RESEARCH ARTICLE

Quantitative Developmental Data in a Phylogenetic Framework

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MOLECULAR AND DEVELOPMENTAL EVOLUTION

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ABSTRACT

Following the embryonic period of organogenesis, most development is allometric growth, which is thought to produce most of the evolutionary morphological divergence between related species. Bivariate or multivariate coefficients of allometry are used to describe quantitative developmental data and are comparable across taxa; as such, these coefficients are amenable to direct treatment in a phylogenetic framework. Mapping of actual allometric coefficients onto phylogenetic trees is supported on the basis of the evolving nature of growth programs and the type of character (continuous) that they represent. This procedure depicts evolutionary allometry accurately and allows for the generation of reliable reconstructions of ancestral allometry, as shown here with a previously published case study on rodent cranial ontogeny. Results reconstructed the signature allometric patterns of rodents to the root of the phylogeny, which could be traced back into a (minimum) Paleocene age. Both character and statistical dependence need to be addressed, so this approach can be integrated with phylogenetic comparative methods that deal with those issues. It is shown that, in this particular sample of rodents, common ancestry explains little allometric variation given the level of divergence present within, and convergence between, major rodent lineages. Furthermore, all that variation is independent of body mass. Thus, from an evolutionary perspective, allometry appears to have a strong functional and likely adaptive basis. *J. Exp. Zool. (Mol. Dev. Evol.) 9999B: 1–9, 2014.* © 2014 Wiley Periodicals, Inc.

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The specific way in which development unfolds can be described quantitatively by an ontogenetic trajectory. If character states can be compared in adult specimens to establish their homologies, then comparing their development along those trajectories equates to tracing the recognized homology back into ontogeny. This is sensible because ontogenetic trajectories evolve (Zelditch et al., 2003; Adams and Nistri, 2010; Wilson and Sánchez-Villagra, 2010; Piras et al., 2011; Porto et al., 2013; Urosevic et al., 2013). While the development of any two species that share a homologous structure can be readily compared without any especial consideration, a broader, multispecific comparison requires specific information on relative ancestry (phylogenetic relatedness) of the various terminals of analysis. The issue is then the specific manner in which the multispecific comparison should be made.

The ontogenetic trajectory of a continuously developing organism such as a vertebrate has been conveniently divided into a relatively short, embryonic period during which most organogenesis occurs, and a usually longer, fetal postnatal period during which most development is allometric growth. Allometry is key because it is thought that its adaptive variation drives morphological evolution (e.g., Frankino et al., 2005). Allometric scaling "laws" have been derived from first-principle relationships of either metabolic or constructional variables with body size (e.g.,

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West et al., 2001; Demetrius, 2006; Rampal et al., 2006). In morphology, allometry uses a (general) linear-model framework, either bivariate or multivariate, to describe growth quantitatively, which yields accurate, stable, and repeatable estimates of developmental change (see the foundational article by Jolicoeur, '63). These estimates are the coefficients of allometry, which have been widely used to compare ontogeny because they vary intraspecifically and extensively across taxa (e.g., Klingenberg, '98, and references therein; Weston, 2003; Flores et al., 2013; Wilson and Sánchez-Villagra, 2010, 2011; Sheets and Zelditch, 2013). In addition, allometry has been demonstrated to express highly significant genetic variation (e.g., in rodents; Pavlicev et al., 2008). Therefore, variation plus inheritability unequivocally indicates that allometry evolves and lends strong support to the validity of interspecific comparisons. This in turn leads to the direct extension of allometric studies into the phylogenetic field.

Recent studies have used a variety of approaches for studying allometry in an evolutionary framework, including mapping of shape characters using least squares parsimony, regression of independent contrasts of shape on independent contrasts of size, and the like (see Klingenberg and Marugán-Lobón, 2013, and citations therein). Here I examine an alternative option of analysis. It is widely accepted that ontogeny contains rich evolutionary information; if allometries evolve, then interspecific divergence in their estimates—allometric coefficients—can be traced onto a tree. So in its simplest formulation, a phylogenetic approach to ontogeny should consider that for a given character, sister taxa with similar allometric parameter estimates share a developmental pattern by virtue of common ancestry. Practically, direct mapping of allometric coefficients onto phylogenetic trees is in order; however, a number of conditions should be met for analyses of ontogenetic evolution be performed in this framework. Optimization of continuous characters as such, and access to all character reconstructions (see Goloboff et al., 2006), are required to achieve reliable reconstructions of ontogenetic trajectories that project deep into the past of a lineage. With the aid of specific phylogenetic comparative methods (PCMs), I explore whether absolute body size may have an additional effect on interspecific allometric patterns, as well as how much variation is expected to be explained by phylogeny in a case studied previously by Wilson and Sánchez-Villagra (2010) of a diverse clade of mammals, Rodentia.

