EVOLUTION

A Better View of Eras of Life

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Principles of Social Evolution
by Andrew F. G. Bourke
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Many biology classrooms and lecture theaters are adorned with posters that depict the history of life on Earth as a succession of different taxonomic groups. These posters tell the standard story of the age of invertebrates giving rise to the age of fishes, which gave rise to the age of reptiles, which gave rise to the age of mammals, which culminates with us at the pinnacle. In *Principles of Social Evolution*, Andrew Bourke makes an excellent case for replacing this history, which is biased toward relatively humanlike organisms, with a hierarchical approach based on how organisms come together to form higher-level collectives, tracing the steps from genes to complex societies. He has written a superb book, one that should change how we teach and think about life on our planet.

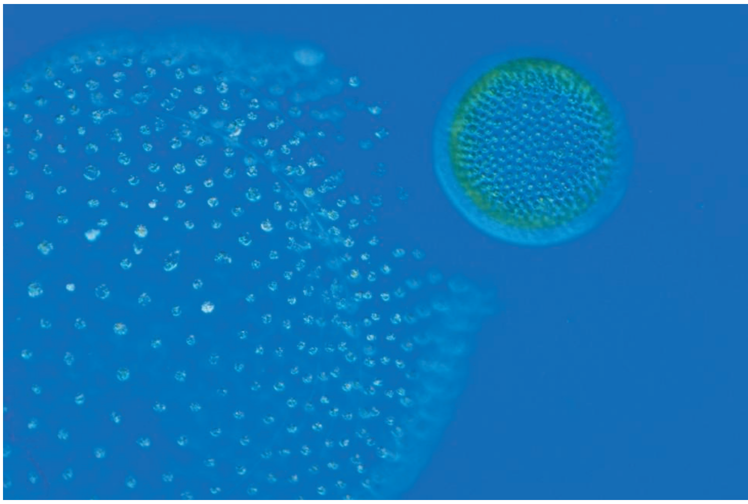
Bourke, an evolutionary biologist at the University of East Anglia, takes a two-pronged approach. First, he builds on previous work by other researchers (*1*–*3*) to emphasize how evolution has involved a number of major transitions, through which a group of individuals that could previously replicate independently come together to cooperatively form a new, more complex form of individual that can only replicate as a whole. Genes joined to form genomes, prokaryotic cells incorporated protobacteria as mitochondria to become eukaryotic cells, single-celled organisms joined together to become multicellular organisms, multicellular organisms became eusocial societies, and multicellular species joined with either unicellular species or other multicellular species to become interspecific mutualisms. Over several chapters, the author compares and contrasts these transitions, dissecting them into three principal steps through which social groups are initially formed, maintained, and then transformed into the new level of individuality.

Second, Bourke uses Hamilton's inclusive fitness theory to provide an overarching conceptual framework to explain all of these major transitions. This elucidates how the cooperation that drives these transitions is driven by either a direct benefit to the individual concerned or an indirect benefit from helping relatives. The beauty of this approach is that it allows enlightening comparisons across the transitions. Particularly lucid, and worth the price of the book alone, is Bourke's exposition of how the factors shaping the evolution of complex multicellular organisms and eusocial societies are remarkably similar. Both instances involve social groups that develop from a single propagule (a single cell that then reproduces clonally or a single monogamously mated female), the same type of social group formation (offspring stay with parents), and a collection of overlapping and nonoverlapping ecological factors (such as defense against predators).

As well as offering a good explanation for the major transitions, Bourke clarifies why such transitions have not developed in other cases. For example, slime molds and allodapine bees can have life cycles with, respectively, some multicellularity and sociality. But it isn't surprising that they haven't gone all the way to the next level, because they have a method of group formation different from groups that have. In these slime molds and bees, same-generation individuals come together to form social groups, and so relatedness isn't as high as when offspring stay with parents. This stresses that while there is a continuum of sociality, there is something special (and predictable) about what carries groups all the way through a major transition.

Bourke's book will no doubt be compared with John Maynard Smith and Eörs Szathmáry's *The Major Transitions in Evolution* (*1*). That earlier book did an excellent job of setting out the major-transitions view as an approach to understanding life's evolutionary history. However, Maynard Smith and Szathmáry did not offer a unified conceptual framework but instead provided a mixed bag of explanations for the different transitions. Building on Hamilton's theory and the more recent work in this area, especially that of David Queller and Koos Boomsma, Bourke has fixed that problem. In an important step forward, he has made the major-transitions approach both more approachable and more obviously fundamental.

Principles of Social Evolution provides an accessible, comprehensive, and highly readable overview, which will be invaluable in undergraduate teaching (although I would have liked to have found more figures). In addition, Bourke clarifies the future research that is required, making the book equally suitable for frontline researchers from postgraduate to professorial levels. In dividing the major transitions into three successive steps, he demonstrates how we understand the first two (the formation and maintenance of social groups) fairly well and the third (the transformation to the next level of individual) relatively poorly. The book does exhibit a bias toward the social insects. Although Bourke suggests this may reflect his background, the tilt is probably more a reflection of the fact that theirs is the transition that has attracted the most attention. Hopefully, his book will resolve that problem.



From many, one. In the colonial green algae *Volvox aureus* (here releasing a daughter colony), individual cells work together in a coordinated fashion and exhibit cellular differentation.

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