Reviews

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SPECIES CONCEPTS AND SPECIATION

Speciation and its Consequences.—Daniel Otte and John A. Endler (eds.). 1989. Sinauer Associates, Inc., Sunderland, Massachusetts. xiii + 679 pp. cloth \$50.00, paper \$29.95.

Speciation and its Consequences is the first book in recent years to deal largely with species concepts and the process of speciation. It is the outgrowth of a symposium held at the Academy of Natural Sciences of Philadelphia in November, 1987. Twenty-five chapters are organized into six sections (and a conclusion): concepts of species, genetic structure of species boundaries, effects of population structure on speciation, biogeography and ecology of speciation (background and theory; empirical studies), and evolutionary consequences of speciation. The three stated purposes of the book are (1) to illustrate "the inhomogeneity among diverse taxa in their patterns and processes of speciation and differentiation," (2) consider "some of the ecological, paleontological, and systematic consequences of different patterns of speciation," and (3) to present "the extreme diversity of concepts and viewpoints on the subject." Each of these goals was achieved. Like most symposium volumes, there are chapters that provide general reviews and others that treat specific topics or organisms. Likewise, the quality of the individual chapters varies considerably, but most are well-written and interesting (unfortunately, all of those chapters cannot be mentioned here). The book has a moderate number of typographical errors. It is separately indexed by author and subject, and the cover illustration is exquisite.

In an attempt to develop a species concept that applies to all organisms, Templeton introduces the cohesion species concept in the first chapter: "the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability" (p. 25). But this concept does not appear to differ substantially from the biological species concept when applied to sexually reproducing organisms, where genetic exchangeability (or its absence) is more important than demographic exchangeability (p. 21). The idea of a universal species concept is challenged by Endler in a later chapter, who argues that "it is unproductive, and often positively misleading, to apply one species concept to all species or to answer all questions" (p. 644).

In the second chapter, Cracraft asserts that the biological species concept cannot define discrete evolutionary units because it is based entirely on reproductive cohesion, which "manifests a primitive morphogenetic organization" (p. 34). He introduces the phylogenetic species concept as "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent" (p. 34-35). Such a definition by itself would lead to taxonomic chaos if actually applied, because literally thousands of phylogenetic species could be defined within a single "biological" species. However, Cracraft later points out (p. 35) that "the phylogenetic species concept, as all species concepts must, recognizes the critical importance of reproductive cohesion." Most of the examples offered by Cracraft as failures of the biological species concept in recognizing "evolutionary units" are subspecies of birds showing some degree of hybridization. But the biological species concept is not normally applied so rigidly as to exclude hybridizing taxa. Like Cracraft, many systematists would recognize those taxa as species. However, it is unrealistic to believe that any species concept will always lead to objective decisions regarding species status. Speciation is a dynamic process and we should expect borderline cases. The phylogenetic species concept thus appears to be nothing more than the biological species concept as it is normally applied in systematics: monophyletic groups that show reproductive cohesion and which are reproductively isolated (completely, or nearly so) from other such groups.

Hybrid zones and their relationship to speciation are discussed in several chapters. Hewitt reviews the hybrid zone literature and concludes that "many species may be divided into compartments among which gene flow is greatly reduced." This view is supported by Harrison and Rand, who suggest that there is a fundamental difference between steep multilocus clines and what they call mosaic hybrid zones. Wake et al. provide further detailed analyses (from their previous papers) of hybrid zones in an unusual "ring species" of salamander. Butlin concludes that the once popular theory of reinforcement (selection against hybrids) is possible but the necessary conditions are so restrictive that it must be rare. However, Diehl and Bush argue in a later chapter (p. 361) that the conditions necessary for reinforcement are not as stringent. Coyne and Orr elaborate a model based on pleiotropy that explains two common patterns: (1) the inviability or sterility of heterogametic offspring in crosses between two animal races (Haldane's rule), and (2) the large effect of the X chromosome on hybrid inviability or sterility.

Sympatric speciation is discussed in several chapters, with Tauber and Tauber concluding that it may be an important mechanism in a large number of insect groups (references were excessive, comprising nearly one-third of this chapter). In a chapter that

was nicely developed from a poster at the symposium, Lynch outlines a method of quantifying the potential cases of allopatric versus sympatric speciation using distribution and phylogeny. He finds that sympatric speciation may be more frequent (6%) than is commonly recognized, but is still a minor mechanism. Although Lynch draws his examples from vertebrate taxa, Barrett concludes in another chapter (p. 279) that allopatric speciation also is the most common mode in plants.

Taxon cycles are discussed in two chapters. In one, Roughgarden and Pacala describe a situation involving three pairs of West Indian lizard species. Although the authors maintain that the taxon cycle is real, they offer some very convincing counterarguments. Some errors that I noted were: the categories

of species group and series are reversed in their classification (p. 405) compared with normal usage, the Bahamas do have taxonomically distinct populations (four species) of *Anolis* (p. 406), and a subspecies is raised to species status by mistake (p. 407).

In general, this is a high-quality volume that should be of interest to most evolutionary biologists. It could provide an ideal subject of discussion for a graduate course, and an up-to-date reference source for the many different species concepts currently debated in the literature. Above all, this book brings together a healthy diversity of viewpoints and ideas on speciation that will certainly stimulate further research.

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