METHODS

Allometry Analysis

Intraspecific allometric change is described by coefficients of allometry (C). In bivariate allometry analyses, C_i is the regression slope b of the character of interest i (dependent variable) on any descriptor of size (predictor, or independent, variable). Isometry can be defined as the slope predicted by a dimensional analysis. For instance, for a linear character $b = 1$ if the size proxy is any length, or $b = 0.33$ if size is expressed as body mass or volume (see Niklas, '94). Departures from isometry are evidenced by slopes greater or smaller than expected, referred to as "positive" or "negative" allometry, respectively. In multivariate allometry, size is a latent constituent of variation differentially affecting all characters. The genetic basis of this effect has been investigated in the mouse (epistatic interactions differentially affecting variation in traits of a pleiotropic domain; see Pavlicev et al., 2008). Quantitatively, all characters are analyzed simultaneously using principal components analysis (hereafter PCA). Here, C_i is the corresponding ith element of the first eigenvector of a variance–covariance PCA of log-transformed linear data, with eigenvectors scaled to unity (Jolicoeur, '63). While this scaling masks the absolute amount of ontogenetic variation, it allows detection of allometry, which is relative to an expectation of isometry. For a given character i, positive or negative allometry are represented by the corresponding eigenvector element that is either greater or smaller than a pre-calculated isometric value V, which depends only on the number of characters p, such that $V = 1/p^{0.5}$ (see Jolicoeur, '63).

While in bivariate allometry testing for departures of isometry involves t-tests with the null slope set to the predicted (isometric) slope (e.g., $b = 1$ in linear cases), the statistical recognition of multivariate allometry has relied upon resampling procedures such as bootstrapping (e.g., Weston, 2003) or jackknifing (e.g., Giannini et al., 2004, 2010). With both techniques, a confidence interval is estimated from specific simulated values (i.e., resampled with replacement in bootstrapping, or calculated from pseudo-values in jackknifing), such that allometries are identified whenever V is excluded from the interval.

Allometric Characters

The statistical departure from isometry is key in understanding variation in developmental trajectories in any comparative case study. Allometry coefficients are continuous variables, but for interpretation they are usually recoded in an ordinal scale. For instance, Wilson and Sánchez-Villagra (2011) converted allometry values into a three-state character (i.e., negative allometry = 0, isometry = 1, positive allometry = 2) in their evolutionary study of cranial ontogeny in chelid turtles. This procedure is of great help in describing the overall growth pattern in a simple way for many variables and greatly facilitates comparison across taxa, so it has been widely adopted (e.g., Abdala and Giannini, 2000; Giannini et al., 2004). While recognizing the value of recoded allometry coefficients for descriptive and basic comparative purposes (as here in Table 1), I suggest that using coefficients as continuous characters is more appropriate in an explicit phylogenetic framework.

First, recoded coefficients may mask available information of ontogenetic change because, as happens in categorical representations of continuous variation, a simplification is introduced. For

Table 1. Evolutionary reconstruction of rodent cranial allometry.

		Reconstructed interval			
Characters	Steps	Lower limit	Upper limit	Width	Allometric trends
0. Premaxilla ventral length	0.966	0.249	0.292	0.043	+
1. Premaxilla width	0.793	0.207	0.217	0.010	–
2. Palatine length	1.381	0.221	0.277	0.056	=
3. Palatine width	2.105	0.243	0.312	0.069	(+)
4. Occipital condyles width	1.029	0.158	0.172	0.014	–
5. Skull length	0.057	0.244	0.246	0.002	(+)
6. Nasal length	0.752	0.220	0.254	0.034	=
7. Nasal width	0.934	0.204	0.226	0.022	–
8. Frontal midline length	0.752	0.209	0.222	0.013	–
9. Parietal midline length	1.470	0.199	0.271	0.072	=
10. Jugal length	0.947	0.227	0.228	0.001	–
11. Length of dental diastema	0.765	0.245	0.256	0.011	(+)
12. Max interorbital width	1.106	0.190	0.191	0.001	–
13. Basioccipital length	0.828	0.235	0.247	0.012	=
14. Basioccipital width	0.657	0.214	0.216	0.002	–
15. Basisphenoid length	0.829	0.226	0.230	0.004	–
16. Basisphenoid width	1.194	0.199	0.208	0.009	–

