Reviews

Syst. Biol. 41(2):264–266, 1992

Principles of Systematic Zoology, 2nd edition.—Ernst Mayr and Peter D. Ashlock. 1991. McGraw-Hill, New York. xx + 475 pp. $39.95 (cloth).

In 1969, Mayr's *Principles of Systematic Zoology* was probably the best systematic text and reference book available (Michener, 1969), and it retained a prominent place among such works for years after its publication. When first published, it was current, authoritative, and comprehensive, and even more than 20 years after its heyday I continue to use my copy frequently. Although several excellent books on the subject have been published subsequently, only Wiley's (1981) *Phylogenetics* serves as many different purposes. But a lot has happened since 1969. No book about systematics published that long ago is current today. Consequently, the publication of a revised edition of *Principles of Systematic Zoology* raises hopes of a new standard for the field.

The new edition has been reorganized and, compared with its predecessor, places greater emphasis on concepts and theory. It consists of 14 chapters, the first of which is an introduction to the science of taxonomy, including a brief history and a discussion of the role of taxonomy in biology. The remaining 13 chapters are divided among three major sections. The first two of these sections, which were devoted to principles and methods in the first edition, are now devoted to "Microtaxonomy," dealing with species and infraspecific categories, and "Macrotaxonomy," dealing with higher taxa. The last major section, titled "Methodological Issues," covers issues relating to systematic collections, taxonomic publications, and the rules of zoological nomenclature. Also included are a glossary, a bibliography, and a combined subject and author index. The volume is reasonably well produced, with only a moderate number of typographical errors, and its size is comfortable in the hand.

The section on microtaxonomy covers a diversity of topics, including species concepts, the ontology of species, infraspecific categories, population structure, different kinds of variation within species, methods for comparing population samples, and speciation. Given Mayr's prior writings on species, it is not surprising to find strong advocacy for the biological species concept. I was, however, surprised to find logical inconsistencies reflecting incomplete acceptance of that concept. For example, Mayr and Ashlock seem unable to decide whether asexual organisms form species (p. 32), and at one point they suggest that reproductively separate entities that are not distinct in other respects should not be recognized as separate species (p. 93). The authors admit their bias concerning species concepts (p. xix), but that does not excuse their failure to mention one concept that has received considerable attention in the recent systematic literature, namely, the phylogenetic species concept (e.g., Cracraft, 1987; Mishler and Brandon, 1987; Nixon and Wheeler, 1990). If nothing else, phylogenetic perspectives on the species problem have drawn attention to the fact that interbreeding is not the only interesting phenomenon that occurs at the microtaxonomic level (de Queiroz and Donoghue, 1988).

Mayr and Ashlock also dismiss too hastily Paterson's (e.g., 1985) critique of the biological species concept. Paterson called for replacement of what he views as the traditional version of that concept, which he calls the isolation concept, with an alternative that emphasizes mate recognition instead of reproductive isolation. He has attempted to discredit the biological species concept because of a supposed tie to the concept of reinforcement, the idea that characters responsible for the absence of interbreeding between the organisms of different species ("isolating mechanisms") have evolved as a result of selection against hybrids. In Mayr and Ashlock's defense, even if Paterson is correct in concluding that reinforcement is unimportant in the evolution of intrinsic reproductive barriers, the biological species concept need not be replaced. Regardless of historical associations between the concepts of biological species and reinforcement, the two are not tied logically to one another. As a general species concept based on interbreeding, the biological species concept can be adopted regardless of whether intrinsic reproductive barriers result from reinforcement or, as Paterson believes, they are by-products of the adaptation of mate recognition systems to different environments.

Nevertheless, other aspects of Paterson's critique deserve consideration. For example, according to Mayr and Ashlock, the term "*species* is a relational term like the word *brother*" (p. 39). This proposition implies that it is nonsensical to speak, even hypothetically, of the existence of only a single species. In contrast, Paterson's emphasis on recognition, rather than isolation, led him to reject the idea that the term "species" is relational (e.g., Paterson, 1984). Paterson's position is more congruent with the view, endorsed by Mayr and Ashlock themselves (p. 40), that species are "individuals" (composite wholes). Organisms form composite wholes called populations as a result of interbreeding with one another, not as a result of avoiding interbreeding with the organisms of other populations.

