

Part I

Carnival of the Animals



The Monkey Dance
Albrecht Dürer, 1523

1 Quo Vadis?

One of the great joys of biology is the realization that there is no end of wonders to discover, to describe, and to attempt to understand.

Janet Leonard (2010)

Representatives of the Class Mammalia are to be found on every continent, and in every ocean of the world. They comprise a handful of extraordinary egg-laying species (the monotremes), as well as 7 orders of marsupials and 19 orders of placental mammals. Phylogeny, and modes of life, as well as sexual selection (via sperm competition and cryptic female choice) have all profoundly influenced mammalian reproductive biology. The reproductive adaptations of these animals have been forged over vast spans of time, beginning some 297–252 million years ago, during the Permian Period, when one branch of the synapsid reptiles (the Therapsida) gave rise to the furry, warm-blooded forerunners of the Class Mammalia (Kemp, 2005). Some therapsids survived a major extinction event that occurred at the close of the Permian; their modern descendants include the echidnas, kangaroos and possums, elephants, whales, rodents, bats and primates, as well as a host of other taxa.

Post-copulatory sexual selection is a relatively new addition to the field of evolutionary biology. This type of selection was unknown to Charles Darwin when he wrote *The Origin of Species* (1859) and *Sexual Selection and the Descent of Man* (1871). At that time, and for almost a century after his death, sexual selection was thought to operate solely with respect to events that take place before the act of mating. Inter-male competition for access to females, and female mate choices for the most attractive males, were viewed as the major drivers by which sexual selection influences individual reproductive success. All this began to change, however, once Geoffrey Parker (1970) had identified the phenomenon of sperm competition, and William Eberhard (1985, 1996) expanded discussions of post-copulatory sexual selection to embrace the concept of cryptic female choice.

The potential for sperm competition arises when a fertile female mates with two or more males. In mammals, sperm competition is usually limited to the ‘fertile phase’ of the ovarian cycle, during which ovulation occurs and ova are transported to the oviducts prior to fertilization. In some mammals, copulation itself induces ovulation to occur, but sperm competition is still possible if more than one male succeeds in mating with the same partner during the critical phase when fertilization is possible.

However, multiple-partner matings during non-ovulatory periods are not conducive to sperm competition, except in unusual circumstances (e.g. when females store sperm from multiple males, and fertilization is delayed, as happens in some species of bats). These examples serve as indicators that it is the female's reproductive tract and her physiological responses that determine the conditions under which sperm competition and fertilization take place. In mammals, as in other amniotes, spermatozoa must traverse multiple anatomical and physiological sieves and barriers within the female's reproductive system before gaining access to her ova. Therefore, the female's anatomy and physiology might also influence the fate of gametes from rival males in different ways. It is this hidden potential that constitutes cryptic female choice.

These novel insights concerning post-copulatory sexual selection are the fruits of research conducted initially on insects. The discovery of sperm competition thus owes much to the yellow dung fly (*Scathophaga stercoraria*, Parker, 1970), whilst the concept of cryptic female choice derives from work on scorpion flies (*Harpobittacus nigriceps*, Thornhill, 1983). Indeed, since the 1980s, research on invertebrate taxa has continued to expand apace, whereas investigations of mammalian post-copulatory sexual selection have progressed much more slowly. This may be due, in part, to the practical difficulties inherent in conducting experiments on mammals. However, it is also the case that many mammalian reproductive physiologists were initially unaware of the invertebrate literature, or failed to appreciate its wider significance. That is no longer the case, and much has been accomplished to advance knowledge of post-copulatory sexual selection in mammals and in other vertebrate groups. Dobzhansky's dictum, that 'nothing in biology makes sense except in the light of evolution', most assuredly applies to mammalian reproductive physiology, just as it does to other branches of the biological sciences.

