MARSUPIALS

The last 20 years have seen many exciting discoveries in the study of marsupials, leading to significant developments in our understanding of this unique group of mammals. The impact of these developments has been such that marsupials are coming to be seen as model organisms in studies of life-history evolution, ageing and senescence, sex determination and the development and regeneration of the nervous system. This volume provides a synthesis of current knowledge, bringing together information scattered throughout the primary literature. Coverage includes evolutionary history and management strategies as well as all aspects of basic biology. A complete listing of currently known species and a comprehensive list of references make this a unique repository of information on this fascinating group of animals.

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For Hugh Tyndale-Biscoe, who, more than any other single person, has championed the study of marsupials both as models for biomedical research and as animals worthy of study in their own right – a wonderful scientist, inspirational teacher and scholar who unselfishly supported the editors throughout their careers.

Contents

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Preface

It is now more than 30 years since Hugh Tyndale-Biscoe's student text *Life of Marsupials* (1973) was published, and almost 30 years since the first compendia on marsupial biology appeared. Both bore the same title, *The Biology of Marsupials*, and were edited by B. Stonehouse and D. Gilmour (1977) and D. Hunsaker II (1977). Since then numerous more specialised books on various aspects of marsupial biology have appeared. However, with the exception of a new edition of *Life of Marsupials* (Tyndale-Biscoe 2005) that appeared while the current book was in production, none has the breadth of the earlier books. The closest is *Marsupial Biology: Recent Research, New Perspectives*, edited by N. R. Saunders and L. A. Hinds (1997*)*. There is thus a need for a resource book that covers the many facets of marsupial biology, many of which are unique to the mammalian subclass Marsupialia.

In *Marsupials* we have harnessed the collective knowledge and wisdom of a select group of colleagues from the Americas and Australia. The result is a collection of essays that cover marsupials from their beginnings and subsequent evolution, through their genetics, anatomy, physiology, ecology and behaviour, to conservation management concerns. Each chapter stands as a view into the marsupial world by its author(s). Although all chapters have been independently reviewed, then edited for consistency and cross-referencing to other chapters, the original style has been retained in all cases.

We hope that *Marsupials* will be the first place to look, for students (both undergraduate and graduate), research scientists and management professionals in government agencies seeking information on any aspect of marsupial biology. Often this may be as far as the reader needs or wants to go. Other readers will be directed to more specific texts, reviews and research papers. The list of references at the end of the book will serve as a guide to further reading.

So what makes a marsupial a marsupial? The female reproductive tract clearly distinguishes marsupials from all other mammals. There are two distinct oviducts

and two lateral vaginae; a median vagina is patent just for birth, then reverts to connective tissue except in most of the macropods and in the honey-possum *Tarsipes rostratus*. In males, the scrotum enclosing the testes is anterior to the penis, the penis is often bifid at the tip, and in American marsupials the sperm are conjugated in pairs. The X chromosome is significantly shorter than in eutherians, and there is selective inactivation of the paternal X chromosome. The fertilised egg divides to form a unilaminar blastocyst. In the trophoblast there is no inner cell mass present; instead, the cells of the trophoblast form a hollow ball. Gestation is short, as little as 12 days in bandicoots, and a shell membrane is retained for most of gestation but there is no shell. All marsupials have placentas, and many have pouches. Pouches may be permanent or consist of raised folds of skin that develop during gestation but regress at the end of lactation. At birth there is a functional mesonephric kidney (like that of reptiles), but a mammalian metanephric kidney develops soon after birth. The ureters are derived from pronephric ducts and enter the bladder by coursing mesially to the vas deferens or the oviducts. Marsupial neonates are uniformly small, usually no larger than 10 mm long and 500 mg in mass, regardless of maternal size. Young are born with well-developed olfactory bulbs and forelimbs with deciduous claws for the climb from cloaca to pouch. An intranasal epiglottis allows the young to remain continuously attached to the teat during early pouch life. The greater part of development takes place in the pouch rather than *in utero*, so that transmission of maternal antibodies via milk is prolonged. The total cost of reproduction is probably similar to that in eutherians, but the lactational component dominates in marsupials. Milk composition changes during lactation, particularly at the time of permanent pouch evacuation, and milks of different composition can be produced from different mammary glands within the same pouch.

These reproductive features are just some of those that distinguish marsupials from the other two mammalian subclasses (the eutherians and the prototherians or monotremes). Others occur in the skeleton and teeth, and are thus of great importance to palaeontologists. These include the 'marsupial shelf' formed by an inflection of the lower jaw, a bony palate that is fenestrated and thus incompletely separates the nasal and buccal cavities, a jugal that always reaches to the glenoid articulation of the jaw, fully confluent orbital and temporal fossae, the absence of a post-orbital bar, and tricuspid molars. Epipubic bones articulate with the pubis.

The soft tissues of marsupials are blessed with other anatomical features that are diagnostic. For instance, there are paired perianal glands and a cloaca that receives the openings of the alimentary, reproductive and urinary tracts. The cerebral hemispheres are small and do not overlie the cerebellum. Internally the left and right hemispheres are interconnected by the hippocampal and anterior commissures rather than by a corpus callosum as in eutherians. The optic and oculomotor nerves

and the ophthalmic branch of the trigeminal nerve enter the orbit through a single foramen.

These distinguishing features of marsupials often lead to different solutions to common ecological problems, and this is partly why marsupials are so interesting. Marsupials and eutherians are alternative and equally successful forms of mammals. When comparing the Marsupialia with the Eutheria we prefer the adjective 'eutherian' over 'placental' because a placenta is found in both marsupials and eutherians, as already mentioned. Nevertheless, our preference is not shared by all marsupial workers, and readers will find both 'eutherian' and 'placental' used in this book, depending on each author's preference.

Common names of marsupials also vary among authors, but these have been standardised throughout the book to be consistent with the names used by Burbidge and Eisenberg in Chapter 10. The lists of marsupial species and subspecies in Tables 10.3 to 10.5 have been updated to the time of going to press (2005) to take account of changes in nomenclature of previously recognised species and discoveries of new ones since 1996.

The book owes its birth not only to the enthusiasm of the contributing authors but also to Alan Crowden of Cambridge University Press for continuing encouragement in the face of difficulties associated with any multi-authored text, to Michelle Christy for editorial assistance during the early stages of the project, and to Ben Roediger and Nicholas Jufas for their help later in the project. Pavel German kindly provided images of marsupials. Our respective spouses are owed a great debt of gratitude for their support throughout. All chapters were reviewed by at least one independent referee, and for their assistance with this important task we thank Kristin and Tim Argall, Peter Banks, Steve Cooper, Mathew Crowther, Steve Cork, Elizabeth Deane, Alan Newsome, Jim Patton, Jack Pettigrew, Bob Raison, Lynne Selwood and Steve Wroe.