The section on macrotaxonomy consists of chapters devoted to general principles, taxonomic characters,

phenetics, cladistics, evolutionary classification, and numerical methods of phylogeny inference. Mayr and Ashlock favor evolutionary classification over phenetics and cladistics, which is to be expected, but their bias becomes too great when they define certain general terms, such as "biological classification" and "taxon," in a way that precludes the alternative approaches. In any case, the chapters devoted to alternative macrotaxonomic approaches reveal much, both stated and unstated, about how Mayr and Ashlock perceive the alternatives. The chapters on phenetics and cladistics are largely critiques. Unfortunately, Mayr and Ashlock's characterizations of those approaches are inaccurate or outdated. For example, they attribute to pheneticists the claim that grouping according to similarity will automatically produce a phylogenetic classification, and they continue to characterize the cladistic approach to classification as being concerned only with the branching component of phylogeny. Regardless of these problems, the discussion of phenetics receives only 11 pages, whereas cladistics gets 36. Furthermore, the chapter on evolutionary classification (32 pages) is devoted in a large part to continuing the argument against cladistics. Mayr and Ashlock apparently perceive cladistics as posing a serious threat to their preferred approach.

The arrangement of the book into sections devoted to microtaxonomy and macrotaxonomy is supposed to reflect the insight "that taxonomy at the species level is very different from taxonomy at the level of higher taxa" (p. xviii). Although a difference certainly exists, the way in which the difference is conceptualized by Mayr and Ashlock stems from their view of macrotaxonomy, which is currently being replaced. Mayr's conservative stand on this issue is ironic, for in many ways the view that he so vigorously resists is the macrotaxonomic counterpart of a microtaxonomic perspective championed by Mayr himself. An important part of what came to be known as the New Systematics, of which Mayr was one of the principal architects, involved replacing the view that species are groups of similar organisms with the view that species are populations—entities that result from interbreeding. Analogously, what has come to be known as cladistic classification, which Mayr and Ashlock persistently oppose, consists largely of replacing the view that higher taxa are groups of similar organisms with the view that higher taxa are clades—entities resulting from common descent.

The parallels between these two developments are striking. In each case, the definition of a taxonomic term ("species" and "monophyletic taxon") was reformulated so that it would refer to a class of entities resulting from a particular biological process (interbreeding and common descent). In each case, supposedly homogeneous taxa that had been recognized by earlier workers (morphospecies composed of separate interbreeding units and homogeneous but paraphyletic higher taxa) were rejected if they did not fit the new definitions; correspondingly, heterogeneous taxa that might not have been recognized by previous workers (polymorphic species and heterogeneous monophyletic taxa) were accepted if they fit the new definitions. In each case, taxa (those entities given names) were seen to be composite wholes—albeit of different kinds (populations and clades)—rather than classes based on shared organismal characters. And in each case, the new concept of taxa brought a new theoretical context to comparative biology (population thinking and tree thinking) (O'Hara, 1988). From the viewpoint of developing a phylogenetic system of taxonomy, the changes involving the higher taxa are particularly important in that they grant the concept of evolution a more important role in taxonomy. No longer are taxa based on shared characters and only interpreted after the fact as having been produced by evolution; evolution is now fundamental to the very concept of taxa (de Queiroz, 1988).

Although Mayr and Ashlock have made the conceptual shift with regard to species, they have not yet done so for higher taxa. For example, they continue to view higher taxa explicitly as classes (p. 113). They view the entire endeavor of macrotaxonomy as a problem of how best to classify organisms *"according to their similarities"* (p. 115), rather than a question of inferring which organisms or species are descended from a particular common ancestor. For Mayr and Ashlock, macrotaxonomy is a two-step process (p. 243). In the first step, species are sorted into relatively homogeneous groups that reflect their overall similarity. Only after taxa have been formed according to this nonevolutionary criterion are they tested for consistency with evolution, that is, for monophyly in the broad sense. Thus, in Mayr and Ashlock's approach to macrotaxonomy, taxa are based on similarity, and evolution is granted only a relatively weak kind of "veto power." Calling this approach "evolutionary classification" is misleading because it is not the approach that grants the most important role to the concept of evolution.

The third section is titled "Methodological Issues," but such issues are also discussed in both of the previous sections. The section on microtaxonomy covers a variety of simple methods, but several more complicated ones are neglected, including some that are currently in wide use. Ordination techniques, such as principal component analysis and multidimensional scaling, are only mentioned, and other recently developed methods for the analysis of geographic variation (e.g., Sokal, 1983) are not mentioned at all. In the section on macrotaxonomy, the chapter on methods of phylogeny inference is better, possibly as a result of its having been "completely revised by David Maddison" (p. xx). The assortment of authors, however, makes for a heterogeneous presentation, combining straightforward descriptions of methods with digressions on matters such as use of the term "character" versus "signifer."

The chapters in the third section are in some ways the most useful in the book, partly because they cover topics lacking in most other books on systematics. Compared with the preceding chapters, they also exhibit a high ratio of information to disputation, and despite the title of the section, at least the chapter on nomenclature contains a good deal about principles. Here Mayr and Ashlock discuss topics often taken for granted or otherwise neglected, such as the importance and workings of collections, different kinds of

taxonomic publications, and principles of nomenclature. Although some of the practical matters covered seem out of place in a book on the principles of systematics (e.g., how to prepare a manuscript for publication), even these will be appreciated by the beginning student.

