Brain shape convergence in the adaptive radiation of New World monkeys

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Primates constitute one of the most diverse mammalian clades, and a notable feature of their diversification is the evolution of brain morphology. However, the evolutionary processes and ecological factors behind these changes are largely unknown. In this work, we investigate brain shape diversification of New World monkeys during their adaptive radiation in relation to different ecological dimensions. Our results reveal that brain diversification in this clade can be explained by invoking a model of adaptive peak shifts to unique and shared optima, defined by a multidimensional ecological niche hypothesis. Particularly, we show that the evolution of convergent brain phenotypes may be related to ecological factors associated with group size (e.g., social complexity). Together, our results highlight the complexity of brain evolution and the ecological significance of brain shape changes during the evolutionary diversification of a primate clade.

comparative method | primates | adaptive evolution | geometric morphometrics | Platyrrhini

Adaptive radiation, defined as the rapid and exceptional adaptive diversification of a single phylogenetic lineage into a variety of different ecological niches (1, 2), is thought to be one of the main evolutionary processes generating biodiversity on Earth (3). Although several adaptive radiations have now been thoroughly studied (e.g., African cichlids, Caribbean anoles, Galapagos finches, etc.), we still need more studies from which generalizations on this process can be drawn (2). Particularly, under what conditions a lineage will undergo adaptive radiation has long been debated, although both empirical and theoretical models point to the existence of ecological opportunity as a major factor (2, 3). This opportunity may appear, among others, through the colonization of a new area, the extinction of a strong ecological competitor, or the evolution of a new trait—a "key innovation"— that allows the utilization of resources in ways that were not previously possible (3, 4). Therefore, a significant dimension of adaptive radiations is the diversification of ecologically relevant phenotypic traits (2, 5). Among the studied cases of adaptive radiations, several ecologically relevant traits have been identified. For example, relative limb size in anoles lizards (6), beak shape in Darwin's finches (7), or overall body shape in cichlid fishes (8).

Remarkably, a trait that has received less attention in the study of adaptive radiations among vertebrate clades is brain morphology. Brains have substantial ecological and adaptive importance because they underlie the behavior that allows an animal to successfully interact with its environment. In this sense, primates constitute a notable example, as the evolution of brain morphology is one of the most prominent features of their diversification (9). Primates generally engage in complex foraging and social behaviors (10), and therefore, the evolution of enhanced cognitive capacities associated with enlarged and/or more complex brains may constitute a major axis of their adaptive ecological diversification. For example, possessing a large brain is perhaps the single most relevant phenotypic trait of our own species, *Homo sapiens*. Specifically, previous works have pointed out that the evolution

of enlarged brains could be important ecologically because these changes are related to the acquisition of the cognitive abilities required to sustain complex social interactions—a behavioral trait probably involved in the origin and maintenance of the evolutionary success of primates (the social brain hypothesis) (11).

However, although brain size has been traditionally the preferred measured trait in evolutionary studies, brains are not uniform structures but are constituted by several anatomically distinct functional systems or modules (e.g., neocortex, cerebellum, etc.). Previous work has suggested that these modules can vary in their relative size among species of some mammalian clades (including primates) (12–14) and, moreover, that these mosaic changes can better explain neural diversity than total—absolute or relative—brain size changes alone (e.g., among primates) (14). Additionally, in several vertebrate clades, part of this mosaic variation has been related to particular behavioral capacities (e.g., refs. 15 and 16). Thus, brain diversification is probably a complex process involving several dimensions of change occurring during the divergence of the species and along multiple ecological axes. Moreover, as in previous adaptive radiation studies where shape is the most ecologically relevant trait (6, 7), brain shape (i.e., the relative position and size of individual brain components) is probably a more important aspect of brain evolution than its total relative size. However, despite the potential ecological relevance of brain shape variation for primates, its evolutionary dynamics have been less studied in macroevolution (14).

