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The Origins of Larvae

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A Good Review of Our Understanding of Speciation

Speciation. Jerry A. Coyne and H. Allen Orr. Sinauer, Sunderland, MA, 2004. 545 pp., illus. $89.95 (ISBN 0878930914 cloth).

"Why are there are so many species and how did they form?" is a fundamental question in biology. Jerry Coyne and Allen Orr's book is the first major summary of the data and ideas on speciation since *Animal Species and Evolution,* Ernst Mayr's highly influential book published in 1963. Although several books have appeared in the interim, none has been as broad as Coyne and Orr's.

The first two chapters of *Speciation,* which provide the foundations for subsequent arguments, present an admirable discussion of the various concepts of species that have proliferated in the past 20 years. Coyne and Orr opt for a slightly modified version of Mayr's biological species concept: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (p. 30). Species are maintained by isolating barriers, or "those biological features of organisms that impede the exchange of genes with members of other populations" (p. 29).

The real strength of the book lies in these elaborations: "Groups of interbreeding natural populations are distinct species if either (1) their genetic differences preclude them from living in the same area or (2) they inhabit the same area but their genetic differences make them unable to produce fertile hybrids"; and "Distinct species are characterized by substantial but not necessarily complete reproductive isolation" (p. 30). Maintaining the distinction between definition and recognition of species in this way removes many of the problems that plagued earlier approaches. Equating speciation with the formation of isolating mechanisms defines evolutionarily independent entities, which are presumably the units of evolutionary phenomena. This approach will be unsatisfactory to systematists, who are using a different definition to ask entirely different questions, but it is probably the best approach to take in evolutionary biology. However, it ignores processes that lead to anagenesis (which might explain some of the divergence leading to isolation, because anagenesis can occur differently in various populations within species).

Isolating barriers include the premating and postmating isolating mechanisms discussed by others, but Coyne and Orr make a valuable distinction between postmating prezygotic barriers and postmating postzygotic barriers. This allows the inclusion of all of the recent work on cryptic mate choice and sexual selection, which can occur after mating, while keeping them distinct from classic postmating postzygotic barriers. Another refreshing improvement is the explicit inclusion of ecological factors in the list of isolation barriers. Ecological factors appear in both the premating and the postmating postzygotic sections (the first including habitat isolation, temporal isolation, and pollinator isolation, and the second ecological inviability, when hybrids cannot find an appropriate niche or mates). This is an important point because the evolutionary dynamics can be quite different between premating and postmating postzygotic barriers; for example, only postmating postzygotic ecological isolation could lead to reinforcement of isolation.

Ecologically minded readers will be amused by what Coyne and Orr call "ecological"—they actually mean factors other than conventional genetic ones—but this is understandable, given that they both work on ecologically intractable organisms (*Drosophila*). Readers should ignore this quirk and attend to the useful new insights that arise from this approach; ecological and behavioral factors are considered later in the book.

The authors do not define species as "reproductively isolated entities having sufficient divergence to permit their coexistence" (p. 35), because "coexistence of nearly identical species can be maintained by spatial and temporal fluctuation in resources, or by subtle and virtually undetectable differences in ecology" (p. 35). This fact, Coyne and Orr maintain, would make the "sufficient divergence" species concept untestable in practice. A related point is that ecological isolation can arise either directly, by divergent adaptation to the local environments, or incidentally, as a result of competitive divergence unrelated to the habitat differences, again making distinctions untestable. The authors' strongly empirical approach, which permeates the book, sometimes leads to inconsistencies. For example, they point out the important distinction between definition and recognition of species, but later they reject a valid definition because it does not lead to an ability to distinguish species in all cases. They do believe niche differences are necessary to aid the persistence of species, and point out that there is no necessary correlation between reproductive isolation and ecological differentiation.

