Evolution of the House Mouse

The house mouse is the source of almost all genetic variation in laboratory mice; its genome was sequenced alongside that of humans, and it has become the model for mammalian speciation. Featuring contributions from leaders in the field, this volume provides the evolutionary context necessary to interpret these patterns and processes in the age of genomics.

The topics reviewed include mouse phylogeny, phylogeography, origins of commensalism, adaptation, and dynamics of secondary contacts between subspecies. Explorations of mouse behaviour cover the nature of chemical and ultrasonic signalling, recognition, and social environment. The importance of the mouse as an evolutionary model is highlighted in reviews of the first described example of meiotic drive (*t*-haplotype) and the first identified mammalian speciation gene (*Prdm9*). This detailed overview of house mouse evolution is a valuable resource for researchers of mouse biology as well as for those interested in mouse genetics, evolutionary biology, behaviour, parasitology, and archaeozoology.

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Evolution of the House Mouse

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Preface

As we write this preface in May 2011, it is 70 years since publication of the first book on the biology and genetics of the house mouse, authored by the staff of the Jackson Laboratory (*Biology of the Laboratory Mouse* [1941]), and 30 years since publication of R. J. Berry's seminal edited monograph, *Biology of the House Mouse* (1981). In this vein it is perhaps interesting to further explore the historical context of the house mouse in evolutionary biology: this year we celebrate the 145th anniversary of Gregor Mendel's seminal paper 'Versuche über Pflanzen-Hybriden' (*Verhandlungen des naturforschenden Vereins Brünn*, 4, 3–47 [1866]). Though his laws of inheritance are described using experiments on peas, it has been speculated that Mendel initially bred and crossed mice in his rooms of the Augustinian Abbey of St Thomas in Brno, not far from the laboratory of one of the present editors. In 2012, when *Evolution of the House Mouse* is to be published, it will be 110 years since L. Cuénot in France and A. D. Darbishire in the United States used house mice to provide the first independent confirmation of Mendel's laws; 80 and 70 years since J. B. S. Haldane's *The Causes of Evolution* and J. Huxley's *Evolution: The Modern Synthesis*, respectively; 60 years since Ursin's paper on the Danish house mouse hybrid zone; 40 years since K. Theiler's *The House Mouse*; and ten years since the first draft of the mouse genome (Mouse Genome Sequencing Consortium) was made available online.

We are living in an ever-accelerating world of information. Scientific data are gathered with increasing pace, and mouse-related research is at the forefront of this flood. Our intention is to reflect this rapid development and bring together in one easy reference a snapshot of current knowledge regarding the evolution of the house mouse. In this we want to follow in the footsteps of excellent and influential books such as *Origins of Inbred Mice* (Morse, 1978), *Biology of the House Mouse* (Berry, 1981), *The Mouse in Biomedical Research* (Foster *et al*., 1981), *Genetics in Wild Mice* (Moriwaki *et al*., 1994), and special issues of *Current Topics in Microbiology and Immunology* (1978) and the *Biological Journal of the Linnean Society* (1990, 2005). Since the latter publication, which was based on the proceedings of the symposium on *The Genus Mus as a Model for Evolutionary Studies* (edited by J. Britton-Davidian and J. B. Searle, 2005), significant progress in almost every field of mouse research has been published, while areas not covered in the symposium have seen a growth of interest (e.g. olfactory and acoustic communication, morphology and development, MHC, the *t*-haplotype, phylogeography, parasites, hybrid sterility).

Although this book is targeted primarily at professionals working in mouse-related research, we hope it will also be of interest to scholars of evolutionary biology, and perhaps also to scholars of human history, as it appears the genetic record of association between mouse and man can tell us of events for which there is no written record. We hope this book will serve not only as a resource for researchers entering these fields, but also to highlight the cooperative nature of research across labs and generations. In this we are inspired by Barbara Dod, who throughout her career at University of Montpellier, working on the first studied region of the European house mouse hybrid zone, the Jutland peninsula, sought to break down barriers between house mouse research groups, and in doing so started many lasting friendships.

We thank all who helped with preparation of the book, especially all the contributors and those colleagues who took time out from busy schedules to review particular chapters. We are also grateful to Ivan Horáček, Gregg F. Gunnell, and Russell L. Ciochan for encouraging us to edit this monograph and the staff at Cambridge University Press for their help and support throughout its preparation.

