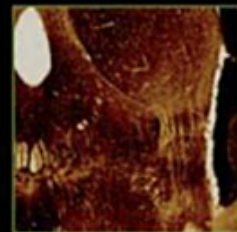
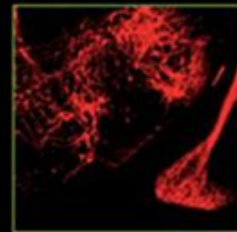
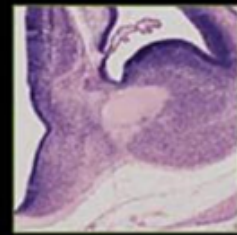


Ken W.S. Ashwell

The Neurobiology of **Australian Marsupials**

Brain evolution in the other mammalian radiation



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Preface

Marsupials in general, and Australian marsupials in particular, have much to offer in broadening our understanding of brain function. Both Charles Darwin and J. L. Johnson recognised that the native Australian mammals represent a 'second creation' or, to couch this in more modern terms, a parallel adaptive radiation. Australian marsupials have made a unique journey through the Tertiary, evolving nervous systems to deal with the special features of the changing Australian environment. For much (but not all) of that time, Australian marsupials were (apparently) completely isolated from placental mammals and many of the megafaunal species of the Pleistocene and recent times evolved large and complex brains. This raises many questions. Have marsupials used the same neural solutions to meet the demands of their environment as their distant placental cousins, or have they explored novel adaptations? How does the dramatically different developmental timetable of the marsupial lifestyle influence brain development and adult structure? Does the marsupial brain mediate sexual behaviour in the same way as the placental brain? These are some of the abiding questions of marsupial neurobiology.

The reader should note that, for the purposes of this work, the term Australian is used to include all those parts of Greater Australia to the east and south of the Wallace line (i.e. including New Guinea and its associated islands, mainland Australia and Tasmania). This corresponds to the continental land mass of Greater Australia (Sahul) as it was at the height of the last glaciation of the Pleistocene when sea-levels were at their lowest and Australian marsupials could move relatively freely between the Australian mainland and surrounding islands.

The textual component of this book has been organised into four broad parts. The first part (Chapters 1 to 3) deals with general aspects of marsupial classification, evolution, brain organisation and brain development. The second (Chapters 4 to 6) deals with the parts of the marsupial brain from a regional approach. The third (Chapters 8 to 12) includes chapters on important systems, while the fourth part (Chapters 14 and 15) is concerned with marsupials as research models. The book also includes three atlases. The first of these (Chapter 16) is a non-stereotaxic atlas of a representative polyprotodont marsupial (*Sminthopsis macroura*), since this species breeds well in captivity and may provide a useful model for studies of brain ageing. The second (Chapter 17) is a stereotaxic atlas of the brain of a representative diprotodont marsupial (the tammar wallaby, *Macropus*

ragens). Since the tammar is also used widely for developmental studies, the third atlas (Chapter 10) is a developmental series of five ages of the tammar pouch young. The atlases are provided in the hope that they will stimulate interest in Australian marsupial neurobiology and facilitate their study.

In these times of fierce competition for government grant money, marsupials are often seen as convenient models for solving human health problems and scientists interested in marsupial biology must often pitch their applications for research money with this in mind. There is no doubt that the special reproductive features and life cycles of Australian marsupials make them excellent models for studying problems relevant to human development and ageing, and, with this in mind, the book includes chapters on those aspects of marsupial neurobiology. On the other hand, I am certain that the neurobiology of Australian marsupials is worthy of study in its own right and will continue to fascinate scientists.

I have prepared this work with two broad audiences in mind. The first group would be students and researchers in zoology who are fully acquainted with the physiology, reproductive biology, evolution and palaeontology of marsupials, but who are interested in knowing more about the nervous systems of marsupials. The second would be neuroscientists who usually study placental mammals, but want to know more about what makes marsupials different. I have endeavoured to place the neurobiology of Australian marsupials in the context of their evolution, general and reproductive physiology. Naturally, as a neuroanatomist my perspectives on these may occasionally suffer from naivety and over-generalisation, and I beg the forgiveness of my zoologist colleagues should this be the case. I welcome any feedback from colleagues to improve future editions.

While I was preparing this book, a colleague asked me if I could have found a more obscure topic to write a book about. The natural answer to this is: 'Yes, monotreme neurobiology!' Unfortunately, marsupials (and monotremes) still suffer from prejudice and misinformation. In some quarters they continue to be seen as 'not quite right', 'primitive', 'evolutionary dead-end' mammals, whose only scientific value

is to inform our thinking on how the 'advanced' mammals evolved. The quotations at the front of this book highlight another approach. As Darwin noted concerning the northern hemisphere and Gondwanan radiations, 'certainly in each case the end is complete.' The Gondwanan mammalian radiation is in no sense incomplete, inferior or deficient, simply intriguingly different.

To paraphrase David Attenborough's lines in the television documentary *Life on Earth*, I see Australian mammals as alternative solutions to the problem of staying alive. As such, study of the unique and convergent features of their nervous system anatomy and physiology has much to teach us about neurological solutions to organism survival. It is my enduring hope that this work will make some contribution to dispelling misconceptions about marsupials and stimulate further research into the nervous systems of these fascinating and beautiful creatures.

This field of study owes much to the work of many outstanding scientists in Australia and internationally. I am fortunate that some of these talented people have contributed to this work, but there are many who are no longer active in science for various reasons. Many of these scientific pioneers have been given due recognition in the body of this book, and I have made every effort to acknowledge their contribution in the text. In my opinion two names in recent times stand out for their foresight, scientific leadership and imagination. These are: Richard F. Mark and John R. Haight, to whom this book is dedicated. Australian science is much richer for their work.

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Summary	"Australian marsupials represent a parallel adaptive radiation to that seen among placental mammals. This great natural experiment has produced a striking array of mammals with structural and behavioural features echoing those seen among primates, rodents, carnivores, edentates and ungulates elsewhere in the world. Many of these adaptations involve profound evolutionary changes in the nervous system, and occurred in isolation from those unfolding among placental mammals. Ashwell provides the first comprehensive review of the scientific literature on the structure and function of the nervous system of Australian marsupials. The book also includes the first comprehensive delineated atlases of brain structure in a representative diprotodont marsupial (the tammar wallaby) and a representative polyprotodont marsupial (the stripe-faced dunnart). For those interested in brain development, the book also provides the first comprehensive delineated atlas of brain development in a diprotodont marsupial (the tammar wallaby) during the critical first 4 weeks of pouch life"--Provided by publisher.
Contents	Classification, evolution and behavioural ecology of Australian marsupials / K. Ashwell Overview of marsupial brain organization and evolution / K. Ashwell Development and sexual dimorphism / K. Ashwell Ventral hindbrain and midbrain / K. Ashwell Cerebellum, vestibular and precerebellar nuclei / K. Ashwell Diencephalon and associated structures / K. Ashwell Deep telencephalic structures / K. Ashwell Cerebral cortex and claustrum/endorhinal complex / K. Ashwell Visual system / L.D. Beazley, C. Arrese and D.M. Hunt Somatosensory system / L. Marotte, C. Leamey and P. Waite Auditory system / L. Aitkin and R.K. Shepherd Olfactory system / K. Ashwell Motor system and spinal cord / K. Ashwell Australian marsupials as models of brain development / L. Marotte, P. Waite and C. Leamey Australian marsupials as models of ageing and disease / B. McAllan and S.J. Richardson 3 More...
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