Thus, although reproductive physiologists have traditionally concentrated on tackling a host of complex proximate questions, such as the control of spermatogenesis, or the biochemistry of sperm and ova, in the nine chapters that follow my goal is to address the ultimate questions about the role played by copulatory behaviour, and by post-copulatory sexual selection, during mammalian evolution. Are the copulatory patterns displayed by male mammals subject to sexual selection, and how did they evolve in the various mammalian lineages? Phallic morphology exhibits considerable diversity, in some cases between closely related taxa. Why should this be the case? Why do mammals have such a complex and variable array of accessory reproductive glands, and what roles might their secretions play during post-copulatory sexual selection? What effects have sperm competition and cryptic female choice had upon the coevolution of the reproductive systems of both sexes, and how far might sexual conflict, as well as cooperation between the sexes, have influenced these matters? How did mating-induced and spontaneous patterns of ovulation come to exhibit their current phylogenetic distributions among the mammals?

With these questions in mind, Part II of this book focuses on the evolution of patterns of mammalian copulatory behaviour. Chapter 3 presents a phylogenetic analysis of mating behaviour, and examines the impact of modes of life and of natural selection upon copulatory traits in the Mammalia. Chapter 4 serves as an introduction

to the concepts of copulatory courtship and post-copulatory sexual selection. This chapter also reviews current knowledge of the prevalence (or absence) of multiple-partner matings by mammals that have primarily polygynandrous, polygynous or monogamous mating systems. Part III comprises five chapters that explore connections between copulatory and post-copulatory sexual selection and the evolution of mammalian reproductive anatomy and physiology. Chapters 5–7 deal with the diversity of phallic structure and function, the testes and spermatozoa, and the accessory reproductive glands and ducts. Chapter 8 focuses on the anatomy and physiology of the female reproductive system in relation to mechanisms of cryptic choice and copulatory courtship. Chapter 9 considers the origins and evolution of mating-induced and spontaneous ovulation in female mammals. Part IV presents conclusions and suggestions for future research in this field, as well as a discussion of its relevance to understanding the evolution of human reproduction. I shall also say something about the decline of mammalian diversity, due to human overpopulation and the continued destruction of the planet's ecosystems.

Before embarking upon these tasks, however, it is essential to establish a firm basis for the comparative discussions of reproductive biology that follow. To this end, Chapter 2 reviews phylogenetic relationships between the various groups of extant mammals, and provides readers with an introduction to the enormous diversity displayed by the Class Mammalia.

2 Mammalian Classification and Evolution

Questions regarding character evolution among living mammals now have the decisive advantage of a relatively well-resolved tree.

Asher, Bennett and Lehmann (2009)

The last 25 years have seen significant developments in the fields of mammalian classification and evolutionary biology. Molecular genetic techniques have increasingly been applied to test traditional classifications that were based upon fossil evidence and comparative anatomical studies of extant taxa. As well as confirming many of the established tenets of mammalian classification, some fresh insights have emerged as a result of these endeavours. The following brief review of the phylogeny and basic biology of the 27 extant orders of mammals is designed to provide the reader with a sound basis for the discussions of copulatory behaviour, reproductive biology and evolution that unfold in the ensuing chapters.

How Many Species of Mammals Are There?

It might be imagined that all the various kinds of mammals were discovered long ago. In 1970, at the beginning of my research career, I thought that all the lemurs, monkeys and apes must be known to science. Surely, no new primates could remain concealed in the world's diminishing rainforests? Happily, I was wrong, and new species, not only of primates, but also of many other types of mammals, have steadily come to light during the last 50 years. In 1982 there were considered to be 4170 extant species of mammals, but this tally had risen to 5341 by the time that the third edition of *Mammal Species of the World* was published (Wilson and Reeder, 2005). A few years later, Schipper *et al.* (2008) included 5487 extant species in their analyses of mammalian diversity, and in 2018 Burgin *et al.* calculated that 6399 species of mammals currently exist (Table 2.1).