Coyne and Orr advocate and then criticize various modes of speciation, presenting an excellent discussion of the recent literature and evidence. However, they made no effort to compare the conditions for each mode and say which predictions or properties are unique to each mode. For example, they list six critical conditions for, and properties of, allopatric speciation, but almost all of these apply also to parapatric speciation, and some apply to sympatric speciation. A table and chapter contrasting the modes and their conditions would have been very helpful. The authors eventually opt for allopatric speciation as the most common mode and as the null hypothesis, but mostly on the basis of testability and simplicity (although genetic drift, which they rightly discard on examination of the empirical evidence, is even simpler). Considerations of the commonness of speci-

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ation modes should, however, also consider the commonness of their necessary conditions; isolation by distance and geographic variation in ecological conditions is more common than absolute isolation, so on that basis parapatric speciation might be thought more common than allopatric speciation. But the strong overlap in properties makes them difficult to distinguish in practice, and Coyne and Orr decide arbitrarily to assume that allopatric speciation should be assumed as a null hypothesis.

After discussing the modes of speciation, the authors present several excellent chapters on various isolating mechanisms: ecological isolation, behavioral and nonecological isolation, postzygotic isolation and its genetics, polyploidy and hybridization, reinforcement, and genetic drift. This is a major advance over previous treatments because each subject is discussed in detail, excellent summaries of the empirical data are given, and we have a chance to consider the strengths and weaknesses of the evidence. It was particularly refreshing to find a chapter on ecological isolation, a subject that has been almost entirely neglected.

In choosing mates, females try to get the best mate that they can find. This would result in (premating) isolation as an incidental by-product of sexual selection, because a mate of the wrong species (with postmating isolation) would not be as good a mate as one of the same species.

These chapters are useful also because they point out glaring holes in our knowledge. For example, the summary of adaptation to new environments revealed that no study has showed that such adaptation yielded behavioral preferences for the new environments, which would be critical for speciation. Another example: Although selection may increase prezygotic isolation as a way to decrease postzygotic isolation effects (reinforcement), selection could also decrease postzygotic isolation directly by purging the deleterious alleles involved. One strong, general, and important new conclusion emerges from recent work on the population genetics of speciation: Reproductive isolation in the form of postzygotic isolation can easily result from natural selection within species (chapter 4), and genetic drift is probably unimportant in most cases of speciation (chapter 11).

The only notable weakness of the book is that only two implications of sexual selection are mentioned: It can cause rapid divergence of mate choice and traits, and hence isolation, and it increases the likelihood of reinforcement (choice is driven both by the need to avoid postmating costs and by indirect selection on preferences from sexual selection itself). But there is more to sexual selection than this. In choosing mates, females try to get the best mate that they can find. This

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would result in (premating) isolation as an incidental by-product of sexual selection, because a mate of the wrong species (with postmating isolation) would not be as good a mate as one of the same species. This in turn implies that in concentrating on isolation and the biological species concept, we may have the wrong end of the stick, and that Coyne and Orr's dismissal of the mate recognition concept may be premature. We might come to different conclusions about speciation and species if we viewed it as a problem of mate choice.

Consideration of sexual selection also reminds us that sexual selection may run in different directions in different populations of the same species. This means that there can be geographic variation in mating preferences, as has been shown in many species; what is a biological species in one location may not be one, using the same criteria, in other locations. This could also be true even with a conventional model of speciation if newly evolved isolating mechanisms have not yet spread throughout the species range. An examination of the factors causing and effecting the evolution of mate choice and mating traits should clarify this problem, but it may also undermine our conception of species if they are more amorphous than we currently think.

The last chapter presents some interesting ideas and speculations about evolution above the species level. The discussion of species selection was particularly objective and welcome. I would, however, have enjoyed a final chapter with general conclusions and questions.

The book is excellent but frustrating. It is an excellent summary of the ideas and data, but the chapters are not well connected to one another and the work does not yield a clear conclusion about the process of speciation or what conditions favor it. In a way, this is a good thing, because the subject was held back for 40 years by overly strong opinions. Nonetheless, it would have been useful to set up a series of general questions and predictions.