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Foreword: Mice and (wo)men – an evolving relationship

House mice and humans have shared their environment over many millennia, presumably ever since mice spread from their origin in northern India and found a welcoming habitat in the cereal stores of early farmers. Mice have made much use of their human hosts, who have fought an often losing battle against their unwanted guests (Meehan, 1984; Young, 1986; Drummond, 2005). In AD 930, a Welsh king, Hywel Dda ('Hywel the Good'), published a standard price list for cats: one penny for a newborn kitten, tuppence [two pennies] for an inexperienced youngster, but fourpence for a cat once it had caught a mouse. Keeler (1931) points out that the word for mouse in Sanskrit (*mūṣaka*) is derived from a verb *mūṣ* [*mush*] meaning 'to steal' and suggests that this implies the species' pilfering habits were well known at least as early as the second millennium BC. Keeler writes of a 'mouse cult' in Asia Minor and records a number of examples of domestication and even worship by the ancient Greeks and Romans. Such familiarity with mice meant that variant animals would be noted. White mice are mentioned by many classical authors. It is said that the first written record of a variant was in a Chinese dictionary around 1100 BC, describing dominant spotting.

The Latin word for a mouse is *mus*. Pliny the Elder (AD 23–79) named the house mouse *musculus*, the little mouse, to distinguish it from the rat, its larger relative. Formally, of course, the binomial *Mus musculus* dates from Linnaeus, who presumably based his knowledge on the light-bellied mice around his home in Uppsala, Sweden, although no specimen exists in his collections. He wrote that it is 'an animal that needs no description: when found white it is very beautiful, the full bright eye appearing to great advantage amidst the snowy fur. It follows mankind, and inhabits all parts of the world except the Arctic.' Because of the priority of naming in taxonomy, the light-bellied species or subspecies is properly labelled *Mus musculus* (or *M. m. musculus*), meaning that another name is needed for the dark-bellied form. Albert Magnus, writing in Paris in the first half of the thirteenth century, referred to *Mus domesticus*, as did Conrad Gesner in Zurich in the mid-sixteenth century, and in Britain, Robert Sibbald in 1684 and John Ray in 1693. The first post-Linnean reference to *M. domesticus* was by John Rutty, who published *An Essay towards a Natural History of the County of Dublin* in 1772. In it, he lists '*Mus domefticus*. The Houfe-Moufe', with no embellishment or description. The International Commission on Zoological Nomenclature (1990) have now agreed that the name *domesticus* is legitimate, and is available for use either as *Mus domesticus* (Schwarz & Schwarz, 1943), or as *Mus musculus domesticus* (Schwarz & Schwarz, 1943).

In the early days of modern science, Robert Hooke (1635–1703) used a mouse to study the effects of increased air pressure. He does not state where the mouse came from. William Harvey (1578–1657) used mice in his anatomical studies, and Joseph Priestley (1733–1804) gives a delightful account in his *Experiments and Observations on Different Kinds of Air* (1775) of his work with mice, including how he trapped and maintained them. Half a century later, a Genevan pharmacist named Coladon bred large numbers of white and 'grey' mice and obtained segregations in agreement with Mendelian expectation 36 years before Mendel published his work on peas (Grüneberg, 1957). Indeed Sturtevant (1965) has even suggested that Mendel originally worked out his 'laws' in mice, but suppressed his results for fear of antagonizing his ecclesiastical superiors – medieval churchmen frequently commented on the 'voluptuous and libidinous habits' of mice (and, it is said, bred them so as surreptitiously to observe their wicked behaviour).

Sturtevant's idea of Mendel as a mouse geneticist is not too far-fetched. R. A. Fisher showed that Mendel's published work on peas was much closer to statistical expectation than expected (Fisher, 1936); he suggested that perhaps the pea work was really a demonstration of a factorial scheme which Mendel had previously discovered. Support for this comes from Mendel's biographer, who notes 'Mendel used to breed mice in his rooms, grey mice as well as white mice, crossing these varieties ... Mendel tells us nothing about this matter ... The silence is readily comprehensible ... [He] had to walk warily, for his bishop had a prejudice against him' (Iltis, 1932: 105).

Keeler (1931: 16) records that '[d]uring the nineteenth century, a number of European zoologists bred fancy mice [mainly coat colour variants] ... They accumulated valuable information, but the meaning of these data remained unknown until the rediscovery of Mendel's work in 1900 (Davenport, 1900).' New breeding experiments were quickly set up to test the truth and extent of Mendel's work, and within months Cuénot (1902) in France, Darbishire (1902) in the United States, and Bateson (1903) in Britain showed unequivocally that Mendelian segregations operated in mice. Haldane *et al.* (1915) used Darbishire's data to demonstrate that linkage, discovered in *Drosophila* by Morgan (1910), operated also in mammals, thus laying the basis for genome mapping. Searle (1981) has described the exponential increase in knowledge of inherited variants and linkage groups. The mouse genome was published in 2002 (Mouse Genome Sequencing Consortium, 2002).

