made commensurable by transforming their elements to Z-scores after which the difference matrix B-C is compared to matrix A using the Mantel's permutation strategy. A statistically significant positive $r_{A,B-C}$ index implies that matrix B is a better fit to matrix A than is matrix C, whereas a significant negative index implies the reverse (Dow and Cheverud 1985). This three-matrix strategy was used to test whether phylogeny (genetic distance matrix) or ecology (diet matrix) had a better fit to covariance structure similarity among Neotropical primate genera.

Finally, a discriminant function analysis was performed

with the 16 genera as the grouping variable and the overall pooled covariance matrix as the measure of within-taxon variability. The canonical scores of the group means were used to calculate Mahalanobis (D^2) morphological distances between genera. The D^2 matrix was then used to see whether variation in covariance structure among Platyrrhine genera corresponds to the distances between their means. Additionally, the D^2 matrix was also compared to phylogenetic distance and diet. All comparisons were made using matrix correlation followed by the Mantel test.

RESULTS

Repeatability calculated separately for each of the 16 genera and 39 characters ranges from 0.80 to 1.00. The average repeatability across all characters and genera is 0.97 with a median of 0.99 and a standard deviation of 0.06. Measurement error is quite low in this study and therefore should have a negligible impact on the results presented below.

Matrix correlations between species-specific correlation matrices within each genus are presented in Table 3. Matrix repeatabilities, maximum correlation, and raw and adjusted matrix correlations are presented for each species pair within genera. All results are significant at the 0.0001 level. Table 3 also presents average vector correlation results between species-specific observed V/CV matrices. Again, matrix repeatabilities, maximum expected vector correlation, and raw and adjusted vector correlations are presented for each species pair within genera. Generally, raw vector correlations for V/CV matrices are higher than their pairwise matrix correlation counterparts. Results indicate a high degree of similarity for nearly all pairwise comparisons of species within genera, suggesting a shared correlation/covariance structure at this biological level. Exceptions include the two *Chiropotes* species, comparisons involving *Saguinus geoffroyi* and *S. oedipus*, and comparisons involving *Callithrix argentata* and *C. jacchus*. Comparisons involving these taxa show only a moderate matrix and vector correlation with their congeners.

The raw and adjusted matrix correlations between observed pooled generic correlation matrices are presented in Table 4. All results are significant at the 0.0001 level. Raw correlations vary between 0.40 and 0.86, and adjusted correlations range from 0.56 to 0.96. The raw and adjusted random skewers vector correlations between observed generic covariance matrices are presented in Table 5. The raw vector correlations range from 0.55 to 0.89, and correlations adjusted for repeatability vary from 0.62 to 0.95. In comparing these tables, note that covariance matrix repeatabilities (along the diagonal) are generally higher than their correlation counterparts. The general pattern emerging from these correlation/covariance structure comparisons is that Neotropical primate genera present a high degree of shared correlation/covariance structure in cranial morphology.

Matrix comparisons at higher taxonomic levels agree with the species- and genus-level comparisons (Table 6). All comparisons present a high degree of similarity, perhaps with the exception of Aotinae and Callitrichinae, which show a moderate degree of shared structure with the other four subfamilies in the matrix correlation results. In general, the matrix similarity results suggest a shared correlation/covariance

TABLE 3. Matrix correlation and random skewers vector correlation, respectively, between pairwise species comparisons within genera. Repeatabilities for species 1 (t_1) and 2 (t_2) are presented. The maximum possible correlations ($\sqrt{t_1 t_2}$) is shown for each species pair compared. Observed and adjusted matrix correlations and random skewers vector correlation are also presented. All matrix correlation comparisons were significant at $P = 0.0001$ in 10,000 permutations, and all vector correlation comparisons were significant at $P = 0.001$ in 1000 random vectors. The average and standard deviation of all observed and adjusted comparisons are presented at the bottom.

Genus	Species 1	Species 2	Correlation matrices					Covariance matrices					
			t_1	t_2	Maximum correlation	Observed correlation	Adjusted correlation	t_1	t_2	Maximum vector correlation	Observed vector correlation	Adjusted vector correlation	
Alouatta	belzebul	caraya	0.816	0.687	0.749	0.714	0.953	0.961	0.966	0.963	0.836	0.868	
	belzebul	fusca	0.816	0.790	0.803	0.706	0.880	0.961	0.959	0.960	0.842	0.877	
	belzebul	palliata	0.816	0.779	0.797	0.735	0.922	0.961	0.963	0.962	0.838	0.871	
	belzebul	senicula	0.816	0.751	0.783	0.824	1.052	0.961	0.953	0.957	0.898	0.939	
	caraya	fusca	0.687	0.790	0.737	0.713	0.968	0.966	0.959	0.962	0.853	0.887	
	caraya	palliata	0.687	0.779	0.732	0.701	0.959	0.966	0.963	0.964	0.856	0.888	
	caraya	senicula	0.687	0.751	0.718	0.752	1.047	0.966	0.953	0.959	0.843	0.879	
	fusca	palliata	0.790	0.779	0.784	0.666	0.849	0.959	0.963	0.961	0.805	0.838	
	fusca	senicula	0.790	0.751	0.770	0.745	0.968	0.959	0.953	0.956	0.847	0.886	
Ateles	palliata	senicula	0.779	0.751	0.765	0.756	0.988	0.963	0.953	0.958	0.822	0.858	
	geoffroy	marginatus	0.820	0.654	0.733	0.648	0.884	0.956	0.946	0.951	0.818	0.860	
	geoffroy	paniscus	0.820	0.626	0.717	0.639	0.892	0.956	0.936	0.946	0.830	0.877	
Callicebus	marginatus	paniscus	0.654	0.626	0.640	0.680	1.062	0.946	0.936	0.941	0.816	0.868	
	brunneus	personatus	0.587	0.619	0.603	0.511	0.848	0.889	0.920	0.905	0.740	0.818	
	brunneus	moloch	0.587	0.802	0.686	0.574	0.837	0.889	0.952	0.920	0.808	0.878	
	brunneus	torquatus	0.587	0.601	0.594	0.543	0.913	0.889	0.918	0.903	0.784	0.868	
	personatus	moloch	0.619	0.802	0.704	0.694	0.985	0.920	0.952	0.936	0.815	0.871	
	personatus	torquatus	0.619	0.601	0.610	0.563	0.924	0.920	0.918	0.919	0.734	0.799	
Chiropotes	moloch	torquatus	0.802	0.601	0.694	0.631	0.909	0.952	0.918	0.935	0.799	0.855	
	albinasus	s. chiropotes	0.644	0.754	0.697	0.431	0.619	0.923	0.938	0.931	0.718	0.771	
	Pithecia	chrysocephala	irrorata	0.544	0.632	0.586	0.555	0.947	0.915	0.936	0.925	0.738	0.798
		chrysocephala	monacha	0.544	0.633	0.587	0.566	0.964	0.915	0.932	0.923	0.805	0.872
		chrysocephala	pithecia	0.544	0.634	0.587	0.569	0.969	0.915	0.928	0.921	0.766	0.831
irrorata		monacha	0.632	0.633	0.633	0.608	0.961	0.936	0.932	0.934	0.782	0.837	
Saimiri	irrorata	pithecia	0.632	0.634	0.633	0.670	1.058	0.936	0.928	0.932	0.815	0.874	
	monacha	pithecia	0.633	0.634	0.633	0.513	0.810	0.932	0.928	0.930	0.738	0.794	
	Saguinus	sciureus	oerstedi	0.809	0.722	0.764	0.701	0.917	0.975	0.933	0.954	0.823	0.863
		geoffroyi	illigeri	0.908	0.726	0.812	0.424	0.522	0.959	0.935	0.947	0.623	0.658
		geoffroyi	lagonotus	0.908	0.622	0.751	0.430	0.572	0.959	0.900	0.929	0.623	0.671
		geoffroyi	midas	0.908	0.586	0.729	0.526	0.721	0.959	0.933	0.946	0.689	0.729
		geoffroyi	mystax	0.908	0.764	0.833	0.710	0.853	0.959	0.946	0.953	0.774	0.812
		geoffroyi	n. graellsii	0.908	0.537	0.698	0.348	0.498	0.959	0.906	0.932	0.581	0.623
		geoffroyi	niger	0.908	0.846	0.877	0.449	0.512	0.959	0.953	0.956	0.677	0.708
		geoffroyi	nigrifons	0.908	0.683	0.788	0.398	0.505	0.959	0.923	0.941	0.612	0.651
		geoffroyi	oedipus	0.908	0.907	0.907	0.694	0.765	0.959	0.958	0.959	0.780	0.814
		geoffroyi	wedelli	0.908	0.740	0.820	0.453	0.552	0.959	0.935	0.947	0.606	0.640
		illigeri	lagonotus	0.726	0.622	0.672	0.625	0.930	0.935	0.900	0.917	0.801	0.873
		illigeri	midas	0.726	0.586	0.652	0.526	0.806	0.935	0.933	0.934	0.767	0.821
		illigeri	mystax	0.726	0.764	0.745	0.552	0.741	0.935	0.946	0.941	0.716	0.761
		illigeri	n. graellsii	0.726	0.537	0.624	0.559	0.896	0.935	0.906	0.920	0.734	0.798
		illigeri	niger	0.726	0.846	0.784	0.575	0.733	0.935	0.953	0.944	0.802	0.849
		illigeri	nigrifons	0.726	0.683	0.704	0.674	0.956	0.935	0.923	0.929	0.800	0.862
		illigeri	oedipus	0.726	0.907	0.811	0.444	0.547	0.935	0.958	0.946	0.693	0.733
		illigeri	wedelli	0.726	0.740	0.733	0.563	0.768	0.935	0.935	0.935	0.780	0.835
		lagonotus	midas	0.622	0.586	0.604	0.592	0.981	0.900	0.933	0.916	0.742	0.809
		lagonotus	mystax	0.622	0.764	0.689	0.507	0.736	0.900	0.946	0.923	0.682	0.739
		lagonotus	n. graellsii	0.622	0.537	0.578	0.479	0.829	0.900	0.906	0.903	0.695	0.769
		lagonotus	niger	0.622	0.846	0.725	0.515	0.710	0.900	0.953	0.926	0.754	0.814
		lagonotus	nigrifons	0.622	0.683	0.652	0.617	0.946	0.900	0.923	0.911	0.782	0.859
		lagonotus	oedipus	0.622	0.907	0.751	0.482	0.642	0.900	0.958	0.929	0.685	0.738
		lagonotus	wedelli	0.622	0.740	0.678	0.527	0.777	0.900	0.935	0.917	0.713	0.778
		midas	mystax	0.586	0.764	0.669	0.607	0.907	0.933	0.946	0.940	0.747	0.794
		midas	n. graellsii	0.586	0.537	0.561	0.466	0.831	0.933	0.906	0.919	0.688	0.748
		midas	niger	0.586	0.846	0.704	0.573	0.813	0.933	0.953	0.943	0.815	0.864
		midas	nigrifons	0.586	0.683	0.633	0.571	0.903	0.933	0.923	0.928	0.751	0.810
		midas	oedipus	0.586	0.907	0.729	0.461	0.632	0.933	0.958	0.945	0.687	0.727
		midas	wedelli	0.586	0.740	0.658	0.585	0.888	0.933	0.935	0.934	0.749	0.802
		mystax	n. graellsii	0.764	0.537	0.640	0.472	0.736	0.946	0.906	0.926	0.661	0.714
		mystax	niger	0.764	0.846	0.804	0.607	0.755	0.946	0.953	0.950	0.743	0.782
		mystax	nigrifons	0.764	0.683	0.723	0.571	0.790	0.946	0.923	0.934	0.707	0.757
mystax		oedipus	0.764	0.907	0.832	0.575	0.691	0.946	0.958	0.952	0.728	0.764	

TABLE 3. Continued.

