Congruence of hierarchical, localized variation in cranial shape and molecular phylogenetic structure in spiny rats, genus *Trinomys* (Rodentia: Echimyidae)

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Received 5 December 2002; accepted for publication 7 April 2003

Congruence between patterns of localized, hierarchical variation in cranial shape and topological, molecular phylogenetic structure was investigated in a monophyletic lineage of Neotropical spiny rats of the genus *Trinomys*. Levels of organizational complexity in shape were assessed from two-dimensional coordinates of anatomical landmarks for dorsal, ventral and lateral views of the cranium, and the scale of variation in cranial shape was decomposed hierarchically using the statistical formalism of geometric morphometrics. The patterns of variation in cranial shape were evaluated for the five taxa of *Trinomys* in terms of ordinations in the reduced space of relative warps, with the scores of partial warps weighted to emphasize the hierarchical localization of shape differences in different geometric scales. The fit of the morphological shape data to the molecular phylogeny and analysis of the correlation between measures of the differences in shape and molecular phylogenetic distances demonstrated that only variation in small, localized scales in cranial shape in the lateral view of the cranium was congruent with molecular phylogenetic structure. The significance and perspectives of the application of geometric descriptors of shape and the identification of scales of variation for the study of morphological and molecular evolution are discussed. © 2003 The Linnean Society of London, Biological Journal of the Linnean Society, 2003, 80, 385–396.


INTRODUCTION

A fundamental question in evolutionary biology is whether estimated patterns of evolution at the morphological and molecular levels in any given monophyletic lineage are congruent (Singh & Krimbas, 2000). This problem has been approached primarily by examining the correlation between the rates of evolution in regulatory and non-regulatory genes in species that have undergone marked morphological diversifi-
cation relative to a sister lineage (e.g. Barrier, Robichaux & Purugganan, 2001) and by determining the congruence between phylogenies derived from molecular and discrete morphological character states (Thomas et al., 2000). In neither of these approaches has morphological evolution been quantified or modelled in terms of shape. The shape of any complex morphological structure results from the interfacing of and mappings between morphogenetic rules, ecological phenomena and deterministic and stochastic evolutionary forces (Murray, 1990; Smith, 1997; Lewontin, 2000). In this dynamic framework, it is to be expected that the description of variability in shape will be conditional on the chosen level of organizational complexity and scale (Bar-Yam, 1997; Murray, 1990, 2000; Levin, 1992, 2003; Lewontin, 2000). Given this perspective, a question that emerges in the study of morphological and molecular evolution is whether there is any level of organizational complexity and scale of variation in shape that is congruent with molecular evolution inferred from molecular phylogenetic structure.

In this study, we sought for congruence between patterns of morphological evolution, described in terms of variation in shape, and molecular evolution, indexed as the molecular phylogenetic structure based on mitochondrial DNA sequences. Shape variation was described using the recently developed formalism of geometric morphometrics (Bookstein, 1991), which allows the description of shape variation and change in terms of localized, hierarchical shape processes (Bookstein, 1996). We used a monophyletic lineage of spiny rats, genus *Trinomys*, as a model system to determine whether any perspective of variation in cranial shape, in terms of organizational complexity and geometric scale, can be mapped onto phylogenetic structure derived from sequences of the mitochondrial cytochrome *b* gene. The nature of this mapping was assessed by fitting the morphological data to the molecular phylogeny applying a recently derived protocol based on the squared-change parsimony criterion (Rohlf, 2002). Specifically, we searched for congruence between the patterns of ordination of localized, hierarchical variation in cranial shape and topological, molecular phylogenetic structure.

