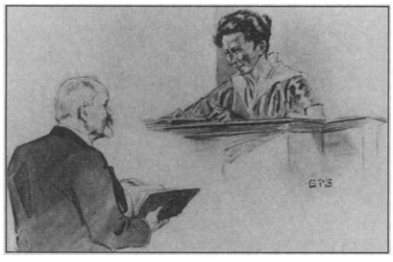
BOOK REVIEWS

Partners in Physiology

August and Marie Krogh. Lives in Science. BODIL SCHMIDT-NIELSEN. An American Physiological Society book from Oxford University Press, New York, 1995. xii, 295 pp., illus. $49.95 or £37.50.

Partnership and friendship are recurrent themes in the history of science. Some collaborators (such as James D. Watson and Francis Crick) have been friends, others have been lovers or spouses. Some partnerships flourish for a short period of time—like that of the most famous of all scientific couples, Marie and Pierre Curie—and others last for a lifetime. The Danish physiologists August and Marie Krogh constitute one of the most stable scientific couples of all times, living and working together for almost 40 years in what was seemingly a happy and harmonious marriage.

Whereas the Curies were equals in standing, the roles were allocated more traditionally between the Kroghs. Marie was an independent and very able scientist (she was the fourth woman ever to defend her medical dissertation in Denmark), and the two spouses worked closely together for long periods of time, continuously exchanging results and ideas. Yet August was by far the more successful of the two. He started his career in Copenhagen as a student of Christian Bohr (the father of Niels Bohr) but soon came in conflict with his mentor when demonstrating that oxygen uptake in the lungs takes place entirely by means of diffusion and not by secretion, a discovery that brought him immediate international recognition. An unusually skillful experimentalist, he constructed a series of ingenious devices for the measurement of respiratory and metabolic processes. For his elucidation of the structure and function of capillaries in the supply of oxygen to muscles he was awarded the Nobel Prize in 1920.

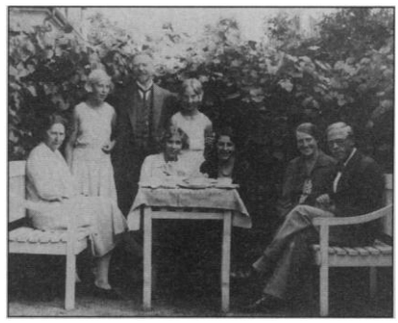


Marie Krogh defends her doctoral dissertation, 1914. [From *August and Marie Krogh*]

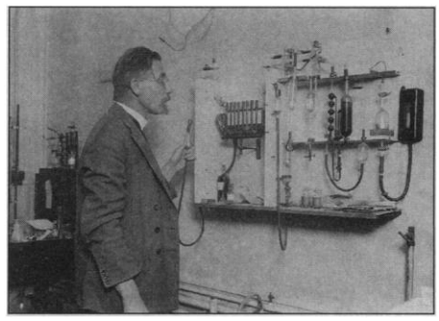
The following 30 years were equally productive. Supported by the Rockefeller Foundation, August Krogh laid the ground for a new and internationally attractive physiological institute in Copenhagen and continued to explore new vistas of research: in the 1930s he introduced the use of heavy water and other isotopes for the measurement of membrane function and performed a series of studies of osmotic regulation that have had a lasting impact. Krogh was known as an independent and uncompromising person: after having tried in vain to rejuvenate the venerable but politically impotent Danish Royal Academy of Science, he left it demonstratively in 1949.

For several reasons, then, August and Marie Krogh deserve a biography. The 81 boxes of letters and other documents in the Royal Library in Copenhagen (released to the public in 1992) provide a gold mine of information about them. It is difficult to write a good scientific biography, however, and even more difficult to write a dual portrait. One must get the biographical facts straight, understand the work, and be able to explain the scientific ideas and results in relation to the larger disciplinary and cultural context. One must get into the minds of the subjects—their thoughts, emotions, and even body feelings—and try to view both the social world and the phenomena in the laboratory the way they did. And finally one must possess the gift of writing: style and composition are necessary skills even for the biographer of scientists.

Bodil Schmidt-Nielsen, the Kroghs' youngest daughter, followed her parents' footsteps and became a physiologist. It is not surprising, therefore, that her account of their lives is well documented and accurate, full of insights into their physiological work and knowledge about their relations with other scientists. Many informative passages cast valuable new light on August Krogh's impressive work and character and give witness to the close and loving relationship between man and wife. Being an observant daughter, Schmidt-Nielsen has also had rich opportunities to collect a number of amusing anecdotes.



"The Krogh family at afternoon tea in the garden at the Rockefeller Institute, 1929." [From *August and Marie Krogh*]



August Krogh "with his very accurate gas analysis apparatus," 1928. [From *August and Marie Krogh*]

This book is excellent for information about the Kroghs' scientific work and whereabouts. But as a contribution to the history of science and as a scientific biography it is burdened by several weaknesses. The degree of contextualization is low: with few exceptions, for example an account of the background of the research on capillaries, Krogh's laboratory work is not satisfactorily placed in its wider scientific context. The author gives a detailed account of the activities of the Kroghs but no deeper understanding of what moved them, their motives, visions, or emotional lives. The description of the parents' personalities is often stereotyped.

