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The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating.—Mark Ridley. 1983. Clarendon Press, Oxford. vi + 272 pp. \$37.50.

Two notorious disciplines in biology seem to be lurching toward each other, groping for mutual understanding and even fusion into a more powerful version of evolutionary

biology. The two disciplines are cladistics and adaptationist theory, and their rapprochement is the refreshing news announced in Ridley's book. The two fields obviously need each other. The current estrangement between adaptationist theory and "pure" cladistics (which tends to focus on character patterns rather than on evolutionary processes) finds its metaphor in a Greek explanation of sex. Plato believed that each male and female once formed a perfect hermaphroditic whole, but through some misunderstanding (nb!) were sundered into different, individually sterile genders. As such they are condemned to wander, miserably seeking their complementary half. With Ridley, I would also advise cladists and adaptationists to give up, join up, and procreate.

At present, adaptationists and cladists are usually each other's worst critics. Ridley himself published a diatribe against "pattern" or "transformed" cladism (Ridley, 1983) and cladists have reviled the adaptationist research program. To any biologist on the sidelines who accepts the evidence for evolution on the one hand, and the rather overwhelming, although circumstantial, evidence for adaptation on the other the fray must be most perplexing. Both camps eschew, however, the chaotic melange bequeathed by the New Synthesis, and the excesses of the past no doubt explain much of the current distrust. In reading the introduction, one senses Ridley's exasperation with that body of thought. He writes, "the comparative method of 1950 was indistinguishable from the comparative method of 350 BC" (p. 6), and "non-systematic studies have no doubt helped to inspire critics who believe that the whole concept of adaptation is untestable. They will notice that the adaptationists count only confirmatory instances. . . [instead] cases that refute, as well as cases that confirm, can easily be counted, and in so doing we are moving towards a scientific test. . . [this criterion] is sufficient to rule out the entire literature (with one exception) from before about 1960" (p. 8). The issue in adaptationist theory, then, is pragmatic tests of natural selection and its product, adaptation, just as in taxonomy the issue has become tests of genealogical hypotheses.

Eating crow is never easy on the ego, but adaptationists seem to be realizing that while one can infer phylogeny without positing natural selection or adaptation, one can't demonstrate adaptation without correct phylogenies. The sting of that asymmetric need may explain the often petulant tone Ridley uses when discussing cladism. For example, "we do not have to make up our minds about Hennig's argument. We do not have to decide whether cladism is a sensible philosophy" (p. 20). How can Ridley rely on cladism in his research and not, at least implicitly, admit its validity? Another defiance is especially relevant: "we do not have to suppress categories such as 'fish' and 'reptiles'." By that I assume he means that paraphyletic or polyphyletic groups are adequate for his purposes. For someone who wants quantitative estimates of convergence in evolution, this blasé attitude about monophyly must lead to inaccurate results.

So much for ideological milieux. What is Ridley's purpose? He wants first and foremost to write a book about method, about how to test and corroborate adaptive hypotheses, and only secondarily to write about particular adaptations. Ultimately, he wants to talk about why traits that interest him evolved, specifically precopulatory mate guarding (termed "precopula") and assortative mating for size. In this review I address mainly his methods, and only briefly his work on precopulatory mate guarding. My overall impression is that he does a moderate job of devising a method, but that its application to the data is uneven, and that the data themselves are lousy, at least in the case of precopulatory mate guarding.

Ridley starts off by identifying two comparative biologies (p. 5):

The two comparative biologies, in their techniques, in their concepts, and in their produce, make up complementary pairs. One seeks homologies, the other analogies; one (in Gregory's terms) studies heritage, the other habitus; one classifies divergence, the other explains convergence; and (more dangerously, Cain, 1964) the one ancestral, the other adaptive characters. This book is concerned with the second of the two traditions. It is about adaptation.