New World monkeys or platyrrhines, one of the three major primate clades, constitute an example of a major mammalian adaptive radiation that unfolded in isolation in Central and

Significance

The evolutionary diversification of brain morphology is one of the most prominent features of the primate adaptive radiation and a likely determinant of primate evolutionary success. However, the ecological factors responsible for the diversification of the primate brain are largely unknown. In this work, we use a comparative approach to study brain diversification during the adaptive radiation of a major primate clade—the New World monkeys. We show that brain morphology evolved in association with the occupation of several ecological niches, and that convergence in brain morphology among clades may be associated with an evolutionary increase in the complexity of social behaviors.

South America during the last 25–35 Ma, resulting in broad ecological and morphological diversity (17, 18). Noticeably, previous works have pointed to the putative occurrence of several evolutionary independent processes of increase and decrease in relative brain size (19–21) in this clade, indicating an extensive diversification of brain morphology. However, it is unknown how brain shape has evolved in the context of this primate adaptive radiation.

In this study, we investigate the process of brain shape diversification of New World monkeys during their adaptive radiation in relation to different ecological dimensions. We first quantify brain shape variation using virtual reconstructions of cranial endocasts and geometric morphometrics methods, and then explore the evolutionary processes underlying brain diversification using phylogenetic comparative methods. We hypothesized that, if brain shape is an ecologically relevant trait for platyrrhines, a pattern of variation that departs from neutral models of evolution would be expected. To address this hypothesis, we analyzed the relationship between phenotypic variation and the branching process of the species based on a Brownian (random) model of evolution. Next, we investigated whether a model involving changes in adaptive peaks in a macroevolutionary landscape for brain shape can better account for the observed diversity. Moreover, considering that a likely outcome of an adaptive radiation, given the importance of ecological factors in shaping diversity, is the repeated evolution of similar phenotypes (22), we explicitly test for the existence of brain morphological convergence in the platyrrhine radiation. Finally, we explore previously hypothesized ecological factors (e.g., group size) (11) driving brain shape diversification and convergence in this primate clade.

Results

Brain Shape Variation. To study the pattern of variation in brain shape in the platyrrhine clade we performed a principal-component analysis (PCA) on the Procrustes shape coordinates of 399 landmarks and semilandmarks measured on 49 species (Table S1) that describe each species external brain morphology (Fig. 1A and Table S2). Fig. 1A shows the main trends in shape variation, as represented by the first two principal components (PCs), which together account for ~61% of the total variation, along a projection of the phylogeny on the morphospace. A general separation among families, and a largely phylogenetically structured occupation of the morphospace can be observed, although remarkable shape proximity occurs among members from the three families (the atelids *Ateles*, *Brachyteles*, and *Lagothrix*; the pithecids *Chiropotes* and *Cacajao*; and the cebid *Cebus*) showing high and similar encephalization (i.e., total relative brain size) values [relative endocranial volume (rECV)] (Figs. S1 and S2), suggesting the existence of brain shape convergence among these clades. Furthermore, *Alouatta* and *Saimiri* species, extremes on the encephalization scale, also appear as extremes in shape space. Although these results may suggest that shape and total relative size describe the same morphological properties of the brain, only a fraction of the total shape variation can be accounted by encephalization [phylogenetic generalized least-squares regression (PGLS): $\lambda = 0.74$; $R^2 = 0.11$; $P = 0.010$]. Brain shape differences along PC1 (Fig. 1B and Movie S1), which explains ~43% of variation, are mainly related to general enlargement of the neocortex area with respect to the stem and cerebellum areas; and the relative position of the stem, which contrasts the posterior location in *Alouatta* with the more ventral position in *Saimiri*. Specifically, shape changes in the neocortex are concentrated mainly in the frontal, parietal, and occipital lobes, with the largest variation observed in the occipital lobe, which expands posteriorly and in a dorsoventral direction. These changes contribute to an overall more globular brain shape for positive scores. Additionally, the brain base exhibits a more ventrally flexed morphology among species with more positive scores. Furthermore, although PC1 is highly correlated with rECV (PGLS: $\lambda = 0.87$; $R^2 = 0.77$, $P = 0.001$; Fig. S3), our results clearly show that PC1

describes complex morphological changes that cannot be characterized merely by relative total brain volume measurements.