**Spiny rats of the genus Trinomys and mitochondrial phylogenetic structure**

Currently, three molecular clades encompassing nine taxa at the species level are recognized for the genus *Trinomys* (Lara & Patton, 2000). The clade chosen to investigate congruence at the molecular and morphological levels includes *T. yonenagae*, *T. setosus setosus*, *T. setosus denigratus*, *T. eliasi* and *T. paratus*. This clade was chosen because one species in this lineage, *T. yonenagae*, has diverged uniquely in ecology and morphology from all other taxa (Rocha, 1995; Pessôa, Von Zuben & Reis, 1998; Manaf & Oliveira, 2000). Contrary to species in this genus, which are ground dwellers in forest habitats (Moojen, 1948; Bergallo & Magnuson, 1999), *T. yonenagae* inhabits fossil sand dunes in a restricted area in the left bank of the São Francisco river in the state of Bahia in north-eastern Brazil, where it burrows underground tunnels (Rocha, 1995; Manaf & Oliveira, 2000). The sand dunes are part of the Caatinga biome characterized by unpredictable rainfall and semiarid conditions, with vegetation dominated by plants of the families Cactaceae and Bromeliaceae (Ab’Saber, 1974). The differentiation of *T. yonenagae* in this particular habitat has produced a strikingly distinct morphology involving a combination of traits such as a light-coloured pelage, a well-developed tail brush, large hind feet and cranial modifications, including an inflated bulla (Rocha, 1995; Pessôa et al., 1998), all of which are usually associated with rodents found in arid environments (Mares, 1980; Vaughan, Ryan & Czaplewski, 2000).

The uniqueness of the ecological life history and morphological traits of *T. yonenagae* are not paralleled by molecular differentiation as inferred from mitochondrial cytochrome *b* gene sequences, since *T. yonenagae* is well nested within a lineage which includes *T. setosus*, *T. paratus* and *T. eliasi* (Lara & Patton, 2000; Fig. 1). Thus, there is a disparity between divergences at the organismal (ecological and morphological) and molecular (mitochondrial DNA sequences) levels.

The patterns of morphological evolution were assessed here in terms of changes in cranial shape in the taxa that comprise the monophyletic lineage of *Trinomys*. The cranium was chosen because it is a complex morphological structure that contains the trophic apparatus, brain and sense organs (Voss, Marcus & Escalante, 1990; Hanken & Thorogood, 1993;...
Herring, 1993). Furthermore, qualitative and quantitative analyses of cranial shape have classically been used to derive information for phylogenetic inference and systematic decisions (Carleton, 1988; Atchley et al., 1992; Lessa & Cook, 1998; Mora, Olivasers & Vassallo, 2003) and to investigate patterns of heterochronic evolution (Haas, 1996; Smith, 2001; Fenin, Berge & Baylac, 2002; Reiss, 2002; Schoch, 2002). Organizational complexity was assessed by two-dimensional projections of the dorsal, ventral and lateral views of the cranium and the scale of variation in shape was decomposed using partial warps (Bookstein, 1989, 1991, 1996; Rohlf, 1996).

MATERIAL AND METHODS

GEOMETRIC FORMALISM OF SHAPE ANALYSIS

Conceptually, the geometric formalism of shape analysis involves the study of variation in the shape of landmark configurations archived in a convenient system of coordinates (Bookstein, 1991). The shape of an object consists of those geometric properties of a configuration of landmark coordinates that do not change with changes in its scale, location, and orientation (Bookstein, 1991; Rohlf, 1996). The extraction of a set of shape variables for N, k-dimensional objects begins by first computing an average configuration of points. This is done by performing a generalized Procrustes analysis (the method iteratively centres, scales, and optimally rotates configurations of points until the sum of squared differences between the specimens and their average is minimized). This average or reference configuration is also often called the ‘consensus configuration’.

The average configuration thus obtained can be visualized geometrically as the point of tangency between the exact non-linear shape space and the approximating linear tangent space (Rohlf, Loy & Corti, 1996) in which multivariate analyses can be performed. The specimens are optimally superimposed on the average configuration prior to the computation of partial warp scores (see below). These operations have been described by Rohlf & Slice (1990). Next, the shape information in these aligned coordinates can be expressed in several ways. Because it was of interest to partition shape variation according to spatial scale, shape variation was partitioned into the uniform component of shape (that describes changes in shape that are not localizable to any particular region in the configuration and are thus of infinite scale) and nonaffine shape (which describes localizable shape changes). The uniform component was computed using the linearized Procrustes method of Bookstein (1996). Partial warps were used as shape variables to capture the nonaffine shape component of shape variation and provided further partitioning according to spatial scale.

