Obituary

Contributions by Ross Crozier on genetics and phylogeny of ants and other organisms

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Myrmecol. News 15: V-XXII
ISSN 1994-4136 (print), ISSN 1997-3500 (online)
Received 5 October 2010; accepted 6 October 2010

Abstract

In 1969, Ross Crozier completed his doctoral degree at Cornell University (USA). The title of his PhD thesis was *Genetic and phylogenetic studies on ants*. During the following four decades he devoted his time to this same topic, and he also expanded his research projects to include other social insects and many other evolutionary questions. His active career came to a sudden and unexpected stop when in November 2009 he died at his work place at the campus of James Cook University in Townsville (Australia). During the past 40 years he achieved a great deal scientifically, established and pioneered the research field of social insect evolutionary genetics, and at the time of his death was still at the peak of his scientific career.

Key words: Social insects, ants, genetics, evolution, karyotype, kin recognition, kin selection, caste determination, sex determination, immune defense.

Early interests

Rossiter (Ross) Crozier was born during the Second World War in India and he spent his childhood largely in South-East Asia where his father worked in various countries. Already during that time, at the age of five, he became fascinated by social insects, when encouraged by his mother he cut open a termite nest with a kitchen knife and discovered the wonderful society inside the nest. That fascination remained throughout the rest of his life. He was sent to Geelong Grammar boarding school in Australia from where he returned to the family in Asia for school holidays. This allowed him to become familiar with the biodiversity on both sides of the Wallace line, a factor which may have contributed to his deep interest in studying and preserving biodiversity.

After finishing school, Ross considered a career as a journalist but instead decided to start studying biology at the University of Melbourne, where he graduated in 1966. His Master's thesis was supervised by his genetics teacher, the famous evolutionary cytogeneticist Michael J.D. White. The title of the thesis was *Cytotaxonomic studies on Australian Formicidae*. The thesis made clear his two great interests: social insects (especially ants) and genetics. He had actively collected ants during his school years and that interest was now developing into a scientific career. His first four scientific papers appeared in 1968, the first one in his CV was on chromosome staining techniques (CROZIER 1968).

For his doctoral studies, Ross moved to Cornell University, a central place for studies on ant systematics and biology, and he was supervised by William L. Brown Jr. He completed his PhD in 1969 with a thesis entitled *Genetic and phylogenetic studies on ants*. The work was based on the best methods available at that time, karyotyping. While in Cornell, Ross was also supervised and influenced by one of the leading population geneticists, Bruce Wallace. Of his teachers, Michael White had been influenced by J.B.S. Haldane at the University College London, and Bruce Wallace was a student of Theodosius Dobzhansky. We can thus see that his two academic grandfathers were central architects of the synthetic evolutionary theory. This was reflected in everything Ross did – he was always keen to understand the genetic and evolutionary mechanisms and processes that underlie the patterns of current biodiversity.

From Cornell Ross moved to Athens, University of Georgia where he stayed until 1974. While continuing the work with ant karyotypes and chromosome polymorphisms, he started to develop his research in new directions. A few years after receiving his PhD, Ross reviewed what was known about hymenopteran chromosomes, largely based on his own work, in a book published in the series *Animal Cytogenetics* (CROZIER 1975). In that book he discussed, in addition to chromosomes, other important aspects of hymenopteran reproductive systems and social life, and demonstrated his ability to write excellent reviews, to summarize and synthesize information and to introduce new ideas. Ross later continued cytogenetic research together with Hirotami Imai (see IMAI 2011), examining the evolutionary processes of karyotype change in animals, not only ants but also vertebrates. His studies on ant chromosomes revealed extreme variability in the chromosome numbers, with a haploid number ranging from 1 to 16 within the *Myrmecia pilosula* complex alone (CROSLAND & CROZIER 1986). He worked with Imai on a minimum interaction theory, according to which selection favours karyotype rearrangements which reduce deleterious chromosomal mutations, and hence chromosome numbers are expected to increase (IMAI & al. 1986). The conclusions from the *Myrmecia* species were consistent with the predictions of this theory as chromosome evolution of the complex seems to have proceeded towards an increase in chromosome number by centric fission and inversions converting chromosomes from acro- to metacentrics (IMAI & al. 1994).

Beginning of social insect evolutionary genetics

It is fair to state that Ross was the person who established the field of social insect evolutionary genetics or sociogenetics, largely during the 1970's. Based on his early-born and long-lasting interest in social insects, he focused his scientific research on sociality. His formal training in genetics and evolutionary biology together with his intellect and curiosity made him ask questions on the evolution of sociality nobody had asked earlier. He also introduced the theoretical framework of population genetics into research on social insects. This combination of research interests quickly led to several important contributions. There were renowned geneticists working with social insects, mainly bees (e.g., Warwick Kerr) but nobody interested in the ecological and evolutionary aspects in the same way as Ross. He had the whole field open in front of him and he identified several important questions that should be explored. His ability to identify essential questions and capacity to suggest useful approaches and solutions resembled the touch of the mythological king Midas – almost every question Ross touched transferred into a new and flourishing line of research.