Genus	Species 1	Species 2	Correlation matrices					Covariance matrices				
			t_1	t_2	Maximum correlation	Observed correlation	Adjusted correlation	t_1	t_2	Maximum vector correlation	Observed vector correlation	Adjusted vector correlation
<i>Callithrix</i>	<i>mystax</i>	<i>wedelli</i>	0.764	0.740	0.752	0.570	0.758	0.946	0.935	0.940	0.688	0.732
	<i>n. graellsii</i>	<i>wedelli</i>	0.537	0.740	0.630	0.443	0.704	0.906	0.935	0.920	0.689	0.749
	<i>niger</i>	<i>n. graellsii</i>	0.846	0.537	0.674	0.434	0.645	0.953	0.906	0.929	0.696	0.749
	<i>niger</i>	<i>nigrifrons</i>	0.846	0.683	0.760	0.497	0.654	0.953	0.923	0.938	0.744	0.793
	<i>niger</i>	<i>oedipus</i>	0.846	0.907	0.876	0.415	0.473	0.953	0.958	0.956	0.690	0.722
	<i>niger</i>	<i>wedelli</i>	0.846	0.740	0.791	0.542	0.685	0.953	0.935	0.944	0.757	0.802
	<i>nigrifrons</i>	<i>n. graellsii</i>	0.683	0.537	0.605	0.478	0.790	0.923	0.906	0.914	0.701	0.766
	<i>nigrifrons</i>	<i>oedipus</i>	0.683	0.907	0.787	0.492	0.625	0.923	0.958	0.940	0.700	0.744
	<i>nigrifrons</i>	<i>wedelli</i>	0.683	0.740	0.711	0.564	0.794	0.923	0.935	0.929	0.751	0.809
	<i>oedipus</i>	<i>n. graellsii</i>	0.907	0.537	0.698	0.327	0.469	0.958	0.906	0.932	0.604	0.648
	<i>oedipus</i>	<i>wedelli</i>	0.907	0.740	0.819	0.424	0.517	0.958	0.935	0.946	0.662	0.699
	<i>argentata</i>	<i>geoffroyi</i>	0.707	0.626	0.665	0.399	0.600	0.926	0.918	0.922	0.644	0.699
	<i>argentata</i>	<i>jacchus</i>	0.707	0.767	0.737	0.489	0.663	0.926	0.938	0.932	0.634	0.681
	<i>argentata</i>	<i>kuhlii</i>	0.707	0.814	0.759	0.535	0.705	0.926	0.951	0.939	0.765	0.815
	<i>argentata</i>	<i>penicillata</i>	0.707	0.759	0.733	0.436	0.595	0.926	0.952	0.939	0.699	0.744
	<i>geoffroyi</i>	<i>jacchus</i>	0.626	0.767	0.693	0.394	0.568	0.918	0.938	0.928	0.495	0.533
	<i>geoffroyi</i>	<i>kuhlii</i>	0.626	0.814	0.714	0.609	0.853	0.918	0.951	0.935	0.773	0.827
	<i>geoffroyi</i>	<i>penicillata</i>	0.626	0.759	0.689	0.516	0.748	0.918	0.952	0.935	0.706	0.756
	<i>jacchus</i>	<i>kuhlii</i>	0.767	0.814	0.790	0.603	0.762	0.938	0.951	0.945	0.713	0.754
	<i>jacchus</i>	<i>penicillata</i>	0.767	0.759	0.763	0.497	0.651	0.938	0.952	0.945	0.654	0.692
<i>Cebus</i>	<i>kuhlii</i>	<i>penicillata</i>	0.814	0.759	0.786	0.707	0.899	0.951	0.952	0.952	0.863	0.907
	<i>albifrons</i>	<i>apella</i>	0.667	0.829	0.743	0.666	0.896	0.932	0.968	0.950	0.825	0.868
	<i>albifrons</i>	<i>libidinosus</i>	0.667	0.737	0.701	0.610	0.870	0.932	0.937	0.935	0.801	0.857
	<i>albifrons</i>	<i>nigritus</i>	0.667	0.794	0.728	0.612	0.841	0.932	0.960	0.946	0.783	0.828
	<i>albifrons</i>	<i>robustus</i>	0.667	0.664	0.665	0.520	0.782	0.932	0.930	0.931	0.722	0.775
	<i>apella</i>	<i>libidinosus</i>	0.829	0.737	0.781	0.803	1.028	0.968	0.937	0.953	0.873	0.917
	<i>apella</i>	<i>nigritus</i>	0.829	0.794	0.811	0.844	1.040	0.968	0.960	0.964	0.915	0.948
	<i>apella</i>	<i>robustus</i>	0.829	0.664	0.742	0.739	0.997	0.968	0.930	0.949	0.872	0.919
	<i>libidinosus</i>	<i>nigritus</i>	0.737	0.794	0.765	0.728	0.951	0.937	0.960	0.949	0.804	0.848
	<i>libidinosus</i>	<i>robustus</i>	0.737	0.664	0.699	0.831	1.188	0.937	0.930	0.934	0.878	0.940
Average						0.576	0.807				0.750	0.800
SD						0.115	0.162				0.078	0.079

structure among all Platyrrhine primates. Figure 2 summarizes the comparison of correlation and covariance matrices at all the taxonomic levels examined here. Generally, raw and adjusted comparisons of correlation and covariance matrices follow the same general trend. There is an apparent

increase in average phenotypic covariance structure similarity with increasing taxonomic rank, from the average of all species compared to the average of all families and superfamilies. Given that taxonomic rank is intended to be an indication of phylogenetic relatedness, this trend suggests

TABLE 4. Correlations between correlation matrices for each pairwise New World monkey genera comparison. The bolded diagonal contains the matrix repeatability for each genus. Raw matrix correlations are in the lower half, and adjusted matrix correlations are above the diagonal. All comparisons were significant at $P = 0.0001$ in 10,000 permutations.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Ateles</i>	0.890	0.869	0.825	0.896	0.898	0.916	0.903	0.906	0.717	0.901	0.934	0.559	0.608	0.684	0.687	0.654
<i>Alouatta</i>	0.796	0.942	0.888	0.832	0.810	0.890	0.794	0.823	0.588	0.856	0.827	0.634	0.610	0.706	0.666	0.589
<i>Brachyteles</i>	0.509	0.564	0.428	0.883	0.719	0.852	0.877	0.858	0.772	0.779	0.869	0.753	0.805	0.776	0.808	0.720
<i>Lagothrix</i>	0.723	0.691	0.494	0.732	0.781	0.873	0.838	0.811	0.589	0.797	0.853	0.577	0.584	0.697	0.663	0.702
<i>Cacajao</i>	0.736	0.683	0.409	0.581	0.755	0.954	0.895	0.947	0.821	0.958	0.923	0.633	0.643	0.812	0.756	0.727
<i>Pithecia</i>	0.811	0.810	0.523	0.700	0.777	0.879	0.915	0.945	0.788	0.936	0.921	0.673	0.701	0.790	0.768	0.717
<i>Chiropotes</i>	0.773	0.700	0.521	0.651	0.706	0.778	0.824	0.917	0.759	0.890	0.895	0.631	0.669	0.689	0.732	0.669
<i>Callicebus</i>	0.822	0.769	0.540	0.668	0.792	0.853	0.801	0.926	0.840	0.935	0.892	0.660	0.728	0.781	0.777	0.740
<i>Aotus</i>	0.630	0.531	0.470	0.469	0.663	0.687	0.640	0.752	0.865	0.784	0.767	0.650	0.777	0.718	0.803	0.663
<i>Saimiri</i>	0.809	0.791	0.485	0.649	0.792	0.836	0.769	0.857	0.694	0.906	0.931	0.674	0.668	0.831	0.754	0.711
<i>Cebus</i>	0.857	0.781	0.553	0.710	0.781	0.840	0.791	0.835	0.694	0.843	0.947	0.666	0.605	0.736	0.725	0.650
<i>Leontopithecus</i>	0.451	0.526	0.421	0.422	0.470	0.539	0.489	0.543	0.517	0.548	0.553	0.730	0.739	0.845	0.829	0.688
<i>Saguinus</i>	0.566	0.584	0.520	0.493	0.552	0.649	0.599	0.691	0.713	0.628	0.581	0.623	0.974	0.854	0.856	0.651
<i>Callimico</i>	0.474	0.503	0.373	0.438	0.518	0.544	0.459	0.552	0.490	0.581	0.525	0.622	0.619	0.539	0.945	0.841
<i>Callithrix</i>	0.630	0.628	0.514	0.552	0.639	0.700	0.645	0.727	0.726	0.697	0.686	0.689	0.821	0.675	0.945	0.699
<i>Cebulla</i>	0.524	0.486	0.401	0.510	0.536	0.571	0.516	0.605	0.524	0.575	0.537	0.499	0.546	0.524	0.577	0.722

TABLE 5. Average vector correlations between variance/covariance matrices responses to 1000 random selection vectors for each pairwise New World monkey genera comparison. The bolded diagonal contains the matrix repeatability for each genus. Raw average vector correlations are in the lower half, and adjusted vector correlations are above the diagonal. All comparisons were significant at $P = 0.001$.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Ateles</i>	0.967	0.798	0.696	0.895	0.832	0.870	0.918	0.871	0.833	0.860	0.937	0.695	0.834	0.716	0.895	0.754
<i>Alouatta</i>	0.775	0.976	0.723	0.871	0.849	0.919	0.851	0.892	0.748	0.835	0.830	0.722	0.801	0.677	0.755	0.756
<i>Brachyteles</i>	0.646	0.674	0.890	0.754	0.726	0.742	0.791	0.794	0.755	0.679	0.722	0.643	0.773	0.620	0.731	0.722
<i>Lagothrix</i>	0.855	0.836	0.691	0.945	0.861	0.904	0.878	0.898	0.801	0.855	0.888	0.728	0.839	0.702	0.834	0.797
<i>Cacajao</i>	0.792	0.813	0.664	0.811	0.938	0.923	0.889	0.926	0.839	0.900	0.862	0.747	0.834	0.725	0.823	0.773
<i>Pithecia</i>	0.839	0.891	0.687	0.862	0.877	0.963	0.909	0.949	0.864	0.901	0.908	0.778	0.892	0.766	0.861	0.810
<i>Chiropotes</i>	0.882	0.821	0.729	0.833	0.841	0.871	0.954	0.916	0.862	0.876	0.908	0.752	0.878	0.717	0.883	0.794
<i>Callicebus</i>	0.841	0.866	0.735	0.858	0.881	0.915	0.879	0.965	0.911	0.890	0.915	0.766	0.897	0.757	0.868	0.842
<i>Aotus</i>	0.799	0.721	0.695	0.760	0.793	0.827	0.821	0.872	0.952	0.813	0.864	0.748	0.890	0.702	0.872	0.810
<i>Saimiri</i>	0.835	0.815	0.632	0.821	0.860	0.873	0.845	0.863	0.783	0.975	0.883	0.772	0.846	0.815	0.850	0.752
<i>Cebus</i>	0.910	0.810	0.673	0.853	0.825	0.880	0.877	0.888	0.833	0.862	0.977	0.732	0.832	0.719	0.871	0.763
<i>Leontopithecus</i>	0.657	0.685	0.582	0.679	0.695	0.733	0.705	0.722	0.701	0.732	0.695	0.922	0.834	0.775	0.791	0.759
<i>Saguinus</i>	0.805	0.776	0.715	0.801	0.793	0.859	0.842	0.865	0.852	0.820	0.807	0.786	0.963	0.799	0.920	0.840
<i>Callimico</i>	0.664	0.632	0.552	0.644	0.663	0.710	0.661	0.702	0.647	0.760	0.671	0.706	0.740	0.891	0.865	0.739
<i>Callithrix</i>	0.866	0.734	0.678	0.797	0.784	0.831	0.848	0.839	0.837	0.826	0.846	0.746	0.888	0.803	0.967	0.802
<i>Cebulla</i>	0.716	0.720	0.658	0.747	0.723	0.766	0.749	0.798	0.762	0.716	0.728	0.703	0.796	0.673	0.760	0.931

TABLE 6. Matrix correlation and average vector correlation of random selection vectors between Platyrrhine higher taxa (subfamilies, families, and superfamilies). Dotted lines separate comparisons at different taxonomic ranks. The maximum possible correlation ($\sqrt{t_1/t_2}$) is shown for each taxon pair compared. Observed and adjusted matrix correlations or average vector correlations are also presented. All matrix correlations are significant at $P = 0.0001$ and all average vector correlations are significant at $P = 0.001$. The average and standard deviation of all comparisons is presented at the bottom. na, values not available because covariance matrices had sample sizes that were too large to allow matrix repeatability estimation with our software.