The number of species recognized by various authorities is affected by the penchant of taxonomists either to 'lump' taxa together or, more commonly, to 'split' existing taxa into separate species. Subspecies of certain well-known mammals are sometimes raised to specific rank, often on the basis of molecular genetic evidence. For example, the giraffe has long been considered as a single species (*Giraffa camelopardalis*). However, a wide-ranging study of giraffe population genetics by Fennessy *et al.*

Table 2.1 Estimates of mammalian taxonomic diversity: 1982–2018 (based on Burgin *et al.*, 2018)

Taxa	1982	1993	2005	2017	2018
Orders	20	26	29	27	27
Families	135	132	153	159	167
Genera	1033	1135	1230	1267	1314
Species (extant)	4170	4631	5341	5475	6399

Data are from *Mammal Species of the World*, the IUCN Red List, and the Mammal Diversity Database (Burgin *et al.*, 2018).

(2016) led them to conclude that there are four species of giraffes. This has been disputed, however (Bercovitch *et al.*, 2017). Another example concerns an isolated population of orang-utans in a mountainous region in Sumatra that has been proposed to represent a new species (*Pongo tapanuliensis*: Nater *et al.*, 2017). Whether this truly is a new species or a subspecies of the Sumatran orang-utan (*P. abelii*) is debatable.

Yet, every so often, truly novel species of mammals come to light. Recent welcome surprises include a pygmy sloth (*Bradypus pygmaeus*) from Panamá (Anderson and Handley, 2001), new monkeys such as *Macaca munzala* from India (Sinha *et al.*, 2005) and the lesula (*Cercopithecus lomamiensis*) from the Democratic Republic of the Congo (Hart *et al.*, 2012), a previously unknown tapir (*Tapirus kabomani*) from the depths of the Amazon rainforest (Cuzzuol *et al.*, 2013) and a tree hyrax from western Nigeria (Bearder *et al.*, 2015). A new river dolphin has been discovered in Brazil (*Inia araguaiaensis*: Hrbek *et al.*, 2014) and there is even a new beaked-whale species, belonging to the Genus *Berardius* (Morin *et al.*, 2017). Such discoveries are not evenly distributed across the mammalian phylogeny. Thus, 323 of the 408 new mammals (i.e. 84 per cent of new species) described between 1993 and 2009 were bats, rodents, primates, or small insectivorous species belonging to the Order Eulipotyphla (Ceballos and Ehrlich, 2009). The bats and rodents combined comprise 65 per cent of all mammalian species. The great diversity represented by these two orders, and the fact that molecular studies are revealing that cryptic species are often concealed among morphologically similar taxa, makes it likely that many more new species of bats and rodents have yet to be described.

Subclasses of the Mammalia

There are three subclasses of living mammals: Monotremata, Marsupialia and Placentalia. The marsupials and placental mammals derive from common ancestors belonging to the Theria, a mammalian group that diverged from the egg-laying ancestors of monotremes (Prototheria) at some time between 161 and 217 million years ago (Mya). The Theria subsequently became separated (143–178 Mya) into two lineages: the Metatheria, which gave rise to the marsupials, and the Eutheria, which

gave rise to the ‘crown group’ Placentalia (Figure 2.1). The latter comprises all extant eutherian mammals as well as their common ancestor and all extinct taxa that also share that common ancestor. All of today’s eutherians thus belong to the Placentalia but, as we shall see, most of the fossil stem eutherians, which existed during the Cretaceous Period (145–66 Mya), are not considered to be members of the crown group Placentalia.

The Placentalia is the most diverse and successful of the three subclasses of living mammals in terms of its worldwide distribution, as well as its taxonomic and ecological diversity. Placental mammals currently comprise about 6000 living species belonging to 19 orders. They include diminutive representatives such as the mice, shrews and insectivorous bats, as well as megafauna such as elephants, whales, bears, sea lions, apes, buffalos and a host of others. Most agricultural livestock, such as pigs, cattle and sheep, as well as domestic pets, such as dogs, cats and hamsters, also belong to the Placentalia. By contrast, the Marsupialia or pouched mammals are represented currently by 350+ species; 3 orders of these are found in South America, and 4 orders occur in Australia, on New Guinea and some small neighbouring islands. The third and most ancient subclass is represented by the single order Monotremata, which comprises just five species of remarkable egg-laying mammals that are confined to Australia and New Guinea. The following sections describe the members of these three subclasses, focusing on their phylogenetic relationships, evolution and general biology.