Cost of each allometric character (numbered 0–16) on the tree of Figure 1 is given (steps column), together with the lower limit, upper limit, and width of the reconstructed interval at the root of the rodent tree. Symbols for allometric trends are "=" (isometry; i.e., reconstructed interval included the expected isometry value of 0.243); "+" (positive allometry); and "−" (negative allometry). These intervals are not statistical (see text).

instance, a given ontogenetic character may exhibit a wide interspecific variation within, say, the positive spectrum of allometry, but all taxa will be scored "2" in a recoded framework, rendering the character uninformative (Fig. 1A). Second, and by the same logic, recoded characters may alter the perceived similarity between states across taxa. Using another contrived example, if taxon A is deemed positively allometric by only a short distance (e.g., with $0.28 < C_A < 0.29$ as compared with $V = 0.27$) it will be coded "2" together with more allometric taxa (e.g., taxon B with $0.40 < C_B < 0.43$); in fact, values of taxon A are much closer to those of an isometric taxon (e.g., taxon C) than to those of the positively allometric taxon B (Fig. 1B). These artifacts result from the broken continuity of the allometric scale.

Evolution of Ontogeny

To avoid the limitations and simplification introduced by creating discrete categories in continuous variation, as described in the previous section, I mapped allometry coefficients onto the phylogenetic trees of interest (see example below), treating them as continuous characters. The problems detected above are avoided entirely if allometric characters are not rescaled and their continuous condition is maintained. This is because steps at ancestral nodes of the phylogenetic tree directly reflect the differences between the allometries of descendants from which they are calculated. For instance, the step difference between taxon A in the example above (Fig. 1) and an isometric sister taxon C would be 0 (i.e., intervals overlap), whereas the step difference with, say, a sister taxon B would be appreciable (i.e., 0.11 = 0.40–0.29; see Fig. 1B).

Optimization of continuous characters has been described as an extension of Farris' ('70) algorithm for optimization of additive (ordered) discrete characters (see Goloboff et al., 2006) and implemented in the phylogenetic program TNT (Goloboff et al., 2008). In this implementation, continuous characters can be entered either as point estimates (a single value per taxon) or as a range; e.g., minimum–maximum values for the character in a taxon, or any estimated confidence interval (including those of allometry coefficients). Using intervals removes the justified concern of Wilson and Sánchez-Villagra (2011), specifically that the variation around allometry estimates, discovered by resampling, be lost when using just the point estimates of slopes in a continuous character.

In addition, I applied two PCMs, each for a specific goal. First, I performed canonical phylogenetic ordination (CPO; Giannini, 2003) to determine which tree partitions (clades in a rooted tree) are significantly associated with the variation in ontogenetic trajectories, and how much of the total variation in allometries is accounted for by phylogeny. CPO is a linear model that relates a matrix of binary characters that code clade membership, the tree matrix X, with a dependent Y vector