Taxon 1	Taxon 2	Covariance matrices			Correlation matrices		
		Maximum vector correlation	Observed vector correlation	Adjusted vector correlation	Maximum matrix correlation	Observed matrix correlation	Adjusted matrix correlation
Atelinae	Alouattinae	0.970	0.826	0.851	0.967	0.825	0.854
Atelinae	Pithecinae	0.966	0.909	0.942	0.991	0.866	0.875
Atelinae	Callicebinae	0.965	0.882	0.914	0.992	0.834	0.840
Atelinae	Cebinae	0.973	0.928	0.954	0.978	0.883	0.902
Atelinae	Aotinae	0.958	0.824	0.860	0.926	0.634	0.684
Atelinae	Callitrichinae	0.975	0.859	0.881	0.987	0.661	0.669
Alouattinae	Pithecinae	0.969	0.887	0.915	0.965	0.812	0.841
Alouattinae	Callicebinae	0.968	0.866	0.895	0.966	0.769	0.796
Alouattinae	Cebinae	0.976	0.820	0.840	0.953	0.815	0.855
Alouattinae	Aotinae	0.961	0.720	0.749	0.902	0.531	0.588
Alouattinae	Callitrichinae	0.978	0.785	0.803	0.962	0.635	0.660
Pithecinae	Callicebinae	0.964	0.939	0.974	0.990	0.893	0.902
Pithecinae	Cebinae	0.972	0.924	0.951	0.976	0.912	0.934
Pithecinae	Aotinae	0.957	0.854	0.893	0.925	0.723	0.782
Pithecinae	Callitrichinae	0.974	0.889	0.913	0.985	0.726	0.736
Callicebinae	Cebinae	0.971	0.902	0.929	0.978	0.876	0.896
Callicebinae	Aotinae	0.956	0.872	0.913	0.926	0.752	0.812
Callicebinae	Callitrichinae	0.973	0.875	0.899	0.987	0.744	0.753
Cebinae	Aotinae	0.964	0.845	0.877	0.913	0.721	0.789
Cebinae	Callitrichinae	0.981	0.838	0.854	0.973	0.694	0.714
Aotinae	Callitrichinae	0.966	0.857	0.888	0.922	0.751	0.814
.....							
Atelidae	Pitheciidae	0.970	0.942	0.972	0.963	0.880	0.914
Atelidae	Cebidae	na	0.923	na	0.974	0.789	0.810
Atelidae	Aotidae	0.961	0.797	0.830	0.912	0.604	0.662
Pitheciidae	Cebidae	na	0.953	na	0.975	0.859	0.881
Pitheciidae	Aotidae	0.958	0.871	0.909	0.913	0.757	0.829
.....							
Cebidae	Aotidae	na	0.883	na	0.924	0.794	0.859
Ateloidea	Ceboidea	na	0.937	na	0.984	0.853	0.867
.....							
Average			0.871	0.892		0.771	0.804
SD			0.055	0.054		0.097	0.090

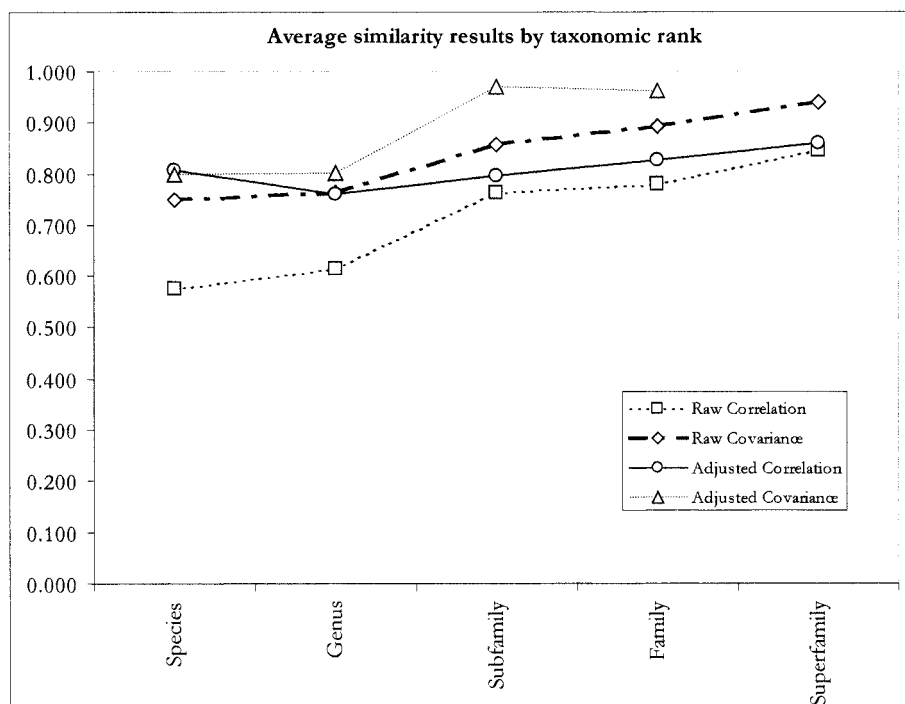


FIG. 2. Average similarity of raw and adjusted comparisons of correlation and variance/covariance matrices among New World monkeys. Average values are shown for all species compared, all genera, and so on until reach Superfamily, which is simply the value found between Ceboidea and Ateloidea. Adjusted covariance is not presented for superfamily because it was not possible to calculate repeatability for Ceboidea given their high sample size (see Appendix) and limitations in our software.

that covariance structure similarity might be largely independent of evolutionary relatedness.

Table 7 provides the Mahalanobis D^2 distances among genera. These distances clearly show the morphological unity of the Callitrichines, Atelines, and Pitheciines (Fig. 3). Morphological relationships among the remaining taxa are less clear, although *Cebus* aligns with the Pitheciines; *Alouatta* with the Atelines and Pitheciines; and *Callicebus*, *Aotus*, and *Saimiri* together.

The neighbor-joining phylogenetic tree obtained for the 16 Platyrrhine genera is shown in Figure 4, with BCL values below and CP values above each node. This tree has strong support from both statistics at nearly all nodes and is fully congruent with the single maximum-parsimony tree obtained by Schneider (2000) with the same dataset used here. Only *Aotus*'s position in the tree is not well resolved, showing a tricotomy with the *Cebus-Saimiri* clade and the Callitrichini clade (*Saguinus*, *Leontopithecus*, *Callimico*, *Cebuella*, and *Callithrix*). Additionally, *Callimico* also does not present a high value in the CP and BCL tests, although its position as the sister group of *Callithrix-Cebuella* clade is corroborated by other analyses (Horovitz and Meyer 1995; Chaves et al. 1999). The Jukes-Cantor genetic distances among genera corresponding to this tree are presented in Table 8 along with the measure of dietary similarity.

Matrix correlations have been used to examine the relationships between phylogenetic distance and dietary similarity and morphological and variance pattern similarity measures among genera. Dietary similarity has a significant negative correlation ($r = -0.65$; $P < 0.001$) with phylogenetic

distance, indicating that phylogenetically related genera have more similar diets. To separate the effects of these two factors on morphological and V/CV pattern similarity, the residual matrix of the regression of dietary similarity on phylogenetic distance was used. This procedure allows a test of the partial correlation between dietary similarity and other factors, independent of phylogenetic propinquity. Also, the three-way Mantel test was used to determine which of these two factors had a greater effect on morphological and V/CV pattern similarity. Matrix correlations between correlation matrix similarity, V/CV matrix similarity, and morphological distance with phylogenetic distance, and dietary similarity are given in Table 9. Measures of correlation and V/CV pattern similarity do not correlate significantly with phylogenetic distance, but they are significantly associated with dietary similarity. The three-way Mantel's test indicates that diet is more strongly correlated with correlation and covariance matrix similarity than is phylogeny. The correlations between dietary similarity and correlation and V/CV matrix pattern similarity is maintained, indeed enhanced, when phylogenetic distance is controlled for in the analysis. Morphological distance correlates significantly with both dietary similarity and phylogenetic distance to about the same extent.

Table 10 presents morphological integration results at the generic level. Species-level results follow the same patterns as described here for the genera. Matrix correlations between observed and theoretical total integration matrices reveal positive and significant morphological integration in all genera. Correlations among functionally and developmentally related traits are 44% higher than those among unrelated traits.

TABLE 7. Morphological distances among genera. Mahalanobis D^2 distances between the means (centroids) of all paired New World monkeys genera are presented below the diagonal.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Ateles</i>	0															
<i>Alouatta</i>	474.7	0														
<i>Brachyteles</i>	209.0	325.1	0													
<i>Lagothrix</i>	89.3	285.6	144.6	0												
<i>Cacajao</i>	244.8	502.8	402.7	209.1	0											
<i>Pithecia</i>	396.7	376.7	495.8	301.9	145.6	0										
<i>Chiropotes</i>	281.3	515.0	423.2	237.4	44.7	136.4	0									
<i>Callicebus</i>	542.0	382.2	564.0	378.3	291.8	105.4	252.1	0								
<i>Aotus</i>	556.5	455.0	596.2	410.8	345.3	180.2	296.1	80.9	0							
<i>Saimiri</i>	448.5	565.8	610.8	398.9	223.1	164.6	198.1	122.2	205.0	0						
<i>Cebus</i>	236.2	484.3	329.6	218.6	188.8	204.5	196.6	336.3	390.5	221.6	0					
<i>Leontopithecus</i>	691.4	602.1	820.4	565.5	341.0	140.9	298.8	95.5	196.2	141.3	388.2	0				
<i>Saguinus</i>	758.1	652.5	863.6	615.0	411.7	207.8	349.7	105.9	231.1	148.6	464.0	34.4	0			
<i>Callimico</i>	677.2	555.1	745.2	548.0	400.5	180.5	347.9	79.4	165.5	124.6	404.0	59.9	53.4	0		
<i>Callithrix</i>	783.6	635.0	859.8	634.0	447.0	208.5	372.0	95.4	224.3	158.6	498.3	47.0	14.3	59.0	0	
<i>Cebuella</i>	963.3	723.7	1029.5	781.8	606.0	333.2	506.6	169.9	296.6	249.0	674.3	117.4	47.9	110.1	32.3	0

Squared correlations among related traits are double those among unrelated traits. This same pattern holds for the general integration of facial versus neurocranial traits. Over all the genera, correlation among facial traits is, in general, stron-

ger than among neurocranial traits—the squared correlation among related facial traits being more than double the value for unrelated traits, whereas neurocranial traits only show a 50% enhancement of squared correlation. The stronger correlation among facial traits is largely due to the relative lack of neural integration in most of the taxa. Where significant neural integration exists, it is as strong as average facial integration. The most highly integrated trait set is the set of oral traits: Correlations among oral traits average double and squared correlations quadruple the average value among other kinds of traits. Other restricted anatomical regions, such as the orbital, nasal, zygomatic, cranial base, and cranial vault regions, show only sporadic enhancement of average correlation among related traits in these taxa.