We used these techniques to derive hierarchical, localizable descriptors of cranial shape for the taxa in the Trinomys lineage. The partial warps were obtained from a spectral (eigenvalues-eigenvector) decomposition of the bending energy matrix, the elements of which are functions of the distance between all pairs of landmarks in the consensus configuration (Bookstein, 1991). The eigenvalues are inversely proportional to the spatial scale of their corresponding eigenvector. This allows the eigenvectors to be used to describe shape variation as deformation at successively smaller spatial scales. The eigenvectors of the bending energy matrix are called principal warps (Bookstein, 1989: 574). The separate projection of the x- and y-coordinates of each specimen’s landmarks onto the principal warps generates the partial warp scores that we interpreted as spatial, hierarchical description of shape variation (Bookstein, 1996: 340).

The matrix of partial warp scores was computed as:

$$W = V \Lambda^{\alpha/2},$$

where $V$ is a matrix of specimen coordinates expressed as deviations from the consensus, $\Lambda$ is a matrix of principal warps, $E$ is a diagonal matrix of eigenvalues and the exponent $\alpha$ allows differential weighting of partial warps according to spatial scale on the consensus configuration (Bookstein, 1996; Rohlf, 1996). The partial warp scores are shape variables and can be subjected to the usual multivariate analyses. A principal components analysis (called an analysis of relative warps when applied to partial warps, Bookstein, 1991) yields directions of maximal variation in shape relative to bending energy (Rohlf et al., 1996). The computations were done using the TPSRELM (version 1.25) program developed by Rohlf (1997).

The molecular phylogenetic relationships among the taxa of Trinomys analysed were estimated by maximum parsimony analysis of 726 base pairs (bp) of cytochrome b gene sequences (Lara & Patton, 2000). Molecular distances between pairs of taxa were estimated as corrected percent sequence divergence using the two-parameter model based on the 726 bp of cytochrome b gene sequences (Kimura, 1980; Lara & Patton, 2000). The ancestral cranial shape for each internal node (hypothetical taxonomic units – HTUs) of the phylogenetic tree derived from the DNA sequences was estimated by the squared-change parsimony method, as described in Rohlf (2002). The HTU scores in the relative warp ordinations were used to draw and visualize the phylogenetic tree superimposed on the morphometric space. The correlation between cranial shape ordinations in the space of relative warps and molecular distances was examined using matrix correlations (Mantel, 1967; Manly, 1997).
associating morphometric Euclidean distances measured in the entire space of relative warps and the molecular phylogenetic distances derived from the cytochrome \( b \) gene sequences. The significance of matrix correlations was obtained by comparing the observed correlation to the results of 100 random permutations.

**SAMPLES**

The specimens examined are housed in the mammal collections of the Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Museu de Zoologia da Universidade de São Paulo, São Paulo and Museu de Biologia Professor Mello Leitão, Espírito Santo. All specimens analysed were adults, based on the patterns of dental eruption and wear (Pessôa & Reis, 1991). Sample sizes were as follows: \( T. \text{yonenagae} \) (\( N = 17 \)), \( T. \text{s. elegans} \) (\( N = 8 \)), \( T. \text{s. denigratus} \) (\( N = 17 \)), \( T. \text{eliasi} \) (\( N = 13 \)) and \( T. \text{paratus} \) (\( N = 11 \)). No samples were available for \( T. \text{s. setosus} \).

**LANDMARKS**

Two-dimensional landmarks, assumed to be homologous from individual to individual, were identified for the dorsal, ventral, and lateral views of the cranium (Fig. 2) and described as follows.

**Dorsal view**

1 – anterior extremity of the suture between the nasals; 2 – anterior-most point of the suture between the nasals and premaxillary; 3 – suture between the premaxillary, maxillary and frontal; 4 – suture between the nasal, frontal and premaxillary; 5 –

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Figure 2. Morphological landmarks defined for the dorsal (A), ventral (B) and lateral (C) views of the cranium of *Trinomys yonenagae*.
suture between the nasals and frontals; 6 – suture between the frontal and maxillary in the lachrymal region; 7 – suture between the maxillary and jugal in the zygomatic arch; 8 – suture between the jugal and squamosal in the zygomatic arch; 9 – suture between the frontal, parietal and squamosal; 10 – suture between the frontals and parietal; 11 – suture between the parietal, occipital, and posterior process of the squamosal; 12 – posterior-most point of the occipital.