The first tradition, studying homology, he calls taxonomy, and the second, studying analogy, he does not name but describes as taxonomy's poor cousin: "not as rich, made up of only a few passages in works on other subjects. . . easily outweighed by the hundreds of great volumes of taxonomy" (p. 4). Well, descriptive taxonomy, perhaps, but we are interested in analysis, not cataloging, and from that point of view, the instances of useful taxonomy are precious few. Ridley's second, innominate tradition seems identical to gradism. As he says, "the tradition does exist, flickering in many strange places" (an apt epitaph). Why isn't good old gradism sufficient? Because gradism confuses convergence or symplesiomorphy with monophyly, and Ridley wants as many instances of convergence as possible, not just one. These independent cases of convergence make Ridley's case for general adaptive value. If a trait evolves only once, and thus defines a monophyletic group, Ridley is unclear about its status as an adaptation.

I think most cladists would agree that studies on the adaptive nature of homologies are what evolutionary biology needs, so I was disappointed to see Ridley opt for the second. He reasons that "comparative studies of convergence have a much closer relationship with the principle of adaptation" (p. 5). This is egregious understatement. In fact, convergence is always explained by natural selection and adaptation because no other process explanation for substantial convergence exists. To my mind, this theoretical poverty makes analyses of convergence somewhat dull, since one knows in advance the author's basic conclusions. Adaptationist study of homology could be more interesting, because simple heritage forms such a strong alternative hypothesis to stabilizing or directional selection. Ridley thus avoids the main issue in process theory relevant to phylogenetics, and opts for restating a method that has been around for quite some time.

To continue, Ridley's method comes down to this. Following Clutton-Brock and Harvey (1977), he realizes that the standard adaptationist approach (counting all terminal taxa as confirmatory instances) will wildly overestimate the number of convergences if the trait is primitive for the group. That approach is bankrupt, due to what he quaintly calls "taxonomic artefact." (Indeed, a minor part of the book does investigate this centerpiece of the cladistic research program, and I will consider his success in that endeavor below.) On the other hand, he doesn't want to underestimate convergences, because they make his case. His main use of cladistics is to specify the nodes on a cladogram where each instance of homoplasy has arisen, and thus the total number of homoplasies on the tree. If he can show that two features are consistently correlated and occur convergently with some frequency, adaptation has been demonstrated.

In his précis of cladistics, Ridley agrees that synapomorphy is the only kind of similarity relevant to phylogeny, although he does not call such characters synapomorphies. In his *New Scientist* article he insisted on what he considered to be original Hennigian terms, calling them 'derived characters.' In the same article, by the way, he accuses pattern cladists of preferring "to substitute their own terms, such as 'synapomorphy' and 'symplesiomorphy' which barbarously disguise their [Hennig's terms] evolutionary meaning" (p. 651). Willi Hennig coined synapomorphy and symplesiomorphy, and although minor, this mistake in etymology does reflect Ridley's unfamiliarity with current (or even relatively old) cladistic theory. For example, he still thinks that cladists insist that speciation is dichotomous. That *was* an original Hennigian thought, but it was dropped long, long ago by working cladists.

He outlines three-taxon statements and conveys the gist of outgroup comparison, but not much of its subtlety. He seems blithely unaware of problems caused by uncertainty in outgroups themselves. He also is either unaware of or reluctant to use step-counting parsimony procedures in polarity analysis, preferring instead plausibility arguments about ancestral states. The point of outgroup comparison is, however, adequately expressed (p. 21): "outgroup comparison thus minimizes the number of (estimated) evolutionary events," but he relapses in his next sentence: "Although the

method minimizes convergence, it does not eliminate it entirely." A relapse because convergence in cladistics is just a post hoc explanation invoked to explain parsimony's residue. Ridley worries about the "real" frequency of convergence, but laboriously convinces himself that outgroup comparison is still the best method, though in a very curious way.