DISCUSSION

Correlation and Variance/Covariance Structure

Both trait and matrix repeatability in this study are fairly high, so that measurement and estimation error should not affect substantially our comparisons of phenotypic covariance structure among Platyrrhines. The only exceptions are the estimated correlation matrices of *Brachyteles* ($n = 40$) and *Callimico* ($n = 27$) that present moderate repeatabilities

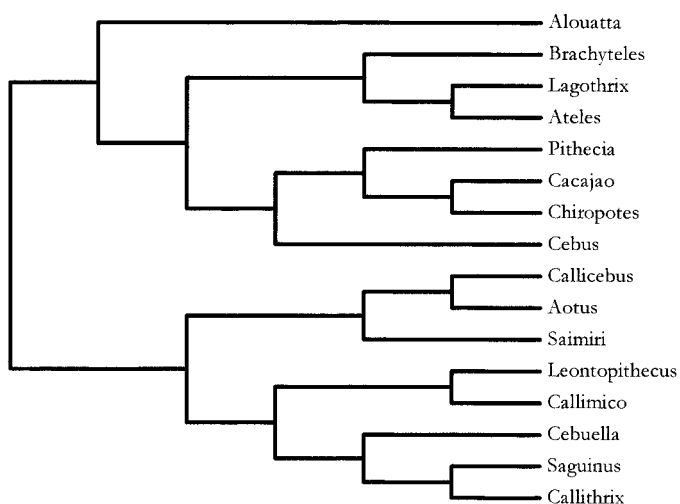


FIG. 3. Cluster diagram constructed from morphological distances between genus means (D^2) using the UPGMA method.

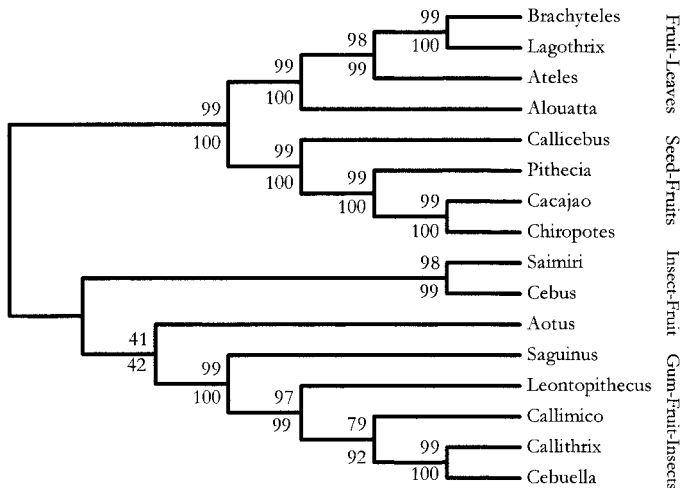


FIG. 4. Phylogenetic tree obtained with Jukes-Cantor distance model and neighbor-joining method applied to the pooled datasets of four genes (ϵ -globin, β 2m, G6PD, and IRBP) aligned in tandem. Numbers below each node correspond to bootstrap values found in 5000 replications. Numbers above each node correspond to standard error values testing for nonzero branch lengths. The four basic diet types are presented.

TABLE 9. Matrix correlations between phylogeny, diet, and correlation matrix and variance/covariance matrix similarity and morphological distance among New World Monkey genera. Significant results ($P > 0.05$) are shown in bold.

Matrix	Correlation matrix similarity	Covariance matrix similarity	Morphological distance
Phylogeny	-0.12	0.04	0.41
Dietary similarity	0.40	0.32	-0.58
Dietary similarity residuals	0.42	0.39	-0.41
Phylogeny-dietary similarity	-0.33	-0.34	0.20

0.43 and 0.54, respectively. Generally, phenotypic covariance matrices were estimated with less error than correlation matrices, as revealed by their higher repeatabilities. Also, the pattern and level of within-group correlation and V/CV among New World monkey species, genera, and higher taxa are relatively stable, presenting a moderate to high degree of shared structure. When the sampling error resulting from the limited sample size used for matrix estimation is taken in to account by controlling for matrix repeatability, correlation and covariance matrix similarity results are generally high. These high correlations are an encouraging result for those interested in applying quantitative genetic models to interpretations of morphological diversification. Some exceptions

TABLE 8. Phylogenetic and ecological matrices. Jukes-Cantor genetic distances between all genera pairs among New World monkeys are presented below the diagonal. Diet similarity matrix between all genera pairs are presented above the diagonal.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Ateles</i>	1	0.966	0.866	1.000	0.612	0.612	0.612	0.750	0.612	0.612	0.612	0.433	0.497	0.612	0.497	0.194
<i>Alouatta</i>	0.035	1	0.966	0.966	0.500	0.500	0.500	0.612	0.500	0.500	0.500	0.354	0.406	0.500	0.406	0.158
<i>Brachyteles</i>	0.028	0.038	1	0.866	0.354	0.354	0.354	0.433	0.354	0.354	0.354	0.250	0.287	0.354	0.287	0.112
<i>Lagothrix</i>	0.029	0.038	0.026	1	0.612	0.612	0.612	0.750	0.612	0.612	0.612	0.433	0.497	0.612	0.497	0.194
<i>Cacajao</i>	0.052	0.057	0.057	0.056	1	1.000	1.000	0.966	0.500	0.500	0.500	0.354	0.680	0.500	0.406	0.158
<i>Pithecia</i>	0.049	0.054	0.053	0.053	0.029	1	1.000	0.966	0.500	0.500	0.500	0.354	0.680	0.500	0.406	0.158
<i>Chiropotes</i>	0.054	0.059	0.057	0.058	0.019	0.028	1	0.966	0.500	0.500	0.500	0.354	0.680	0.500	0.406	0.158
<i>Callicebus</i>	0.051	0.056	0.054	0.055	0.049	0.043	0.047	1	0.612	0.612	0.612	0.433	0.691	0.612	0.497	0.194
<i>Aotus</i>	0.053	0.059	0.057	0.055	0.060	0.056	0.061	0.058	1	1.000	1.000	0.854	0.819	1.000	0.812	0.474
<i>Saimiri</i>	0.066	0.067	0.069	0.068	0.071	0.067	0.072	0.069	0.057	1	1.000	0.854	0.819	1.000	0.812	0.474
<i>Cebus</i>	0.058	0.065	0.063	0.062	0.066	0.063	0.065	0.063	0.052	0.056	1	0.854	0.819	1.000	0.812	0.474
<i>Leontopithecus</i>	0.058	0.063	0.062	0.061	0.064	0.063	0.065	0.064	0.050	0.062	0.059	1	0.912	0.854	0.985	0.861
<i>Saguinus</i>	0.061	0.066	0.064	0.064	0.068	0.065	0.069	0.067	0.054	0.065	0.058	0.040	1	0.819	0.912	0.757
<i>Callimico</i>	0.057	0.062	0.061	0.061	0.065	0.062	0.065	0.062	0.050	0.062	0.058	0.033	0.041	1	0.812	0.474
<i>Callithrix</i>	0.058	0.065	0.062	0.061	0.068	0.065	0.068	0.066	0.052	0.065	0.059	0.036	0.042	0.032	1	0.890
<i>Cebuella</i>	0.061	0.068	0.066	0.066	0.069	0.065	0.070	0.068	0.056	0.064	0.060	0.038	0.042	0.033	0.015	1

TABLE 10. Morphological integration for each Platyrrhine genera, displayed as the matrix correlation between correlation matrices of each taxon and the morphological integration matrices. Observed matrix correlation coefficient, significance level, and average of correlation coefficients of traits included (Avg +) and not included (Avg -) in the effect tested are shown.

Genus	Total	P	Avg (+)	Avg (-)	Neuroface	P	Avg (+)	Avg (-)	Neural	P	Avg (+)	Avg (-)	Face	P	Avg (+)	Avg (-)	Oral	P	Avg (+)	Avg (-)
<i>Alouatta</i>	0.127	0.004	0.38	0.32	0.223	0.000	0.37	0.28	-0.026	0.394	0.29	0.20	0.369	0.001	0.45	0.24	0.278	0.000	0.57	0.30
<i>Ateles</i>	0.125	0.004	0.27	0.20	0.185	0.000	0.25	0.18	0.010	0.428	0.23	0.14	0.278	0.003	0.30	0.18	0.194	0.003	0.38	0.21
<i>Brachyteles</i>	0.134	0.002	0.20	0.12	0.179	0.000	0.17	0.11	0.067	0.132	0.23	0.14	0.211	0.002	0.21	0.12	0.194	0.000	0.32	0.14
<i>Lagothrix</i>	0.127	0.003	0.30	0.23	0.216	0.000	0.29	0.20	0.041	0.285	0.28	0.19	0.312	0.000	0.34	0.21	0.174	0.004	0.40	0.22
<i>Cacajao</i>	0.170	0.000	0.32	0.22	0.204	0.000	0.28	0.19	0.071	0.194	0.29	0.20	0.194	0.035	0.30	0.22	0.161	0.017	0.40	0.22
<i>Pithecia</i>	0.156	0.001	0.31	0.23	0.232	0.000	0.29	0.20	0.027	0.357	0.28	0.17	0.308	0.002	0.34	0.20	0.229	0.001	0.43	0.23
<i>Chiropotes</i>	0.124	0.004	0.25	0.19	0.216	0.000	0.25	0.17	0.001	0.478	0.29	0.20	0.260	0.005	0.28	0.17	0.194	0.005	0.37	0.19
<i>Callicebus</i>	0.198	0.000	0.29	0.19	0.213	0.000	0.25	0.17	0.132	0.053	0.23	0.14	0.214	0.018	0.27	0.18	0.174	0.012	0.35	0.20
<i>Aotus</i>	0.165	0.000	0.21	0.13	0.128	0.002	0.17	0.12	0.116	0.051	0.23	0.14	0.073	0.180	0.42	0.29	0.166	0.009	0.29	0.15
<i>Saimiri</i>	0.174	0.000	0.43	0.34	0.159	0.000	0.39	0.32	0.076	0.183	0.28	0.19	0.196	0.043	0.37	0.22	0.205	0.005	0.53	0.32
<i>Cebus</i>	0.168	0.000	0.34	0.25	0.235	0.000	0.32	0.22	-0.007	0.469	0.28	0.16	0.319	0.000	0.37	0.22	0.268	0.000	0.52	0.25
<i>Leontopithecus</i>	0.182	0.000	0.34	0.20	0.134	0.003	0.27	0.19	0.089	0.109	0.28	0.16	0.166	0.036	0.30	0.20	0.270	0.000	0.57	0.21
<i>Saguinus</i>	0.194	0.000	0.25	0.16	0.125	0.001	0.20	0.15	0.166	0.020	0.41	0.28	0.064	0.236	0.22	0.17	0.202	0.005	0.33	0.18
<i>Callimico</i>	0.167	0.000	0.39	0.27	0.133	0.002	0.33	0.25	0.124	0.068	0.23	0.16	0.110	0.147	0.22	0.17	0.181	0.008	0.52	0.28
<i>Callithrix</i>	0.142	0.002	0.24	0.17	0.125	0.002	0.21	0.16	0.052	0.230	0.23	0.14	0.127	0.088	0.22	0.17	0.239	0.001	0.38	0.17
<i>Cebuella</i>	0.144	0.001	0.21	0.14	0.188	0.000	0.19	0.11	0.108	0.050	0.23	0.14	0.180	0.017	0.21	0.13	0.170	0.004	0.30	0.14