Readers will come away thinking that speciation research is a mess, but at least—thanks to Coyne and Orr—it is now an organized mess, and we can get on with figuring out how speciation works and when we should and should not see it.

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EXTINCTION OF THE ROCKY MOUNTAIN LOCUST

Locust: The Devastating Rise and Mysterious Disappearance of the Insect that Shaped the American Frontier. Jeffrey A. Lockwood. Basic Books, New York, 2004. 288 pages, illus. $25.00 (ISBN 0738208949 cloth).

The Rocky Mountain grasshopper, or locust, was a migratory insect that in peak population years spread over the Great Plains from Canada to Texas and periodically devastated the crops of homesteaders and farmers. The mystery began late in the 19th century: Instead of another invasion during the next drought cycle, the locust completely disappeared over the course of a few years, without any apparent cause.

Jeffrey Lockwood, professor of natural sciences and humanities at the University of Wyoming, set out to reinvestigate the intriguing disappearance of the Rocky Mountain locust, which he calls "the quintessential ecological mystery of the North American Continent," when existing extinction theories proved untenable. This popular account of his quest to solve this cold-case mystery is a synthesis of his and his students' research over several years.

The Rocky Mountain locust was once the most abundant insect on the Great Plains. In years of peak populations, Lockwood calculates, its numbers rivaled bison populations in both biomass and consumption of forage. Before the plains were settled, periodic swarms of migrating locusts were part of the natural rhythm of the grasslands, particularly during years of drought. That situation had changed by the mid-1870s, however, when farmers and ranchers occupied much of the Great Plains. A drought of several years' duration triggered a massive outbreak of locusts that swept over an immense area, destroying much of the agricultural production and bringing famine to many settlers.

The author recounts several vivid eyewitness accounts of the locust invasion and its aftermath: The swarms of countless flying insects looked like dark storm clouds, and they glittered like snowflakes as they descended out of the sky. They arrived in waves from the more northern regions of the plains during July and August, devouring crops in their path and laying eggs in the soil. The farmers tried desperately to save their crops and to drive the locusts off, but with little success because of the huge numbers of insects. Many families had to abandon their homesteads, and thousands more were threatened by famine, with virtually no food left for themselves or their livestock.

Lockwood's account encompasses the homestead era and the politics of early disaster relief efforts by private, state, and federal agencies. Some limited aid came from frontier Army supplies and other sources, but not enough to avert catastrophe: Settlement of the plains was threatened, and the Rocky Mountain locust was thought to be the greatest obstacle to farming this region.

To deal with this emergency, three prominent entomologists—Charles Valentine Riley, Cyrus Thomas, and Alpheus Packard—were named by the federal government to the newly formed Entomological Commission. They were charged to gather all available information on the locust and to find practical methods for its control. (Lockwood's biographical account of Riley, the brilliant but eccentric head of the commission and later the chief entomologist in the US Department of Agriculture, is particularly entertaining. Riley went on to become the nation's foremost economic entomologist and pioneered the intro-

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duction of biological agents for control of introduced pests.) The commission did indeed gather a remarkable amount of detailed information on the ecology, behavior, anatomy, reproduction, and distribution of the locust, and suggested practical ways for the farmers to battle the insects.

Then in the late 1870s, about the time the commission was publishing its work, a wetter climatic cycle brought about a decrease in locust invasions. The locust depradations were expected to rebound in the next drought cycle, but much to the surprise of entomologists, the species disappeared completely. The Rocky Mountain locust is now considered to be extinct.

