

PHYLOGENIES AND COMPARATIVE BIOLOGY, STAGE II: TESTING CAUSAL HYPOTHESES DERIVED FROM PHYLOGENIES WITH DATA FROM EXTANT TAXA

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The revolution in comparative biology that occurred over the past 15 years stemmed from two related developments. In the early 1980s, a number of workers argued that macroevolutionary phenomena can be interpreted only in an explicitly historical context (e.g., Cracraft, 1981; Lauder, 1981; Gould and Vrba, 1982). Shortly thereafter, workers realized that as a result of shared ancestry, species are not statistically independent entities; consequently, statistical analyses of comparative data are invalid unless phylogenetic information is incorporated (e.g., Gittleman, 1981; Ridley, 1983; Felsenstein, 1985; Harvey and Pagel, 1991). The result is that workers in all fields of biology are now aware that phylogenetic information must be incorporated into any comparative study that investigates causal hypotheses (i.e., studies that are not purely descriptive). The number of journal articles that incorporate phylogenies has increased substantially, not only in those journals traditionally devoted to evolutionary issues but also in journals such as *Animal Behavior*, *Ecology*, and *Development*.

Nonetheless, the phylogenetic revolution is only half complete. Although workers now commonly use phylogenetic methods to evaluate hypotheses developed using other forms of data, the time has come to invert the process and to use phylogenies as the source of testable hypotheses about evolutionary patterns and processes. Phylogenies are statements not only about relationships among taxa but also about the evolution of characters. These statements in turn may suggest causal hypotheses about why character change should occur in a particular manner. In many cases, hy-

potheses deduced from phylogenies make predictions that pertain to both historical events and contemporary phenomena. For example, phylogenetic analysis indicated that in ray-finned fishes the hypochordal longitudinalis muscle arose prior to the evolution of an externally symmetrical tail (Lauder, 1989). One hypothesis that could be derived from this observation is that the muscle alters functional capacities of the tail in such a way as to favor a symmetrical tail, which might not have been beneficial previously. Functional studies of the hypochordal longitudinalis in extant fish support this hypothesis by revealing that the muscle qualitatively alters tail function (Lauder, 1989).

In a similar manner, testable hypotheses can be derived from phylogenies in many fields of comparative biology as the first four papers in this issue of *Systematic Biology* attest. The form that such tests take, however, will vary from field to field. Laboratory examination and manipulations will be most appropriate to fields such as developmental biology, functional morphology, and endocrinology, whereas field observations and/or experiments may be more appropriate in ecological or behavioral studies. In addition, measures of genetic variation and constraint can be useful to test some hypotheses (e.g., Futuyma and McCafferty, 1990). In some situations, one can test hypotheses that certain traits are favored by natural selection in particular selective regimes (sensu Baum and Larson, 1991) as predicted based on phylogenetic evidence; multigeneration experiments can test whether selection leads to evolutionary change in the direction predicted by phylogenetic hypotheses. This

approach applies to all fields of biology that have a comparative aspect; even in the area of conservation biology, this approach may be useful in establishing priorities and conservation strategies (Brooks et al., 1992).

Although suggested by Hennig (1966), this approach to hypothesis generation and testing has been used only in the past few years (e.g., Lauder, 1989; Futuyma and McCafferty, 1990; McLennan, 1991; Futuyma et al., 1994, 1995; Basolo, 1995; Jermann et al., 1995; Ryan and Rand, 1995). As these approaches become more widespread, workers will grapple with the situation in which a causal hypothesis developed from examination of a phylogeny is not supported by tests on extant taxa. Such a finding might indicate that the hypothesis is mistaken, but another possibility is that historical and present conditions are different in some important respect. Processes that operated in the diversification of a lineage might no longer be important agents of selection. For example, interspecific competition might lead to character displacement in early stages of adaptive radiation, but as species adapt to different niches, they might no longer compete with each other. Another possibility is that subsequent evolutionary change, such as the gain or loss of traits, the loss of genetic variation, or the establishment of genetic or functional correlations, may alter the way in which species within a lineage respond to a particular selection agent.

Thus, just as failure to reject a hypothesis does not prove that the hypothesis is correct, rejection of a phylogenetically derived causal hypothesis through examination of extant taxa does not indicate that the hypothesis incorrectly describes the cause of historical events. Testing of historical processes must be seen as an iterative process in which the results of one round of testing inevitably lead to new investigative approaches.

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REFERENCES

- BASOLO, A. L. 1995. Phylogenetic evidence for the role of a pre-existing bias in sexual selection. *Proc. R. Soc. Lond.* 259:307-311.
- BAUM, D. A., AND A. LARSON. 1991. Adaptation reviewed: A phylogenetic methodology for studying character macroevolution. *Syst. Zool.* 40:1-18.
- BROOKS, D. R., R. L. MAYDEN, AND D. A. MCLENNAN. 1992. Phylogeny and biodiversity: Conserving our evolutionary legacy. *Trends Ecol. Evol.* 7:55-59.
- CRACRAFT, J. 1981. The use of functional and adaptive criteria in phylogenetic systematics. *Am. Zool.* 21:21-36.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1-15.
- FUTUYMA, D. J., M. C. KEESE, AND D. J. FUNK. 1995. Genetic constraints on macroevolution: The evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* 49:797-809.
- FUTUYMA, D. J., AND S. S. MCCAFFERTY. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera, Chrysomelidae). *Evolution* 44:1885-1913.
- FUTUYMA, D. J., J. S. WALSH, JR., T. MORTON, D. J. FINK, AND M. C. KEESE. 1994. Genetic variation in a phylogenetic context: Responses of two specialized leaf beetles (Coleoptera: Chrysomelidae) to host plants of their congeners. *J. Evol. Biol.* 7:127-146.
- GITTLEMAN, J. L. 1981. The phylogeny of parental care in fishes. *Anim. Behav.* 29:936-941.
- GOULD, S. J., AND E. S. VRBA. 1982. Exaptation—A missing term in the science of form. *Paleobiology* 8:4-15.
- HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, England.
- HENNIG, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana.
- JERMANN, T. M., J. G. OPITZ, J. STACKHOUSE, AND S. A. BENNER. 1995. Reconstructing the evolutionary history of the artiodactyl ribonuclease superfamily. *Nature* 374:57-59.
- LAUDER, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. *Paleobiology* 7:430-442.
- LAUDER, G. V. 1989. Caudal fin locomotion in ray-finned fishes: Historical and functional analyses. *Am. Zool.* 29:85-102.
- MCLENNAN, D. A. 1991. Integrating phylogeny and experimental ethology: From pattern to process. *Evolution* 45:1773-1789.
- RIDLEY, M. 1983. The explanation of organic diversity: The comparative method and adaptations for mating. Oxford Univ. Press, Oxford, England.
- RYAN, M. J., AND A. S. RAND. 1995. Female responses to ancestral advertisement calls in Túngara frogs. *Science* 269:390-392.