to this stable pattern include the two bearded saki species (*Chiropotes*) and some of the pairwise comparisons among marmosets and tamarins (*Callithrix* and *Saguinus*), particularly those involving *S. oedipus* and *S. geoffroyi* (Ackermann and Cheverud 2000) and *Callithrix jacchus* and *C. argentata*. Comparisons of these taxa with congeners indicate only a moderate level of shared covariance structure, although these two tamarin species are more similar to one another and are close phylogenetic relatives (Cropp et al. 1999). But, generally our combined results point to an overall similarity in the phenotypic covariance structure. For example, when pairwise comparisons among *Callithrix*, *Saguinus*, and *Chiropotes* species are excluded, the average adjusted correlation among correlation matrices is 0.945 (SD = 0.083) and the corresponding figures for adjusted covariance matrices are 0.863 (SD = 0.040). Moreover, the overall level of correlation (Fig. 5) among New World monkeys as indicated by the average r^2 -values is also stable, with some few exceptions among howlers and capuchins.

Consistency of genetic covariance structure can be inferred from comparison of phenotypic variation patterns in related populations (Lande 1979). The hypothesis of strictly constant within-groups covariance patterns is rejected here; although very high matrix correlations are observed among species or genera, these correlations are not strictly equal to one. However, as Roff (1996a) noted, maybe a more relevant question for evolutionary studies is not whether covariance patterns remain strictly constant during morphological diversification, but precisely how much divergence is observed and at what point during phylogenetic history disruption of covariance structure appears.

In judging similarity and dissimilarity in covariance patterns, some degree of subjectivity is inevitable, even with rigorous statistical tests based on resampling procedures. What level of divergence in covariance structure could be tolerated to still allow confidence in selection reconstruction analyses? For example, is a highly significant random selection vector correlation of 0.70 between two species' covariance matrices enough to allow the net selection gradient to be estimated with confidence, or is a correlation of 0.80, or 0.90, or even 0.99 necessary? Despite many debates during the last two decades, there is no consensus among evolutionary biologists about what level of similarity in covariance patterns is necessary (Cheverud 1988; Turelli 1988a; Shaw et al. 1995; Arnold and Phillips 1999). However, selection reconstruction analysis is mathematically a form of two-group discriminant function analysis (see above). A long period of experience with this method has led researchers to conclude that as long as diversity among groups in covariance is moderate or less than grotesque, the effects of this diversity on the analysis are minimal (Blackith and Reymont 1971; Manly 1986). Although this question is open to dispute and further theoretical and empirical investigation, researchers should follow Turelli's (1988a) suggestion to check how the reconstructed net selection gradient β varies within the bounds of the additive genetic covariance matrix \mathbf{G} (or the phenotypic matrix, if it is used as a substitute) predicted by its confidence limits. One solution might be the use of resampling procedures to generate confidence intervals for estimates of the net selection gradient (Price et al. 1984; Price

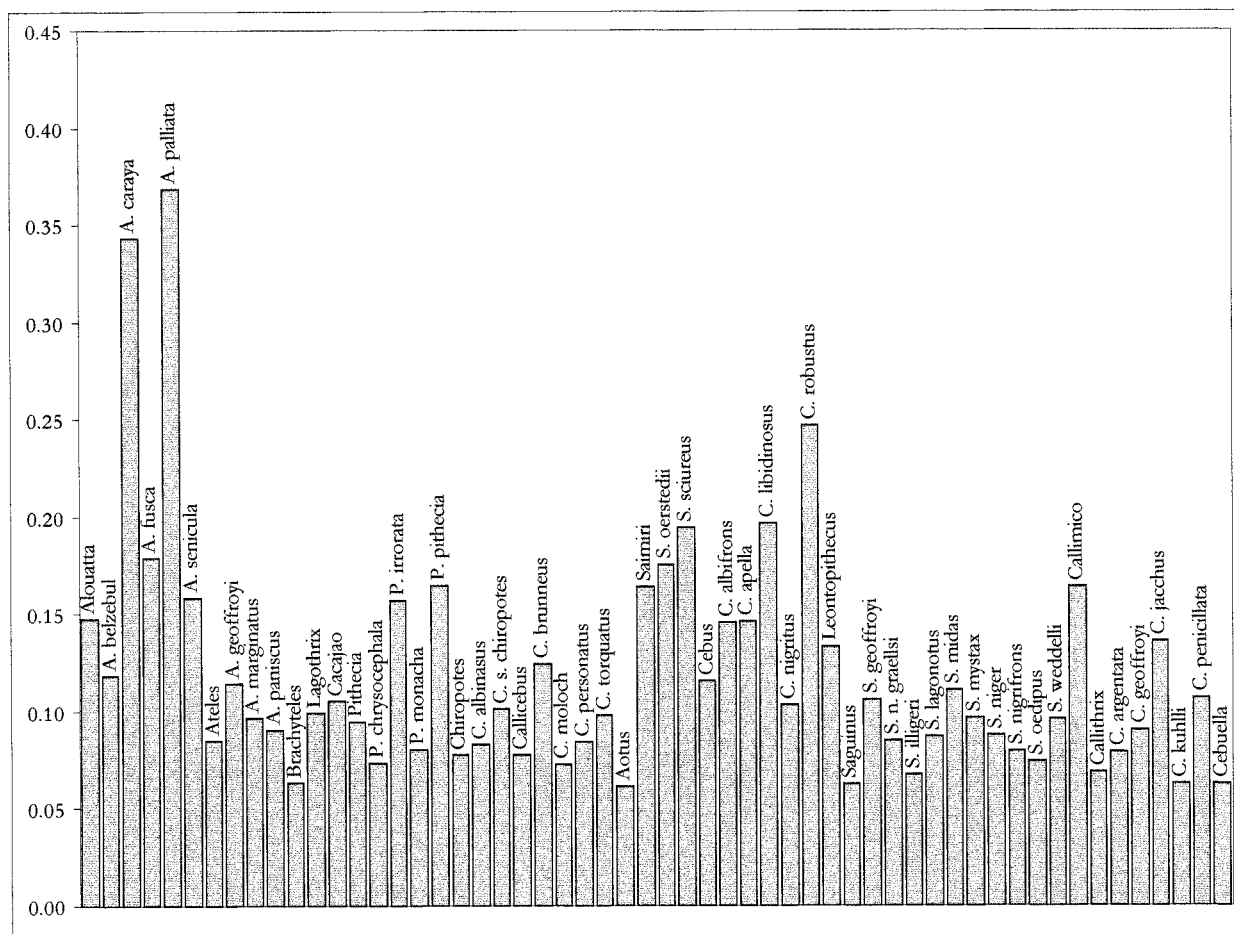


FIG. 5. Integration level among Platyrrhini measured as the average r^2 -value. For each of the 16 genera and 40 species, correlation matrices compared the average r^2 of all 39 traits are shown.

and Grant 1985). Also, if the similarity in covariance patterns is relatively high, pooling covariance matrices among populations, as suggested by Lofsvold (1988), is a viable approach.

Given that phenotypic correlation patterns and levels are relatively stable among Neotropical primates, a reasonable hypothesis is that similarity in phenotypic correlation results from similarity in genetic correlation patterns. Otherwise, if substantial changes in genetic patterns happened during evolutionary divergence of the cranium among the Platyrrhini, complementary changes in environmental correlation would have to occur to explain the relative stability observed among phenotypic matrices. Indeed, Arnold and Phillips (1999) failed to find such complementation in their study of genetic covariance in snake morphology. Cheverud (1984, 1988, 1996a) suggested that if environmentally and genetically based phenotypic variations are produced by similar disruptions of developmental pathways, then genetic and environmental correlations, and hence phenotypic correlations, should all be similar, given that the pattern of developmental relationships among traits structures the pattern of correlation. Arnold and Phillips's (1999) results of constant environmental and slightly varied genetic matrices agree with this similar disruption of developmental pathways hypothesis.

Also, direct comparison of phenotypic, genetic, and environmental correlation matrices in two tamarin species (*Saguinus*) revealed substantial similarity among and between matrices and species (Cheverud 1996b). If this hypothesis is correct, we would expect that developmentally based morphological integration patterns are similar among species and genera of Neotropical primates—precisely what is found comparing observed correlations patterns to theoretical developmental matrices.

Morphological Integration

There is an overall similarity in the morphological integration patterns of New World monkey skulls. The same basic pattern of positive integration at total integration, neural-somatic, face, and oral integration matrices was found for nearly all species and genera. On average, squared correlations among characters within each of the developmental integration regions were double those among characters in different regions. One interesting difference among taxa was found in the face and neural integration results. There is an apparent tight correlation among characters of the face in all South American primates, except some of the Callitrichinii genera (*Saguinus*, *Callimico*, *Aotus*). In contrast, the same

taxa that did not present significant integration in the face did show it in the neural region. With a few exceptions, such as *Cebuella* and *Callicebus*, which are integrated in both the facial and neural regions, taxa that display significant integration in the face do not present neural integration and vice versa. This contrast between neurally integrated and facially integrated taxa is most likely due to differences in the relative magnitude of intercorrelations among facial and neurocranial traits in these taxa. If correlations among facial characters are high relative to correlations among neural characters, facial integration will be apparent but not neurocranial integration because correlations between the "unrelated" traits in the neural analysis will include correlations among facial traits and will, therefore, be high relative to correlations among neurocranial traits. The mirror image of this phenomenon occurs in taxa displaying neurocranial integration in the absence of facial integration. Thus, taxa showing neurocranial integration have relatively higher correlation among neurocranial traits than those showing facial integration and vice versa. The lack of strong association among face characters and increased neural integration is also observed in the genus *Aotus*, the night monkeys, which with their nocturnal habits represent a unique condition in all Platyrrhini. These differences in facial-neural region integration could explain the smaller shared covariance structure observed when Aotinae (*Aotus*) and Callitrichinae (marmosets and tamarins) are compared with the other four subfamilies of Platyrrhines.

