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Phylogeny, ontogeny and intraspecific variation in *Balsamorhiza* (Asteraceae, Heliantheae): A study of evolutionary phenomena

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PHYLOGENY, ONTOGENY AND INTRASPECIFIC VARIATION IN

BALSAMORHIZA (ASTERACEAE, HELIANTHEAE):

A STUDY OF EVOLUTIONARY PHENOMENA

by

Kathleen A. Robson

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A hierarchical approach to the study of phylogenetic, ontogenetic and environmental variation is demonstrated using a combination of cladistics and principal components analysis (PCA). Intraspecific variation within the genus Balsamorhiza (Asteraceae, Heliantheae) was explored in terms of a partial phylogenetic hypothesis, independently constructed for representative species, and based on a limited set of shared, novel characters. The genus and its presently recognized sections, Artorhiza and Balsamorhiza, appear to be monophyletic. Based upon this, intraspecific variation in the three species of section Artorhiza was further examined through the analysis of data describing the growth of flowering shoots at sequential stages of development. The morphological variation expressed during annual growth in these herbaceous perennials was examined; 1) for the species of Artorhiza; 2) among presumably allopatric sites within the single species B. careyana; 3) and between two successive years of growth repeated in a group of individual plants of this

species. The variables examined were: lengths of shoot internodes; associated cauline leaves; and axillary flowering shoots (when present). Comparable data were collected for a single species in section Balsamorhiza and three outgroup species. These data were subjected to PCA by site and stage. Because the interest here was to describe changing structural organization, graphics consisted of plottings of eigenvector coefficients against the first two principal components. The changing relationships of variables to each other and to the overall variation summarized in the axes was assessed within the cladistic framework. While some variables change at random, two groups, describing lowermost cauline leaves and axillary flowering shoots, show patterns that appear to reflect phylogenetic history within Artorhiza alone, suggesting an independent origin. Among-site and between-year variation in B. careyana is reflected as the rotation of eigenvector coefficients about the major axes, but where patterns among and within these variables remain relatively constant. Applications to the partitioning of phylogenetic and environmental factors in evolutionary phenomena are suggested. The structure of scientific explanation is discussed; concepts and theories regarding biological change through time are examined within this framework.

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General Introduction

Twenty years ago a symposium was held and a volume produced entitled "Beyond Reductionism" (Koestler and Smythies, eds. 1969). The participants represented a wide array of disciplines, including genetics, embryology, economics and psychology. The purpose of the meeting was to discuss the general features of biological organization beyond the atomistic or molecular levels and to explore the concept of hierarchy. Koestler (1969, pp. 192-193) provided the following description: "When one talks about hierarchic organization as a fundamental principle of life, one often encounters a strong emotional resistance. For one thing, hierarchy is an ugly word, loaded with ecclesiastic and military associations, and conveys to some people a wrong impression of a rigid or authoritarian structure... Apart from this, the term is often wrongly used to refer simply to order of rank on a linear scale or ladder... But that is not at all what the term is meant to signify. Its correct symbol is not a rigid ladder but a living tree - a multi-levelled, stratified, out-branching pattern of organization, a system branching into subsystems which branch into subsystems of a lower order... a structure encapsulating sub-structures... a process activating sub-processes..." This is an important aspect of living systems and of evolutionary phenomena, although until very recently it has been generally ignored in "modern" biology. Such a concept of hierarchy will form the central theme of this study.

In the same volume, the problem of molecular reductionism is clearly outlined by Weiss (1969, pp.10-11): "Historically, the term 'molecular biology' was coined almost simultaneously, though independently, by Astbury (1951) and myself; it was to indicate, on the scale of orders of magnitude, the lowest level of investigation relevant to the advancement of biological knowledge. But nothing in the nomenclature insinuated that it should assume the role of pars pro toto. As once I put it, there is no phenomenon in a living system that is not molecular, but there is none that is only molecular, either. It is one thing not to see the forest for the trees, but then to go on to deny the reality of the forest is a more serious matter; for it is not just a case of myopia, but one of self-inflicted blindness... the phenomenon of hierarchic structure is a real one, presented to us by the biological object, and not the fiction of a speculative mind."