The literature references are both a strength and a weakness of the book. The bibliography is extensive (30 pages), although the text citations vary from thorough to less than adequate, depending on the subject. Mayr and Ashlock deliberately did not replace some of the literature cited in the 1969 edition with newer references "to prevent excellent older papers from being forgotten" (p. xix–xx). Including newer references does not, of course, necessitate the replacement of older ones, but in many cases newer references were not added.

Mayr and Ashlock's book has major strengths and weaknesses. The broad range of topics covered and the general organization are things that an instructor looks for in a textbook for use in an introductory course on systematic biology. However, to cover certain important topics even minimally, the text would have to be supplemented by additional readings. Given the exciting developments in macrotaxonomy that have occurred during the last 20 years, Mayr and Ashlock's conservative position on this topic gives the book an anachronistic character; this is perhaps its most disappointing feature from the perspective of potential use as a textbook. As a reference book, its broad scope and extensive bibliography are assets, but coverage of certain topics and recent literature could have been better. Times change, and so must new editions of books if they are to regain their place of prominence. Although the second edition of *Principles of Systematic Zoology* is useful both as a textbook and a reference, I doubt that its importance will come close to matching that of the first edition.

R. J. O'Hara and K. I. Warheit provided valuable comments on a draft of this review.

References

CRACRAFT, J. 1987. Species concepts and the ontology of evolution. Biol. Phil. 2:329–346.

DE QUEIROZ, K. 1988. Systematics and the Darwinian Revolution. Phil. Sci. 55:238–259.

DE QUEIROZ, K., AND M. J. DONOGHUE. 1988. Phylogenetic systematics and the species problem. Cladistics 4:317–338.

MAYR, E. 1969. Principles of systematic zoology. McGraw-Hill, New York.

MICHENER, C. D. 1969. Review of *Principles of Systematic Zoology*, by E. Mayr. Syst. Zool. 18:232–234.

MISHLER, B. D., AND R. N. BRANDON. 1987. Individuality, pluralism, and the phylogenetic species concept. Biol. Phil. 2:397–414.

NIXON, K. C., AND Q. D. WHEELER. 1990. An amplification of the phylogenetic species concept. Cladistics 6:211–223.

O'HARA, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Syst. Zool. 37:142–155.

PATERSON, H. E. H. 1984. The recognition concept of species. South Afr. J. Sci. 80:312–318.

PATERSON, H. E. H. 1985. The recognition concept of species. Pages 21–29 *in* Species and speciation (E. S. Vrba, ed.). Transvaal Museum, Pretoria.

SOKAL, R. R. 1983. Analyzing character variation in geographic space. Pages 384–403 *in* Numerical taxonomy (J. Felsenstein, ed.). Springer-Verlag, Berlin.

WILEY, E. O. 1981. Phylogenetics. John Wiley, New York.

Kevin de Queiroz, Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.

Syst. Biol. 41(2):266–267, 1992

Sex and Death in Protozoa. The History of an Obsession.—Graham Bell. 1988. Cambridge University Press, New York. 199 pp. $47.95 (cloth).

Sex, as imagined by most biologists, is a reproductive process that begins with recombination and reduction during meiosis and gametogenesis, wanders through the vagaries of mating, and concludes with syngamy, restitution of the genome, and the production of offspring. Yet, strictly speaking, sex need only involve the exchange of genetic material between individuals; as such, it seems to be an essential fact of life for nearly all species. Even so minimally construed, sex appears to be genetically and demographically an expensive proposition with respect to asexuality, hence explaining its persistence has been termed "the queen of problems in evolutionary biology" (Bell, 1982).

In his first book on the evolution of sex, Graham Bell (1982) began the task of unraveling the components, consequences, and functions of sex, largely in the context of metazoans. He primarily sought an ecological scenario that would give individuals that engage in sexual reproduction a sufficient selective advantage over those engaged in asexual propagation to overcome (or at least balance) the genetic and demographic costs of sex. His conclusion, one that remains favored (but is by no means a consensus), is that spatial or temporal variation in selective regimes can produce the necessary advantage over ecological time.

In *Sex and Death in Protozoa*, Bell remains true to the challenge of understanding how sex is maintained (rather than how it originated) but shifts his attack on the problem in two important respects. First, rather than seeking an explanation that suffices at the level of the individual and in ecological time, he considers higher levels of selection over longer time spans to explain the prevalence of sex. Second, he focuses on ciliate protozoans, in which sex is generally unencumbered by recombination, gametogenesis, and reproduction; rather, there is only a reciprocal exchange of some genetic material (the micronucleus) between partners, a process termed conjugation. The micronucleus itself is not somatically active; it primarily directs the course of replication of the macronucleus, which in turn regulates vegetative function. From