IN MEMORIAM

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ROSS H. CROZIER
(1943–2009)

Professor Rossiter (Ross) Henry Crozier, one of the world's most distinguished insect geneticists, died at the age of 66 from heart attack on November 12th, 2009 while working near his lab at James Cook University in Townsville, Australia. His death diminishes the fields of evolutionary biology, entomology, genetics, and sociobiology and deprives them of one of their most significant thinkers. Crozier was a true gentleman, always displaying modesty, kindness, high standards of conduct, and intellectual elegance. His lasting influence will be felt not only through his extensive personal scientific contributions, but also through the numerous junior scientists he mentored during his career.

Crozier was born in India in 1943. But early in life he moved to his true home, Australia, where he was educated at Geelong Grammar School and Melbourne University. He then traveled overseas to the United States to obtain his PhD at Cornell University. While a student at Cornell, Crozier married his wife Yuen Ching Kok, who would go on to be his most important life and research partner. Crozier stayed in the United States for his first academic appointment as assistant professor at the University of Georgia from 1970–1974. He then moved back to Australia to take a position as lecturer at the University of New South Wales in 1975. He rapidly progressed up the academic ranks and ultimately obtained a personal chair and professorship in 1989. Crozier then accepted a position as professor and head of genetics at La Trobe University from 1990–2000. Finally, he moved to James Cook University in 2000 where he was professor until his passing.

Crozier's major research accomplishments centered on understanding the social biology of insects. He was on the forefront of advancing ideas of how genetic relationships among individuals might influence social behavior. For example, Crozier helped develop the view that social behavior might be particularly likely to evolve in hymenopteran insects. An early, but important, contribution was to correct and extend metrics of relationships for male haploid or X-linked genetic systems (Crozier, 1970), originally discussed by William D. Hamilton in his seminal introduction to kin selection theory (Hamilton, 1964).

Crozier was also among the first scientists to investigate and study the genetic structure of social insect populations using effective empirical and statistical methods. For example, his 1984 study on *Rhytidoponera* ants (Crozier et al., 1984) helped demonstrate how genetic relationships among social groups could be assessed and understood. Crozier also was enthusiastic about a study he coauthored that announced the discovery of an ant that had only N = 1 chromosomes, the minimum number possible for any species (Crosland and Crozier, 1986). His affection for this study demonstrated his love and fascination of the genetic details of social insect species.

One of Crozier's most significant contributions was the complete sequencing of the mitochondrial genome of the honeybee *Apis mellifera* (Crozier and Crozier, 1993). It is notable that the only other author on this paper was his wife, Y. Ching Crozier. The honeybee mitochondrial genome sequence was the first complete mitochondrial sequence of a non-dipteran insect. Importantly, Crozier showed that gene order within the mitochondrial genome could readily change over evolutionary time. In addition, this paper demonstrated how comparative studies in genomics should be undertaken.

Crozier was also an important contributor to our understanding of why social insect females mate multiply. This issue poses a major evolutionary challenge because multiple mating by social insect females tends to depress the relatedness among interacting colonymates, thereby restricting the conditions under which social behavior might evolve. Crozier coauthored important papers that provided frameworks for understanding the reasons why social insect females might mate multiply (Crozier and Page, 1985; Crozier and Fjerdingstad, 2001).

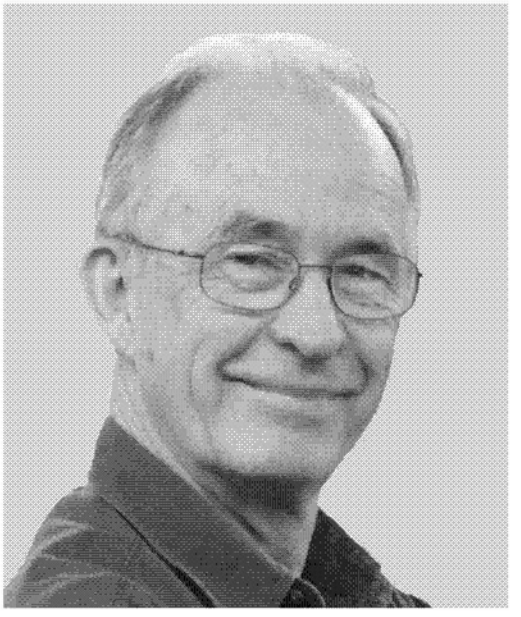
Crozier discussed the genetic underpinnings of social evolution in insects in the book *Evolution of*

social insect colonies: Sex allocation and kin selection, which he coauthored with his longtime collaborator, Pekka Pamilo (Crozier and Pamilo, 1996). This book represented a theoretical tour de force and described the processes underlying the evolution of social behavior in insects and the importance of sex allocation decisions by social insect colonies. This work demonstrated Crozier's aptitude and interest for understanding the exact mathematical and genetic details underlying social behavior. However, it did not lose sight of the interesting questions in social insect biology. Indeed, the memorable opening sentence of the book, "Social insects fascinate because of the finely coordinated organization of their societies and because of their great ecological success in many biotypes" reminds us of Crozier's fundamental interests in the field.

Crozier recently authored an entertaining and thought-provoking paper in the *Australian Journal of Entomology*, which acted in defense of the concept of kin selection (Crozier, 2008). This paper was spurred by a recent challenge to kin selection theory coauthored by the father of sociobiology, E. O. Wilson (Wilson and Hölldobler, 2005), who suggested that certain forms of group selection, rather than kin selection, may better explain the evolution of altruism in insects. Crozier's (2008) response represents one of the best examples of his expression and ideas, as he effectively and incisively explains the importance of kin selection. Indeed, one can hear his quiet, confident voice when he states "Kin selection does remain unchallengeable..." and "[W]ithout a kin selection component, group selection cannot lead to the evolution of sterile castes."

The research accomplishments of Crozier are deserving of great tribute. However, his greatest impact in science may ultimately come from the academic lineage he generated by mentoring students and postdoctoral fellows. Crozier supervised over 50 honors and postgraduate students, and acted as advisor to almost 20 postdoctoral fellows. His collaborations and mentorships resulted in his having coauthored papers with over 200 different scientists. Overall, his research group provided a dynamic setting for both scientific advancement and the formation of lifelong bonds of friendship.

Crozier received many awards and accolades for his scientific contributions. He was elected as an American Association for the Advancement of Science Fellow in 2002 and a Fellow of the Australian Academy of Science in 2003. He was then awarded an Australian Research Council Professorial Fellowship in 2006. The same year, Crozier received the first Hamilton Award from the International Union for the Study of Social Insects (IUSSI). This award, conferred only once every four years, represents the highest honor given by the IUSSI and recognizes outstanding lifetime achievements in the area of social insect research.



Ross H. Crozier at the Global Ant Project summit meeting on November 6, 2009. Photo credit: Alex Wild.

Crozier also held many important administrative posts. He served as president of the Genetics Society of Australia and the IUSSI. He was vice president of the Society for the Study of Evolution and a member of the council of the Society for Molecular Biology and Evolution. Crozier also served in various capacities on editorial boards for several major journals including *Annual Review of Ecology & Systematics*, *Behavioral Ecology & Sociobiology*, *Ecology Letters*, *Evolution*, *Insectes Sociaux*, *Journal of Molecular Evolution*, and *Molecular Biology & Evolution*.

Crozier was brilliant, yet remarkably humble. He was a world-class scientist, a gentleman of great integrity, and, above all, a kind man who enjoyed the company of others. His passing leaves a great emptiness and he will be sorely missed by all those he influenced throughout his distinguished scientific career.—*Michael A. D. Goodis-*

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