Weiss (1969, p.193) goes on to describe the need in biology for considering the holistic or emergent properties of living systems: "When people use the phrase 'the whole is more than the sum of its parts', the term 'more' is often interpreted as an algebraic term referring to numbers. However, a living cell certainly does not have more content, mass or volume than is constituted by the aggregate mass of molecules which it comprises... the 'more' (than the sum of parts) in the above tenet does not at all refer to any measurable quantity in the observed systems themselves; it refers solely to the necessity for the

observer to supplement the sum of statements that can be made about the separate parts by any such additional statements as will be needed to describe the collective behaviour of the parts, when in an organized group. In carrying out this upgrading process, he is in effect doing no more than restoring information content that has been lost on the way down in the progressive analysis of the unitary universe into abstracted elements." (Emphasis in the original.)

At one level, this study explores the relationships between phylogeny, ontogeny and intraspecific variation in perennial sunflowers of the genus Balsamorhiza in an attempt to differentiate between phylogenetic and environmental sources of constraint and variation. At another level, some established methods are used in a novel combination through which I hope to provide a more accurate description of the hierarchical organization of a biological system and the structural variations that manifest evolutionary change. By "hierarchical organization" I mean, at least in operational terms, demonstrable features expressed by organisms that show a pattern of nested levels of differentiation through time. Individual organisms, species and monophyletic groups of species, for instance, make up some of the levels that are part of this hierarchical pattern. This study constitutes, in part, an empirical exploration to the concept of hierarchy described above. Regardless of which actual features may signal pattern at a given level among organisms, I believe such an outlook can only improve the accuracy of evolutionary

studies, for morphogenesis clearly expresses the properties of a hierarchical, emergent phenomenon. As long as these properties are ignored, I do not see how a general understanding of life and its change through time can possibly deepen beyond descriptions of biochemical minutiae.

The subject of biological organization is an extremely complex one, but two of the levels within this hierarchy - organisms and species - are assumed to be real here, so they must be defined in at least some simple, operational fashion. The level of individual organisms is usually easy to defend as having an objective existence in nature. An individual balsamroot plant is a taprooted entity composed of physically integrated parts that are organized in a non-random fashion. A balsamroot would seem to be real and cohesive, with discrete boundaries and an objective existence independent of our perception. This is not to say that we can never be deceived by our senses, but there is no evidence in this case to suggest that the plant is an illusion. To deny reality to a being such as a balsamroot, an oak tree or a frog is to indulge in skepticism so extreme that constructive rationality is lost (Watkins 1984) and scientific curiosity becomes self-defeating. Belief in objective reality is nothing more than that, but such a belief is necessary.

The case for species cannot be argued in so straightforward a manner, in balsamroots or in anything else. Debate over the ontology of species has continued in the literature for many years

and has recently become more heated as dissatisfaction with older species concepts has deepened. Mayr (1987, p.217) still asserts that, "...what makes species 'individuals' is the interaction of the members of the species. They exchange genes with each other in each generation, they form a common gene pool, and stabilizing selection controls the limits of their variation." Mayr (1987, p.214) adds a new criterion to the traditional "biological" definition of species: "Two populations may not be able to coexist because they are not reproductively isolated, that is they would immediately interbreed and fuse into a single species. However, two populations may also not be able to coexist at one locality because they have not yet acquired such niche exploiting capacities as would preclude competitive exclusion...superimposed on the primary criterion of reproductive isolation...the process of speciation is not complete until such mutual ecological tolerance has been achieved."

