EVOLUTION

How Species Arise

Benjamin K. Blackman and Loren H. Rieseberg

One of the most important legacies of the modern synthesis is the articulation of the biological species concept (BSC). In his seminal 1942 work, *Systematics and the Origin of Species* (*1*), Ernst Mayr defined species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Explicitly relating the definition of species to the process of speciation, the BSC has thrived—despite numerous hopeful alternatives—by inspiring a wealth of literature on reproductive isolation and gene flow. The last two decades in particular have brought major advances in molecular genetics, comparative analysis, mathematical theory, and molecular phylogenetics; speciation has consequently matured from a field fraught with untestable ideas to one reaching clear, well-supported conclusions.

Speciation
by Jerry A. Coyne and H. Allen Orr

Sinauer, Sunderland, MA, 2004. 557 pp. $89.95. ISBN 0-87893-091-4. Paper, $54.95, £34.99. ISBN 0-87893-089-2.

Jerry Coyne and Allen Orr's *Speciation* provides a much-needed review of these developments. The exceedingly well-written and persuasive text eschews speculation. The authors instead resolutely develop testable criteria for distinguishing alternative hypotheses about evolutionary processes that may result in similar biological patterns, critically evaluate how theoretical and empirical results meet the burden of proof, and actively confront important caveats and unresolved questions with practical suggestions. It is a testament both to the authors and to the state of the field that the book provides such a robust picture of the origin of species.

The "species problem" that Coyne and Orr consider in the book is how do species arise. More specifically, why do sexually reproducing organisms fall into discrete clusters? With this question in mind, they choose a relaxed version of the BSC that allows for some gene flow among species as long as distinctiveness is maintained. Although Coyne and Orr recognize that the segregation of biological diversity into distinct clusters likely has multiple causes including ecology and history, the book concentrates almost exclusively on reproductive isolation. Given that the bulk of speciation research has focused on the origin of reproductive barriers, the authors' predominant focus is, if nothing else, appropriate for their chosen task. And although the book's subject matter and neontological approach may prove unhelpful to systematists or paleontologists, such readers may find some appeasement in the favorable treatment of species selection and the thorough yet concise appendix that discusses the relative merits and pitfalls of several major species concepts.

Proceeding from their premise that studying speciation is largely synonymous with studying reproductive isolation, Coyne and Orr explore what we know about where, when, and how isolating barriers evolve. Following Mayr, they argue that speciation most often occurs where populations are geographically isolated or "allopatric." The broad range of theoretical conditions under which reproductive isolation evolves in allopatry, experimental evolution of reproductive barriers in isolated laboratory populations, and abundant examples of speciation events associated with vicariance events or isolation on islands all strongly support this position. However, unlike Mayr, Coyne and Orr reach a more favorable though still unenthusiastic view of sympatric speciation, one largely based on the development of theoretical models with increasingly realistic assumptions that indicate sympatric speciation could occur. They find empirical data to be less compelling: only three case studies not involving polyploid or hybrid speciation meet their criteria for a biogeographic and evolutionary history that makes an allopatric phase highly unlikely.

Evidence for allopatry. These three congeneric Pacific wrasse (top to bottom: *Halichoeres trimaculatus*, *H. margaritaceus*, and *H. hortulanus*) were painted for David Starr Jordan and Alvin Seale's *The Fishes of Samoa* (*5*) by the Japanese artist Kako Morita. (Morita's work was published with the help of Theodore Roosevelt, who interceded after a government committee ruled the plates were too expensive to print.) Jordan argued that geographical barriers were required for speciation.

An examination of when and how isolating barriers evolve forms the core of *Speciation*. Far from being a dry catalog of mechanisms and well-known examples, these chapters offer engaging discussions that aim to sharpen how we define, detect, and measure isolating barriers; challenge us to decipher the evolutionary rather than current importance of these barriers; and synthesize evidence regarding their genetics and evolution. The treatment of mechanical isolation is an often-entertaining read, and the overall attempt to outline and then disentangle how natural and sexual selection may act to promote nonecological or behavioral forms of isolation is methodical and enlightening.