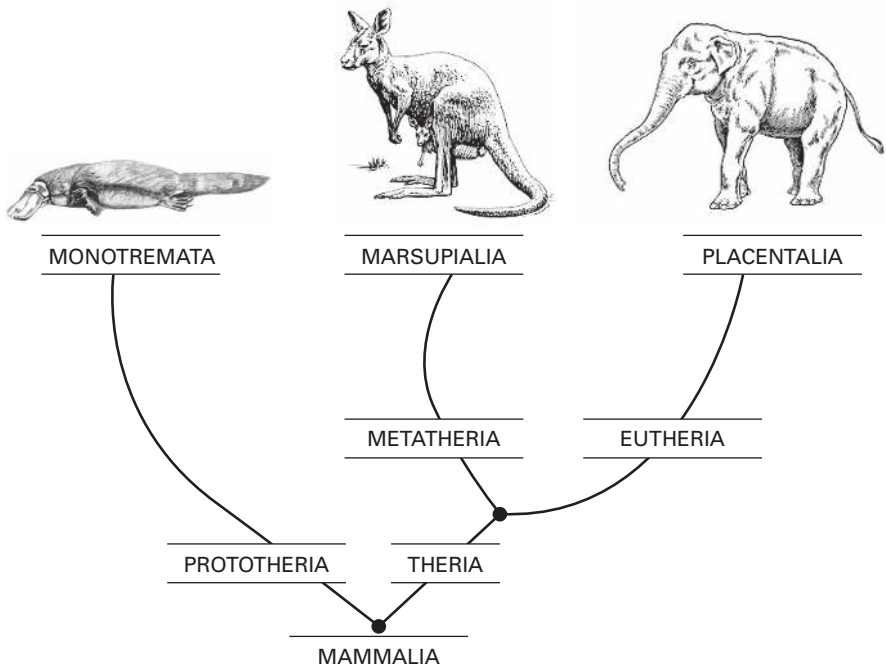


Figure 2.1 Phylogenetic relationships among the three subclasses of the Mammalia.

Subclass Monotremata

‘Molecular clock’ studies indicate that the earliest monotremes originated at some time between 161 and 217 Mya, during the Lower Jurassic (Phillips *et al.*, 2009). However, the earliest known fossil monotreme (*Teinolophus*) has been dated at 112–121 Mya, from the lower Cretaceous of Australia (Rich *et al.*, 2001). Both fossil and genetic evidence confirms that the monotremes were already established in Australia long before the arrival of marsupials there, at some time between 71 and 54.6 Mya (Beck, 2008; Godthelp *et al.*, 1992; Phillips *et al.*, 2009).

Only two types of echidna and a single species of the platypus have survived to the present day (Figure 2.2). The short-beaked echidna (*Tachyglossus aculeatus*) is very widely distributed throughout Australia. It is clothed in short hairs, interspersed with robust spines, and is equipped with long digging claws on its short, powerful limbs. The echidna is toothless, and it employs its long, sticky tongue to capture ants and other small invertebrates. Three species of a larger, long-beaked echidna, belonging to the Genus *Zaglossus*, occur on the Island of New Guinea. Long-beaked echidnas may weigh up to 15 kg, whereas adults of the short-beaked species vary from 2 to 7.5 kg in weight. Both types of echidna probably occurred in Australia until quite recently. This is known because a museum specimen of *Zaglossus bruijnii* originates from the Kimberley region of Western Australia; it was collected there in 1901 (Helgen *et al.*, 2012).

