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Putting Protozoa in Their Place

The Illustrated Guide to the Protozoa. 2nd ed. John J. Lee, Gordon Leedale, and Phyllis Bradbury, eds. Allen Press, for the Society of Protozoologists, Lawrence, KS, 2002. 1423 pp., illus. $125.00 (ISBN 1891276220 paper).

This massive, beautifully produced, two-volume work is a compendium of information on the structure and diversity of groups of unicellular eukaryotic organisms that have traditionally been included among the protozoa. It will be of value to researchers working on protists, to teachers of courses on protists or eukaryote diversity, and to libraries. This book, the most extensive compendium of its kind, greatly expands the first edition's treatment of many groups.

The concept of protozoa has little meaning at present other than as a general category for unicellular eukaryotes that are either nonphotosynthetic or both photosynthetic and motile. The traditional taxonomy of protozoa, based on the categories amoebae, flagellates, ciliates, and sporozoa, has almost completely broken down, and a new phylogenetic taxonomy is struggling to be born. These volumes reflect the uncomfortable state of the art. The rather bewildering array of 44 chapters on different groups of organisms is presented in alphabetical order within broad categories (alveolates, stramenopiles, amoebae, and flagellates), with no attempt to place related groups adjacent to one another or to fit them into a higher versus lower evolutionary sequence. As editor John Lee notes on the first page, "While this order of chapters may disappoint some readers, there are sufficient gaps in our knowledge to leave the relatedness of many groups in doubt. Others will respect our decision to defer judgment until a clearer overall picture emerges from unfolding studies."

This unsettled state of affairs is the consequence of the 40-year revolution—extensive but incomplete—in the small world of evolutionary and systematic studies on protists (unicellular eukaryotes that encompass the traditional categories of protozoa) and unicellular algae and fungi. These organisms, from which all multicellular plants, animals, and fungi have arisen, comprise the basal radiation of eukaryotic life and encompass the vast majority of eukaryotic diversity at the cellular level.

This revolution began in the 1960s with electron microscopic studies on protists, which revealed a wealth of hitherto unrealized structural detail and diversity. These studies revealed the remarkable consistency of basic cellular architecture within most protist groups (for example, in the structures of mitochondrial cristae, of flagella and their associated microtubular bundles and striated fibres, and of chloroplast envelopes, thylakoids, and photosynthetic pigments in photosynthetic forms). On the basis of these similarities, a number of researchers argued that the traditional classification of these organisms was both inadequate and artificial, and that an integrated approach to the study of unicellular eukaryotes was needed, independent of their formal plant, animal, or fungal taxonomic affinities.

The second major idea propelling the change in thinking about protists arose from the realization that mitochondria and chloroplasts represent symbiotic prokaryotes that have become integrated into their host organisms. This finding was important, because it made biologists consider the relationship between photosynthetic and nonphotosynthetic organisms in a new way. If chloroplasts could be acquired either as primary symbionts from cyanobacteria, or through secondary symbiotic events from other chloroplast-containing protists, then the evolutionary relationships between photosynthetic and nonphotosynthetic groups could be much more intimate and varied than biologists had previously supposed.

While these factors led to a breakdown of the traditional view of protozoa and algae in the 1970s, there was no clear scheme to take the place of the traditional system, and so most texts and monographs continued to repeat the traditional systematic structures, with only minor changes. For example, the first edition of the *Illustrated Guide to the Protozoa,* published in 1985, reaffirmed the traditional division of protozoa into the four major groups—amoebae, flagellates, ciliates, and sporozoa—in use since the 1880s, despite the widespread feeling of many, if not most, workers in the field that this view was both artificial and inadequate.

Although structural studies made it possible to establish substantial numbers of structurally consistent eukaryotic groups, working out the relationships among these groups was problematic. Some early linkages between groups (e.g., euglenoids and kinetoplastids) were suggested in the early 1970s solely on the basis of structural features of the organisms, but deducing the relationships between most of the major assemblages of organisms requires a combination of gene sequence information and structural features. A lot of this information has come from ribosomal DNA sequences, and in the last few years an increasing number of genes (such as actin, EF-1, EF-2, tubulins, HSPs) have been used to provide phyletic information about relationships between protist groups. Consequently, although much work remains to be done to fully illuminate the relationships among all of the diverse protist groups, the phyletic structure of large clusters of eukaryotic groups—alveolates, euglenozoa, opisthokonts, and heterokonts—has been established. These groupings will undoubtedly form the basis of a new taxonomy of protists when one emerges.

In the meantime, D. J. Patterson, in his excellent essay in the introductory section of the *Illustrated Guide to the*

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Protozoa, outlines the ways in which the traditional protozoan taxonomic scheme has fallen apart. Patterson also describes the problems that researchers face as they try to develop a modern replacement for the traditional scheme.

Other chapters typically include an introductory essay describing general features of the group, its taxonomy and evolution, keys to orders and families, and a brief synopsis of each genus, with references to descriptions in the primary literature and, often, an illustration. They focus on a mixture of larger, apparently monophyletic, assemblages (alveolates, stramenopiles) where possible, and rather arbitrary clusters of groups based on more or less traditional categories (amoeboid protists, flagellated protists). While this combination of fairly well-established monophyletic assemblages of organisms and other somewhat artificial groupings is not particularly satisfying, it represents a conservative interpretation of the state of the art and gives biologists a good overview of the work needed to resolve the many remaining problems of eukaryote phylogeny.

The chapter bibliographies have generally been greatly expanded: A quarter to half of the references are to works that appeared after the publication of the first edition of the guide. For example, the chapter on apicomplexa has 472 references; the earlier publication had 118.

The endpapers consist of a useful list of groups with their common names and an indication of how they fit into the traditional grouping of amoebae, flagellates, sporozoa, and ciliates. It is unfortunate that botanical synonyms are not included for groups in the botanical classification scheme.

The chapters of this second edition are more consistent in depth and treatment than are those of the first edition; virtually all sections of the new version have been brought up to the very high standard of the best sections of the earlier one.

The vast majority of the thousands of figures in this work are of very high quality. However, there are some losses. In the ciliate chapter, the drawings associated with the keys have lost resolution relative to those in the first edition. They look like photocopies of photocopies. Clearer drawings are found with the descriptions of the genera.

It is perhaps unfair to ask for more from a work that already is so voluminous, but I would have liked to see a collection of phyletic trees based on DNA sequence information for each of the major groups. Obviously, the trees currently available cannot provide the last word on the relationships among protist groups, yet they do contain a lot of information that would strongly complement the information in this marvelous compilation.

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