Ross was undoubtedly one of the first to understand the importance of HAMILTON's (1964a, b) theory on social evolution. He was, however, not satisfied with the way HAMILTON (1964b) had presented the coefficients of genetic relatedness for male haploid organisms. He pointed out (CROZIER 1970) that the relatedness of a haploid male to a diploid female is not the same as the reverse relatedness of a female to a male, and he also corrected a value presented by Hamilton. Ross denoted his coefficients of relatedness with a symbol G, and these have later been called Crozier's coefficients (UYENOYAMA & FELDMAN 1981) or pedigree coefficients (CROZIER & PAMILO 1980). This was a very important contribution with regard to the central place of the concept of relatedness in kin selection and the later development of conflict models. It should be emphasized that at the time when Ross published this note, Hamilton's work was not yet much appreciated and had been cited altogether less than 20 times.

Later Ross developed, together with his student Robin Craig, a method for estimating relatedness from empirical genotypic data (CRAIG & CROZIER 1979). The method was based on a suggestion by ORLOVE (1975), and Craig & Crozier applied it to estimate relatedness in the colonies of the ant *Myrmecia pilosula*. It was later shown that this original method is statistically biased as it does not take into account the sample sizes (number of colonies, number of individuals per colony) and the method has been revised accordingly (PAMILO & CROZIER 1982, QUELLER & GOODNIGHT 1989). However, the 1979 paper demonstrates nicely the way Ross worked between empirical and theoretical research. He considered it important to develop methods with which we can estimate parameters that are important in the models. He also wanted to develop theoretical models which can usefully direct empirical work.

An excellent example of the latter type of work is given by his studies on kin recognition. It was well known in the 1970's that ants (and other social insects) have specific colony odours, but there were only weak hints to the genetic source of odour variation. CROZIER & DIX (1979) suggested that both environmental and genetic factors can contribute to odour profiles, and they proposed the very first genetic models for the innate colony-odour differences, the Gestalt model and individualistic model. The Gestalt model suggested that individuals acquire odour compounds from nest mates through trophallaxis or grooming and therefore share a similar cocktail of odours. The individualistic model assumed that each individual has a specific odour determined (or influenced) by the genotype, and the similarities between colony members originate through shared alleles. Both models, as presented in 1979, assumed that individuals recognize nest mates on the basis of shared odours. This differed from the suggestion by Ross' supervisor Bill BROWN (1968) who had proposed that odours function by marking strangers rather than by indicating nestmates. Some recent studies (GUERRIERI & al. 2009) favour Brown's proposal. Nevertheless, CROZIER & DIX (1979) laid an important basis for conceptual studies of kin recognition and all studies on this topic are still built upon the basic models and concepts that were developed in the 1970's. LACY & SHERMAN (1983) further developed the models by introducing the concepts of labels, templates and referents. Ross later reviewed the rapidly expanding literature on kin recognition, both empirical and theoretical studies, in influential papers (CROZIER 1987a, 1988, CROZIER & PAMILO 1996). His laboratory also conducted a series of empirical studies on kin recognition in the ant genus *Rhytidoponera* (e.g., PEETERS 1988, CROSLAND 1989a, b).

Ross extended kin recognition models further to clonal invertebrates (CROZIER 1986) and introduced what is commonly known as Crozier's paradox (e.g., TSUTSUI & al. 2003, GARDNER & WEST 2009). Namely, in clonal organisms new mutations cannot ally with anyone else and are therefore selected against. It therefore becomes difficult to explain the maintenance of genetic diversity in such a system – thus a paradox.

Another modeling exercise from the mid seventies was on colony-level selection (CROZIER & CONSUL 1976). Ross was always keen on the levels or units of selection, and he approached the problem with great philosophical attitude in several reviews (CROZIER 1987b, 2008). The first theoretical model developed by CROZIER & CONSUL (1976) was relatively simple, focusing on the conditions of maintaining genetic variation. At that time, mid 1970's, population geneticists had started to explore allozyme variation in natural populations and discovered that populations harboured more genetic variation than had been anticipated. This observation led to an active debate between the neutralist and selectionist schools (see e.g., LEWONTIN 1974). The classical view in population genetics had been that organisms commonly carry so called wild type alleles, and mutants are often inferior in fitness and hence relatively rare. The neutral theory expanded from this view by assuming that many mutations are selectively neutral. The selectionist hypothesis assumed that most polymorphisms are maintained by some type of balancing selection. As a part of this debate, the study of Crozier & Consul addressed an essential question. In a wider perspective and considering social evolution, the important point in their paper was that the fitness values were assigned to the colonies or the mating types rather than to individual queens. Conceptually this use of colony-level fitness was novel and the discussion of the paper showed what the authors had in their mind. They referred to a possible genetic bias in task specialization and to different susceptibilities of different worker genotypes and wrote: "Where worker task specialization has a genetic basis, the colonies founded by heterozygous queens would have a broader range of worker competencies … Another possibility would arise when different worker genotypes have different susceptibilities to different environments." (CROZIER & CONSUL 1976). This line of thinking has later led to many interesting studies on the role of genetic diversity within colonies and on the evolution of polyandry and polygyny.

Consequently, it was no wonder that Ross was also puzzled by the evolution of polyandry and polygyny as well as by the evolution of the caste systems. He made important contributions in the studies of polyandry by discussing sperm clumping (CROZIER & BRÜCKNER 1981) and summarizing and developing the hypotheses on the evolution of polyandry (CROZIER & PAGE 1985 and again later CROZIER & FJERDINGSTAD 2001). The possibility of sperm clumping in ants with multiple mating has recently been revitalized (WIERNASZ & COLE 2010), and observations on the high level of polyandry in some ants have given new insights into the factors affecting the evolution of polyandry (HUGHES & al. 2008). As concluded by CROZIER & FJERDINGSTAD (2001), it is likely that no single hypothesis explains all the cases of polyandry.