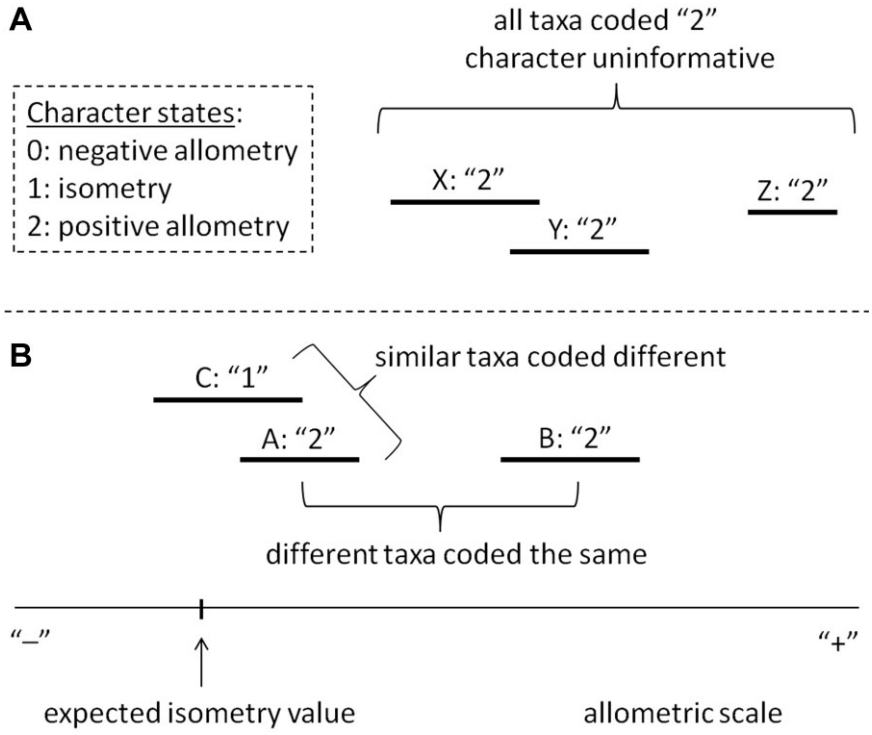

Figure 1. Problems with recoding allometry as multistate discrete characters (additive). Here, the original allometric character is a continuous variable and for each taxon the observed states comprise an interval (represented by thick horizontal lines). The character varies along a continuous allometric scale (bottom). The value expected under isometry is marked with an arrow (bottom). Transformation of the allometric character into a discrete additive character involves defining states for negative allometry (state "0"), isometry (state "1"), and positive allometry (state "2"; inset). In example A (above horizontal dotted line) taxa *X*, *Y*, and *Z* have distinct allometry values, with *Z* being much more positively allometric than *X* and *Y*; however all are coded "2" rendering the character uninformative. In example B (below horizontal dotted line), a narrowly allometric taxon A (recoded "2") is very similar to one isometric taxon C, with their intervals overlapping. However taxon A shares coding with the widely different taxon B instead (A and B recoded "2"), which is much more positively allometric. The evolutionary cost (steps) between taxon A and C is zero (because their intervals overlap) whereas the cost between taxon A and B is the inner distance between their non-overlapping intervals (i.e., the distance between the upper interval limit in A and the lower interval limit in B).

(univariate case) or matrix (multivariate case), here composed of the allometric coefficients of each cranial variable per taxon. The specific model depends on the nature of the data; in this case of continuously varying characters, the model is redundancy analysis (RDA; Rao, '64), the canonical extension of PCA (see Ter Braak, '95). Each clade character of X was tested by means of resampling (4,999 unrestricted permutations), and all individually significant clades (alpha set to 0.01) were submitted to a stepwise forward selection process. The resulting reduced tree matrix was used to calculate the final model fit. This was done for the whole matrix (multivariate case) and the analysis was executed in CANOCO v. 4 (Ter Braak et al., '98).

Second, I applied delayed-response correlation (DELCOR; Giannini and Goloboff, 2010) in order to determine the association through phylogeny of the change of each allometric character with evolutionary change in body mass. DELCOR is a way of correlation/regression that connects inner-node reconstructions of two characters of interest to form corresponding pairs, with the particular that these pairs do not need to match at the same node; that is, the response change in the dependent character can be delayed with respect to change in the other character, forming a pair of changes occurring at different nodes. Thus, a lagged response of one character to the other is allowed, but penalized relative to an immediate response in the corresponding node with a function (the delay factor) such that matches at distant nodes are less influential in the analysis than same-nodematches. All possible reconstructions are generated initially, and then a random set of reconstructions ($n = 100$ by default) are used. This generates an observed range of r (or b, which are equivalent test statistics; see Manly, '97). The significance test is done by shuffling inner-node assignations of a chosen character reconstruction and re-matching the now randomly placed changes with the fixed

reconstructions of the other character. The observed parameter range is compared with the resampled distribution. The pair-matching process can proceed tree-down or tree-up, depending on the research question. Here I set body mass as the independent variable and so I explored whether ontogenetic change responded to change in body size (tree-up testing). Analyses were run using the script DELCOR.run written in the macro language of TNT (Goloboff et al., 2008), which is available from the authors (Giannini and Goloboff, 2010).