He first supposes that in truth convergences outnumber homologies, and concludes that since outgroup comparison minimizes convergence, it will be a woeful underestimate. He misses the point. If Ridley can recognize convergence without an implicit phylogenetic scheme, he should tell us. That method would be a greater contribution than the subject of this book. How can we possibly know that a similarity between two taxa is convergent unless we know by other evidence that the taxa are not each other's closest relatives? If what Ridley calls "convergence" is truly more common than "homology," and we are deceived by it, then our impression of the true phylogeny simply inverts, and the former "convergences" become the justifying "homologies" of the new phylogeny, and vice versa. That is a simple, basic, point of any scientific method which Ridley seems to have missed. Although presumably published too late for Ridley to have seen it, Farris (1983) offers several other reasons why the actual frequency of convergence is unimportant.

He also dwells for an amazingly long time on ingroup comparison. He concludes with a lukewarm preference for outgroup techniques, but remains uncommitted, and even uses ingroup comparison to settle polarity issues when outgroup relationships are unresolved (p. 106).

Ridley has other, more deep-set problems to confront about "convergence." His intent in the case of precopula is to show that where female receptivity to mating is both limited and predictable, precopulatory mate guiding will evolve. But his definition of precopula is any situation where the male is adjacent to the female for at least twenty-four hours before she becomes sexually receptive. This definition is inadequate because males can be adjacent to females for other reasons. In other words, although Ridley wants to study the evolution of analogies, he still has to worry about the homology of his analogies. In this case, an essential aspect of the definition of precopula should be the reason it evolved, not merely its behavioral form. The stipulation arises because in analogy it is common cause that distinguishes true convergence from mere superficial similarity, just as in the case of homology it is common inheritance that essentially defines the term. Second, Ridley dismisses courtships which are longer than twenty-four hours, such as characterize many birds and mammals, because the male is more active than in a precopula, and because that activity itself makes the female more ready to mate. According to Ridley, "courtship, therefore, by definition, makes the female more ready to mate: she mates quicker if courted than if not. A precopula has relatively little effect on how long the female waits until mating" (p. 60). But he does not demonstrate that such is the case, and admits that precopulas do affect the duration of the last subadult molt cycle in some crustaceans. In fact, he is willing to accept as a precopula the case of a mite in which the female will not molt to maturity unless joined by a male, but apparently would reject as courtship behaviors in such animals as pigeons and cats where ovulation is dependent on male presence. Thus to identify a behavior as a precopula, Ridley first would have to show that it doesn't affect the interval to female maturity (thus distinguishing it from courtship), and second, that the guarding arose because of a trade-off between time invested in guarding immature females versus searching for receptive females. In his subsequent literature review, Ridley ignores these necessary criteria, and usually accepts as a precopula any association between the sexes prior to female receptivity and longer than a day.

Despite these criticisms, Ridley's method is basically sound, or could be made to be so. It is as possible to talk about the evolution of behavioral or functional traits using

cladistic techniques as it is to talk about evolution in morphology. If Ridley had corroborated cladograms, and wanted to test for the association of two features, in principle he could determine how often each had evolved, and then use a contingency test to demonstrate association.

Generally Ridley doesn't discuss any category more restrictive than families. That weakness is directly contradicted by his own methodological advice. Early in the work he explains why one should ignore the taxonomic hierarchy in such studies. The answer, of course, is that the Linnaean hierarchy is hopelessly inadequate to show detailed cladistic structure in any large group. Cladists merely name the cladogram nodes that interest them, and thus Ridley should be searching for those nodes where a precopula evolved, whether formally named or not. To his credit, Ridley rejects the Procrustean system advocated by Clutton-Brock and Harvey (1977), which uses that taxonomic category in which (on average) the trait shows maximum variance, because nomenclatorial categories are artificial. In effect, he says (p. 15) that he'll work with whatever group the data define, but he ends up using families, and forcing them into the categories of precopula or no precopula.