Evolution of polygyny is in several respects harder to explain than the evolution of polyandry, because the effects on colony-level relatedness are greater and polygyny also includes a strong behavioural dimension as several queens must coexist in a single nest. One approach Ross took with Paul Schmid-Hempel was to test the association of polygyny and parasite load. Logically, this continued directly from the assumption on genetic specialization among workers (CROZIER & CONSUL 1976, CROZIER & PAGE 1985) and incorporated the suggestion by HAMILTON (1987) that such specialization can extend to resistance against pathogens and parasites. The study (SCHMID-HEMPEL & CROZIER 1999) combined two great interests of Ross – sociobiology and phylogenetics – as it was based on a comparative method with phylogenetic contrasts. Their results showed that parasite load is higher in ants with one queen and especially when the queen is monandrous, and the pattern remains when the phylogeny is taken into account.

The question of parasites and pathogens later led to important studies on immunity, focusing both on colony-level immune response and on long-term evolution of immunity genes (SCHLÜNS & CROZIER 2009). Ross started the work with immune genes by looking at the effects of exposure to an entomopathogenic fungus in the termite *Mastotermes darwiniensis*. Infection led to a significant increase in transferrin expression, but no clear evidence for positive selection in insect transferrin sequences was detected (THOMPSON & al. 2003). Innate immunity in insects has different pathways with proteins (and genes) responsible for pathogen recognition, signal transduction and antimicrobial destruction. Together with Mark Bulmer, Ross showed that the antimicrobial peptides of termites, the termicins, have duplicated and diverged under directional selection (BULMER & CROZIER 2004) and that a host-pathogen arms race has also in termites driven the evolution of some recognition proteins and the Relish protein which has a central role in the intracellular signaling cascade of the Imd pathway (BULMER & CROZIER 2006). Such studies have shed new light on the long-term evolution of the immunity genes in social insects and shown interesting differences when comparing with evolution in other insects (see also VILJAKAINEN & al. 2009). However, we are still at the beginning of a long journey if we want to get a clear picture on the role of immunity as a factor affecting the evolution of social insects and their colonial organizations.

In his influential review on hymenopteran genetics (CROZIER 1977), Ross had a long chapter on caste determination which is the core of the evolution of eusocial insects. He also made some early attempts to check whether genetic factors influence caste determination, focusing first on the role of heterozygosity by using allozymes (CRAIG & CROZIER 1978). More important than the answer (no effect was found) was the question itself. He later returned to genetic caste differences in *Camponotus* workers and showed that families (each produced by a single queen) differed in caste proportions within colonies, whereas intercolony differences in allometry were negligible (FRASER & al. 2000). In a different (phylogenetic) context he also turned attention to the evolution of workers in termites and concluded that the phylogenetic pattern is consistent with the hypothesis that the most recent common ancestor to all living termites was characterized by a "true" worker caste (THOMPSON & al. 2004).

Ontogeny of the female castes includes a switch point somewhere during development. Another, earlier switch point is that determining the sex of the developing individual. Ross presented a multilocus model (CROZIER 1971) to complement WHITING's (1939) one-locus multiallele model and CUNHA & KERR's (1957) genic balance model. Today, when data from complete genomes are accumulating, we can expect new information on this interesting topic. Ross later reviewed the population biological aspects of sex determination (COOK & CROZIER 1995) and started mapping the honeybee sex locus (BEYE & al. 1996) – a project finally completed by BEYE & al. (2003).

Genetics spreads in social insect research

As described above, during the 1970's Ross raised many relevant questions concerning the evolution of social insect colonies focusing strongly on genetic aspects. At that time he was a true pioneer and more or less working alone in this area. It is justified to say that he established the field of evolutionary genetics in social insects. Personally, when I became interested in similar questions as a student, it was natural for me to contact Ross and I joined his lab in 1978 and asked him to supervise my doctoral thesis together with a Finnish colleague Rainer Rosengren. That was an interesting time, because after one year in Australia I returned to Finland to do my PhD. I was in Finland and my supervisor was on the other side of the globe. Every time I had a question or Ross made a comment, we had to write letters, which might take weeks to arrive. This worked very well and led to a thirty-year collaboration and friendship. Our joint interests and studies were later summarized in a co-authored volume (CROZIER & PAMILO 1996).

One way to understand and appreciate Ross' contributions in the 1970's is to compare his research interests with the program of a congress of the International Union for the Study of Social Insects (IUSSI) at the same time. The IUSSI congress in 1977 was an excellent meeting. The congress volume had 133 abstracts, 1 - 3 pages each, and they included a total of one thousand references. Two papers used genetic methods, one for taxonomy and one for studying inbreeding. Nothing on kin selection was included. Only one paper referred to kin selection and Hamilton – in that paper Murray BLUM (1977) in very broad terms appreciated the importance of kin selection and concluded that it has become necessary to start studying the genetic bases of specific behaviours. The type of research Ross was carrying out during the 1970's had not yet penetrated the rest of the research community.

The change was coming soon. The organizer of the next IUSSI congress, Charles Michener, invited Ross to give a plenary talk. There were two plenary talks, one by E.O. Wilson and the other one by Ross. Ross' talk and the short version of it in the congress volume have several features so typical to him. Ross opened his presentation with a clear statement on the role of kin selection behind the evolution of worker caste. He showed his knowledge of the classical scientific literature and he also showed his wide cultural knowledge and interest in ancient history and mythology. According to his son Michael, the favourite book of Ross was the *History of the Peloponnesian War* by Thucydides. Enclosed is a quote from the beginning of his presentation (CROZIER 1982).