Several theories to explain the extinction—and one positing that the locust was still alive, masquerading as an extreme migratory form of a common related grasshopper—were put forward over the years, but most have been refuted by Lockwood and other grasshopper specialists through new research and analysis of data. One of the most interesting of these theories was that the ecology of the locust was somehow linked to the great herds of bison, and that the extermination of the latter from most of its range brought about the extinction of the former. These two major and competing grazers had coexisted on the plains for thousands of years, so the idea was advanced that the bison somehow altered the ecology of the grasslands to favor reproduction and survival of the locust. Another theory was that the planting of alfalfa throughout the locust's breeding area in the latter part of the 19th century could have played a role in the insect's extinction; alfalfa, which is palatable to grasshoppers, was shown in laboratory studies to be deleterious to the growth of the insect's immature stages. That the Rocky Mountain locust was a distinct species, and not a migratory form of an extant species, was proved by taxonomic studies on male genitalia and more recently by DNA analysis of specimens recovered from glaciers by Lockwood and his colleagues.

On the basis of a synthesis of the detailed information gathered by the Entomological Commission, settlement records, and other evidence, Lockwood has arrived at a new explanation of the locust's disappearance, which he calls "my habitat destruction theory." He maintains that cattle grazing and homesteaders' cultivation of a restricted region of the plains—the permanent breeding grounds of the insect—during a population recession of the locust in the 1880s may have irreversibly disrupted locust reproduction. Others had shown that grasshopper eggs fail to hatch if the soil they are deposited in is disturbed by plowing or by other means.

The book is replete with odd facts and interesting characters involved in the locust story. (Among them was the Canadian entomologist Norman Criddle, who collected the last live specimens of the Rocky Mountain locust in 1902. He also invented a grasshopper poison bait known as Criddle's Mixture, composed of horse manure, arsenic, and molasses, that was state of the art in grasshopper control in the early days.) Lockwood works into the book a wide range of information, including the biology of grasshoppers and locusts, the history and politics of the homestead era, and his and his colleagues' expeditions to remote glaciers in the Rocky Mountains to collect rare specimens of the extinct locust, which had been preserved in ice.

Moreover, this tale of a unique case of extinction of an insect pest that threatened settlement of the Great Plains is written in an entertaining and often humorous style. It should be of wide interest not only to biologists but also to Western historians and the general reading public.

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IS OUR VIEW OF ANIMAL PHYLOGENY FUNDAMENTALLY WRONG?

The Origins of Larvae. Donald I. Williamson. Kluwer Academic, Dordrecht, The Netherlands, 2003. 264 pp., illus. $99.00 (ISBN 1402015143 cloth).

This book is a revised and enlarged edition of Donald I. Williamson's *Larvae and Evolution: Toward a New Zoology,* published in 1992 (Chapman and Hall). Williamson's goal is to present, and provide evidence for, the hypothesis that "larval forms (or the genes that specify them) have been transferred between groups of animals." Instead of a bifurcating "tree" (cladograms), where major branches once separated do not rejoin, Williamson suggests that animal evolution is in fact reticulate, with hybridization occurring across large sections of the tree. He also argues that animals have hybridized several times with unicellular protists. If Williamson is correct, then our current understanding of animal evolution is fundamentally wrong, and many scientific careers have essentially been wasted. Williamson, now retired, is an honorary research fellow at the University of Liverpool's Port Erin Marine Biology Laboratory; apart from a series of publications on the topic outlined in this book, he has mainly published on Crustacea.

The Origins of Larvae begins with a general introduction in which Williamson defines *larva* as an immature phase of an animal that differs significantly from the adult and must, to become an adult, metamorphose (unfortunately, he does not define what amount of change this metamorphosis amounts to). He then points out that the larvae of some distantly related groups are more similar to each other than are the adults of those groups. The contemporary explanation for this, combined with phylogenetic hypotheses for the various groups, suggests either that there has been convergence in the evolution of larval forms or that

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basic larval forms have been retained as animals have diversified.

