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STUDIES IN THE ADAPTATION AND EVOLUTION OF THE AUSTRALASIAN FAUNA



A collection submitted for the Degree of Doctor of Science
in the University of Adelaide

by

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Details of research activities relating to submission

My PhD research centred on the mechanisms used by a lizard to cope with temperature extremes and water stresses in Western Australia (5, 6, 23). S.D. Bradshaw was one of the supervisors of this thesis, otherwise the work is my own.

When I began work in my present laboratory in 1972, I extended this work to include studies of response to water stress in Australian desert mammals (1, 11). These studies followed a standard procedure and were unremarkable other than showing the very high tolerance of some Australian desert rodents to water stress. Here, the work is my own except for C.H.S. Watts overseeing the animal breeding colonies and providing background knowledge of Australian rodent biology.

During the course of this work it occurred to me that while many studies had been made of responses of animals to water stress, no studies had been made of the mechanisms a lactating female desert animal might use to conserve water. This led to studies of the water balance of lactation in desert animals (4, 7). Here, all the work reported is my own except that again C.H.S. Watts oversaw the animal breeding colonies, while L. Spencer and C. Pollard provided technical assistance.

This work showed that desert mammals were indeed better able to sustain lactation in the face of water-stress, but the exact mechanism used eluded me. The solution to this dilemma came with the discovery of water recycling in lactating mammals (2, 10). Here, the female drinks the urine of the lactating young, a feature which returns the water problem to the mother, whose kidney copes with the problem.

Because adult desert mammals have such a high capacity to handle these

problems (1), they are better able to sustain lactation under waterstress. This work was done with B. Green who, in a remarkable
coincidence, independently discovered water-recylcing in dingoes.
Here, I did the work on marsupials and rodents, and B. Green did the
work on dingoes. Subsequent studies were aimed at determining
precisely how efficient this mechanism was in rodents, and its effect
on water balance of the mother (24, 26, 39). Here, the work is my own
except for C.H.S. Watts overseeing the animal husbandry, L. Spencer
providing technical assistance, and S. Elhay providing mathematical
and computational advice and analysis.

As a result of this work, it soon became apparent that, in order to adequately interpret the adaptations I was observing, I needed to know more of the evolutionary history of the rodents of Australia. A number of modern genetic techniques had become available for such studies, and so I applied the techniques of chromosomes (8, 13, 17, 18, 19, 27, 31, 32, 33, 47, 52, 53), and allozyme electrophoresis (12, 16, 20, 43, 63, 67) to investigate the evolution of the Australian rodents.

All of the work reported in the chromosome papers 8, 13, 17, 18, 19 is my own except for C.H.S. Watts overseeing the husbandry of laboratory animals and supervising the collection of animals from the field, A.C. Robinson and J.F. Robinson collecting the animals from the field, and J.T. Hogarth providing technical assistance. The work reported in 31, 32, 33, 47, 52 and 53 is my own except that W.G. Breed conducted the reproductive anatomy and physiology in 31 and 33, M. Gelder and A. Jahnke provided technical assistance, C.H.S. Watts oversaw collection of animals from the field, and in 32, M. Adams conducted the electrophoresis. The allozyme studies represent my own work except for the following contributions: S. Cole provided

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technical assistance in 12, 16, 20, 43; J. Covacevich supplied the animals in 12; C.H.S. Watts supervised the collection and husbandry of animals in 16, 20, 43 and 67; and M. Adams conducted the electrophoresis in 43, 63 and 67. For 63, my contribution involved mathematical analysis of the electrophoretic data.

These studies led to a much clearer understanding of the evolutionary history of this group, summarized in a number of papers (41, 44, 61). In 44, I wrote the section on phylogenetic history and taxonomy.

A group whose evolutionary history is now very well known as a result of this work is the Australian Rattus, and consequently this group has proved useful for testing evolutionary hypotheses on DNA evolution (29, 34, 35, 60, 81, 82). My contribution to these studies was to conduct the genetic crosses, supply the tissue samples, and provide the evolutionary interpretations of the data.

The studies of evolution in the Australian rodents showed how morphological evolution and genetic evolution were often decoupled. Hence it became apparent that a full understanding of the evolutionary history of Australian vertebrates would only come from the application of these modern genetic techniques. I therefore extended the genetic approach to include other vertebrates such as marsupials (36, 42, 49, 56, 57, 71, 72, 74), bats (37, 45, 75, 76, 77), dingoes (21), birds (46, 54), and snakes (65, 66). In 21, 36, 37, 42, 45, 46, 49, 54, 57, 75, 76, and 77 I coordinated the research and acted as the major writer of the papers. Most of these papers are co-authored by M. Adams, who did the electrophoretic work. Papers 56, 71 and 72 represent my own work with the technical assistance of J. Birrell and M. Krieg, while T. Flannery

and K. Aplin provided samples for 71 and assisted with the manuscript preparation. In 65, I wrote all sections except that on immunodiffusion, while for 66 I conducted the microcomplement analyses and phylogenetic analysis. In 74, I wrote the sections on chromosomes and provided the albumin immunologic data and analysis.

The results of these studies may be generally summarized as follows:-

- 1) Among the Australian rodents, marsupials and bats there are many "sibling" species. That is, species that are so similar at the morphological level that their specific distinctiveness was not recognised until the genetic studies had been conducted. Indeed, as a result of this work, over 20 new species of mammals have been added to the Australian list since the publication of Strahan's "Complete Book of Australian Mammals" in 1983.
- 2) Sibling species are themselves a manifestation of the decoupling of genetic and morphological evolution i.e. genetic evolution proceeds to the point of speciation but morphological evolution is undetected. The studies of dingoes, birds and snakes showed the opposite extreme of rapid morphological evolution with little genetic evolution. Thus dingoes and domestic dogs are indistinguishable at the molecular genetic level, yet are morphologically distinct. Among the birds and snakes, morphologically very distinct species are very similar at the genetic level.
- 3) A large body of evidence suggests that evolution at the molecular genetic level proceeds at a relatively constant rate.

 Therefore molecular genetic evolution can be used as a "clock" to date

past evolutionary events. When the "molecular clock" concept is applied to Australian vertebrates using the data I have accumulated, some surprising results emerge. For example, the Australian elapid snakes (the "poisonous snakes") have a very recent history in Australia. They appear to be only distantly related to the cobras of India and the mambas of Africa, and to have evolved here from sea-snakes a mere 7 million years ago. The molecular genetic studies of marsupials are similarly allowing dates to be placed on events in their evolutionary history.

As a result of these studies, I have developed considerable expertise in the areas of genetic approaches to studying evolutionary history (28, 62, 70, 73, 80), culminating in co-authorization of a book on allozyme electrophoresis (69). For 28, the basic idea and the writing of the paper were shared equally by B.J. Richardson and myself. Papers 62, 70 and 73 represent my own work with Adams supplying critical comments for 62 and 70. The book (69) was a joint effort, equally among the three authors.

evolution seen in vertebrates, it seemed that the phenomenon might be even more apparent in invertebrates, particularly among the parasites. This is a major area of my current research, and early indications support the hypothesis (64, 68, 79, 83). I conceived the idea of the study in 64, and coordinated the project, while in 68, 79 and 83 the idea of the project was mine.

With the revolution currently occurring in the field of molecular biology, it is apparent that much of the DNA technology being developed will prove to be valuable for evolutionary studies. It is in this area

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that my future research efforts are being concentrated. I have been involved in one such study (78), where I conducted the phylogenetic analyses of the data.

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