"We generally credit Hamilton with ushering the present era of theoretical exploration of the problem of eusociality, or the existence of the worker caste. But no train of thought springs full-grown from nowhere, as Athena is supposed to have sprung from the head of Zeus. Relatively immediate predecessors of Hamilton include Williams and Williams and Haldane. And Charles Darwin wrestled with the problem, and has been interpreted as taking a parental-manipulational stance. Before Darwin, Shakespeare proved himself no biologist with his description of kingly rule in honey bee life. Marcus Aurelius could be interpreted as an early group selectionist, and Solomon noted both the female-dominated and democratic (anarchic?) characteristics of ant society."

Ross returned to the question on the origin of eusociality 26 years later in an overview paper (CROZIER 2008). He argued firmly for the role of kin selection as the unchallenged explanation of eusociality: "Kin selection does remain unchallengeable but, for some, the role of male haploidy has lost favour recently despite several modelling efforts all finding that it favours the evolution of eusociality" (CROZIER 2008). In this paper, as also in his other publications, he emphasized the point that both genetic factors (genetic relatedness) and ecological factors (costs and benefits) are intertwined and essential in kin selection. He discussed the levels of selection in the context of Eliot Sober's source laws and consequence laws and he showed his sense of humour when discussing the evolution of the sterile caste. "As one graffito puts it: Sterility is hereditary – if you don't have kids, they won't either" (CROZIER 2008). His papers are good reading in several meanings. Furthermore, in that paper he identified two important directions of research on eusocial insects. One stems from genome sequences by identifying the gene networks that allow caste differentiation, and the other one builds upon the diversity of social insects and explores how they adapt as self-organizing systems.

Combining field and lab

Besides the theoretical and conceptual issues, Ross conducted and supervised throughout his career empirical studies both in the lab and in the field. He had become interested in ants in his school years, and he was a good naturalist. He knew his ants and carried out a series of important studies on genetic colony structures and phylogeny, especially in his favourite genera *Rhytidoponera*, *Myrmecia* and more recently *Oecophylla* (e.g., CROZIER & al. 1984, TAY & CROZIER 2000, HASEGAWA & CROZIER 2006, CROZIER & al. 2010).

As described above, he pioneered many research areas by developing the conceptual framework, and he was also known as a person who introduced new techniques in social insect research. He started working with chromosomes and his air-drying technique (CROZIER 1968) became widely used. He was one of the first who applied allozymes to study social insects (CROZIER 1973), and when DNA sequencing became available, he initiated sequencing projects first with rosellas (OVENDEN & al. 1987) and bats (BENNETT & al. 1988) and then with the honeybee (CROZIER & al. 1989). That was the time before PCR when such work was tedious and time-consuming. Together with his wife Ching, he sequenced the complete honeybee mitochondrial genome (CROZIER & CROZIER 1993). They showed that the genome is extremely AT rich and the tRNA genes in insect mitochondrial genomes have changed positions. The sequence served also as an important source for primer sequences in many studies on other hymenopterans. The study was a real landmark as the same had been earlier done with only one other insect, *Drosophila yakuba* by CLARY & WOLSTENHOLME (1985). For example Marjorie HOY (1994) in her book has a list of significant events in genetics, molecular biology, and insect molecular genetics and the honeybee mtDNA sequencing is one of the three events listed in 1993 (one of the others being Kary Mullis receiving the Nobel Prize for PCR).

Ross was keen with all kinds of technical equipment and he designed devices that helped his research. He liked to apply new equipment and methods – except that he hated Windows PC's and was devoted to Macintosh. Already in the early 1980's he planned to test methods to determine the age of individual ants for his project, and he finally did that together with Simon Robson by using lipofuscins (ROBSON & CROZIER 2009). He was equally interested in new statistical methods. When we at the end of the 70's and early 80's worked with relatedness estimators, Ross suggested using jackknifing and bootstrapping to estimate the standard errors. That was one of the very first times these methods were applied in evolutionary biology (CROZIER & al. 1984, PAMILO 1984). One of his favourite topics was phylogenetics, especially phylogeny of ants. He carried out empirical projects to resolve the phylogeny of his favourite genera and to determine the origin of ants (CROZIER & al. 1997, CROZIER 2006). He was also broadly interested in phylogenetic methods from both the methodological and evolutionary points of view. He developed ways to compare phylogenetic trees and to use phylogenetic information to assess and preserve biodiversity (CROZIER 1997). The title of his first paper on this topic was typical to Ross: "*Genetic diversity and the agony of choice*" (CROZIER 1992). He developed a method to measure phylogenetic information and applied it to analyse microbial communities (CROZIER & al. 1999). Besides, he also made many other contributions in conservation biology, he studied the stress tolerance of fish and supervised many projects with non-social organisms.

If we look at his research career through publication statistics, the number of papers published per year remained rather constant during the early part of his career. From the University of Georgia he moved in 1975 back to Australia, University of New South Wales in Sydney. He was first appointed as a lecturer and was gradually promoted and received a personal chair in 1989. In UNSW he worked in the zoological department which was later agglomerated into a School of Biological Sciences. He established a genetic laboratory, but had to struggle to equip it properly. His personal success made this easier and he attracted many international visitors who stayed various periods in the lab. During those years, population and evolutionary genetics started to transform from the allozyme era to DNA era. Ross was among those who very early made this shift successfully. At that time sequencing was done manually, first by cloning, and the lab even started to carry out PCR before there were machines for that. The tubes were manually moved between different temperatures.