The extraordinary, amphibious, platypus (*Ornithorhynchus anatinus*) is the sole surviving representative of an ancient monotreme lineage. The limb bones and teeth of a platypus-like creature (*Monotrematum sudamericanum*), dated to approximately 61 Mya, have been discovered in Patagonia, and these fossils closely resemble those of a platypus (*Obdurodon*) which lived in Australia at around 25 Mya (Pascual *et al.*, 1992; Phillips *et al.*, 2009). Several species of *Obdurodon* have been described, and

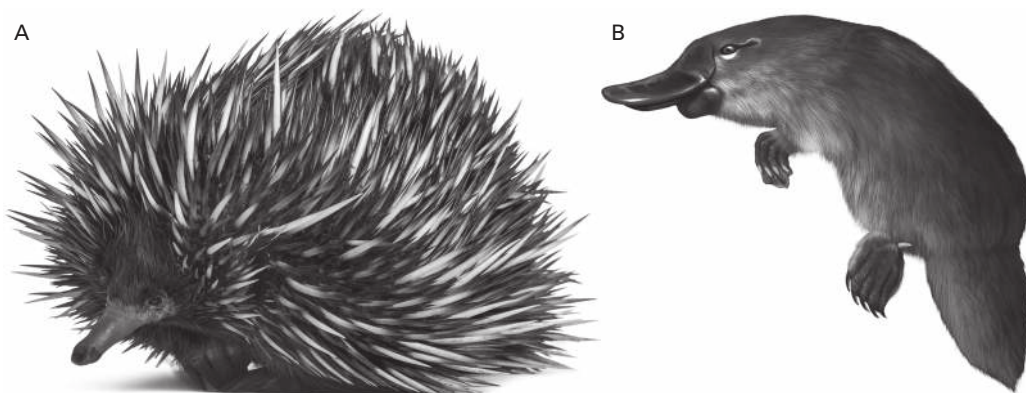


Figure 2.2 Australian monotremes. **A:** The short-beaked echidna (*Tachyglossus aculeatus*). **B:** The platypus (*Ornithorhynchus anatinus*). (Images: © Shutterstock.com.)

one of them was a giant of its kind, almost a metre in length and twice as large as today's platypus.

The distribution range of the platypus extends along the eastern seaboard of Australia, and includes the island of Tasmania in the south. It is found in rivers, lakes and streams, and is an adept swimmer, using its flattened, webbed forefeet for propulsion. The bill of the platypus is soft and leathery; it contains a battery of tactile and electro-receptors which assist the animal in locating the small aquatic invertebrates which form the bulk of its diet (Pettigrew, 1999). The adult is toothless, but a series of horny plates and ridges inside the bill allow it to grind up its food. The hind feet have claws and there is also a sharp hollow spur which, in adult males, receives the secretions of a venom gland situated in the thigh. The functions of these poison glands have been much debated. It is known that they enlarge during the breeding season, and they may play some role during inter-male competition, as males sometimes have puncture wounds in their tails at this time (Grant and Temple-Smith, 1998). Intra-sexual selection may also have influenced the evolution of body size in the platypus (adult males weigh 40 per cent more than females).

Like the echidna, the platypus is non-gregarious and each adult occupies its own burrow, close to the water's edge. During the breeding season the female platypus constructs a much longer burrow terminating in a nest chamber in which she deposits her eggs. Figure 2.3 shows the map of a platypus burrow made by Harry Burrell (1873–1945), a pioneering amateur naturalist and self-styled 'platypoditudinarian' who wrote an excellent book about his researches (Burrell, 1927). The female platypus usually lays two eggs in her nest chamber and incubates them for 1–2 weeks. Once they hatch, she feeds the young with milk from ducts that open directly onto the

