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Rodentia: a model order?

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In the UK, every good discussion takes place over a nice cup of tea. Our book was no exception, with the first seeds of the idea being sown during teatime in the tearoom of the Department of Zoology of the University of Cambridge (United Kingdom). Our original thought was to write a review on the evolution of the masticatory apparatus of rodents, but we quickly realised that such a review could be as long as a book, and that no journal would accept it for publication. Thus, the idea for this volume was first voiced as a joke: 'what about writing a book then?'. Sometimes, a small joke can have long-term consequences and this one has been running for over two years.

At some point, the conversation turned to the fact that the last authoritative work on the Rodentia, *Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis*, edited by W. Patrick Luckett and Jean-Louis Hartenberger (1985a), was nearly 30 years old. That volume was the result of a NATO Advanced Research Workshop held in Paris in July 1984 (Figure 1.1). Similarly, the current volume was preceded by a symposium on rodent evolution at the 10th International Congress of Vertebrate Morphology in Barcelona in July 2013, convened by the editors and Robert Druzinsky. Although not precisely the same in content, many of the chapters in this volume were presented at that symposium. Despite the apparent lack of enthusiasm for rodents in the intervening 30 years between these two volumes and symposia, it was clear to us that the study of rodents is currently going through a renaissance period. The widespread use of mouse models in developmental, behavioural and genetic studies has sparked interest in the biology of rodents as a whole, and developments in computing technology have enabled great leaps forward in our understanding of the rodents. Advances in the use of molecular data in phylogenetic studies are leading to consensus on the relationships within this large order (e.g. Blanga-Kanfi *et al.*, 2009; Fabre *et al.*, 2012), whilst recent fossil and extant finds have greatly increased our understanding of the evolutionary history of the rodents (e.g. Jenkins *et al.*, 2005; Antoine *et al.*, 2012). In addition, improved morphometric techniques are enabling a greater comprehension of how the skull, mandible and skeleton have evolved (e.g. Hautier *et al.*, 2011, 2012), and complex computer simulation methods are allowing the functional implications of rodent morphology to be inferred (e.g. Cox *et al.*, 2012, 2013).

Our goal in developing this book is to provide the best, most comprehensive review of current research on the order Rodentia as a whole. Similar to the Rodentia itself, the rodent research community is very diverse and we cannot claim that this volume

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Figure 1.1 Photograph taken at the NATO Advanced Research Workshop held in Paris in July 1984. In the foreground, from left to right, Patrick Luckett, Christiane Denys and Jean-Louis Hartenberger. In the background, from left to right, Albert Elmer Wood and René Lavocat.

represents all aspects of rodent biology studied today. However, this volume brings together active researchers from many different disciplines within rodent biology to review the current understanding and new developments within their particular field. Within this broad remit, the volume covers many disciplines, such as comparative anatomy, molecular biology, functional morphology, palaeontology, developmental biology, phylogenetics and biomechanics. We hope that this book will be held in the same high esteem as the Luckett and Hartenberger *Evolutionary Relationships Among Rodents* volume, and will inspire new research as well as stimulate interest in rodent evolution. Our goal in this introduction is therefore not to achieve an overview of the diversity of rodents but to introduce the order as a whole, to review their evolutionary relationships within the mammals and to consider the field of rodentology: what it has achieved, where it stands at present and what directions it may take in the future.

Incisive and Diverse: an ID portrait of rodents

Entering into the world of rodents is nontrivial as there are, at the time of writing, 2277 living species of rodents (Wilson and Reeder, 2005). This number may not appear huge to specialists who study amphibians (6433 species), reptiles (9084 species),