Ross had a heavy administrative load when he became the head of the School of Biological Sciences in UNSW. In 1990 he moved to Melbourne, La Trobe University as a professor of genetics, and as the head of the school. The laboratory at La Trobe was better equipped for the kind of molecular genetic work Ross was doing, and he had some good colleagues with related scientific interests. The size and productivity of his research group started to increase significantly during the years in Melbourne. However, departmental intrigues and poor university management support were very wearing for Ross and contributed to his decision to move to James Cook University in Townsville in 2000. Other prominent evolutionary geneticists also left La Trobe soon after him. Ross built again an active and productive research group around him in Townsville, and it was easy to see that he really enjoyed being at James Cook University. In 2006 he received the prestigious professorial fellowship of the Australian Research Council.

Supervisor, mentor and colleague

Ross did not change much during the years, neither in his appearance nor in the way he encouraged and supported his students. His lab meetings were inspiring with intellectual discussions, often supported with a glass of wine and good cheese. He also generously hosted many visitors and he had a habit of keeping contact with his former lab members and with many other colleagues. This way he inspired much research around him. I have never seen any other person with such a network of correspondence. When he offered me a postdoc position in the early 80's, he said the reason was financial. He argued that when present in his lab in Sydney, I would occupy less space than our correspondence and he would save all the time that he otherwise spent when writing letters.

It was easy to discuss with him science, science policy, university administration, politics or any other matter (and we enjoyed the pleasures of the opera houses in Sydney and Melbourne). He was willing to exchange ideas and give good advice, and he presented his comments in a constructive and polite way. These characteristics made him also a highly appreciated editor and reviewer. He served many scientific societies and journals. He did editorial work for *Annual Review of Ecology & Systematics*, *Australian Journal of Zoology*, *Behavioral Ecology and Sociobiology*, *Ecology Letters*, *Evolution*, *Genetic Selection Evolution*, *Insectes Sociaux*, *Journal of Molecular Evolution*, *Molecular Biology and Evolution*, and *Myrmecological News*. He served as the president of the International Union for the Study of Social Insects and Genetics Society of Australia, as a vice president of the Society for the Study of Evolution, and as a councilor of the Society for Molecular Biology and Evolution. The amount of work he put into these tasks was enormous since he always wanted to do things well. The same characteristics made him a good administrator, but administrative work took his time as he was fair and conscientious.

Ross trained many students and hosted many visitors. When the former lab members, the Crozierites, gathered together for a joint dinner in an IUSSI congress in Sapporo, Japan in 2002, it was an impressive group of prominent researchers. During the 2006 congress, the International Union for the Study of Social Insects honoured Ross by awarding him the inaugural Hamilton Award. The award was given to him for his life-time contribution to the knowledge of the evolution of social insects, for studies of their evolutionary genetics and for fostering the careers of many current leading researchers. He was elected to the Australian Academy of Science and as a fellow of the American Association for the Advancement of Science in recognition of his significant scientific contributions.

His most important collaborator and companion over the years was his wife Ching. They met during their student years in Melbourne in 1962 and were married at Cornell in 1968. Ching is a trained bioscientist and she took care of the lab, supervised people in the lab and collaborated in all the important projects. In addition to Ching, Ross is survived by two sons, Michael and Ken, and a granddaughter, Madeleine.

The doctoral thesis of Ross had a broad title, *Genetic and phylogenetic studies on ants*. In retrospect we can say that the title characterized his life-long research career, except that he expanded it to other social insects as well as to many other organisms. A week before he died, he participated in a general ant project meeting in Chicago. He was very enthusiastic about the current development of our research field, especially the era of new genomics which he himself had so forcefully promoted. The large number of obituaries in scientific journals demonstrates how much the colleagues will miss his advice and initiatives when entering this new genomic era (ANONYMOUS 2009, 2010, BOOMSMA & PAMILO 2010, COOK & OLDROYD 2010, GOODISMAN 2010, JOHNSON 2010, ROBSON 2010, THOMPSON 2010).

Acknowledgements

I am grateful to Ching Crozier, Ary Hoffmann, Elina Leskinen and Simon Robson for various kinds of support while preparing the manuscript. My own work on social insects has been supported by a grant from the Academy of Finland (122210).