Unfortunately, when he tries to do this in the case of precopulatory mate guarding, he still doesn't follow his own rules. First, Ridley breezily dismisses inadequacies in the data. For example, Ridley admits that he requires phylogenies to estimate convergence, but his source for phylogenies is existing classifications, and he is avowedly indiscriminate (p. 24):

Taxonomy is not only usually not adequate; it is also usually not phylogenetic. What should we do when we know a taxonomy is not a phylogeny but we have nothing else to go on? The answer is that we take the taxonomy as the best estimate of phylogeny that we have, and use it as if it were true. Even if it is a purely numerical taxonomy it will be a better estimate of the phylogeny than to assume that all the species in the whole group are equally related.

As would any serious investigator, I object to this statement on grounds of 'garbage in, garbage out.' But one detects this attitude throughout the book. He generalizes about large taxa on very few observations: for example, about Mygalomorphae (an entire suborder of spiders) on the basis of old references on three species. He says, "The mygalomorphs, on this scant evidence, lack a precopula. We can conclude that a precopula was originally absent in the group to which the mygalomorphs are the outgroup, the araneomorphs" (p. 135). I think a more accurate conclusion would be that discussion of that group will be worthless until more primary research is completed. Further, Ridley admits that the spider taxon Haplogynae is polyphyletic (p. 135), but still shows the group as monophyletic on his naive cladograms (p. 142). Worse, he doesn't point out that the polyphyly of Haplogynae renders its contrast set, Entelegynae, equally suspect, although that conclusion has been general (and repeatedly published) among spider workers for a decade. Within "Entelegynae" he also treats Lycosoidea and Clubionoidea as monophyletic without justification. Another example is his statement (p. 64): "During the evolution of arthropods precopulas have been gained and lost many times, but, their outgroups all lacking it, we can assume that the common ancestor of all the arthropodan groups lacked a precopula." Most cladists would agree that in such a case the state for the stem taxon is equivocal. While on the subject of arthropods, Ridley misrepresents Manton's argument for arthropod polyphyly as merely a rearrangement of arthropod subphyla. Manton believed rather emphatically (without a shred of evidence) that Arthropoda was polyphyletic.

Generalist's works must always run the gauntlet of specialists' criticisms, and I do not want to belittle Ridley's efforts at synthesis merely because of his mediocre knowledge of spiders (his mediocre knowledge of cladistics is more damning). However, he does seem to rely heavily on secondary sources, summaries and anthologies of spider biology,

and the like. A brief perusal of his bibliography suggests that he does the same for other groups. If his synthesis of the biology of those taxa is as mistaken as that for spiders, I worry that most of the generalizations in this book are completely unreliable.

In sum, Ridley's intention to inculcate phylogeny into the study of adaptation can only be applauded. He outlines a serviceable method for the study of convergence, but insofar as I can judge, does only a fair job of applying the method to the study of pre-copulatory mate guarding. The book also has a chapter on homogamy for size as a function of male choice—perhaps that is more carefully done. Both theories still stand as viable explanations, but the vast scope of Ridley's synthesis (the Animal Kingdom) and its superficiality discredit the test. Cladistic studies of behavioral and ecological data probably will soon sweep the field, but those that gain respect will be comprehensive biologies of small monophyletic groups, not armchair syntheses on all animals.—*Jonathan Coddington, Department of Entomology, National Museum of Natural History, Washington DC 20560.*

LITERATURE CITED

- CLUTTON-BROCK, T. H., and P.H.HARVEY. 1977. Species differences in feeding and ranging behaviour in primates. *In* Clutton-Brock, T. H. (ed.), *Primate ecology*. Academic Press, London, pp. 557-584.
- FARRIS, J. S. 1983. The logical basis of phylogenetic analysis. *In* Platnick, N. I., and V. A. Funk (eds.), *Advances in cladistics, volume 2: Proceedings of the second meeting of the Willi Hennig Society*. Columbia Univ. Press, New York, pp. 7-36.
- RIDLEY, M. 1983. Can classification do without evolution? *New Scientist* (Dec. 1983): 647-651.