Ventral view
1 – anterior extremity of the suture between the nasals; 2 – antero-lateral extremity of the incisive alveolus; 3 – anterior-most point on the premaxillary in the incisive foramen; 4 – suture between the premaxillary and maxillary in the outline of the cranium (in the photographic plane); 5 – suture between the vomerine portion of the premaxillary and maxillary in the incisive foramen; 6 – intersection between the anterior end of the premolar and maxillary; 7 – anterior-most point in the mesopterygoid fossa; 8 – suture between the maxillary and jugal; 9 – intersection between the posterior end of the third molar and maxillary; 10 – lateral-most point in the suture between the presphenoid and basisphenoid; 11 – tip of the jugal process; 12 – tip of the process between the jugal and squamosal; 13 – suture between the squamosal, alisphenoid and tympanic; 14 – point where the suture between the basisphenoid and basioccipital contacts the tympanic bulla; 15 – anterior-most point of the foramen magnum; 16 – posterior-most point of the occipital.

Lateral view
1 – anterior extremity of the suture between the nasals; 2 – anterior-most point of the suture between the nasal and premaxillary; 3 – point of intersection between the premaxillary and anterior end of the incisor; 4 – point of intersection between the premaxillary and posterior end of the incisor; 5 – suture between the premaxillary and maxillary in the outline of the cranium (in the photographic plane); 6 – suture between the premaxillary, frontal and antorbital bridge of the maxillary; 7 – suture between the premaxillary, frontal and maxillary; 8 – suture between the frontal and maxillary in the lachrymal region; 9 – superior-posterior suture between the maxillary and jugal; 10 – inferior-posterior suture between the maxillary and jugal; 11 – anterior suture between the jugal and squamosal; 12 – tip of the posterior process of the jugal; 13 – posterior process of the squamosal; 14 – suture between the frontal, parietal and squamosal; 15 – point of the posterolateral intersection between the squamosal and alisphenoid; 16 – base of the paroccipital process; 17 – posterior-most point of the occipital.

Each cranium was placed parallel to the focal plane under a Pixera (Pixera Corporation, Los Gatos, California) digital camera system and the x- and y-coordinates of each landmark for the dorsal, ventral, and lateral views of the cranium were obtained using tpsDig, version 1.18 software (Rohlf, 1999a).

RESULTS

The average shape configurations for the two-dimensional dorsal, ventral and lateral views of the cranium of the five Trinomys taxa were computed separately using the generalized Procrustes analysis (Rohlf & Slice, 1990). Three matrices of partial warp scores were computed, one for each view. The number of partial warps depends on the number of landmarks according to $2p−6$ for $p$ two-dimensional landmarks (Rohlf, 1996). The dorsal, ventral, and lateral views of the cranium had 12, 16 and 17 landmarks so that 18, 26 and 28 partial warps were derived for each view of the cranium, respectively.

The partial warp score matrices, $W$, were subjected to a relative warp analysis (Bookstein, 1991; Rohlf, 1993; Rohlf et al., 1996), and the mean scores for each of the five taxa of Trinomys were plotted on the first two relative warps. In all cases, i.e. for all views of the cranium and three values of the exponent $\alpha$ ($−1$, 0 and $+1$), the first relative warp accounted for a substantially larger amount of the variation in shape among the taxa. For all three views of the cranium, relative warp analysis for the partial warps and uniform components combined gave identical results, in terms of ordination of the taxa in the first and second relative warps, to those obtained using partial-warp variables alone. The uniform component therefore does not contribute to the observed pattern of variation in cranial shape among taxa of Trinomys. The results shown here are for the partial-warp variables only.

The first two relative warps for landmarks of the dorsal view of the cranium (Fig. 3A) for $\alpha=0,+1$ and $−1$ explained between 78% and 90% of the variation in cranial shape among the taxa (Fig. 3B). For all three values of $\alpha$, the ordination of the mean values for relative warps 1 and 2 revealed the distinctiveness of cranial shape in $T$. yonenagae, which was separated from other Trinomys taxa along relative warp 1 (Fig. 3B). In no case was the pattern of ordination in the space of relative warps congruent with the phylogenetic relationships inferred from the cytochrome $b$ gene sequences (Figs 1, 3B).