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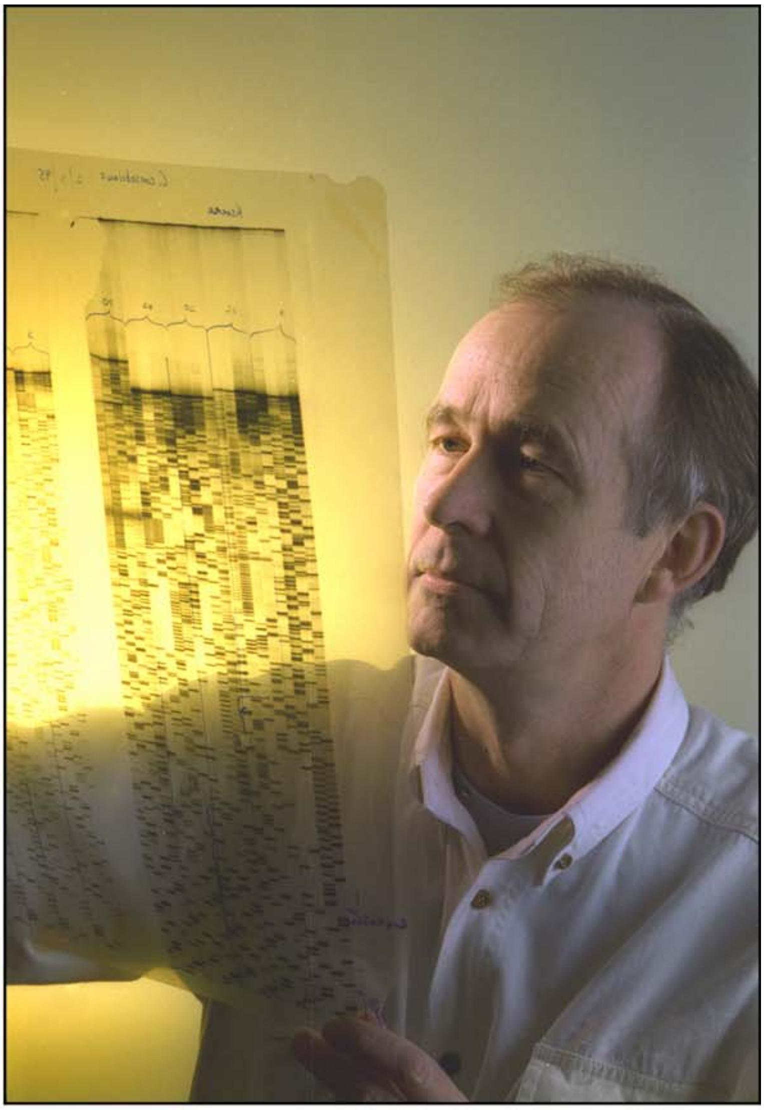
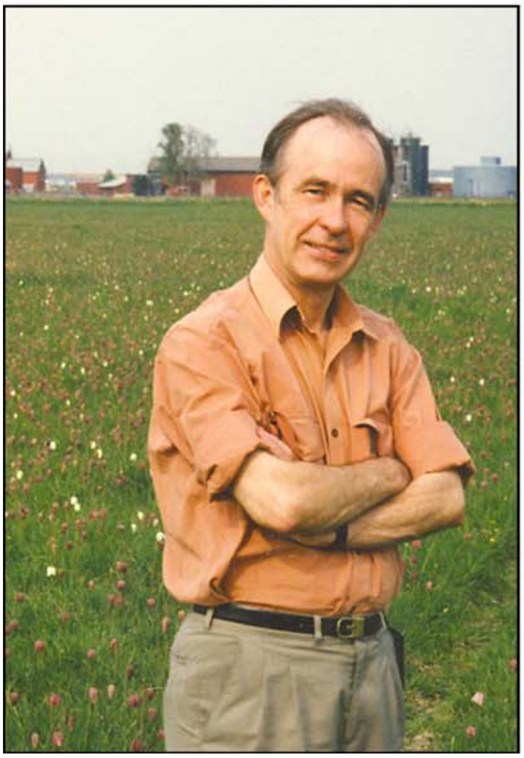
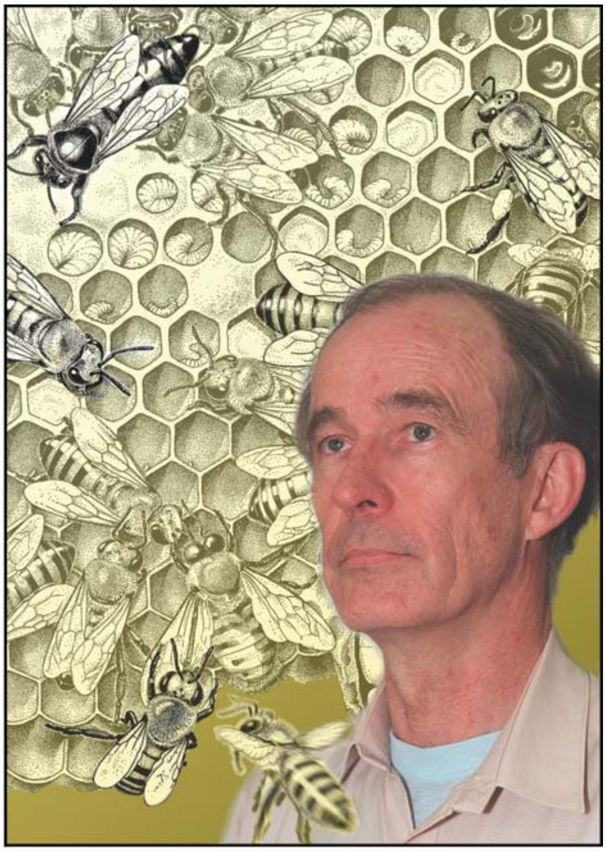
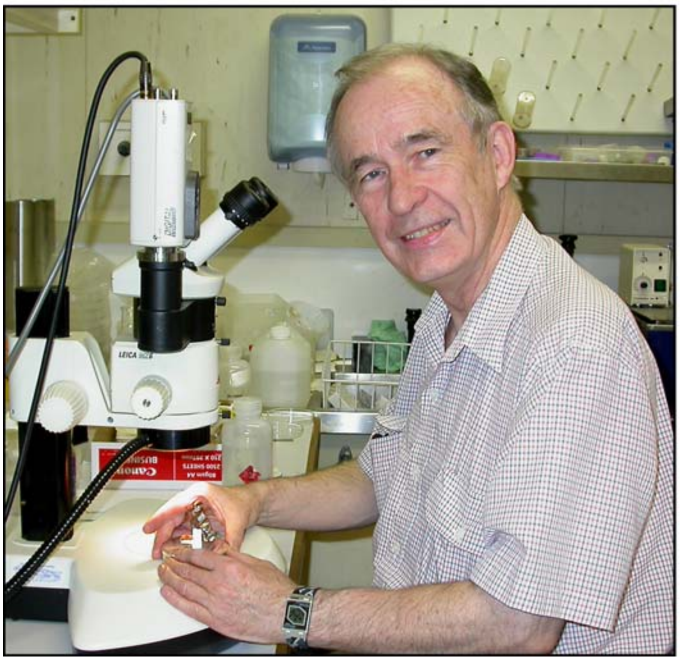