These results also shed some light on the question of whether morphological integration evolves. Our results point to a general shared pattern of developmentally based morphological integration, but also show differences in some details of how different taxa had their crania integrated, indicating that morphological integration evolves to some extent. The observed changes in facial-neural integration discussed above probably result from changes in signaling factors (like growth hormone or homeobox genes) occurring during early and late ontogenetic periods (Kim et al. 1998). In mammals, including primates, various cranial organs grow at different rates during different life stages and under influence of different physiological systems. In particular, early (neural) and late (somatic) growth factors can be distinguished during eutherian mammal ontogeny. The brain and eye complete their growth early, before the influence of the growth hormone axis is manifest. Facial features, especially those influenced by the size of attaching muscles and the oral cavity, continue to grow under the influence of the growth hormone. Therefore, taxa that show a neural integrated pattern (like marmosets and tamarins) probably had a more pronounced contribution of early developmental factors to their overall integration, whereas facially integrated taxa have more influence from late developmental integration. This interpretation is also supported by the significant integration observed among nearly all Platyrrhini with the neurosomatic developmental matrix, which tests for an overall effect of early and late growth factors. This also suggests that while a neurosomatic integration pattern is shared among all New World monkeys, taxa differ in whether facial or neurocranial traits are more highly intercorrelated.

An explanation for changes in early and late developmental integration patterns in New World monkeys may be based

on a modular genetic architecture where pleiotropic effects of single genes are generally restricted to functionally and developmentally related traits, leaving unrelated traits relatively uncorrelated. The lack of strong association among facial characters and increased neural integration observed in marmosets, tamarins, and night monkeys could result from evolutionary changes in modularity of pleiotropic effects. These changes in modularity could happen in two ways, parcellation (or desintegration) and integration (Wagner and Altenberg 1996, fig. 2). Parcellation is the differential suppression of preexisting pleiotropic effects between groups of characters and could explain the relative lack of integration in the face of the Callitrichinae and Aotinae. Modularity through integration consists in the acquisition of pleiotropy among characters from the same functional/developmental group and could explain the increased neural integration observed in Callitrichinae and Aotinae when compared to the rest of the New World monkeys. Recent surveys of the effects of quantitative trait loci (QTLs) on morphological characters in mammals are consistent with a modular model (Cheverud et al. 1996, 1997; Leamy et al. 1999; Mezey et al. 2000; Cheverud 2001). Pleiotropic effects were restricted to functionally/developmentally related traits in mouse mandibular morphology (Cheverud et al. 1997; Mezey et al. 2000; Cheverud 2001) and in cranial morphology (Leamy et al. 1999). Cheverud et al. (1996; see also Vaughn et al. 1999) also found that early and late murine growth were influenced by different sets of QTLs, mapping to different chromosomal locations, indicating separate genetic and physiological systems for early and later murine growth. Pleiotropic effects were mostly restricted to early or later weight growth indicating that mice also present a modular genetic architecture through ontogeny.

Phylogeny and Ecology

Phylogeny was not significantly similar to V/CV or correlation matrix similarity among Platyrrhines. The independence of covariance structure similarity and phylogenetic distance is an indication that changes and maintenance of covariance patterns is to some extent dissociated from phylogeny. In contrast, morphological changes in character means are strongly dependent on history, as indicated by the correlation between Mahalanobis distance (D^2) and phylogenetic distance (see Figs. 3, 4). This result supports Lande's (1980) mutation-selection balance model, because while the phenotypic means were evolving during the diversification of modern Neotropical primates, the covariance structure (the pattern and level of the covariance matrices) remained relatively stable. This model is also supported by the morphological integration results, which uncovered common patterns of developmental integration in New World monkeys. Lande (1980) showed that at equilibrium the genetic variance-covariance matrix (\mathbf{G}) will be, $\mathbf{G} = \mathbf{W}^{1/2}(\mathbf{W}^{-1/2} \mathbf{U} \mathbf{W}^{-1/2})^{1/2} \mathbf{W}^{1/2}$, where \mathbf{U} is the mutation matrix measuring the pattern of phenotypic variation produced by mutation each generation and \mathbf{W} is the fitness surface relative to the additive genetic values measuring the pattern and extent of stabilizing selection. Generally, this means that the pattern of coinheritance will evolve to match the pattern of stabilizing selection and the pattern of mutational effects (Cheverud 1996a). Both,

internal and external stabilizing selection are important in determine the pattern of stabilizing selection (**W**). External selection is stabilizing selection due to the interaction of the phenotype with the external environment. Internal selection is the stabilizing selection due to the interaction of the phenotype with other, internal characteristics of an organism and relates to the need for coadaptation of traits one to another rather than to the external environment. The pattern of internal stabilizing selection is that exerted by the epigenetic system on its parts. Through its effects on patterns of genetic correlation (Cheverud 1984) internal stabilizing selection will constrain the pattern of variation available for selection by the external environment. Only developmentally consistent mutations will be offered as potential adaptations for selection by the external environment. The common pattern of developmental integration found among New World monkeys is an indication of common patterns of internal stabilizing selection among them produced by the epigenetic developmental system. Therefore, shared developmental patterns among Platyrrhini represent internal stabilizing selection forces accounting at least partially for the phenotypic covariance structure being relatively stable during their evolutionary diversification in trait means, as suggested by the mutation-selection hypothesis.

Adaptive landscapes have a dual role in evolution, influencing both stasis and changes of the covariance structure. First, stasis might occur via stabilizing selection acting through a common epigenetic developmental system, as discussed above, to keep genetic patterns similar. Conversely, directional selection might directly or indirectly change the covariance structure. Indirect changes in covariance structure might result from directional selection acting to differentiate population means and concomitantly changing variances and covariances. Direct changes might result from directional selection for new functional and developmental morphological integration patterns, such as those changes associated with diet types among New World monkeys.

Four major dietary groups can be recognized among Platyrrhines based upon the types of food items and their relative proportion consumed (Table 8). The distribution of these four diets groups (fruits-leaves, insects-fruits, seeds-fruits, and gums-insects-fruits) across the New World monkey phylogeny (Fig. 4) demonstrates their association with major clades (family or subfamily rank) of Platyrrhini, which is also apparent in the correlation ($r = -0.65$) between diet and phylogenetic distance. Whereas covariance structure similarity was shown to be independent from phylogenetic history, patterns of cranial variation and covariation in New World monkeys are at least partially dependent upon dietary habits. There is a significant correlation between correlation and covariance structure similarity with diet, even when considered independently of phylogenetic history. This result suggests that interrelationships among skull traits are dependent, in part upon the feeding habits of Platyrrhine genera.

A detailed analysis of the differences between dietary groups will be presented elsewhere. However, a comparison of the pooled within-group correlation matrices of these four diet types suggests some interesting patterns. First, there is a general size factor accounting for about 30% of the total variation that is highly correlated (vector correlation ranging

from 0.94 to 0.99) among all four diet types. This means that cranial allometry is similar across these dietary groups. Second, after removing this general size factor from the correlation matrices and fitting secondary factors for each of the six functional/developmental groups of traits, the comparisons of the resulting factors suggest that correlations among facial traits account for most of the differences among diet groups. In particular, correlations in the zygomatic region of the gum-insect-fruit eating type are most divergent from the other types. When absolute differences in the correlation coefficients (only those greater than 0.15) of the four diet matrices are compared, the emerging picture is that almost all differences between the gum diet type and the other three types involve a decrease in the general level (magnitude) of the correlations. This is true for both facial and neural regions. The decreasing level of correlation among facial traits is consistent with the overall lower level of integration shown by Callitrichines (Fig. 5) when compared to other primates and also consistent with the lack of significant integration in the face (Table 10). These results indicate that during evolutionary diversification of Callitrichines, their general secondary trend to reduce body size was associated with a general trend toward reducing the overall level of integration, with more pronounced effects upon the face.

Conclusions

Phenotypic correlation and V/CV structures of New World monkey species were found to be quite similar, although not strictly constant. After approximately 30 million years of evolutionary diversification, phenotypic V/CV structure is broadly similar at all taxonomic levels considered, from the species to the superfamily level. Variations in phenotypic correlation and covariance structure are largely independent of phylogenetic history, whereas changes in character means are historically structured. Even while New World monkey cranial morphology was undergoing large-scale diversification, covariance patterns remained relatively stable. Changes in phenotypic correlation structure are shown to be associated with ecology because genera sharing more of their dietary habits also tend to present stronger similarity in correlation/covariance patterns providing specific hypotheses for future work.

Given the relative stability of V/CV patterns across the New World monkeys, selection reconstruction analysis becomes a real possibility, but should be done with care. One possible way to conduct such studies in the future is to incorporate information relative to factors influencing covariance patterns in the analyses. If such a factor influences covariance patterns in a way that could be predicted a priori from other sources of information, such factors could be taken into account. For example, diet is a potential factor that could be incorporated into the model given its effects on covariance stability. Additionally, simulations could be performed to verify how reliable reconstructed selection gradient coefficients are given the observed changes in the covariance structure among populations or species.

Morphological integration resulting from common patterns of development is ubiquitous among Platyrrhines. Pleiotropy is a common property of gene effects and the observed com-

mon patterns of integration indicate the likelihood of pleiotropy effects largely restricted to functionally and developmentally related traits. The modular representation of the genotype-phenotype map function as shown by the comparison of morphological integration patterns to theoretically derived developmental patterns argue for a bounded net of pleiotropic genes, where there are more pleiotropic effects on the characters within each complex than between them.

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LITERATURE CITED

- Ackermann, R. G., and J. M. Cheverud. 2000. 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.
- Anderson, T. W. 1958. An introduction to multivariate statistical analysis. Wiley, New York.
- Arnold, S. J. 1981. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. *Evolution* 35:489–509.
- . 1992. Constraints on phenotypic evolution. *Am. Nat.* 140: S85–S107.
- Arnold, S. J., and P. C. Phillips. 1999. Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-island divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53: 1516–1527.
- Atchley, W. R., J. J. Rutledge, and D. E. Cowley. 1981. Genetic components of size and shape. II. Multivariate covariance patterns in the rat and mouse skull. *Evolution* 35:1037–1055.
- Barroso, C. M. L., H. Schneider, M. P. C. Schneider, I. Sampaio, M. L. Harada, J. Czelusniak, and M. Goodman. 1997. Update on the phylogenetic systematics of New World monkeys: further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the genus *Callithrix*. *Int. J. Primatol.* 18:651–674.
- Barton, N. H., and M. Turelli. 1989. Evolutionary quantitative genetics: How little do we know? *Annu. Rev. Genet.* 23:337–370.
- Blackith, R. E., and R. A. Reyment. 1971. Multivariate morphometrics. Academic Press, London.
- Canavez, F. C., M. A. M. Moreira, J. J. Ladasky, A. Pissinatti, P. Parham, and H. N. Seuánez. 1999. Molecular phylogeny of New World primates (Platyrrhini) based on β_2 -microglobulin DNA sequences. *Mol. Phylogenet. Evol.* 12:74–82.
- Chaves, R., I. Sampaio, M. P. Schneider, H. Schneider, S. L. Page, and M. Goodman. 1999. The place of *Callimico goeldii* in the Callitrichine phylogenetic tree: evidence from von Willebrand factor gene intron II sequences. *Mol. Phylogenet. Evol.* 13: 392–404.
- Chernoff, B., and P. Magwene. 1999. Morphological integration: forty years later. Pp. 319–353 in E. C. Olson and R. L. Miller, eds. *Morphological integration*. Univ. of Chicago Press, Chicago, IL.
- Cheverud, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36:499–516.
- . 1984. Quantitative genetics and developmental constraints on evolution by selection. *J. Theor. Biol.* 110:155–171.
- . 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42:958–968.
- . 1989. A comparative analysis of morphological variation patterns in the papionins. *Evolution* 43:1737–1747.
- . 1995. Morphological integration in the saddle-back tamarin (*Saguinus fuscicollis*) cranium. *Am. Nat.* 145:63–89.
- . 1996a. Developmental integration and the evolution of pleiotropy. *Am. Zool.* 36:44–50.
- . 1996b. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*S. fuscicollis*) tamarins. *J. Evol. Biol.* 9:5–42.
- . 2001. The genetic architecture of pleiotropic relations and differential epistasis. Pp. 411–434 in G. Wagner, ed. *The character concept in evolutionary biology*. Academic Press, New York.
- Cheverud, J. M., G. P. Wagner, and M. C. Dow. 1989. Methods for the comparative analysis of variation patterns. *Syst. Zool.* 38:201–213.
- Cheverud, J. M., E. J. Routman, F. A. M. Duarte, B. van Swinderen, K. Cothran, and C. Perel. 1996. Quantitative trait loci for murine growth. *Genetics* 142:1305–1319.
- Cheverud, J. M., E. J. Routman, and D. J. Irschick. 1997. Pleiotropic effects of individual gene loci on mandibular morphology. *Evolution* 51:2006–2016.
- Coimbra-Filho, A. F., and R. A. Mittermeier. 1981. Ecology and behavior of Neotropical primates. Vol. 1. Academia Brasileira de Ciências, Rio de Janeiro.
- Cowley, D. E., and W. R. Atchley. 1992. Comparison of quantitative genetic parameters. *Evolution* 46:1965–1967.
- Cropp, S. J., A. Larson, and J. M. Cheverud. 1999. Historical biogeography of the tamarins, genus *Saguinus*: the molecular phylogenetic evidence. *Am. J. Phys. Anthropol.* 108:65–89.
- Dow, M., and J. Cheverud. 1985. Comparison of distance matrices in studies of population structure and genetic microdifferentiation: quadratic assignment. *Am. J. Phys. Anthropol.* 68:367–374.
- Emerson, S. B., and P. A. Hastings. 1998. Morphological correlations in evolution: consequences for phylogenetic analysis. *Q. Rev. Biol.* 73:141–162.
- Falconer, D. S. 1989. Introduction to quantitative genetics. Longman, Essex, U.K.