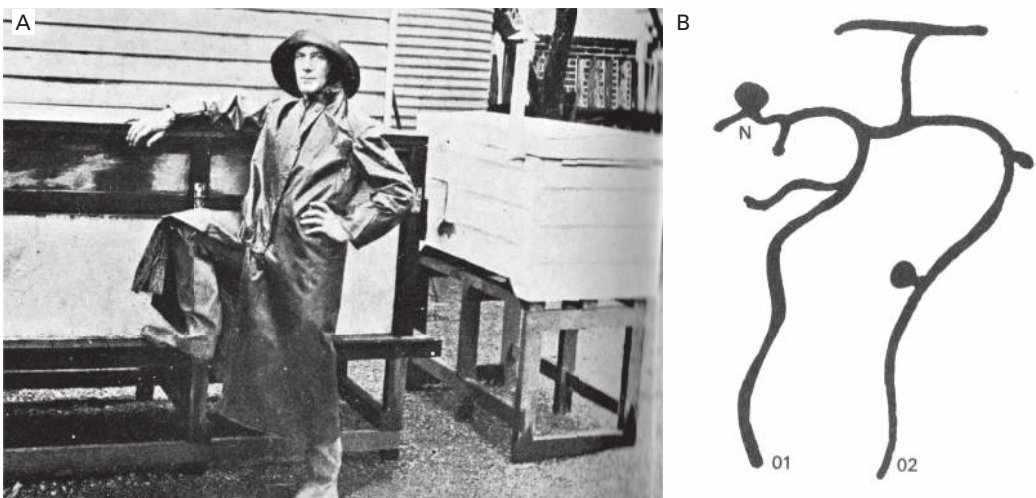


Figure 2.3 **A:** Harry Burrell (1873–1945), pictured beside his 'portable platypusary'. **B:** Map of a platypus breeding burrow, with two entrances (01 and 02). N = the female's nest chamber. (After Burrell, 1927.)

surface of her abdomen (female monotremes do not have nipples). Lactation lasts for 4–5 months, by which time the offspring are ready to leave the burrow.

The female echidna deposits her egg not in a nest chamber, but into a shallow, muscular pouch-like depression situated on her abdomen (Griffiths, 1998; Rismiller, 1999). Once hatched, the tiny offspring, which weighs barely one-third of a gram, remains in the pouch and begins to feed and to grow rapidly. Its body mass increases 100-fold during the first 14 days. The young echidna, which has been delightfully named the ‘puggle’ by field researchers (Rismiller, 1999) remains in the mother’s pouch until it is between 50 and 60 days old. At this stage, the mother constructs a simple nursery burrow in which she leaves her offspring, but returns every 5 days in order to supply it with milk. The puggle feeds voraciously, increasing in body weight by up to 40 per cent during a single feed. By 3 months of age the infant is covered in soft hair, but short spines are also present. These emerge gradually and, by the time it is 7 months old, Rismiller records that the offspring has been weaned, and it weighs anywhere between 800 and 1300 g.

Despite obvious differences in their morphology and modes of life, the echidna and platypus share a great many anatomical traits, and they may be phylogenetically more closely related than was originally thought to be the case. The same kinds of specialized tactile and electro-receptors that have been identified in the bill of the platypus also occur, but at a lower density, in the beak of the echidna (Proske *et al.*, 1998). There is a sharp spur on the back foot in both species, but it is atrophic in the echidna, and lacks the venom gland that is present in the male platypus. There are many skeletal similarities between these taxa and echidnas are also surprisingly good swimmers (Rismiller, 1999). Molecular genetic evidence now places the divergence between the echidna and platypus lineages at somewhere between 19 and 48 Mya (Phillips *et al.*, 2009). These authors posit that echidnas ‘had aquatically foraging ancestors that reinvaded terrestrial ecosystems’. These ancestors may have gained an ecological advantage when transitioning to terrestrial life by foraging on ants, because only one type of marsupial (the numbat) specializes in exploiting similar prey. The common ancestor of the platypus and echidna may also have prospered because it occupied a niche that was inaccessible to Australian marsupials, none of which is amphibious. Marsupial reproduction involves pouch infants remaining firmly attached to the mother’s nipples for extended periods. These traits are not conducive to an aquatic life and, in fact, only one marsupial (the South American yapok) is known to forage in this way.

Some preliminary remarks are necessary regarding the reproductive organs of the monotremes. Given that all extant members of this infraorder reproduce by laying eggs, and that the platypus lineage is phylogenetically ancient, it seems likely that the Monotremata as a whole derives from oviparous ancestors (Temple-Smith and Grant, 2001). In the female echidna each ovary is enclosed within an infundibulum which leads to an oviduct, and uterus; both sides of the system open into a central urogenital sinus which connects, in turn, with the female’s cloaca. However, in the platypus, only the left ovary is functional, as is also the case in most kinds of birds. In the male platypus and echidna, the testes are very large and are retained inside the abdomen