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.

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On the Origin of Phyla
by James W. Valentine
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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.

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

The reviewer is in the Division of Biology, Mail Code 139-74, 1200 East California Boulevard, California Institute of Technology, Pasadena, CA 91125, USA. E-mail: acameron@caltech.edu



An odd ecdysozoan. Phylogenetic analyses using morphological traits place *Opabinia* and the anomalocarids in a clade basal to Arthropoda or Onychophora. But an alternative interpretation of the imputed lobopodial structures in this predator from the Burgess Shale suggests it is a stem-group arthropod. (*6*)

Darwin's *The Origin of Species* has. Perhaps this is due in part to the modern fragmentation of studies in biology and geology into specialized areas, which must be integrated to build an explanation, for as Valentine points out, ecologists have sought environmental explanations, developmental biologists have offered mechanisms for achieving variety of form, and so on. But there has recently been a convergence of new data from several areas of research that is especially relevant to these questions. Witness the new finds of fossil pre-Cambrian embryos from the Doushantuo Formation of southwest China, estimated to be 40 to 55 million years older than the base of the Cambrian (*2*); the maturing consensus emerging from molecular phylogenetics; and advances in the comparative molecular biology of development. Valentine has organized the book into sections that reflect these converging areas of study.

The question of when and how higher taxonomic groups like phyla evolved differs markedly from the one Darwin addressed 145 years ago in *The Origin of Species*. It is not simply different in scale but also in quality. Although it is somewhat easier to see how changes in single genes can lead to differences among species that render some more capable of surviving in particular environments, it is more difficult to account for the many changes that lead to entirely different bodyplans as a simple accumulation of single-gene effects. For example, marine stickleback fishes possess bony plates and spines that presumably prevent predation, while their freshwater relatives show a loss of this armor through changes that can be attributed to a single gene (*3*, *4*). However, entire organ systems or embryonic germ layers, features that distinguish higher taxa, can be explained in terms of the gene regulatory networks whose architecture is hardwired into the genome. The simplest of these networks leads to the specification of differentiated cell types, something like the cell morphotypes that Valentine defines.

Networks that underlie morphogenetic pattern formation programs defining clade-specific body parts and bodyplans are more complex (*5*). These networks are assembled from cis-regulatory interactions that operate at the genome level. They represent the heritable process by which the genome specifies the organism. From the structure of these networks emerge obvious ways that major changes can happen through changes in the links among regulatory genes like transcription factors. For instance, a morphogenetic program may evolve with relatively minimal changes to establish a new spatial domain of expression for a cell-differentiation program, and the resultant animal has a new body part. Although Valentine skirts around this mechanistic model for the evolution of developmental programs in his definitions of the hierarchy of genomes, genes, and their possible sources of change, he does not incorporate a molecular model in his final synthesis.

The intellectually greedy might flip to the back of the book, skipping over the sections on the evidence for the origins of metazoan phyla and the descriptions of the phyla themselves, even though these compilations (particularly the section on the fossil record) are the work's strong points. In the third section, Valentine paints his view of the evolution of the phyla, with an emphasis on the work of morphologists and paleontologists (a portion of which he contributed). He fleshes out a scenario of variation and extinction that unites the detailed descriptions of the first two sections. The pictures he delineates here reveal correlations uniting different levels of biological organization, but absent are firm statements about causal mechanisms from which predictions could be made. Only in the section's closing pages are genomes considered.

In view of the volatility of the ideas and the controversy that still exist in this particular area of evolutionary biology, one might argue that it is too early to explain the causes of the origin of phyla. But as Valentine aptly points out, the time will never be exactly right: there are always more information to incorporate and more ideas to organize. Though too heavy with data to be carried in the kit bag, *On the Origin of Phyla* is a likely candidate for the bookshelves of those who hunt for pre-Cambrian fossils or the historical patterns in DNA sequences.

References and Notes

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