Shape variation along PC2 (18.5% of total variation) is mainly related to changes in the prefrontal area, which becomes less expanded, particularly along the brain base midline, in the positive scores direction; and with a general increase in globularity for negative scores (Fig. 1B and Movie S2). Importantly, although New World monkeys exhibit a remarkable body size diversity (~0.01–10 kg.), brain shape variation cannot be merely attributed to evolutionary allometric effects (PGLS: $\lambda = 0.69$; $R^2 = 0.15$; $P = 0.003$).

Brain Shape Convergence. Next, we explicitly test whether the pattern of shape proximity exhibited by members of the three families departs from what can be expected by chance. We calculated two pattern-based measures of morphological convergence (C1 and C5) using the first two PCs and compared them against a null distribution obtained using simulations under a random model of evolution (Brownian motion). Although only the first measure showed a strong convergence signal (C1 = 0.63; $P = 0.01$; C5 = 5; $P = 0.22$), these analyses point to the existence of nonrandom evolutionary processes generating brain shape similarity among these clades.

The Evolution of Brain Shape. Phylogenetic signal analyses allowed to further unravel the evolutionary dynamics of brain shape diversification. Complementing the observed cladewise convergence, K statistic values both for PC1 ($K = 1.30$, $P = 0.001$) and PC2 ($K = 2.32$, $P = 0.001$) showed that variance was concentrated among clades rather than within clades, indicating, besides a considerable phylogenetic signal, a pattern of early brain morphological diversification that departs from neutral expectations. Disparity-through-time (DTT) plots further support this view: an early fast diversification of the morphological aspects represented by PC2 is observed (Fig. 2); whereas, for PC1, a drop in disparity beyond the neutral expectation can be seen between ~17 and 12 Ma, pointing to a burst of brain shape evolution approximately associated with the origin of the extant subfamilies (Fig. 2 and Fig. S2), followed by a slowdown in disparity changes until present times. Moreover, these results also point to the existence of separate bursts of brain evolution during the platyrrhine radiation, each affecting different aspects of brain morphology.

Finally, we explicitly asked whether a model of adaptive evolution could be invoked to explain brain shape diversification in platyrrhine monkeys, and particularly, to explain the observed pattern of shape convergence. To do this, we implement a model selection approach, in which the likelihoods of several alternative evolutionary scenarios are compared using an information content criterion [corrected Akaike information criterion (AICc)] to find the best-fitting model. The explored models were a random walk [modeled as Brownian motion (BM)]; early burst (where the rate of Brownian evolution decays exponentially through time); and several adaptive evolution scenarios modeled as Ornstein–Uhlenbeck (OU) processes (Fig. S4). In OU models, nodes and branches of the phylogeny are assigned to different selective regimes representing phenotypic adaptive peaks on a Simpsonian macroevolutionary landscape. This way, directional and stabilizing selection can be modeled. To construct these scenarios, we combined a priori biological hypotheses with the use of the SURFACE method (*Supporting Information* and Figs. S4 and S5), which, using a data-driven algorithm, finds the model that has the best statistical fit. By combining these approaches, we generated a likely biological hypothesis with a high absolute statistical support, excluding the possibility of choosing only the best among several bad biological hypotheses (see *Supporting Information* for details). Our results support as the best fit an OU model based on a multidimensional ecological niche hypothesis (AICc weight = 0.94; Fig. 3 and Table S3) in which diet composition, locomotion strategy, and group size are
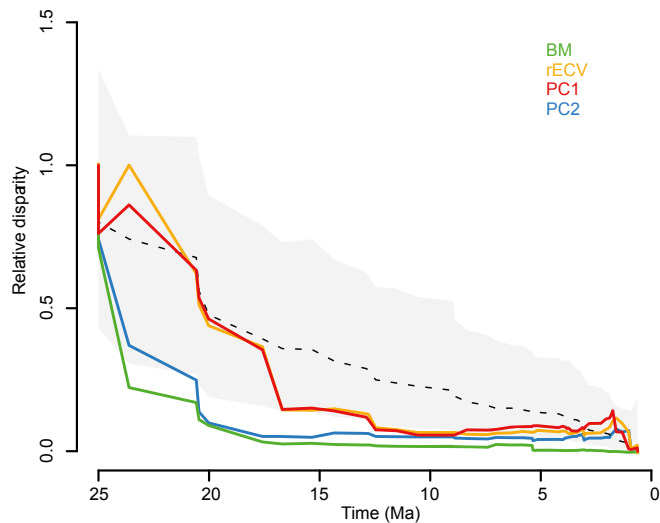
<div style="text-align: right">EVOLUTION</div>