Empirical Example

Here I extended the evolutionary analysis of Wilson and Sánchez-Villagra (2010) on rodent cranial ontogeny, applying the techniques outlined above. In mammals, and rodents in particular, allometry patterns shift significantly after birth (Wilson, 2011). The present analysis covers the postnatal ontogeny of representative members of two major rodent clades. Briefly, Wilson and Sánchez-Villagra (2010) described the ontogenetic trajectories of the rodent skull as defined by 17 measurements (Fig. 2) taken on 34 rodent species chosen to represent families from the major clades of hystricognath and muroid rodents. With these, an allometric space was defined using a PCA on the 17 multivariate coefficients of allometry for each rodent species; metrics within this space, defined as angles between species, were used to compare members across major clades and across dietary categories. Wilson and Sánchez-Villagra (2010) reported a continuous occupation of, and extensive overlap in, allometric space by rodent species from both major clades. Here I applied the concepts and analyses outlined above to this rodent dataset, which represent a complement to the original data analyses done by Wilson and Sánchez-Villagra (2010). For the body size analysis using DELCOR (see above), data were obtained from Smith et al. (2003) except for *Myospalax fontanierii* (obtained from Zou et al., '98).

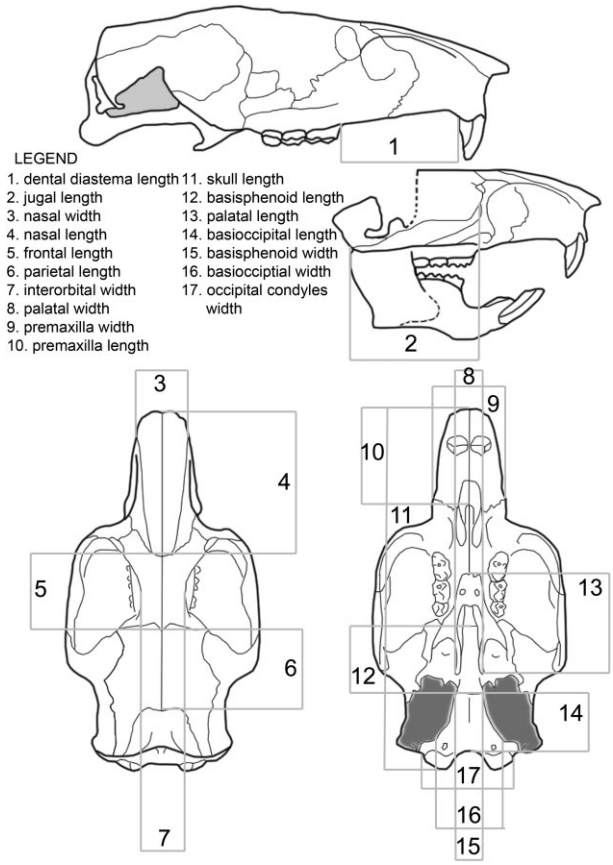

Figure 2. Skull characters used in this study. Character names are given with corresponding numbers (inset) that refer to distances indicated in the skull views: lateral partial (without zygomatic arch) and rostral lateral (top), dorsal (bottom left), and ventral (bottom right). See full description of characters in Wilson and Sánchez-Villagra (2010) and Wilson (2013). Splanchnocranial components include characters 1, 2, 3, 4, 8, 9, 10, and 13; neurocranial components include characters 5, 6, 7, 12, 14, 15, 16, and 17. Auditory bullae are shaded in gray. A usual proxy of absolute skull size (see text) is skull length (character 11). From Wilson (2013; see also Carrasco and Wahlert, '99).

RESULTS

The optimization cost of all allometric characters was 16.565 steps distributed in the tree as shown in Figure 3. These are minimum branch lengths, with the branch leading to *Castor* (0.541 steps) and nine other branches exhibiting the greatest amount of change in the tree (>0.400 steps each, bold branches in tree in Fig. 3). Only a couple of terminal branches accumulated <0.100 steps (*Myocastor*, *Dicrostonyx*). Conversely, basal branches had the least changes, even zero length, most notably the basal hystricognath–muroid dichotomy and the first divergences within hystricognaths (Fig. 3). The number of allometric characters changing at a given branch varied from 0 (at zero-length branches) to a maximum of 14 (at the branch leading to *Microtus*). Overall, the total amount of change (numbers below branches in Fig. 3) was highly correlated with the number of characters changing at the node ($r = 0.92$, $r^2 = 0.85$, $P = 0.001$ on the basis of 999 permutations of original values). The allometric character with the greatest amount of change was palatine width (2.105 steps); significantly, the one with the most conserved ontogeny was skull length (0.057 steps; Table 1).