Meanwhile, Robert Yerkes (1876–1956) at Harvard began a series of investigations in 1903 on behaviour in 'waltzing' or 'dancing' mice, a variant known in China from at least AD 80, although Yerkes obtained his animals from animal dealers in the eastern United States (Yerkes, 1907). His technique of comparing genetically related variant and non-variant animals to explore the effects of genetic change was very powerful and has burgeoned ever since.

Early mouse studies were carried out on mice obtained from a variety of sources. Laboratory mice in the modern sense can be said to date from 1907, when a Harvard undergraduate, C. C. Little (1888–1971), began to study the inheritance of coat colour under the supervision of W. E. Castle (1867–1962) at the Bussey Institute of Harvard University. Two years later, Little obtained, probably from Miss Lathrop (see below), a pair of 'fancy mice' carrying alleles for the recessively inherited traits dilute (*d*), brown (*b*) and non-agouti (*a*). He inbred their descendants by brother–sister mating, and produced thereby the first inbred mouse strain (DBA).

Castle did not believe in the value of so-called 'pure strains', and after army service in the First World War, Little moved to the Carnegie Institute at Cold Spring Harbor, where he was joined by L. C. Strong (1894–1982) and began the development of a range of inbred strains, largely descended from mice provided by Abbie Lathrop. Strong joined at a time when a paratyphoid epidemic had killed most of Little's animals. Strong (1978: 49) recorded,

> I was obliged to capture wild mice and start sorting out their hereditary traits through the tedious processes of mate, wait, select, and mate again . . . We kept the wild mice under the bed in our honeymoon tent . . . Meanwhile it became obvious that susceptibility and resistance to transplanted tumours were indeed genetically controlled [which] bent my mind to the task of remodelling *Mus musculus*.

Abbie Lathrop (1868–1918) was a failed poultry farmer, who turned to raising small animals for sale as pets. She started with a single pair of waltzing mice she obtained near her home in Granby, Massachusetts, and advertised for more animals as orders came in. The *Springfield Sunday Republican* for 5 October 1913 (cited by Morse, 1978: 11) wrote of her: 'After she had sold 200 or 300 mice, Miss Lathrop thought that the resource of mouse farming as a business must be very nearly at an end, since the offspring from that number would be enough to supply pets for the entire younger generation, but the orders continued to come in.' More and more of these orders came from research laboratories, including the Bussey Institute where Castle and Little were working. From around 1910 until her death in 1918, Miss Lathrop's sheds contained more than 11 000 mice, several hundred guinea pigs, rabbits, and rats, and occasional ferrets and canaries.

Little left Cold Spring Harbor in 1922 to become President of the University of Maine, and then in 1925 President of the University of Michigan at Ann Arbor, taking his mice with him on both occasions. Disagreements over administration issues forced him to leave Ann Arbor, and he moved with his mice to a site on

Mount Desert Island in Maine, to land donated by a family friend, George Dorr. There he established the Roscoe B. Jackson Memorial Laboratory, largely financed by Roscoe Jackson, head of the Hudson Motor Company, and by Edsel Ford, son of Henry Ford, founder of the Ford Motor Company. The Jackson Laboratory is now a world centre of mouse research (Lauber, 1971; Holstein, 1979; Rader, 2004). Festing and Fisher (2000) list 17 Nobel Prizes awarded for research associated with or stemming from the Jackson Laboratory; five more prizes have been given since their 2000 list. Little's main emphasis was on the determinants of cancer; he saw his and the laboratory's task as 'building a better mouse' for research (Rader, 2004: 11). The staff of the Laboratory collaborated in a major volume of information about laboratory mice, which summarized most of the information available at the time (Snell, 1941; Green, 1966).

For many years, research at the Jackson Laboratory and other centres used mice as little more than experimental tools, with strictly enforced breeding protocols and defined husbandry techniques, developing animal strains which performed uniformly in controlled experiments (Fox and Witham, 1997; Taft *et al.*, 2006). However, increasingly, signs appeared that standardized laboratory mice might give an incomplete or even a biased picture of mouse biology. Interest in transplantation led to mice being brought into laboratories from many places (Klein, 1975, 1986). Inherited variation was the basis of the differences between inbred strains, but the commonly used strains only carried a small part of the variation found in wild mice. House mice are found almost throughout the world – in deserts and tropical islands, from sea level to 3000 metres or so above, in mountains, usually but certainly not always in contact with humans. Genes are certainly not distributed uniformly throughout the animals' range. Taxonomists have long recognized local forms of the species (or species group). At least some of this diversity is related to maintaining body temperature. Many authors have shown that energy-dependent traits are variable and adaptive (Berry and Bronson, 1992). Lynch (1994) found that the architectural complexity of mouse nests (which is an inherited trait) is greater in mice from cold latitudes than from warm ones. Furthermore, in regions where they have no enemies, mouse populations may reach plague proportions, with the amplitude of different outbreaks dependent on environmental factors (Singleton *et al.*, 2003).