Williamson's radical hypothesis is that through cross-fertilization of very different organisms, the whole genome of one animal is added to that of another. However, they do not merge to form a bizarre chimera. Rather, Williamson's idea is that "metamorphosis" is the change from one taxon to another. The implications of this are that the caterpillar larval stage of a butterfly was "gained" by cross-fertilization between a velvet worm (Onychophora) and an ancestral lepidopteran. In fact, he posits that the caterpillar form found in various kinds of insects has been acquired through separate hybridizations with some onychophorans.

The bulk of Williamson's book is a survey of animal adults and larvae and a sweeping range of poorly supported hypotheses as to how larvae were gained in these various animal groups. For example, there is a large group of animals, including segmented worms (Annelida), molluscs, peanut worms (Sipuncula), and ribbon worms (Nemertea), that have a larval form referred to as a trochophore. While some, including myself (Rouse 1999), would suggest that these animals had a common ancestor that had a trochophore, Williamson proposes that the origin of the trochophore in each of these groups was through a hybridization event with a rotifer. Other propositions are that the various larvae found in echinoderms were acquired several different times from hemichordates, and that the zoea larvae found in some shrimps originated from hybridization with mysid crustaceans.

In his earlier book, Williamson suggested that the basic forms of some larvae in eight animal phyla had been transferred from other phyla. In the new book, he now claims that all embryos and larvae were transferred from other taxa, and all transfers can be traced back to animals without larvae. He provides a table to summarize his views, and he offers many other off-the-cuff proposals throughout; there is also a series of line drawings, but, unfortunately, they are often pixelated and of poor quality.

Beyond the fact that this proposal flies in the face of much of what we know about developmental genetics, the simple question this book raises is this: Is Williamson's hypothesis heuristic? In my opinion, the answer is no. Williamson would rather invoke an extraordinarily complicated series of hybridizations across animals than accept that some convergence may have happened in larval forms, or that our understanding of the animal phylogenetic tree is still (rapidly) developing. Williamson sees some of the incongruities from phylogenetic analysis of DNA, particularly the 18S rRNA gene, as providing support for some of his hybridization hypotheses, while ignoring the inference problems that this particular gene can present (Abouheif et al. 1998). Unfortunately, he disregards many of the recent papers on larval forms and the phylogeny of animals, and he takes no note of errors pointed out in a review of the first edition of his book (Strathmann 1993).

Apart from his broad comparative survey of larvae across animals, Williamson's major piece of evidence in support of his thesis is based on an experiment in which he produced hybrids from two very different animals. The frontispiece for *The Origins of Larvae* shows four adult sea urchins that are said to be hybrids of eggs from a tunicate, *Ascidia mentula,* and the sperm of the sea urchin *Echinus esculentus.* Williamson reported on this experiment in his earlier book and provides more details on the procedure here. Unfortunately, he has not repeated it or performed any other experiments, and an elegant paper by Hart (1996) proved that Williamson's hybrids were unlikely to be hybrids at all. Eggs contain numerous mitochondria and a nucleus, both containing DNA. Sperm also contain both of these DNA-bearing components, but the mitochondria found in sperm do not persist after fertilization. Thus an offspring of a sea urchin and a tunicate should have a mixture of parental nuclear genes but only maternal mitochondrial genes. Hart (1996) sequenced both mitochondrial and nuclear genes from one of Williamson's "hybrids" as well as individuals from "pure" *A. mentula* and *E. esculentus.* His results showed that the putative hybrid contained only sea urchin DNA and probably lacked tunicate DNA, thus making a hybrid origin very unlikely. Williamson discusses the paper by Hart (1996), but he rejects it and reiterates that he made no errors.

So, do I think that there are research themes worth following up in this book? No, I don't, not on the evidence presented here. Williamson presented a challenge to scientists in his 1992 book. This was taken up, and his one solid piece of evidence was shown to probably be an error. Williamson provides no other new evidence from the intervening years to back his claims, he has gathered no collaborators, and he provides no new experiments or detailed phylogenetic analyses. Rather, he has simply expanded his theory and rhetoric.

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