Tracing the allometric changes back into the root of the rodent lineage produced the allometric character reconstructions listed in Table 1. These represent the allometric states of the rodent ancestor, or more precisely for the hystricognath–muroid ancestor. Four of the reconstructed intervals included the expected isometric value for this dataset ($V = 0.243$; see the Methods

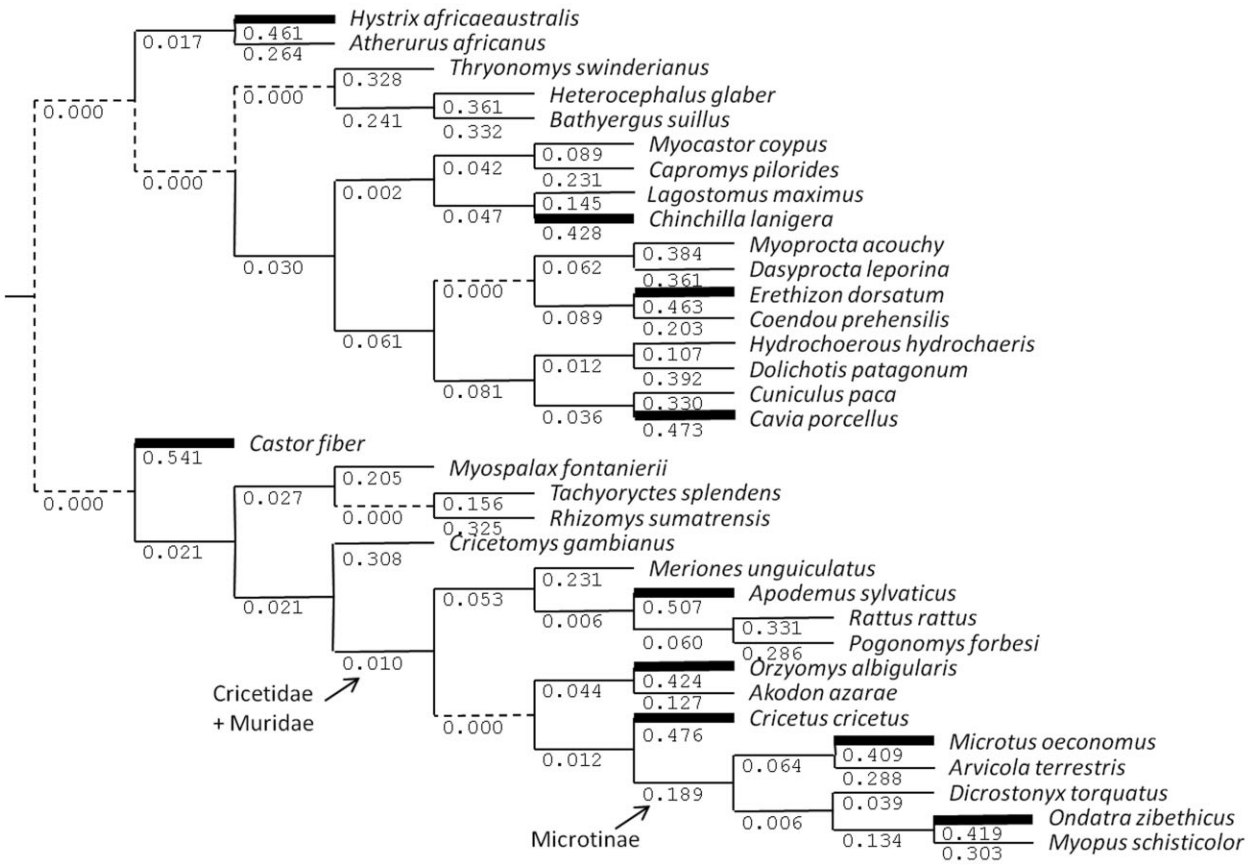

Figure 3. Evolution of allometry in rodents. The tree follows Wilson and Sánchez-Villagra (2010). Numbers in the rodent tree are branch lengths as net evolutionary changes across all allometric characters. Branch thickness (from dotted lines to bold lines) codes amount of total net change (summed over all 17 allometric characters). Arrows indicate the tree partitions that significantly explained some allometric divergence according to results of canonical phylogenetic ordination (CPO) analysis (see text).

Section). The remainder of intervals were allometric, of which four exceeded V and thus were considered positively allometric, whereas nine were negatively allometric (Table 1). Neurocranial components were negative or isometric, whereas splanchnocranial components exhibited a balanced mixture of allometric trends. The largest interval width corresponded to parietal midline length (0.072) and palatine width (0.069), whereas the narrowest intervals were those of jugal length and interorbital width (both 0.001; Table 1).