Fig. 1. Morphometric analysis of New World monkey's brain shape. (*A*) Ordination of 49 platyrrhine species in the morphospace defined by the first two principal components (PCs) of brain shape variation, which together account for ~61% of total variance. Endocast at *Left* shows the measured landmarks (red), and curves (green) and surfaces (blue) semilandmarks on each individual (see also Fig. S6 and Table S2). Encephalization values (relative ECV) for each species are depicted by the color of each data point. Additionally, the three platyrrhine families are indicated, along with the genus *Aotus*, whose position in the platyrrhine tree is contentious. (*B*) Brain shape changes associated with the main axes of variation. Models were obtained by warping a surface model of the mean platyrrhine shape along PC1 and PC2 scores. See also Movies S1 and S2.

the main adaptive landscape-defining variables. Moreover, this suggests that ecological factors represented by group size could be responsible for the observed cladewise convergence in platyrrhines, as further indicated by significant shape differences between species with large (i.e., more than 15 individuals) and small groups (phylogenetic multivariate ANOVA for PC1 and PC2; $P = 0.001$, $R^2 = 0.74$). Overall, our results indicate that adaptive brain shape diversification in platyrrhines can be invoked as a plausible

explanation for the observed patterns, and particularly, to account for brain shape convergence in the clade.

Discussion

The evolution of relatively large and complex brains is perhaps one of the key determinants of primate evolutionary success. Additionally, several extant and extinct primate clades constitute putative examples of adaptive radiations (10), where one of the

Fig. 2. Disparity-through-time (DTT) plots for brain shape, encephalization (rECV), and log body mass (BM). Relative disparity at each point indicates the average extant disparity of the subclades that had an ancestor at that time with respect to the whole clade disparity. Dashed line and gray shadow represent the expectation under a BM model of evolution, estimated via simulations, and its 95% confidence interval, respectively.

expected outcomes is the marked adaptive diversification of ecologically relevant phenotypic traits. However, brain morphology has received little attention in the study of primate adaptive radiations despite its manifest ecological importance. Moreover, most previous comparative studies of primate brain evolution have mainly explored the diversification of relative brain size, having generally overlooked the evolutionary and ecological importance of variation in other phenotypic dimensions of the process of brain evolution, e.g., variation in the relative size and position—shape—of the different brain modules.

Our results indicate that New World monkeys present an extensive variation in brain shape and, importantly, that only a fraction of this variation is related to total relative brain size, indicating that a significant amount of information is not captured by this variable, as other workers have pointed out (23). Relative brain size changes are mostly associated with a relative enlargement of the neocortex, with most localized shape changes concentrated on the frontal and occipital areas, and correlated changes in other brain modules (Fig. S3). Additionally, in species exhibiting this neocortex enlargement, the brainstem shifts its relative position to a more downwardly oriented location (Fig. 1B and Movie S1). Therefore, although our approach (i.e., virtual endocasts and geometric morphometrics methods) only allowed quantification of external brain morphology, it can contribute valuable information that may be otherwise overlooked, as the conjoint changes in relative size and position of brain components or structures—as described above—cannot be measured only with volumetric assessments of the whole brain (i.e., its absolute or relative volume) or brain parts.

Our results also show that platyrrhines display a significantly high phylogenetic structure in brain shape variation, as in other previously studied phenotypic traits (e.g., refs. 21 and 24). Although this is not unexpected at macroevolutionary scales (25), our results additionally show that several clades exhibit significantly convergent brain morphologies, suggesting the existence of ecological or nonneutral evolutionary factors structuring brain shape variation. Moreover, our model selection results indicate that, beyond this clear phylogenetic structure, brain diversification among platyrrhines can be explained invoking a Simpsonian model of adaptive peak shifts to unique and shared