All this means that genetic variation and its distribution cannot properly be neglected in mouse studies. House mice are very variable: Ellerman (1941) listed 189 house mouse taxa in 43 species. Schwarz and Schwarz (1943) sought to bring some order to this. They lumped 133 named forms into 15 subspecies of a single polytypic species, *Mus musculus Linnaeus*, which they bunched into four groups (*wagneri, spicilegus*, *manchu*, and *spretus*). They believed *M. musculus wagneri* had given rise to nine commensal forms, including the common western European form, *domesticus*, while *spicilegus* and *manchu* gave rise to one each; in their scheme, Linnaeus' *musculus* was derived from *spicilegus*. This somewhat crude taxonomy has been progressively refined, with the genetic relationships and origins of the different groups codified and clarified. The results of many of these studies are described in this volume.

Two positive outcomes of the classical period of taxonomy are worth noting. Gropp *et al*. (1970) found that a population of mice from a Swiss valley originally described as a distinct species (*Mus poschiavinus*) on the basis of its colour and size (Fatio, 1869) had seven pairs of Robertsonian translocations in its chromosome set, giving a diploid count of 26 instead of the normal 40. Such Robertsonian races have been found to be comparatively widespread, particularly in *domesticus*. Second, Selander *et al*. (1969) used inherited biochemical variants to investigate a hybrid zone between *domesticus* and *musculus* in Denmark, originally described by Ursin (1952). Both of these studies have given rise to enormously profitable research, described herein.

Laboratory mice have contributed enormously to our knowledge of the genetics and reaction systems of mammals under prescribed and repeatable conditions, but they can only be indicators of what happens in the real world (Berry, 1980; Miller *et al*., 2000, 2002). The findings of multiple Robertsonian races and the intricacies of the hybrid zone leads to the crucial consideration that house mice have an ecology as well as a limited existence as constrained confinement as laboratory animals. Although humans have long fought with mice as pests and indulged in them as show animals, it was only when the necessity of reducing the damage to stored food during the Second World War was faced that the lack of knowledge of mouse ecology was realized. The Oxford University ecologist Charles Elton was commissioned by the British government to study and advise on the control of rodent pests. He assigned H. N. Southern to work on mice. Southern's work (Southern, 1954) was continued by Crowcroft (1966) and led the way to a host of ecological and behavioural investigations.

Geneticists (or evolutionists) and ecologists routinely proclaim the need to integrate their findings, but too often ignore results outside their own discipline. This lack of cooperation began early: with the hiatus about evolutionary mechanisms which lasted for decades following the findings of the geneticists in the early 1900s; it was only finally repaired by the publication of Julian Huxley's *Evolution: The Modern Synthesis* in 1942 (Mayr and Provine, 1980). Then another period of mutual misunderstanding arose during the 1970s and 1980s, precipitated by the discovery of the large amounts of inherited variation shown by applying electrophoresis to population samples, destroying the wisdom of the time which stated that evolutionary change was constrained by limits imposed by genetic loads and the cost of natural selection. The resulting debates again drove the recognition that geneticists and ecologists need each other to fully understand evolutionary situations (Berry *et al.*, 1992). This book is a mature fruit of that recognition. It is a fitting successor to a number of publications which have integrated mice into evolutionary disciplines with varying but growing success (Lindzey and Thiessen, 1970; Berry, 1981; Foster *et al.*, 1981; Potter *et al.*, 1986; Brain *et al.*, 1989; Berry and Corti, 1990; Moriwaki *et al.*, 1994; Britton-Davidian and Searle, 2005). It will not be the last word on the subject, but it is an indispensable milestone for those taking the mouse route to understand evolutionary processes.

The house mouse has been a model and a tool for biology ever since its first recorded use in comparative anatomy by William Harvey in 1616. It has illuminated evolutionary thought since the earliest days of genetics (and, as noted above, perhaps even earlier). It took its place in the neo-Darwinian synthesis alongside *Oenothera*, *Gammarus*, *Drosophila*, *Equus*, and other classical organisms. It has become a model in evo-developmental comparisons and as such gives increasing grist to biomedical pathology. And as our knowledge of its genetics and ecology grows, the species must have considerable potential to act as a motor to drive evolutionary understanding to new heights (Berry and Scriven, 2005).

Professor R. J. Berry

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