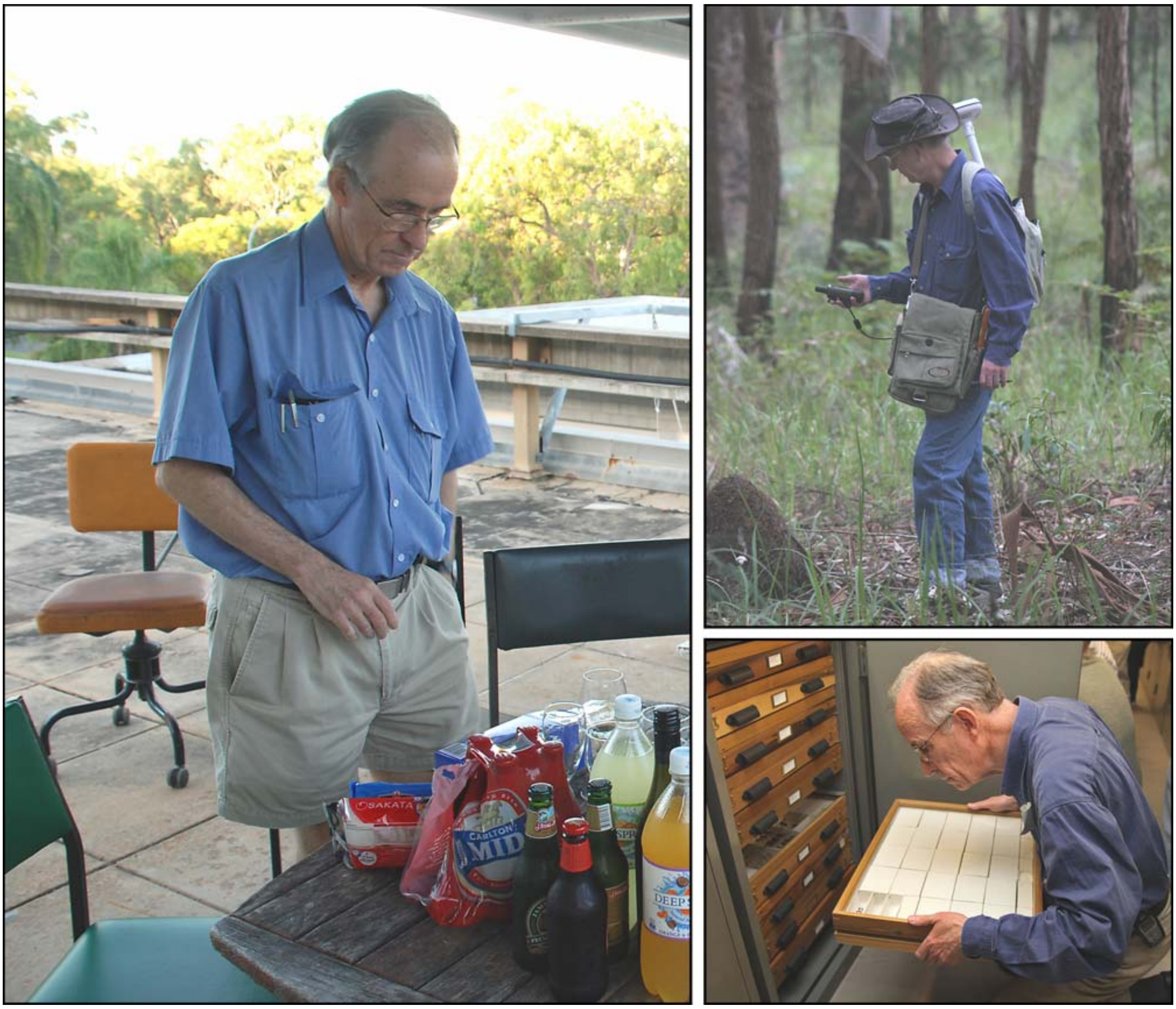






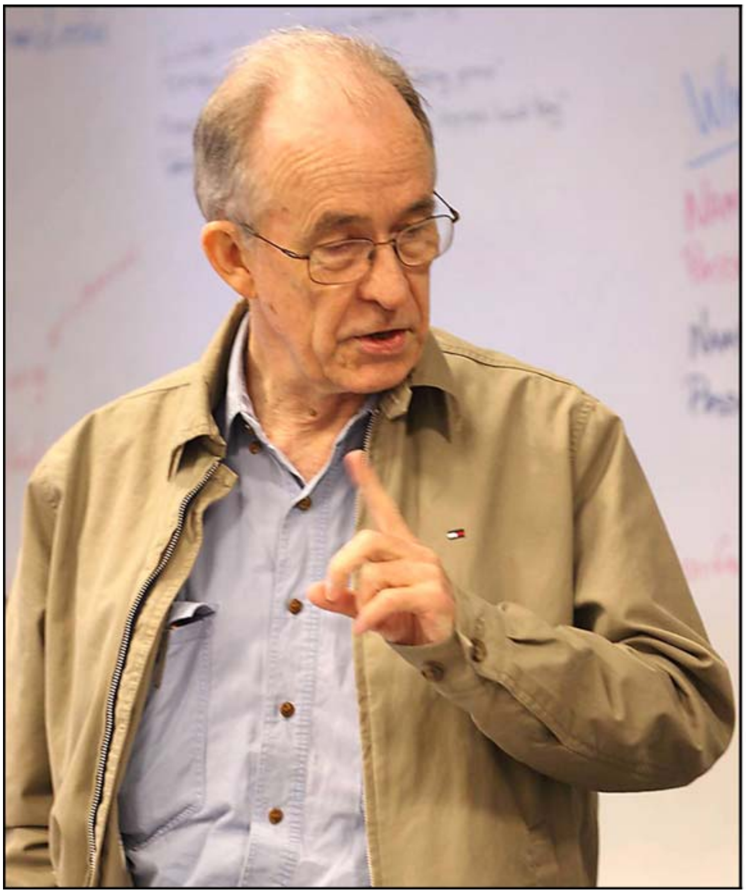
Above (clockwise from top left): Science Talent Search and presentation of prizes to students in the Moat Theatre at La Trobe University, Melbourne, 23 October 1990 (© Photography and Digital Imaging Unit, La Trobe University). Digital image for an article titled "Dance: the language of the honeybees" in the March 1999 edition of La Trobe published news magazine "The Bulletin" (© Photography and Digital Imaging Unit, La Trobe University). The Crozier lab in Sydney in the era of enzyme electrophoresis at the end of 1970's; buffer containers and staining trays occupied most of the space ((© Pekka Pamilo). At James Cook University, Townsville, October 2005 (© Faye Christidis).

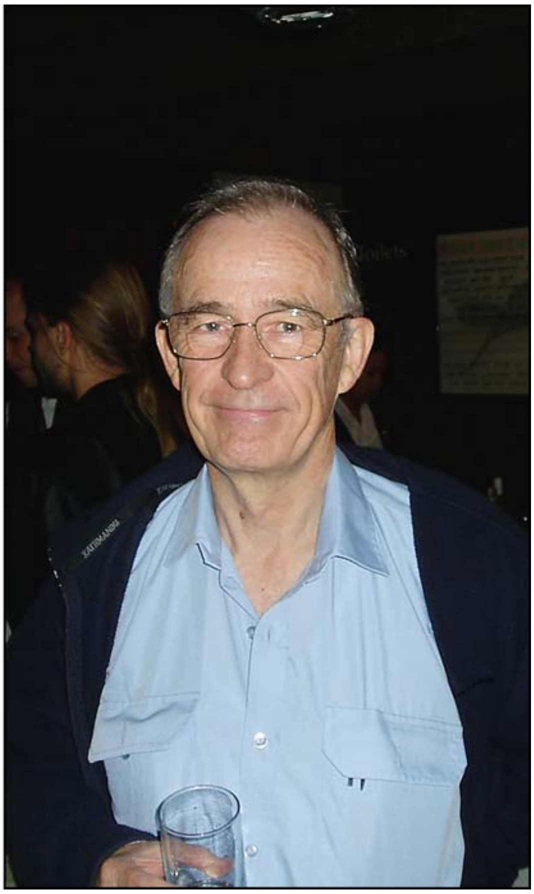
Left page (clockwise from top left): Ross (right) refreshing during a field trip with student Tony Bishop in 1978 (© Pekka Pamilo). At La Trobe University, Melbourne, October 1995 (© Photography and Digital Imaging Unit, La Trobe University). The Crozier lab at La Trobe University, 1998 (© Michelle Guzik). In Uppsala, 1993 (© Pekka Pamilo). With Ching Crozier at La Trobe University, March 1993 (© Photography and Digital Imaging Unit, La Trobe University).



Above (clockwise from left): On "poop deck" at James Cook University, 18 April 2008 (© Birgit C. Schlick-Steiner & Florian M. Steiner). In Paluma, Queensland, with GPS and auxilliary antenna, collecting *Myrmecia*, 7 June 2006 (© Richard J. Rowe). At the Global Ant Project meeting, Field Museum, Chicago, 6 November 2009 (© Hamish Robertson).

Right page (left – right): At the Global Ant Project meeting, Field Museum, Chicago, 6 November 2009 (© Alexander L. Wild). At conference dinner for the Australian Society for the Study of Animal Behaviour, Australian National Botanic Gardens, Canberra, 14 April 2007 (© Graham J. Thompson).





Publications by Ross H. Crozier

Compiled in December 2010, this list covers over 250 mainly but not exclusively peer-reviewed publications that Ross H. Crozier produced in his outstanding scientific career. Every effort was taken to make the list as complete as possible, although inadvertent omissions may exist. – Helge Schlüns

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