optima, mainly defined by a multidimensional ecological hypothesis. Particularly, our results suggest that brain shape diversification in the platyrrhine radiation may have unfolded in at least two stages (Fig. 3): an early differentiation (i.e., among families) within an ecological adaptive landscape mainly defined by diet and locomotion strategy axes, followed by several shifts at the subfamily level to a shared adaptive peak defined by social group size, generating shape convergence. The first stage may be related—although not exclusively—to the changes represented by PC2, which shows a strong early diversification pattern, strikingly similar to that of body mass (Fig. 2), which previous works proposed to have diversified within an adaptive landscape associated with diet and locomotion strategies (17, 18).
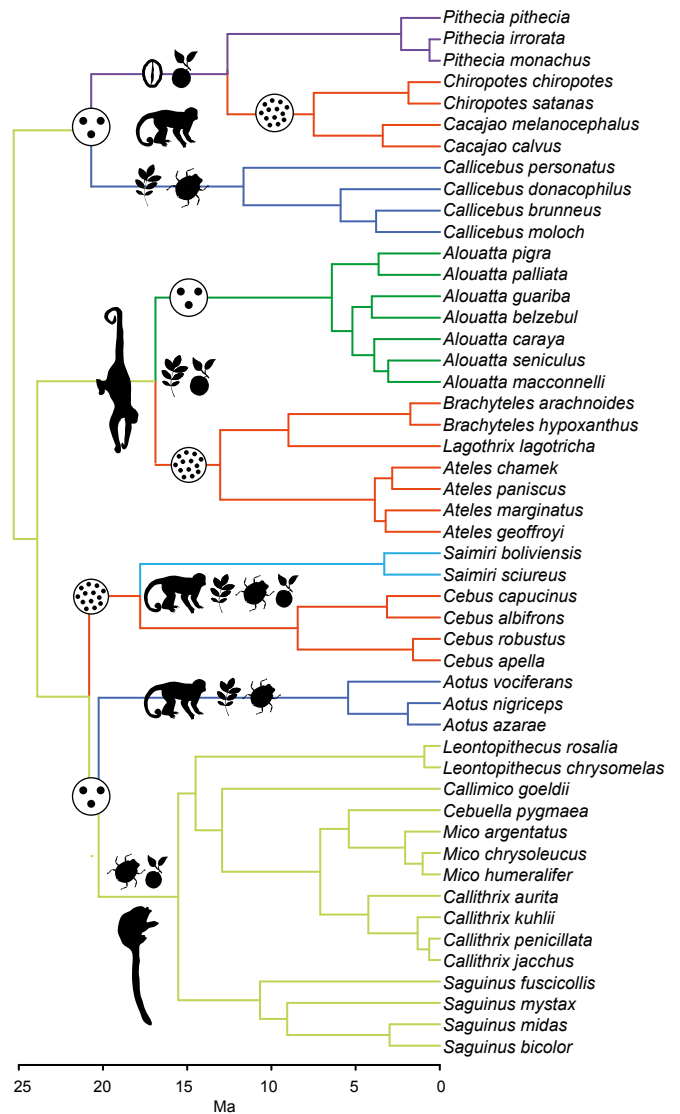

Fig. 3. Time-calibrated phylogenetic tree for the studied New World monkey species showing adaptive regimes for the best-fitting model of brain shape evolution. Regimes were assigned based on diet composition, locomotion strategy, and group size with exception of *Saimiri*, which was assigned based on the SURFACE results (*Supporting Information*). Drawings broadly depict the ecological categories that define these regimes and are not intended to represent ancestral states. Diets are represented by niche-defining food items (17). Locomotion is represented by typical behaviors. Group size (small and large) is represented by encircled dots. Convergent regimes are defined by having large group size. *Aotus* and *Callicebus* are considered by some workers to be sister clades.

This similarity in the patterns of diversification of body mass and a component of brain shape may point to the action of common selective factors on both traits, or alternatively, to the existence of developmental constraints. Interestingly, we only found evidence for a moderate evolutionary allometry linking variation in both traits (PGLS: $\lambda = 0.92$; $R^2 = 0.25$; $P = 0.001$); thus, modular over integrated explanations may be favored. However, we cannot rule out completely the existence of integrated changes affecting brain morphology. For example, correlated structural changes with the face—which may reflect dietary adaptations—could be a major source of the ecological signal in brain shape.