For the ventral view of the cranium (Fig. 4A), the variance explained by the first two relative warps ranged from 83% to 93% of the variation in cranial
shape (Fig. 4B). For all three values of the exponent \( \alpha \), there were two groups along relative warp 1: one formed by \( T. s. elegans \), \( T. s. denigratus \) and \( T. eliasi \) and the other by \( T. paratus \) and \( T. yonenagae \) (Fig. 4B). Again, there was no congruence between the pattern of ordination of mean values of partial warps and the molecular phylogeny (Figs 1, 4B).

The variance in shape explained by the first two relative warps for the lateral view of the cranium (Fig. 5A) ranged from 68% to 87% of the variation in cranial shape (Fig. 5B). For \( \alpha = 0 \) \( T. eliasi \), \( T. s. denigratus \) and \( T. s. elegans \) were clustered at one end of relative warp 1, whereas \( T. paratus \) and \( T. yonenagae \) were distributed further down the first relative warp (Fig. 5B). For \( \alpha = 1 \), the distribution of taxa along relative warp 1 revealed two groups, one which included \( T. paratus \) and \( T. yonenagae \) and the other formed by \( T. s. elegans \), \( T. s. denigratus \) and \( T. eliasi \). For both \( \alpha = 0 \) and \( \alpha = 1 \), the pattern of ordination of the taxa showed no congruence with the molecular phylogeny (Figs 1, 5B). For \( \alpha = -1 \), there were two clusters, one formed by \( T. eliasi \) and \( T. paratus \) and another that included \( T. yonenagae \), \( T. s. elegans \) and \( T. s. denigratus \) (Fig. 5B). These two clusters corresponded to the molecular phylogeny in that the major branching in the topology separated the lineage leading to \( T. eliasi \) and \( T. paratus \) from that leading to \( T. yonenagae \), \( T. s. elegans \) and \( T. s. denigratus \) (Figs 1, 5B).

The association between the shape data and molecular phylogeny was further quantified by calculating the correlations between Euclidean distances between taxa in the space of the first two relative warps and the molecular distances derived from the cytochrome \( b \) gene sequences (Table 1). As expected from the results shown above, only the ordination of taxa derived from the lateral view of the cranium for \( \alpha = -1 \) was significantly associated with distances based on molecular data.

**DISCUSSION**

**CONGRUENCE OF HIERARCHICAL VARIATION IN CRANIAL SHAPE AND MOLECULAR PHYLOGENETIC STRUCTURE**

Shape variation in the dorsal view of the cranium in the three geometric scales defined by the exponent \( \alpha \)
pointed out the morphological uniqueness of *T. yonenagae* relative to the taxa in the monophyletic lineage of *Trinomys*. The ventral view of the cranium for all values of \(a\) and the lateral view of the cranium for \(a = 1\) identified two groups, one formed by *T. s. elegans*, *T. s. denigratus* and *T. eliasi* and the other by *T. paratus* and *T. yonenagae*. A unique pattern of ordination was revealed by the lateral view of the cranium for \(a = 0\). In none of these cases did the pattern of variation in cranial shape that emerged from the geometric analyses agree with the hierarchical branching inferred from the DNA sequences of the mitochondrial cytochrome *b* gene. The only exception was the lateral view of the cranium for \(a = -1\), for which variation in cranial shape in terms of the ordination of taxa in the reduced space of relative warps 1 and 2 was congruent with the molecular phylogeny inferred from the mitochondrial cytochrome *b* gene sequences. This association was also found to be statistically significant in the correlation analysis.

These results show that different levels of organizational complexity, represented by each of the two-dimensional views of the cranium, and geometric scale, measured by different values of the exponent \(a\), displayed characteristic variability and differed in their information content on phylogenetic structure. Congruence between patterns of ordination of localized, hierarchical variation in cranial shape and topological, molecular phylogenetic structure of the *Trinomys* lineage was found only in the lateral view of the cranium and the scaling of partial warps with \(a = -1\). That different perspectives of the cranium differ in their information content with regard to phylogenetic structure has already been demonstrated in several studies (e.g. Straney & Patton, 1980; Corti, Aguilera & Capanna, 2001). For example, Corti *et al.* (2001) reported that in spiny rats of the genus *Proechimys*, non-uniform shape changes measured in the dorsal view of the cranium were more strongly correlated with chromosomal differentiation than they were with shape changes measured in the ventral view of the cranium.