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birds (9998 species), fishes (31300) or insects (>1000000 species), but it is a big deal to a mammalian biologist. When compared to the 5490 species of mammals, which still make up one of the smallest animal groups, rodents represent almost half of the extant mammalian diversity (41% to be precise) and it will be difficult to find a single chapter of this book that does not allude to the extreme diversity of the order. You would probably expect all biologists to wax lyrical about the species they study, but rodents truly are a group to which superlatives apply, and their tremendous diversity makes them a unique mammalian model. Of course, people who study something unique tend to feel they are unique themselves, and we like to call ourselves 'rodentologists', probably just to distinguish ourselves from other mammalogists, or to copy primatologists who study that trendier but poorly diversified sister clade to rodents. While there probably are more primatologists than gorillas in the wild, rodentologists are unlikely to ever become as numerous as most rodent species; however, this book aims to contribute a little to the very optimistic dream of reversing that trend. Over the past century, the house mouse has emerged as the mammalian 'model organism' *par excellence* (Macholán *et al.*, 2012), in part due to its ease of maintenance, short reproductive cycle, and scope for genetic manipulation. However, as we try to imply in the title of this introductory chapter, it is unfair to reduce rodents to a bunch of rats and mice. Owing to their small-to-medium size, short breeding cycle and high adaptability, rodents have repeatedly occupied similar niches and colonised similar environments at different times during their long and blooming evolutionary history. If the mouse can be considered as a model organism for various studies, Rodentia as a whole should be considered as a 'model group' for studying convergent evolution and for investigation of macroevolutionary patterns.

While mice are often considered as the best mammalian model organism, it is nevertheless clear that mammals frequently depart from phenotypic and developmental patterns seen in mice and this is particularly true with regard to their dentition. Mice, like all rodents, are equipped for gnawing with a masticatory apparatus showing chisel-like incisors associated with complex cranial musculature. Rodents are so specialised that their masticatory apparatus can even be seen as a gnawing machine (Druzinsky, this volume, Chapter 12). The word 'rodent' itself refers to this unique morphological characteristic; it comes from the Latin *rodere*, which means 'to gnaw'. However, chisel-like incisors are not restricted to Rodentia, and the mammalian evolutionary history shows many examples of independent acquisition of diprotodont skulls, including primates (e.g. Daubentoniidae, Plesiadapidae, Carpolestidae, Paromomyidae), hyraxes (Procaviidae), notoungulates (Toxodonta), tillodonts (Esthonychidae), 'insectivorans' (Microsyopidae, Mixodectidae, Apatemyidae), marsupials (Diprotodontia) and multituberculates (Allotheria), as well as, of course, other Glires (Lagomorpha, Eurymylidae). In fact, several autapomorphic features allow rodents to be distinguished from all these mammals (Hartenberger, 1985; Druzinsky, this volume, Chapter 12): a single pair of enlarged upper and lower ever-growing incisors (with the loss of I^3); an incisor with enamel restricted to its anterior face; a long diastema between the incisors and cheek teeth on both the mandible and the skull; loss of the paraconid on the lower

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cheek teeth; the orbital cavity lying just dorsal to the cheek teeth; the ramus of the zygoma lying anterior to the first cheek teeth; and a trough-like glenoid fossa (with the loss of the postglenoid process). Landry (1999) tentatively recognised four other autapomorphic features: the hamulus reaching back to the ear region; the possession of a flat 'falciform' bone; a medial tarsal bone (modified sesamoid); and a sensory bristle on the wrist. Most of these autapomorphic features have been defined on the skull probably because this is where the most distinctive characters of the order are concentrated. This association of morphological characters is so distinctive that, in comparison to other placentals, the first representatives of the clade were easily recognisable in the Paleogene fossil record. Indeed, from a quick look at the fossil record, it is easy to get the impression that rodents have always been rodents. Paradoxically, the apparent simplicity of this ordinal classification masks a number of serious challenges. First, the early acquisition of the diprotodonty and associated rodent-like features during the evolutionary history of rodents has made it difficult to recognise the potential ancestral condition for the group. Second, strong functional constraints linked to the acquisition of a diprotodont skull may have limited the number of possible evolutionary pathways and promoted convergent evolution, which in return has hampered attempts to establish an intraordinal classification (see Hautier *et al.*, this volume, Chapter 10).