Following this initial divergence process, our results suggest that ensuing shifts to a shared adaptive peak (Fig. 3), generating cladewise convergence at the subfamily level in particular aspects of brain morphology (e.g., expansion of the neocortex and its correlated increase in relative brain size; Fig. S3), could be a significant mode of brain shape change in platyrrhine evolution. Particularly, a model explicitly incorporating brain shape convergence (Fig. 3) in relation to the several ecological factors that are likely represented by group size (e.g., social complexity; see below) (16) was strongly favored over several nonconvergent models (Fig. S4). Recent studies have suggested that phenotypic convergence could be a frequent phenomenon in macroevolutionary radiations (26–28), although this is typically observed in radiations where the convergent species evolved in geographic isolation from each other. Although some theoretical models (29) and empirical examples (8) describe the emergence of morphological convergence in the same geographic area, these cases refer to communities where the number of species largely exceeds the number of available ecological niches. Alternatively, our results suggest that brain shape convergence was likely attained at a late stage of the radiation, as described above, only after divergence in several other dimensions of the niche space was achieved.

This scenario may be in agreement with proposed general models and examples of vertebrate adaptive radiations (4, 30), in which clades diversify in stages, for example, first diverging in traits allowing differential exploitation of the macrohabitat [e.g., body size for platyrrhines (17, 18)], followed by more narrow sequential partitioning of niche dimensions (e.g., microhabitat, diet specializations, behavior, communication, etc.). In the case of platyrrhines, one of this late niche dimensions could be represented by the complexity of social interactions (i.e., a cognitive dimension of the niche). Convergent phenotypes exhibit, although not exclusively, encephalization-related shape changes. Particularly, the neocortex is the main structure exhibiting a relative enlargement. Because brain size in primates scales almost isometrically with cell number (31), relatively larger brain structures would have relatively higher computational power (14), indicating an increase in the cognitive abilities related with the enlarging neocortex. In this sense, our results suggests that the social brain hypothesis, which posits that the large neocortex of primates evolved in response to the cognitive demands arising from living in complex social groups (16, 32), can be invoked to better understand the evolution at macroevolutionary scales of brain shape and encephalized phenotypes in an ecological context, and particularly, the factors generating brain morphological convergence among primate species. In the case of *Saimiri*, which is the most encephalized genus and which our results showed to occupy its own adaptive peak, additional factors beyond those considered here may be driving its evolution.

Summarizing, we show that brain shape constitutes an ecologically relevant phenotypic trait in the platyrrhine adaptive radiation, and particularly, that the evolution of specific aspects of brain shape probably allowed the exploitation of additional dimensions of the platyrrhine ecological niche space. Overall, this further indicates that brain shape evolution could be of relevance for understanding other cases of primate and, more generally, vertebrate adaptive radiations.

Materials and Methods

Sample. Our sample consisted of 179 adult skulls of both sexes from 49 platyrrhine species belonging to all 17 broadly recognized genera (Table S1). This represents a large sample of platyrrhine phylogenetic diversity (∼40–60% of extant species) (33, 34).

Morphological Analyses. For each specimen X-ray computed tomography or micro-computed tomography scans were acquired or downloaded from public repositories (21). Three-dimensional virtual endocasts were generated from these data following a threshold-based 2D segmentation procedure (21, 35). From the segmented images, a surface 3D model—the virtual endocast—was generated, and the endocranial volume (ECV) was measured as the volume enclosed by this surface.

A total of 26 anatomical landmarks (Table S2) and 373 semilandmarks along curves and surfaces were digitized on each endocast (Fig. 1A and Fig. S6). To digitize the surface semilandmarks, a mesh of 268 roughly equidistant points was generated automatically on one specimen and then projected onto every other endocast, using the landmarks and curve semilandmarks as reference points for alignment and a thin-plate spline interpolation (36), as implemented in the geomorph package for R (37). To remove nonshape variation, a generalized Procrustes analysis (GPA) was performed. GPA also returns the centroid size (CS) of each configuration, a measure of the size of the structure. Additionally, semilandmarks were allowed to slide along tangents and tangent planes to the curves and surfaces, respectively, minimizing the bending energy distance between semilandmarks in each specimen and the consensus configuration (38). The resulting Procrustes shape coordinates were extracted.