There is a difficulty here in that many organisms, including Balsamorhiza, do not fit at all comfortably into this definition. Hybridization in balsamroots is common and generally occurs between morphological species that are not each other's closest relatives (Ownbey and Weber 1943). Furthermore, how would one go about testing the criterion of "niche exploiting capacities" between two sister species that are isolated geographically and ecologically in nature and show no instance of coexistence? I fully agree with Mayr (1987, p. 220) that we should be able "...to

demonstrate the reality of species as aspects of nature without invoking the theory of evolution." But I suspect that this is just the opposite of what he is doing here. Morphologically distinguishable species that hybridize or that reproduce asexually can either be excluded from further consideration as "unreal" or they can be considered falsifiers of the universality of the "biological species concept". I think they may qualify as falsifers.

There has been much discussion of the philosophical and ontological implications of calling a species an "individual" as opposed to calling it a "class" (especially Hull 1987; Ghiselin 1987 and references therein). The "species as individual" has been viewed as the sexually interconnected cluster that evolves. Most importantly, according to Hull (1987) individuality is expressed as "spatiotemporal restrictedness" and he further insists (p. 175): "Anyone who finds the relevant distinction between spatiotemporal restrictedness and unrestrictedness I am laboring to elucidate incomprehensible or biologically irrelevant is going to have a very difficult time in understanding biological phenomena."

But Stebbins (1987), who surely has some little understanding of biology, disagrees (p.200): "Philosophers must accept facts long recognized by botanists: most plant species, including those that in other characteristics conform to the biological species concept, are not discrete, unified individuals in either space or

time." Kitcher (1987) also considers spatiotemporal limitations unnecessary, but for different reasons.

Either way, I must agree with Cracraft (1987, p.210) that "...discussion about 'species as individuals' has been almost entirely within the context of the (biological species concept). Because of this, some critical philosophical and biological problems within evolutionary theory have gone unexplored." Such a theory-laden species concept is exemplified by the opinion of Ghiselin (1987, p. 210): "Allopatric populations evolve as if they were species until they become sympatric with other parts of their species." This is a simplistic assertion, and it suggests that we have little more to learn about either species or evolution. The advocates of a "pluralistic" species concept (e.g. de Queiroz and Donoghue 1988; Mishler and Brandon 1987) rightly argue that the biological species concept, because it is based solely on interbreeding, is so restrictive as to make it of very limited use in comparative and systematic biology.

I do not wish to engage in a longer description of the controversies over species concepts, but this sample from the recent literature serves to illustrate the difficulties. The following pages outline a study of evolutionary phenomena that requires some empirical reference to the collections of organisms I will call species. However, while it is necessary to assume the existence of species and to provide features by which they might be distinguished, I intend to assume little more about them for

the present. No attempt will be made here to assess gene flow or any other aspect of reproduction. Instead, I will rely on Cracraft's "phylogenetic species concept" (1987, 1989), for it assumes little about the nature of species beyond apparent differentiation. Although "differentiation" may not always be obvious, the requisite of a demonstrable character unique to the organisms collectively called a species is a simple demand for empirical content, and this is a good place to start.

Several aspects of this research are studies in themselves and outline, for instance, new approaches to character analysis and the use of descriptive statistics in the study of morphogenesis. The subject of homology is brought up more than once, perhaps because it is of central importance in evolutionary studies and many different roads lead back to it. Homologies here are hypotheses of some novel similarity shared between two or more organisms, and they remain testable through comparative studies. If, at the level of interest, no clear piece of information will serve to show differences in a feature shared among organisms, the sharing is assumed to be real, and a common origin is implied. A phylogeny can be constructed from internesting sets of these hypotheses of unique similarity, where homologies that remain unrefuted may serve, at their appropriate level, as corroboration or falsification of any given cladogram.

Finally, I am interested in finding ways of using my descriptions of biological organization as tests of evolutionary

explanations. The structure of causal explanations and the comparison of evolutionary theories are complex issues and they are left for the closing discussion.

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