- Fooden, J. 1963. A revision of the woolly monkeys (genus *Lagothrix*). *J. Mamm.* 44:213–247.
- Froehlich, J. W., J. Supriatna, and P. H. Froehlich. 1991. Morphometric analyses of *Ateles*: systematic and biogeographic implications. *Am. J. Primatol.* 25:1–22.
- Garber, P. A., and S. R. Leigh. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol.* 68:1–22.
- Hershkovitz, P. 1977. Living New World monkeys (Platyrrhini) with an introduction to Primates. Vol. I. Univ. of Chicago Press, Chicago, IL.
- . 1983. Two new species of night monkeys, genus *Aotus* (Cebidae, Platyrrhini): a preliminary report on *Aotus* taxonomy. *Am. J. Primatol.* 4:209–243.
- . 1984. Taxonomy of squirrel monkeys genus *Saimiri* (Cebidae, Platyrrhini): a preliminary report with description of a hitherto unnamed form. *Am. J. Primatol.* 7:155–210.
- . 1985. A preliminary taxonomic review of the South American bearded saki monkeys genus *Chiropotes* (Cebidae, Platyrrhini), with the description of a new subspecies. *Fieldiana Zool.* (new ser.) 27:1–46.
- . 1987a. Uacaries, New World monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. *Am. J. Primatol.* 12:1–53.
- . 1987b. The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): a preliminary report and critical review with the description of a new species and a new subspecies. *Am. J. Primatol.* 12:387–468.
- . 1990. Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. *Fieldiana Zool.* (new ser.) 55:1–109.
- Horovitz, I. 1999. A phylogenetic study of living and fossil Platyrrhines. *Am. Mus. Novitates* 3269:1–40.
- Horovitz, I., and A. Meyer. 1995. Systematics of New World monkeys (Platyrrhini, Primates) based on 16S mitochondrial DNA sequences: a comparative analysis of different weighting methods in cladistic analysis. *Mol. Phylogenet. Evol.* 4:448–456.
- Kim, H.-J., D. P. C. Rice, P. J. Kettunen, and I. Thesleff. 1998. FGF-, BMP- and Shh-mediated signalling pathways in the regulation of cranial suture morphogenesis and calvarial bone development. *Development* 125:1241–1251.
- Kimura, M. 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proc. Natl. Acad. Sci. USA* 54:731–736.
- Kinsey, W. G. 1997. New World primates: ecology, evolution, and behavior. Walter de Gruyter, Inc., New York.
- Klecka, W. R. 1980. Discriminant analysis. Sage, Beverly Hills, CA.
- Kohn, L. A., and W. R. Atchley. 1988. How similar are genetic correlation structures? Data from mice and rats. *Evolution* 42:467–481.
- Kumar, S., K. Tamura, and M. Nei. 1993. MEGA: Molecular evolutionary genetics analysis. Ver. 1.01. The Pennsylvania State University, University Park, PA.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- . 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416.
- . 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94:203–215.
- Leamy, L., E. Routman, and J. Cheverud. 1999. Quantitative trait loci for early and late developing skull characters in mice: a test of the genetic independence model of morphological integration. *Am. Nat.* 153:201–214.
- Lofsvold, D. 1986. Quantitative genetics of morphological differentiation in *Peromyscus*. I. Tests of the homogeneity of genetic covariance structure among species and subspecies. *Evolution* 40:559–573.
- . 1988. Quantitative genetics of morphological differentiation in *Peromyscus*. II. Analysis of selection and drift. *Evolution* 42:54–67.
- Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, MA.
- Manly, B. F. J. 1986. Multivariate statistical methods: a primer. Chapman and Hall, New York.
- . 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York.
- Marroig, G., and R. Cerqueira. 1997. Plio-pleistocene South America history and the Amazon lagoon hypothesis: a piece in the puzzle of Amazonian diversification. *J. Comp. Biol.* 2:103–119.
- Mezey, J., J. Cheverud, and G. Wagner. 2000. Is the genotype-phenotype map modular? A statistical approach using mouse QTL data. *Genetics* 156:305–311.
- Mittermeier, R. A., A. B. Rylands, A. F. Coimbra-Filho, and G. A. B. Fonseca. 1988. Ecology and behavior of Neotropical primates. Vol. 2. World Wildlife Fund, Washington, D.C.
- Morrison, D. F. 1976. Multivariate statistical methods. McGraw-Hill, New York.
- Norconk, M. A., A. L. Rosenberger, and P. A. Garber. 1996. Adaptive radiations of Neotropical Primates. Plenum, New York.
- Olson, E. C., and R. L. Miller. 1958. Morphological integration. Univ. of Chicago Press, Chicago, IL.
- Paulsen, S. M. 1996. Quantitative genetics of the wing color pattern in the buckeye butterfly (*Precis coenia* and *Precis evarete*): evidence against the constancy of G. *Evolution* 50:1585–1597.
- Pielou, E. C. 1984. Probing multivariate data with random skewers: a preliminary to direct gradient analysis. *Oikos* 42:161–165.
- Phillips, P. C., and S. J. Arnold. 1999. Hierarchical comparison of genetic variance-covariance matrices. I. Using the Flury hierarchy. *Evolution* 53:1506–1515.
- Price, T. D., and P. R. Grant. 1985. The evolution of ontogeny in Darwin's finches: a quantitative genetic approach. *Am. Nat.* 125:169–188.
- Price, T. D., P. R. Grant, and P. T. Boag. 1984. Genetic changes in the morphological differentiation of Darwin's ground finches. Pp. 50–66 in K. Wöhrmann and V. Loescheke, eds. Population biology and evolution. Springer, Berlin.
- Price, T. D., M. Turelli, and M. Slatkin. 1993. Peak shifts produced by correlated response to selection. *Evolution* 47:280–290.
- Raff, R. A. 1996. The shape of life: genes, development, and the evolution of animal form. Univ. of Chicago Press, Chicago, IL.
- Riska, B. 1985. Group size factors and geographic variation of morphometric correlation. *Evolution* 39:792–803.
- Roff, D. A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* 74:481–490.
- . 1996a. Evolutionary quantitative genetics. Chapman and Hall, New York.
- . 1996b. The evolution of genetic correlations: an analysis of patterns. *Evolution* 50:1392–1403.
- Rzhetsky, A., and M. Nei. 1992. A simple method for estimating and testing minimum-evolution trees. *Mol. Biol. Evol.* 9:945–967.
- . 1993. Theoretical foundation of the minimum-evolution method of phylogenetic inference. *Mol. Biol. Evol.* 10:1073–1095.
- Saitou, N., and M. Nei. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4:406–425.
- Schneider, H. 2000. The current status of the New World monkey phylogeny. *An. Acad. Bras. Cienc.* 72:165–172.
- Schneider, H., and A. L. Rosenberger. 1996. Molecules, morphology, and Platyrrhini systematics. Pp. 3–19 in M. A. Norconk, A. L. Rosenberger, and P. A. Garber, eds. Adaptive radiations of Neotropical primates. Plenum, New York.
- Schneider, H., M. P. C. Schneider, I. Sampaio, M. L. Harada, M. Stanhope, and M. Goodman. 1993. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Mol. Phylogenet. Evol.* 2:225–242.
- Schneider, H., I. Sampaio, M. L. Harada, C. M. L. Barroso, M. P. C. Schneider, J. Czelusniak, and M. Goodman. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and epsilon-globin sequences. *Am. J. Phys. Anthropol.* 100:153–179.

