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Between Macro and Molecular

The Evolution of Organ Systems. Andreas Schmidt-Rhaesa. Oxford University Press, New York, 2007. 368 pp., illus. $104.99 (ISBN 9780198566694 paper).

When it comes to evolutionary considerations, relationships among multicellular animals (the Metazoa) have provided a rich source for speculation. What has fueled some of this work for almost 150 years has been the investigation of a variety of organ systems, such as body cavities, excretory systems, photoreceptors, and, by extension, larval forms. An intriguing aspect of organ systems is that they lend themselves to being studied at so many levels of resolution, ranging from the most general anatomical arrangements down to subcellular components.

Yet in recent years, phylogenetic studies of the Metazoa have tended to forgo considerations of organ systems in favor of focusing either on gross comparative morphology or on molecular data—a disparity too often incorrectly referred to as "morphological" and "molecular" systematics. While internal anatomical features occasionally find their way into "morphological" analyses, a comprehensive consideration of organ systems in phylogenetic studies has been neither extensive nor particularly integrative. In *The Evolution of Organ Systems,* Andreas Schmidt-Rhaesa reminds us that there is still a vast realm to be considered in research on metazoan evolution.

According to Schmidt-Rhaesa, the goal of *The Evolution of Organ Systems* is not only to portray organ system diversity, which he does admirably, but also to present it in an evolutionary perspective. This is an ambitious enterprise, with 12 of the 15 chapters covering topics ranging from epidermis, musculature, and body cavities to the more traditional systems (e.g., nervous, sensory, and excretory systems). There is an additional chapter on spermatozoa, which, although not a class of organs, has been recognized as critical to the topic of metazoan evolution.

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Treating metazoan organ systems in an evolutionary context requires first presenting the framework within which the topic is to be developed. It is in chapter 1, "Introduction," that Schmidt-Rhaesa lays out his view of the underlying evolutionary structure upon which subsequent chapters are developed:

> How can we make statements about the evolution of organ systems? We need solid background knowledge about the evolutionary relationships of animals, i.e., their phylogeny. If we have a tree (and "tree" is meant here as the short form of "hypothesis of phylogenetic relationships"), we can map the characters from organ systems onto this tree and then try to "read" its history. I regard this as an enormously important thing. (p. 1)

It is then in chapter 2, "The Phylogenetic Frame," that Schmidt-Rhaesa gives a general overview of current knowledge of metazoan phylogeny, derived from the multitude of disparate phylogenetic analyses of "phyla," principally determined using morphological and molecular data. From these studies, Schmidt-Rhaesa summarizes metazoan phylogenetic relationships by way of a series of cladograms for various groups of phyla. Of course, with disparate sets of data often come contradictory hypotheses, which Schmidt-Rhaesa glosses over far too casually in his endeavor to present branching diagrams. It is these separate cladograms that are then compiled into a single, consensus-like cladogram and used in many of the later chapters to discuss organ system evolution. The problem, however, is that none of the individual cladograms, much less the more inclusive conglomeration of these trees, indicates any attendant empirical justification. Rather, the cladograms are simply branching diagrams derived from various studies.

The consequence is that these diagrams are merely that—they cannot be regarded as phylogenetic hypotheses because they are not the direct consequences of inferences from discernible, relevant sets of observations. I find the book's greatest weakness in these first two chapters, and it is a weakness that extends throughout the book. It is on the basis of an evolutionary tree derived from the host of reviewed phylogenetic analyses that Schmidt-Rhaesa simply maps selected characters of organ systems in later chapters (indicated in the above quote), under the guise that evolutionary transformations can be discerned. The difficulty, however, is that this approach is so fraught with problems that virtually all evolutionary considerations given in this book cannot be taken seriously.

The problem with mapping characters onto preexisting cladograms cannot be overstated. Simply put, mapped characters and cladograms are irrelevant to one another. As cladograms are causal accounts directed at explaining shared similarities, any consideration of characters relative to trees must be in terms of the relations of those trees as answers to our questions regarding observed characters. It is this inferential relation that provides the rational basis for speaking of the evolution of organ systems as well as other classes of characters. In the absence of such a relation, which is the case in almost every instance in which cladograms are presented in *The Evolution of Organ Systems,* virtually no valid evolutionary considerations are to be had.