The composition is problematic as well. The book is full of (sometimes trivial) details but has no clear story line. There is no plot, no sense of urgency behind it. The chapters dealing with the period up to the 1930s are chronological, whereas the rest of the book is organized loosely thematically. The style is hardly conducive to literary enjoyment with its long and not always illuminating quotations from correspondence and much too trite prose (the victims of August's stinging remarks are invariably "not amused"). Oxford University Press is responsible for an unusually sloppy copy-editing job: there are numerous misspellings of names of persons and journals, embarrassing translations (for example, "decan" instead of "dean"), and numerous inconsistencies in the rendering of names of Danish places and institutions.

Probably the greatest problem with this book is that the author seemingly never made up her mind

Vignettes: Math

Those of us with little or no familiarity with formal mathematics are nevertheless used to thinking complex thoughts about complex subjects, namely other people. When we come to study mathematics, we find it hard, perhaps, because we cannot get used to thinking about such simple subjects.

—*A. K. Dewdney*, in *200% of Nothing: An Eye-Opening Tour Through the Twists and Turns of Math Abuse and Innumeracy* (Wiley)

Even among scientists, books dense with equations have always been unpopular, but the general phobia of simple mathematics is nowadays exaggerated. Also to be considered are those who find mathematics useful.

—*Philip Woodward*, in *My Own Right Time: An Exploration of Clockwork Design* (Oxford University Press)

whether she wanted to write a daughter's memoir or a detached, scholarly biography. She has tried to pursue the two projects simultaneously but, unfortunately, neither of them consistently. A thoroughly subjective daughter's portrait would perhaps have been preferable. Nevertheless, the present work is a good point of departure for a deeper and more contextualized portrait of this fascinating partnership in 20th-century biomedical science.

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Evolutionary Pinnacle

Social Evolution in Ants. ANDREW F. G. BOURKE and NIGEL R. FRANKS. Princeton University Press, Princeton, NJ, 1995. xiv, 529 pp., illus. $75 or £55; paper, $29.95 or £19.95. Monographs in Behavior and Ecology.

Ants represent a pinnacle of social evolution in that all species are highly eusocial, except for some that have secondarily lost this social system. Eusocial species have a reproductive division of labor, and highly eusocial species have overlap of generations and have reproductives and worker helpers that are morphologically distinct. Many ants, and many termites, go further and have elaborate caste systems, in which nonreproductives are further differentiated morphologically. Whence came this marvel of nature? What are the characteristics of ant evolution? This thorough and very readable book introduces readers to the evolution of ant eusociality, the evolutionary dynamics of ant society, and the evolution of caste.

The aim of the book is to help bring followers of ant sociobiology up to date following the monumental general treatise by Hölldobler and Wilson. Bourke and Franks use very little quantitative reasoning, basing their approach firmly on Dawkin's view of the gene as the unit of selection, which makes the book very accessible as an introduction to this important subject. This approach is likely seldom to err as to the outcome of selection, and it remains a task for the fairly near future to see how often the conditions necessary for its applicability are violated in nature.

The authors argue convincingly that kin selection is the single crucial factor involved in the evolution of eusociality and that the factors postulated by apparently rival theories of the past (enslavement by parents, mutualism) are but variants of kin selection. The combination of kin selection and sex allocation is vital to understanding ant social evolution, because the male-haploid genetic system of ants leads to drastic asymmetries in relatedness between colony members (a sister may be more closely related to her brother than he is to her!). The resulting conflict expected between queens and their worker progeny over the sex ratio of the colony has intrigued researchers for decades; studies of many species indicate that the workers generally win. This finding, for which this book will help to achieve general acceptance, further erodes the older idea of a truly regal queen dominating her myriad myrmidon offspring, as against the view of a colony as a sea of competing interests. Solomon (Proverbs 6:7) had it right.

Caste is the highest expression of eusociality, and Bourke and Franks give an authoritative and controversial account that deserves to be true even if eventually disproved. A central problem is age polyethism, the apparent dependence on a worker's age of the tasks she performs. The authors show, using simple models and elegant diagrams, how task need have little direct link to age: the relationship might arise simply from workers' switching to tasks for which there are too few attendants. A flow is set up as workers involved in outdoor tasks die off, drawing younger workers from well-tended tasks inside the nest.

This book clearly has a strong populational and behavioral basis, as works at this time must have because of the state of the field. How might the field develop? One way is by the expanding use of better molecular markers to unravel patterns in natural populations, but deeper questions of the molecular architecture of eusociality are becoming approachable. The sociality of the ants has been seen as disqualifying them from being a fit subject for the study of the evolution of sociality. This paradoxical conclusion stems from the fact that all ants are either highly eusocial or clearly descended from highly social ancestors: there are no species on the critical threshold of eusociality. Hence, bees and wasps with simpler social systems are supposedly where to look. But, compared to ants, eusocial bees and wasps remain minimally differentiated from their non-eusocial precursors; indeed, the sociality of such insects is labile, species switching back and forth. This minimal differentiation suggests that there are no significant genetic differences between bees and wasps with simple eusociality and their non-eusocial relatives. The basic genetic architecture is most likely to change only later, as complex morphological differentiation between colony members—caste—arises, better matching them to roles. This increase in complexity favors an increase in gene number, following the pattern by which *Drosophila* has more than twice as many genes as yeast though otherwise these organisms have similar constraints for developmental noise suppression. Termites and those aphids with sterile soldiers provide test comparisons for molecular sociobiologists of the future: do highly eusocial forms have more genes, and do they tend to be the same ones? Such questions would be unaskable without the groundwork laid by such as Bourke and Franks.

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