- Shaw, R. 1991. The comparison of quantitative genetic parameters between populations. *Evolution* 45:143–151.
- . 1992. Comparison of quantitative genetic parameters: reply to Cowley and Atchley. *Evolution* 46:1967–1969.
- Shaw, F. H., R. G. Shaw, G. S. Wilkinson, and M. Turelli. 1995. Changes in genetic variances and covariances: *G* whiz! *Evolution* 49:1260–1267.
- Smith, K. K. 1996. Integration of craniofacial structures during development in mammals. *Am. Zool.* 36:70–79.
- . 1997. Comparative patterns of craniofacial development in Eutherian and Metatherian mammals. *Evolution* 51:1663–1678.
- Stearns, S. C. 1992. *The evolution of life-histories*. Oxford Univ. Press, Oxford, U.K.
- Stephan, S. J. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution* 51:571–586.
- Thompson, D. W. 1961. *On growth and form*. Cambridge Univ. Press, Cambridge, U.K.
- Turelli, M. 1984. Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theor. Popul. Biol.* 25:138–193.
- . 1985. Effects of pleiotropy on predictions concerning mutation-selection balance for polygenic traits. *Genetics* 111:165–195.
- . 1988a. Phenotypic evolution, constant covariances and the maintenance of additive variance. *Evolution* 43:1342–1347.
- . 1988b. Population genetic models for polygenic variation and evolution. Pp. 601–618 in B. S. Weir, E. J. Eisen, M. Goodman, and G. Namkoong, eds. *Proceedings of the second international conference on quantitative genetics*. Sinauer Associates, Sunderland, MA.
- Vaughn, T. T., L. S. Pletscher, A. Peripato, K. King-Ellison, E. Adams, C. Erikson, and J. M. Cheverud. 1999. Mapping quantitative trait loci for murine growth: a closer look at genetic architecture. *Genet. Res.* 74:313–322.
- Venable, D. L., and M. A. Búrquez. 1990. Quantitative genetics of size, shape, life-history, and fruit characteristics of the seed heteromorphic composite *Heterosperma pinnatum*. II. Correlation structure. *Evolution* 44:1748–1763.
- Vivo, M. de. 1991. *Taxonomia de Callithrix* Erxleben, 1777 (Callitrichidae, Primates). Fundação Biodiversitas, Belo Horizonte, Brazil.
- von Dornum, M., and M. Ruvolo. 1999. Phylogenetic relationships of the New World monkeys (Primates, Platyrrhini) based on nuclear G6PD dna sequences. *Mol. Phylogenet. Evol.* 11:459–476.
- Voss, R. S., and L. F. Marcus. 1992. Morphological evolution in muroid rodents. II. Craniometric factor divergence in seven neotropical genera, with experimental results from *Zygodontomys*. *Evolution* 46:1918–1934.
- Voss, R. S., L. F. Marcus, and P. P. Escalante. 1990. Morphological evolution in muroid rodents. I. Conservative patterns of craniometric covariance and their ontogenetic basis in the Neotropical genus *Zygodontomys*. *Evolution* 44:1568–1587.
- Waddington, C. H. 1957. *The strategy of the genes*. George Allen and Unwin Ltd, London.
- Wagner, G. P. 1990. A comparative study of morphological integration in *Apis mellifera*. *Z. Zool. Syst. Evol.* 28:48–61.
- . 1996. Homology natural kinds and the evolution of modularity. *Am. Zool.* 36:36–43.
- Wagner, G. P., and L. Altenberg. 1996. Perspective: complex adaptations and the evolution of evolvability. *Evolution* 50:967–976.
- Wilkinson, G. S., K. Fowler, and L. Partridge. 1990. Resistance of genetic correlation structure to directional selection in *Drosophila melanogaster*. *Evolution* 44:1990–2003.
- Willis, J. H., J. A. Coyne, and M. Kirkpatrick. 1991. Can one predict the evolution of quantitative characters without genetics? *Evolution* 45:441–444.
- Wright, S. 1968. *Evolution and the genetics of populations*. Vol. 1. Genetics and biometric foundations. Univ. of Chicago Press, Chicago, IL.
- Zelditch, M. L., and A. C. Carmichael. 1989. Ontogenetic variation in patterns of developmental and functional integration in skulls of *Sigmodon fulviventer*. *Evolution* 43:814–824.
- Zelditch, M. L., D. O. Straney, D. L. Swiderski, and A. C. Carmichael. 1990. Variation in developmental constraints in *Sigmodon*. *Evolution* 44:1738–1747.

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APPENDIX

Classification employed in this study for New World monkeys. n_1 , the total number of specimens measured per taxa; n_2 , the sample size of correlation and variance/covariance matrices for each taxa.

Superfamily	Family	Subfamily	Genus	Species or subspecies	n_1	n_2	
Ateloidea	Atelidae	Atelinae	Ateles (spider monkey)		1775	1600	
				<i>Ateles belzebulth</i>	827	745	
				<i>Ateles chamek</i>	417	358	
				<i>Ateles geoffroyi</i>	246	226	
				<i>Ateles marginatus</i>	5		
				<i>Ateles paniscus</i>	23		
			Brachyteles (muriqui or wooly spider monkey)		88	87	
					74	71	
			Lagothrix (barrigudo or wooly monkey)		55	54	
					44	40	
			Alouattinae	<i>Brachyteles arachnoides</i>	44	40	
				<i>Lagothrix flavicauda</i>	127	92	
				<i>Lagothrix lagothericha cana</i>	2		
				<i>Lagothrix lagothericha lagothericha</i>	24		
				<i>Lagothrix lagothericha lugens</i>	6		
				<i>Lagothrix lagothericha poeppigii</i>	28		
		33					
		405		387			
		405		387			
		138		130			
	<i>Alouatta belzebul</i>	52		52			
	<i>Alouatta caraya</i>	86		78			
	<i>Alouatta fusca</i>	43		43			
	<i>Alouatta palliata</i>	77		75			
	<i>Alouatta senicula</i>						
	<i>Alouatta villosa</i>	13					
		948		855			
		495		464			
		84	79				
	Pitheciinae	Pitheciidae		Cacajao (uakarie monkey)	<i>Cacajao calvus calvus</i>	8	
					<i>Cacajao calvus novaesi</i>	14	
					<i>Cacajao calvus rubicundus</i>	2	
					<i>Cacajao calvus ucayalii</i>	33	
<i>Cacajao melanocephalus melanocephalus</i>					11		
<i>Cacajao melanocephalus ouakary</i>				16			
Chiropotes (bearded saki monkey)					168	154	
				<i>Chiropotes albinasus</i>	58	54	
				<i>Chiropotes satanas chiropotes</i>	77	74	
				<i>Chiropotes satanas satanas</i>	17		
				<i>Chiropotes satanas utahicki</i>	16		
Pithecia (saki monkey)					243	231	
				<i>Pithecia aequatorialis</i>	2		
				<i>Pithecia albicans</i>	4		
				<i>Pithecia irrorata irrorata</i>	53	47	
				<i>Pithecia irrorata vanzolinii</i>	24		
Callicebinae					68	68	
	<i>Pithecia monacha</i>	51	50				
	<i>Pithecia pithecia chrysocephala</i>	40	38				
	<i>Pithecia pithecia pithecia</i>	453	391				
		453	391				
	Callicebus (titi monkey)	<i>Callicebus baptista</i>	17				
		<i>Callicebus brunneus</i>	39	35			

APPENDIX

Continued.

Superfamily	Family	Subfamily	Genus	Species or subspecies	<i>n</i> ₁	<i>n</i> ₂
Ceboidea	Cebidae	Cebinae	Cebus (capuchin monkey)	<i>Callicebus cinerascens</i>	6	
				<i>Callicebus cupreus</i>	43	
				<i>Callicebus discolor</i>	30	
				<i>Callicebus donacophilus donacophilus</i>	11	
				<i>Callicebus donacophilus pallescens</i>	7	
				<i>Callicebus hoffmanni</i>	22	117
				<i>Callicebus moloch</i>	122	
				<i>Callicebus ornatus</i>	21	52
				<i>Callicebus personatus</i>		
				<i>Callicebus personatus melanochir</i>	24	
				<i>Callicebus personatus nigrifrons</i>	32	49
				<i>Callicebus personatus personatus</i>		
				<i>Callicebus torquatus</i>	8	
				<i>Callicebus torquatus lucifer</i>	38	
				<i>Callicebus torquatus lugens</i>	3	
				<i>Callicebus torquatus purinus</i>	1	
				<i>Callicebus torquatus regulus</i>	3447	2654
					3252	2473
					938	659
					466	396
					42	42
					149	139
					20	
					40	40
					11	
					93	87
					11	
					19	
					39	37
					4	
					472	263
			Saimiri (squirrel monkey)	<i>Saimiri albigena</i>	8	
				<i>Saimiri boliviensis</i>	20	
				<i>Saimiri cassiquiarensis</i>	31	
				<i>Saimiri macrondon</i>	20	
				<i>Saimiri oerstedii</i>	3	
				<i>Saimiri oerstedii</i>	42	42
				<i>Saimiri sciureus</i>	141	105
				<i>Saimiri ustus</i>	19	
				<i>Saimiri vanzolinii</i>	16	
						1814
					40	27
					40	27
					655	
					17	
					1	
					172	143
					56	49
					69	41
					102	81
					92	60
Callitrichinae			Callimico (Goeldi's monkey)	<i>Callimico goeldi</i>		
			Callithrix (marmoset)	<i>Callithrix aurita</i>		
				<i>Callithrix flviceps</i>		
				<i>Callithrix kuhlii</i>		
				<i>Callithrix geoffroyi</i>		
				<i>Callithrix jacchus</i>		
				<i>Callithrix penicillata</i>		
				<i>Callithrix argentata</i>		

APPENDIX

Continued.

Superfamily	Family	Subfamily	Genus	Species or subspecies	n_1	n_2
				<i>Callithrix chrysolaia</i>	26	
				<i>Callithrix emiliae</i>	17	
				<i>Callithrix humeralifera</i>	30	
				<i>Callithrix intermedia</i>	2	
				<i>Callithrix leucippe</i>	12	
				<i>Callithrix mauesi</i>	3	
				<i>Callithrix melanura</i>	19	
				<i>Callithrix nigriceps</i>	6	
				<i>Callithrix saterei</i>	4	89
			<i>Cebuella (pygmy marmoset)</i>	<i>Cebuella pygmaea</i>	116	
					86	
			<i>Leontopithecus (lion tamarin)</i>	<i>Leontopithecus caissara</i>	1	
				<i>Leontopithecus chrysomelas</i>	12	
				<i>Leontopithecus chrysopygus</i>	2	
				<i>Leontopithecus rosalia</i>	68	
					1417	1135
			<i>Saguinus (tamarin)</i>	<i>Saguinus bicolor bicolor</i>	8	
				<i>Saguinus bicolor martinsi</i>	6	
				<i>Saguinus bicolor ochraceus</i>	10	
				<i>Saguinus fuscicollis acensis</i>	2	
				<i>Saguinus fuscicollis avilapirezi</i>	4	
				<i>Saguinus fuscicollis fuscicollis</i>	24	
				<i>Saguinus fuscicollis fuscus</i>	16	
				<i>Saguinus fuscicollis illegeti</i>	121	97
				<i>Saguinus fuscicollis lagonotus</i>	57	45
				<i>Saguinus fuscicollis leucogenys</i>	21	
				<i>Saguinus fuscicollis melanoleucus</i>	29	
				<i>Saguinus fuscicollis nigrifrons</i>	78	63
				<i>Saguinus fuscicollis primitivus</i>	2	
				<i>Saguinus fuscicollis weddelli</i>	76	66
				<i>Saguinus geoffroyi</i>	164	134
				<i>Saguinus imperator imperator</i>	11	
				<i>Saguinus imperator subgriseus</i>	23	
				<i>Saguinus inustus</i>	13	
				<i>Saguinus labiatus labiatus</i>	32	
				<i>Saguinus labiatus thomasi</i>	3	
				<i>Saguinus leucopus</i>	30	
				<i>Saguinus midas</i>	62	54
				<i>Saguinus niger</i>	150	129
				<i>Saguinus sp.</i>	13	
				<i>Saguinus mystax mystax</i>	82	72
				<i>Saguinus mystax pileatus</i>	20	
				<i>Saguinus mystax pluto</i>	8	
				<i>Saguinus nigricollis graellsii</i>	74	44
				<i>Saguinus nigricollis nigricollis</i>	15	
				<i>Saguinus oedipus</i>	230	182
				<i>Saguinus triparititus</i>	16	

APPENDIX

Continued.					
Superfamily	Family	Subfamily	Genus	Species or subspecies	n_1 n_2
Aotidae	Aotinae	Aotinae	Aotus (night monkey)		195 181
					195 181
					195 181
					4
				<i>Aotus azarae azarae</i>	28
				<i>Aotus azarae boliviensis</i>	2
				<i>Aotus brumbacki</i>	30
				<i>Aotus infulatus</i>	18
				<i>Aotus lemurinus griseimembra</i>	44
				<i>Aotus lemurinus lemurinus</i>	9
				<i>Aotus nancymai</i>	27
				<i>Aotus nigriceps</i>	13
				<i>Aotus trivirgatus</i>	11
				<i>Aotus vociferans</i>	