Speciation convincingly presents evidence for several once-unpopular theories that have returned to dominate current thinking. Most important among these is the primacy of natural and sexual selection over drift in driving speciation. Signatures of positive selection on genes involved in postzygotic isolation and reproductive proteins as well as experimental evidence from both the lab and field connect adaptation and sexual selection to reproductive isolation. Another major finding is the congruence of the Dobzhansky-Muller model for the evolution of postzygotic isolation with the genetics of hybrid incompatibilities in many natural systems. In contrast, classical models of chromosomal speciation remain unpopular. Instead, chromosomal rearrangements are now cast as facilitators, rather than causal agents, of reproductive isolation because reduced recombination within these regions restricts gene flow, thereby enabling the accumulation of selected differences and hybrid incompatibilities.

The authors take cautious views on controversial questions like reinforcement, sympatric speciation, and diploid hybrid (or "recombinational") speciation. For al-

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though recent theoretical advances demonstrate each phenomenon can occur under a nontrivial set of conditions, conclusive empirical evidence that they occur in nature only exists for the third process. Even so, the authors believe comparative analyses and further case studies will prove fruitful avenues for determining if and how often these processes operate in nature.

Coyne and Orr, who are *Drosophila* population geneticists at the University of Chicago and the University of Rochester, respectively, provide remarkably lucid explanations of speciation phenomena in other groups of organisms, alleviating prepublication fears that the book would be dominated by flies. Their discussion of polyploidy, for example, is perhaps the best review of a predominantly botanical literature by zoologists. Treatments of other plant-related topics like mating system isolation or hybridization are insightful as well, but may raise eyebrows. For instance, unlike most botanical discussions of mating system evolution (*2*), Coyne and Orr argue that the shift from outbreeding to selfing is not a kind of reproductive isolation because gene flow is reduced as much within as among taxa. Likewise, botanists may find an otherwise excellent treatment of recombinational speciation to be tilted toward the evolution of postzygotic barriers through hybridization as opposed to the contribution of new hybrid gene combinations to ecological differentiation and species establishment. Lastly, the authors downplay increasingly widespread phylogenetic evidence of cryptic introgression or hybrid speciation in the plant, and now even animal, literature.

The book is a rich and thorough review, critique, and synthesis of recent literature that is sure to become a classic read for anyone interested in speciation. As the authors' purpose is to reflect on the value of various approaches to evolutionary questions and point out areas ripe for further investigation, *Speciation* is not a textbook that pauses to give broad introductions; many methods and terms are referred to in passing well before being defined in later chapters. Despite this, Coyne and Orr's descriptions and logical evaluations of theoretical and empirical work are remarkably clear and straightforward, a considerable achievement because the book covers material from complicated mathematics to rigorous molecular genetics. An excellent book for a graduate seminar, *Speciation* should also be interesting and accessible to scientists from diverse backgrounds.

Notably, many important results that support Coyne and Orr's conclusions in the book have only been published in the last year. For instance, two of the four genes known to underlie hybrid incompatibilities were identified only recently, and their analysis adds great support to the role of selection over drift in the evolution of these barriers (*3*, *4*). With such research ongoing, and now with *Speciation* as a guide, the authors' wish that their book "will stimulate younger scientists to pursue their own work on speciation" will certainly be fulfilled.

References

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EVOLUTION

Hunting for Origins

R. Andrew Cameron

The term "Cambrian explosion" is really a metaphor because the phenomenon named here is neither an explosion nor did it happen in the Cambrian. Yes, there appeared in Cambrian rocks (Chengjiang formation) dated 520 million years ago representatives of almost all major groups of animals. But newly estimated rates of change in protein and DNA sequences calibrated to well-dated fossils set the divergences of these major groups to a time well before the Cambrian (*1*). Given this apparent contradiction, many who study animal evolution reckon that the early animals in these lineages were small and soft-bodied, resulting in a poor fossil record. Perhaps the conditions of the Cambrian environment allowed the rapid appearance of hard skeletal parts, greatly favored fossilization, or both.

On the Origin of Phyla
by James W. Valentine
University of Chicago Press, Chicago, 2004. 638 pp. $55, £38.50. ISBN 0-226-84548-6.

In this context James Valentine (an emeritus professor of integrative biology at the University of California, Berkeley) delivers a new book aimed at explaining the origin of the highest taxonomic groups of metazoans, *On the Origin of Phyla*. Considering the great variety of existing animals and the explanations for their elaboration, this is no easy job. There has been a steady trickle of books, some best sellers, offered to incorporate Darwinian evolution into a synthesis explaining the origin of higher taxa, but none have come to represent the field the way that

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