Only two tree partitions were significantly associated to interterminal variation in the set of allometric characters. Results of CPO indicated that the tree partitions separating Microtinae (pseudo-$F = 3.00$, $P = 0.0014$) and Cricetidae + Muridae (pseudo-$F = 2.7$, $P = 0.0064$) from other clades together explain some 15.8% of total variation in rodent skull allometry. Marginally significant ($0.05 < P < 0.01$) tree partitions included muroids (pseudo-$F = 1.9$, $P = 0.0366$) and Cavioidea (pseudo-$F = 2.1$, $P = 0.0236$), but these partitions were excluded from the final model. In addition, none of the allometric characters was significantly associated to body mass through the rodent tree, as evaluated using DELCOR (in all cases, observed $-0.3 < r < +0.3$ and $P > 0.20$; details of results not shown).

DISCUSSION

Wilson and Sánchez-Villagra (2010) revealed the essential nature of comparative cranial ontogeny in rodents: disparity in allometric trends. The allometric space was continuously occupied with major overlap among species from two large, diverging rodent lineages, histricognaths and muroids (Wilson and Sánchez-Villagra, 2010). The results of analyses presented here showed complementary aspects that help understand the evolution of rodent cranial ontogeny in greater detail and more intimate connection with phylogeny, thus providing potential for a more general treatment of evolution of ontogeny.

Mapping of quantitative ontogenetic characters onto the phylogenetic tree of the group is shown here to require optimization of allometric coefficients as continuous characters. Not only the actual intraspecific variation around the coefficients (as detected by resampling) is fully considered for character mapping by using intervals in the terminal values; also, some obvious mistakes (Fig. 1) are prevented given the logic of optimization. Specifically, the operations involved in optimization when considering two descendants of a node, that is, the downpass to calculate local steps, are intersection (when the two descendant intervals overlap, counting 0 steps) and union (when intervals do not overlap and the cost is then the inner distance between them; Farris, '70; Goloboff et al., 2006). When summed over all the nodes, an optimal cost is returned which can be interpreted as minimal (linear) evolutionary changes required by the tree. Optimization also generates minimum branch lengths (or actual branch lengths for each reconstruction) and final states for all nodes, including the root (Goloboff et al., 2008). And here the full value of this application becomes more evident. In the case study from Wilson and Sánchez-Villagra (2010), the states reconstructed at the root of the rodent subtree depict a particular array of allometric trends (Table 1). These are reconstructed intervals that differ in nature from the statistical intervals originally estimated for each terminal from specimen growth series. However, given that the average width of reconstructed intervals across characters was 0.022 in rodents, which result from estimates of divergence between species and is about an order of magnitude greater than the average of actual intervals measured on the terminals (calculated from raw data in Wilson and Sánchez-Villagra, 2010), which represent estimates of intraspecific variation, the reconstructed intervals appear as conservative guides to the range of allometric states in the extinct ancestor. In the ancestral rodent, neurocranial components exhibited the typical mammalian pattern of dominantly negative or isometric tendency, whereas splanchnocranial components exhibited various trends depending on the structure (see Abdala et al., 2001; Weston, 2003; and citations therein). Precisely here we see that the reconstructed rates of growth of the rodent ancestor affected the rostrum to differentially contribute to the configuration of the specialized masticatory apparatus of rodents: the premaxillary ventral length grew positively, together with the length of the dental diastema and the palatine width, while the palatine length and nasal length where isometric, and the premaxilla and nasal width grew negatively. Taken together, these trends indicate a skull growing to yield an elongated and narrow rostrum, in which a long diastema develops separating the incisors from the cheekteeth, and a palate grows transversely posteriorly to accommodate the backward addition of molars as the animal grows. This combination is the signature pattern of the rodent skull and it is nicely reconstructed at the root of the rodent tree (Table 1). So far we can say that it was already present in ancestral rodents, and it is significant to note that this point in time is, at the very least, 55 my old in the Paleocene epoch (O'Leary et al., 2013), but see Fabre et al. (2012) for significantly older estimates that extend well into the Cretaceous. This may compose an allometric pattern shared with lagomorphs (which together with Rodentia compose the unranked clade Glires), so the evolution of this rostral configuration, modeled by the particular allometries just described, need more distant mammalian outgroups to be fully appreciated.

