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"PHYLOGENETIC APPROACHES IN COMPARATIVE VERTEBRATE MORPHOLOGY"

1. Garland, Theodore, Jr.
Recent Developments in Phylogenetically Based Statistical Methods
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Increased phylogenetic information (often based on analyses of DNA sequences) has revolutionized comparative biology. Phylogenies are used to guide the choice of species for comparisons and to identify traits that are homologous versus analogous. They are also used to perform "phylogenetically correct" statistical analyses that attempt to account for the fact that related species tend to resemble each other (exhibit "phylogenetic signal"). The first fully phylogenetic method for continuous-valued traits was "independent contrasts" (Felsenstein, 1985), based on a simple Brownian motion model of character evolution. This algorithm is now viewed as a special case of (phylogenetic) generalized least-squares approaches (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000; Rohlf, 2001). Recent methods to test for and quantify phylogenetic signal show that it is ubiquitous, but stronger in some types of traits (e.g., body size, other morphometric traits) than in others (especially behavior). All of the foregoing approaches may employ Monte Carlo simulations along specified phylogenies (Martins and Garland, 1991; Garland et al., 1993) or randomization tests for hypothesis testing. Current work aims to develop more realistic models of character evolution, sometimes by transformation of branch lengths, to avoid over-correction for possible phylogenetic effects, and to incorporate within-species variation (e.g., measurement error) into phylogenetic comparative analyses. (Methods for categorical traits [e.g., see Ridley, Maddison, Grafen, Pagel] will not be covered.)

2. Vanhooydonck, Bieke and Van Damme, Raoul
Phylogenetic Analyses of Adaptation and Constraint in Lacertid Lizards
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Whereas 'traditional' evolutionary biologists believed in the omnipotent power of evolution by natural selection, emphasis in recent years has been on processes that slow

down or constrain adaptation (e.g. genetic constraints, developmental constraints, phylogenetic inertia, trade-offs). To gain insight into the evolution of locomotor performance in lizards, we test both constraint and adaptive hypotheses. In doing so, we compare locomotor performance (i.e. sprint speed, endurance, climbing speed), limb morphology (i.e. lengths of different limb segments), and ecology (i.e. microhabitat use, anti-predator behaviour) across lacertid lizard species. Since species share (parts of) their evolutionary history and cannot be regarded independent data points in statistical analyses, we use the comparative method to analyze our data. When testing whether species occurring in various microhabitats differ morphologically, the importance of taking the phylogenetic relationships among species into account becomes obvious. While results from traditional statistical analyses suggest that lacertid lizards are adapted to their respective lifestyles, phylogenetic analyses (Monte Carlo simulations) do not support this view. Moreover, simulations show that the statistical power of our test is greatly influenced by the fact that microhabitat use is clustered along the branches of the phylogenetic tree. On the contrary, when testing for the existence of evolutionary trade-offs in locomotor performance among different species, similar results were obtained for both 'traditional' and phylogenetic analyses (independent contrasts).

3. Altshuler, Douglas L.[1], Stiles, F. Gary[2], Graves, Gary R.[3], and McGuire, Jimmy A.[4]
Evolution of Flight Morphology in Hummingbirds
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Hummingbirds are obligate nectarivores, and are the only birds capable of sustained hovering flight. Despite this high degree of ecological and locomotor specialization, hummingbirds are remarkably diverse with over 325 species in the New World, and are also highly variable in body morphology, ranging over an order of magnitude difference in body mass. Here we analyze the phylogenetic patterns in flight morphology using a new phylogeny that contains over 100 taxa based on sequences of one mitochondial and two nuclear genes.

4. Langer, Peter
The Morphology of the Digestive Tract of Cetaceans and Ungulates: Maternal Investment and Phylogenetic Implications
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From twenty discrete anatomical characters of the gastrointestinal tract a phylogenetic tree was constructed for mammals belonging to the PSHM-group (sensu Fischer and Tassy, 1993), Cetacea and Artiodactyla. This tree was used to calculate relationships between body mass and other characters with the help of independent contrasts and to determine residuals of characters on body mass. This was also done in four "manipulated" trees. These were created by shifting the positions of taxa. Relationships between anatomical and life history data, as well as information on food quality (g crude fiber per kg dry matter) and energy contents (MJ per kg food) of food

were determined. In the ungulates, including whales, differentiations of the post-oral digestive tract are independent of life history characters, such as length of gestation and lactation, milk-only and mixed-feeding periods, all expressed as absolute values and as percentages of the length of the total maternal investment period. Relative mixed-feeding periods are not significantly different in the three groups considered here. This period, in which the young animal is weaned, requires about a third of the total time of maternal investment.

5. Hodges, Wendy L.
Integrating CT-Scanning, 3D-Morphometrics, and Phylogenetics to Reconstruct Hypothetical Ancestral Morphologies of Horned Lizards
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Phrynosoma are unique lizards easily recognized by their wide, flat body shape and expanded skulls adorned with parietal and squamosal horns. This genus represents an ideal group for studying character evolution because substantial diversity in morphology and ecology is present, yet it remains a tractable group with 13 extant species. Using morphological and molecular data, Hodges and Zamudio (in press) presented two most parsimonious phylogenies, which I use in studies of character evolution. I will first present analyses of reproductive mode and life history traits (Hodges, in revision). Viviparity, altitude, and latitude exhibit strong phylogenetic signal within *Phrynosoma*. Viviparous species occur at higher minimum and midpoint altitude, which partially supports the cold-climate hypothesis for the evolution of live bearing in squamates (Shine, 1985). Then, I will show how to use phylogeny and mathematical techniques to reconstruct ancestral traits using the evolution of horns in *Phrynosoma* as an example. I apply these methods to 3D-reconstructions of morphological data generated from a high-resolution x-ray, computed tomography scanner. Changes occurring along a phylogeny will be shown via metamorphosis (morphing). Morphing is a dynamic process that allows visualization of transformational changes from one form to another in real time (DeCarlo and Gallier, 1996). All CT data from this project are made available through the NSF-supported, public digital library, www.digimorph.org.

6. Steppan, Scott J.
Phylogenetic Comparative Analysis of Multivariate Data as Exemplified by Comparative Quantitative Genetics and the Evolution of the G-Matrix
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In recent years the development of comparative quantitative genetics and related subjects like phenotypic integration and developmental biology has revealed limitations in several methods of analysis. Most significantly, multivariate data are difficult to analyze in a phylogenetic framework, and there is no standard means of comparing matrices among taxa to examine patterns of variation among traits. I will discuss the challenges presented by multivariate data in comparative studies and illustrate some solutions using comparative quantitative genetics. Quantitative genetics provides one of

the most promising frameworks to unify the fields of macroevolution and microevolution, and the genetic variance-covariance matrix (G) is crucial to quantitative genetic predictions about macroevolution. I will summarize what is known about several key questions in the field and compare the strengths and weaknesses of several statistical and conceptual approaches now being employed, highlighting those approaches using common principle components analysis, ancestral reconstruction, and MANOVA. It is now clear that the key question is no longer if G evolves but how fast and what evolutionary processes affect the rate and direction of evolution.