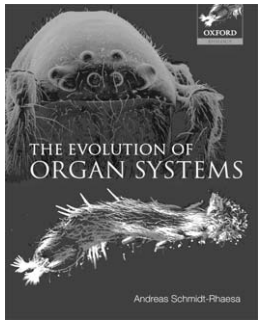
This is a condition that violates what philosophers routinely call "the requirement of total evidence." The requirement—what the philosopher Carl G. Hempel once described as "a maxim for the application of inductive logic"—states that the rational acceptance of a

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particular conclusion is contingent on taking into consideration all *relevant* evidence. Evidence is relevant, either in a positive or negative sense, if it has an effect on the support for a conclusion. Over the past 20 years, this requirement has periodically received attention in phylogenetic systematics, but for the most part it has either been grossly misinterpreted, vaguely acknowledged, or, more often than not, completely ignored. Schmidt-Rhaesa echoes this lack of concern in chapter 2, where he states that "there are attempts to combine morphological and molecular analyses (total evidence [sic] and other methods).... The different data sources and different analytical tools have led to a wide variety of phylogenetic hypotheses. Such hypotheses are sometimes congruent, but incongruence is a common phenomenon" (p. 3).

Schmidt-Rhaesa does not say how to address this issue, but ironically it is in the last chapter (15), "Final Conclusions," that he writes: "If one is interested in the evolution of structures, organs, and organisms, the aim must be to develop an evolutionary scenario that is as complete as possible" (p. 293). One is left wondering why this latter point of view does not form the basis for the entire book. Schmidt-Rhaesa's compilation of observations from the vast literature is a noble effort. But to speak of the evolution of organ systems is to go well beyond compilations of observations and engage in the synthesis of data. It is as a synthetic work, implied by the title, that the book falls far short of its mark.

The Evolution of Organ Systems has a marked redeeming quality: the exhaustive reviews of metazoan organ systems, including spermatozoa, are the strengths of the book. These reviews clearly hint at the wealth of phylogenetic information that still needs to be investigated. The book shows us that it is the observational realm lying between "morphological" and "molecular" that deserves the greatest consideration. If the goal of evolutionary research is to acquire causal understanding of organisms, then there remains a gold mine of research programs waiting to be tapped below the body walls of the Metazoa. I do wish this book had offered a firmer foundation for promoting such pursuits.



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DARWIN'S FINCHES: MULTIPLY AND SUBTRACT

How and Why Species Multiply: The Radiation of Darwin's Finches. Peter R. Grant and B. Rosemary Grant. Princeton University Press, Princeton, NJ, 2007. 272 pp., illus. $35.00 (ISBN 9780691133607 cloth).

How and Why Species Multiply is an odd book. The title suggests it will review the hows and whys of speciation. The authors, Peter and Rosemary Grant, renowned evolutionary ecologists from Princeton University, execute this task quite well in the classic Mayrian framework, invoking isolation of populations and divergence (either adaptive or neutral) in allopatry, followed by the origin of premating or postmating reproductive isolating mechanisms, and eventual secondary contact, where isolating mechanisms might be strengthened (or eroded). The subtitle, however, *The Radiation of Darwin's Finches,* suggests that Darwin's finches will be used as a case study. This is where things get odd, as there is little about the finches that fits the classic model.

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First, allopatry is only approximate, as the authors have documented numerous cases of interisland dispersal, and in historic times populations have been extirpated and replaced, hardly the norm for speciation in isolation. Second, species overlap in phenotypic space, and many congeners are difficult to tell apart in the field and in the museum. In fact, it is sometimes said that "only God and Peter Grant can identify the finches." This is not unique for birds—there are many avian sibling species—but it is atypical for other clear adaptive radiations. Third, interisland movements have also led to considerable hybridization, and the authors now ascribe a significant role to this in finch evolution. Certainly, differentiation can proceed with ongoing hybridization, given strong countering selection, but it is atypical for other adaptive radiations. Last, molecular data fail to discriminate most of the species in the two main genera (*Geospiza* and *Camarhynchus*), a result reminiscent of cichlid fishes (although their morphology is more clear-cut), but unlike other adaptive radiations of birds. Thus, Darwin's finches are not obvious examples of the standard understanding of how speciation proceeds.

The authors present analyses and interpretations that require a robust phylogenetic hypothesis. The simple fact is that there is no established molecular phylogeny apart from the evidence supporting the groups *Geospiza, Camarhynchus, Platyspiza, Cactospiza,* and *Pinaroloxias,* and two species of *Certhidea* (Sato et al. 1999). Importantly, species limits in the genera *Camarhynchus* and *Geospiza,* arguably the most important of the finches in ecological studies, are not supported by mitochondrial DNA (mtDNA) or microsatellite data. The authors ignore the lack of species-level monophyly and present a tree (plate 1) based on a single exemplar for species in *Camarhynchus* and *Geospiza,* which is misleading at best. The topology of the "tree" in plate 1, however, is not the same as that in figure 2.1. The lack of species-level mtDNA and microsatellite diagnosability is exactly what one would predict from the high level of

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