The importance of geometric scale in the organization of shape variation and its relationship with phylogenetic content has nevertheless been underappreciated. In partial warp formalism, the localized description of shape processes is based on the eigenvalues of the bending energy matrix, the magnitude of which is inversely related to geometric scale (Book-
stein, 1991, 1996; Rohlf et al., 1996). Large eigenvalues are associated with small-scale, very localized shape differences that involve deformations in small neighbourhoods of the landmarks, whereas small eigenvalues correspond to large-scale shape differences involving more widely distributed deformations (Bookstein, 1996; Rohlf et al., 1996). Weighting of these eigenvalues by the exponent $\alpha$ allows the description of a series of shape phenomena in a hierarchy of localization (Bookstein, 1996). With $\alpha = 0$, all hierarchical scales are given equal weight, whereas for $\alpha = 1$ and $\alpha = -1$, greater weight is given to larger and smaller scales, respectively (Bookstein, 1996; Rohlf et al., 1996).

Rohlf (1993; see also Rohlf et al., 1996) recommended the use of $\alpha = 0$ in order to study variation in shape in all scales equally. Recent work has followed this suggestion (Corti & Fadda, 1996; Corti & Rohlf, 2001; Corti et al., 2001; Pretorius & Scholtz, 2001). An exception to this rule was the report by Monteiro & Abe (1999) on the functional and historical (phylogenetic) determinants of shape in the scapula of xenarthran mammals, in which these authors demonstrated that small-scale shape phenomena alone ($\alpha = -1$) in the scapula were able to predict the correct phylogenetic position of an arboreal species of anteater. A similar result was found here in that only for $\alpha = -1$ does...
concordance emerge between the ordination of Trinomys taxa based on cranial shape and topological, molecular phylogenetic structure. Such findings seem to indicate that assessing the hierarchical localization of shape change may be fundamentally important when searching for scales of morphological variation that are correlated with a known molecular phylogeny.

GEOMETRIC FORMALISM OF SHAPE ANALYSIS AND THE HIERARCHICAL LOCALIZATION OF SHAPE PHENOMENA

The application of geometric methods to the analysis of biological shape is a recent development (Kendall, 1984; Bookstein, 1991; Goodall, 1991), and the statistical and mathematical implications of this formalism are still being explored and evaluated (Dryden & Mardia, 1998; Rohlf, 1999b, 2000a,b; Bookstein, 2000; Mardia, Bookstein & Moreton, 2000; Monteiro, Bordin & Reis, 2000; Monteiro et al., 2002). From a biological standpoint, the geometric approach to the description and interpretation of shape variation and change has provided powerful, new insights into several classic problems, such as the evolutionary radiation of divergent shapes (Walker, 1997), the diagnosis of cryptic species (Adams & Funk, 1997), the functional basis of ecological character displacement (Adams & Rohlf, 2000; Losos, 2000), the application of models of development and evolution of complex morphological structures to the study of geographical variation in natural populations (Duarte et al., 2000), the ontogenetic basis of cranial diversity in late hominida (Ponce de León & Zollikoffer, 2001), the analysis of allometric patterns within and between species (Rosenberg, 2002), and the definition of morphological boundaries of independent evolutionary units in nature (Reis et al., 2002a,b). Recently, Rohlf (2002) addressed the problem of shape change in the context of mapping shape data onto a phylogeny, including the estimation of ancestral states of shape variables.