Variability in brain shape was characterized by means of a PCA of the species-averaged Procrustes coordinates (Dataset S1). This reduces the dataset dimensionality and generates uncorrelated axes (PCs) describing the main trends in shape variation among species. Subsequently, PC scores were used in the following analyses as brain shape variables.

We measured encephalization (or relative brain size) as the residual values (rECV) from a phylogenetic regression of ECV on basicranial CS (21). Encephalization has been measured in many different ways in primate studies, and the choice mainly depends on the question being asked as all present strengths and weaknesses (39). Our measure is conceptually different from that of other platyrrhine studies, which mainly corrected for body mass (e.g., refs. 19 and 20) but is similar to that used by other workers (e.g., refs. 40 and 41). Using this measurement, we have a more structural encephalization definition, avoiding the use of body mass data, which can be subjected to different selective pressures to that experienced by brain size, affecting evolutionary interpretations (42).

Comparative Analyses. The phylogeny for the platyrrhine species was obtained from the fossil-calibrated Bayesian molecular tree in Aristide et al. (18) and was pruned to match the species in our morphometric dataset (Dataset S2).

PGLSs were used to assess the association between the various analyzed variables. PGLS accounts for the expected lack of independence among samples arising from phylogenetic structure (43) by modeling residual variation assuming Brownian evolution. This assumption can be ameliorated by incorporating an additional parameter to the regression, λ [ranging from 0 to 1 and estimated by maximum likelihood (44)], which measures the phylogenetic signal in the regression residuals.

Convergence was assessed using two pattern-based test statistics (C1 and C5), which quantify independently evolved similarity without making assumptions about the processes generating this similarity (45). This way, investigation of the processes driving convergent evolution can be separated from its identification. C1 quantifies the degree to which the putatively convergent taxa have evolved to be more similar than their reconstructed ancestors were. C5 simply counts the number of lineages entering the region of the morphospace occupied by the hypothesized convergent taxa. Both measures were compared against a null expectation generated using 999 BM trait simulations along the phylogeny (45).

Phylogenetic signal in trait data were estimated by Blomberg's K statistic (25). K measures the association between the pattern of variation in the data and the structure of the phylogenetic tree, considering a BM model of evolution as a null expectation. Values of K near 1 indicate a strong phylogenetic signal, whereas values near 0 indicate a decoupling of phylogenetic and phenotypic divergence. K values above 1 indicate that species are more similar than expected under BM, a pattern that may be associated with early niche-filling scenarios (46).

DTT plots (47) were generated in the GEIGER package for R (48) to examine the temporal pattern of change in relative phenotypic disparity along

the platyrrhine phylogeny. DTT analyses allow comparing the observed pattern of intraclade versus among-clades disparity through time with an expectation under BM. High relative disparity values are indicative of extensive within-clade diversification and among-clades overlap, whereas values near 0 suggest that variation is mainly partitioned among clades (47).

Model selection analyses were performed with the mvMORPH package for R (49), which allows fitting several evolutionary models to trait data and a phylogeny in a multivariate framework. For each model, the relative fit was assessed using the sample size AICc (50). Several models were evaluated, with BM evolution as the simplest. More complex models included early burst (51), were the rates of Brownian evolution decays exponentially with time, mimicking niche-filling scenarios; and several adaptive OU models (Fig. S4). The SURFACE method (52) was used to explore the OU model space to corroborate that our best-fitting biological hypothesis is not markedly different from the best possible statistical hypothesis (Supporting Information and Fig. S5). OU models describe processes where traits values are constrained around one or several optima that can be considered adaptive peaks in a macroevolutionary landscape. These models incorporate to the stochastic BM model a deterministic term representing the action of selection toward an optimum value, and constitute the simplest mathematical expression of an evolutionary model with selection (53). Each OU model is constructed by assigning hypothesized adaptive regimes to each branch and node of the phylogeny following alternative evolutionary scenarios for the traits under study.

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EVOLUTION