Other authors have relied on different methodologies for approaching the evolution of allometries. These include allometric analyses based on independent contrasts for controlling phylogenetic relatedness and reconstructions based on squared-change parsimony (e.g., Klingenberg and Marugán-Lobón, 2013). However, these techniques have shown numerous methodological difficulties and their use should be revised. With regard to independent contrasts, it is widely understood that these transformed-through-phylogeny data only represent sister-node differences in states between descendants (Felsenstein, '85) and therefore not actual estimates of ancestral states that can be used for evolutionary reconstructions. In addition, we have shown that any technique that depends on exclusive node-by-node comparisons (including independent contrasts) may be severely weakened or even biased anytime some evolutionary lags have occurred in the history of the characters (Giannini and Goloboff, 2010); that is, situations in which the same-node comparison breaks down and temporal shifts in the response character requires tracing the explanatory evolutionary change to an older node. The method used here (DELCOR; Giannini and Goloboff, 2010) was developed to deal with such evolutionary delays explicitly. With regard to squared-change parsimony, it does estimate ancestral states with an optimality criterion, but Hormiga et al. (2000) dramatically demonstrated, with a simple numerical example, that "Although this approach is parsimonious, in that it minimizes the sum of the squared changes along the branches, and superficially seems to accord better with gradual phylogenetic change, it perversely ascribes change where none is required and certainly does not minimize ad hoc hypotheses of homoplasy."

Branch lengths as estimates of evolutionary change offered interesting insight in the rodent case study of Wilson and Sánchez-Villagra (2010). The high, positive correlation found between total amount of allometric change (steps) and number of allometric characters changing at corresponding nodes means that on average individual characters made small contributions to the evolutionary change in each branch. Branches with many steps are lineage-specific times in history at which many different parts of the skull changed their ontogeny simultaneously. This may represent indirect evidence of morphological integration in the rodent skull at the evolutionary time scale, as has been reported in other organisms (e.g., birds at the Class level; Klingenberg and Marugán-Lobón, 2013). In addition, it is very significant that the character with the least amount of change in the rodent lineage is skull length, given that it has been the

preferred proxy of size in the traditional literature (e.g., Simpson et al., '60; Radinsky, '81a, b; Emerson and Bramble, '93) and also in more recent contributions (see discussion in Flores et al., 2010).

The rodent lineage demonstrated a relatively low impact of phylogeny on the morphological (allometric) patterns, which contrasts with other mammalian clades in which phylogeny explains a majority ($\gg$70%) of cranial variation (e.g., Morales and Giannini, 2010, 2013a, b). This may be due to a variety of factors, but likely the choice of terminals (taxonomic sampling) had a determinant influence on the rodent pattern reported here. By including a single member of family-level groups within each major rodent clade (hystricognaths and muroids), Wilson and Sánchez-Villagra (2010) sought to maximize lineage representation across rodents. Because these groups are highly divergent within major clades, and partially convergent across clades (see Figure 2 in Wilson and Sánchez-Villagra, 2010), relatively little of the divergence pattern actually correlated with phylogeny. Inclusion of more members of each group (i.e., several cricetines, akodontines, and so on) should help recover the commonalities of closely related species and reveal the true magnitude and location of the phylogenetic effect on the cranial allometry of rodents.

Finally, a possible effect of body size on allometric coefficients (slopes) was decidedly rejected using delayed correlations. This technique demonstrably has power to detect true character associations when present in phylogenetic problems of the size (i.e., terminal number) analyzed here (see simulations in Giannini and Goloboff, 2010). This conclusively demonstrated the evolutionary independence of reconstructed allometric trends and absolute body size in this sample of rodents.

CONCLUSIONS

Allometry may contribute the majority of the evolutionary divergence in morphology between related species. Here I show that the evolution of ontogeny, as estimated by quantitative allometry, can be confidently reconstructed in a given lineage. In an empirical example on rodents, quantitative development was traced back to the root of the rodent phylogeny, indicating a very early establishment, no younger than the Paleocene epoch, of the signature pattern of rodent skull development. The intimate connection of allometric trends with the shaping of the derived masticatory apparatus of rodents, the evolutionary independence of divergence allometric patterns with respect to absolute body size, and the limited impact of phylogeny on its variation at higher-level rodent clades, together suggest that allometric divergence is governed by function and likely is highly adaptive.

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LITERATURE CITED

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