The problem of the hierarchical localization of shape processes and change has received little attention. Conceptually, this is a question of pattern and scale (Levin, 1992, 2003; Bar-Yam, 1997), in that observed patterns of variation in cranial shape are the result of mechanisms that operate on scales different from those in which the patterns are detected and described (Levin, 1992). A fundamental question is thus how information is transferred across scales and how observed patterns should be understood in terms of underlying processes (Sober, 1988; Levin, 1992; Levin & Pacala, 1997; Ruelle, 2001). The complex dynamic process of shape formation and maintenance is governed by genes that code for extracellular proteins, which signal the location, differentiation and fate of cells in a given neighbourhood of the developing embryo. Additional processes involve the control of gene expression in response to the molecular signalling, interactions between gene products and cell-cell interactions responsible for the proper spatial localization of different shapes at their correct positions, thus linking patternning with morphogenesis (Blelloch & Kimble, 1999; Tucker & Sharpe, 1999; Bronner-Fraser & Sternberg, 2000; Gurdon & Bourillot, 2001). Molecular studies of morphogenesis and generation of shape indicate a phenomenon that is essentially spatial and localized (Streicher et al., 2000). The importance of spatial pattern formation also emerges from mathematical modelling where geometry and dispersion relations appear as parameters in the partial differential equations that model morphogenesis (Murray, 1990, 2000).

Molecular studies of development and mathematical modelling emphasize that morphogenetic processes that emerge at the level of morphological structures, such as the cranium, should be seen as variation in shape in which spatial organization and scale are dominant themes. Shape analysis based on partial warps (Bookstein, 1991, 1989, 1996; Rohlf, 1996) seems to be particularly appropriate for uncovering emerging patterns on different scales. As emphasized by Bookstein (1996), the matrix mechanics of the geometric formalism applied to morphometrics involves the minimization of functionals bearing a close parallel to the bending of metal plates subjected to physical constraints. Evidently, the notion of energy needed to bend a metal plate has no parallel in the modelling of biological structures, the cranium analysed here being an example. However, Bookstein (1996) proposed an elegant biomathematical reinterpretation for the energy formalism of continuum mechanics of plates and shells in terms of the hierarchical localization of shape phenomena. This reinterpretation (Bookstein, 1996; 351–352) allows one to search for scales of variation in shape, measured by the scaling of eigenvalues of the bending energy matrix by the exponent \( \alpha \), that are congruent with a molecular phylogeny. The application of these ideas in our study led to the discovery of a scale of localized, hierarchical variation in cranial shape in the Trinomys lineage that was concordant with the topological structure of variation in the cytochrome \( b \) gene sequences.

Our main finding was that congruence between the hierarchical patterns of cranial shape variation and molecular phylogenetic structure is conditional, at least in the case studied here, on the level of organizational complexity and geometric scale. This observation confirms the conjecture that, from the viewpoint of complex dynamic systems, different levels of organizational complexity and scale should display characteristic variability (Levin, 1992, 2003; Bar-Yam, 1997). The geometric-morphometric formalism, by virtue of its biomathematical property to model shape
and shape change as localized, hierarchical phenomena, holds enormous potential for the modelling of morphogenetic and developmental processes. This approach may consequently have important implications for understanding the mechanisms underlying observed patterns of morphological evolution.

ACKNOWLEDGEMENTS

This manuscript profited greatly from comments and suggestions by A. C. R. Alves, J. A. F. Diniz Filho and S. Hyslop. We are indebted to R. Pretorius and an anonymous reviewer for comments that improved the quality of the manuscript. We thank J. A. Oliveira, L. B. F. Oliveira, L. O. Salles (Museu Nacional – MN, Rio de Janeiro), M. de Vivo (Museu de Zoologia – MZUSP, Universidade de São Paulo) and H. Q. B. Fernandes (Museu de Biologia Prof Mello Leitão – MBML, Espírito Santo) for allowing access to specimens. S. M. S. Franco and S. M. Vaz at the Museu Nacional and M. Hofmann and W. A. Hoffmann at the Museu de Biologia Prof Mello Leitão kindly helped with the handling of specimens. J. R. Somera helped with the line drawings. This work was funded by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 99/06845–3) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; Bioinformatics Program 521100/01–1). P. A. Nicola was supported by a graduate scholarship from FAPESP. L. M. Pessôa, F. J. Von Zuben and S. F. dos Reis are supported by research fellowships from Conselho Nacional de Desenvolvimento Científico e Tecnológico. This work was supported in part by a grant (IBM-0090445) from the Ecological and Evolutionary Physiology program of the National Science Foundation. This article is contribution no. 1111 from the Physiology program of the National Science Foundation (IBN-0090445).

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