More than in any other mammalian order, cases of convergent and parallel evolution have repeatedly been reported in Rodentia, especially in relation to their cranial morphology, leading to the impression that homoplasies can affect any morphological component of the body in any of the branches of the rodent tree of life. However, we may simply be lulled into thinking this because of their incredible success in diversifying. As long as 30 years ago, Hartenberger (1985: p. 25) raised the question of whether or not convergent evolution was more frequent in rodents: 'are homoplasies more frequent in rodents than in other mammals? I really do not know, but, if it is the case, Rodentology, more than any other taxonomic group, needs the collaboration of different research fields'. Ironically, it is probably the unique combination of the extreme diversity of the order Rodentia with the extreme morphological specialisation of its members that compelled specialists from different fields to join forces in order to unravel the mystery of this extraordinarily successful radiation, derived from a single common ancestor that lived at least 57 million years ago (Meng and Wyss, 2005).

Seeking rodent relatives: are rodents Glires?

As touched upon in the above section, rodents have many distinctive characteristics, particularly with regard to the dentition, which have led to the Rodentia being recognised as a cohesive group since the time of Linnaeus. However, their position within the mammalian family tree has historically been much less obvious. Indeed, in the conclusion to their volume, Luckett and Hartenberger (1985b) identified the relationship of rodents to other eutherian mammals as one of the major issues to be addressed by rodentologists. Thankfully, over the past 30 years, a broad consensus on these relationships has been reached, largely due to the use of molecular phylogenetics.

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Given that no chapter in this book addresses this topic directly, here we provide a short historical background.

The earliest contender for a sister-group to the rodents was, of course, the lagomorphs (rabbits, hares and pikas). Such is the similarity between lagomorph and rodent dentition, that *Lepus* was included with a number of rodents in the group Glires in the first edition of Systema Naturae (Linnaeus, 1735), and was still there in the much expanded tenth edition (Linnaeus, 1758). Similarly, most other classifications at this time made no distinction between rodents and lagomorphs and placed them together in a group, variously named 'Rosores' (e.g. Storr, 1780), 'Rongeurs' (e.g. Vicq d'Azyr, 1792; Cuvier, 1798, 1800) or 'Prensiculata' (Illiger, 1811), as well as the Linnaean 'Glires' (e.g. Blumenbach, 1779). Classification of species within the rodent group was attempted by Illiger (1811), who erected eight rodent families, one of which contained rabbit-like forms and was termed 'Duplicidentata' to reflect the two pairs of incisors in the upper jaw. This separation of rabbits and hares from all other rodents was adopted by almost all subsequent classifications, although the companion term 'Simplicidentata', for rodents with one pair of upper incisors, was not introduced until over half a century later (Lilljeborg, 1866).

Rodents and rabbits remained separate, but within the same order (named either Glires or Rodentia), in most of mammalian classifications of the late nineteenth century and early twentieth century (e.g. Gill, 1870; Flower, 1883; Cope, 1891; Weber, 1904; Gregory, 1910). However, the suspicion had begun to arise that the origins of rabbits, hares and pikas were sufficiently different from those of other rodents to warrant the creation of a separate order. This was implicit in Tullberg (1899) and was formally proposed by Gidley (1912), who placed rabbits and their relatives into the order Lagomorpha, using the nomenclature of Brandt (1855). As the twentieth century progressed, many researchers began to believe that not only should rabbits and hares be in a separate order to rodents, but also that the Lagomorpha and Rodentia were not particularly closely related (Wood, 1940). Although Simpson (1945), in his seminal classification of mammals, retained the idea of closely related lagomorphs and rodents within the cohort Glires, the accompanying notes indicate that he had little confidence in the grouping. McKenna (1975) abandoned the idea of Glires altogether, placing the lagomorphs in close association with the Macroscelidea (elephant-shrews) in the clade Anagalida. The inter-ordinal relationships of the rodents were not determined at all in the McKenna (1975) classification, with Rodentia simply given the status 'incertae sedis' within the large clade 'Epitheria' (all placental mammals except Xenarthra and Pholidota).

Despite this move towards the separation of rodents and rabbits, morphological analyses from the late 1970s onwards began once again to recover Glires as a monophyletic group (Luckett, 1985; Novacek, 1985, 1986), based on characters of the skull, teeth and foetal membranes. This view of rodent relationships persisted through to McKenna and Bell's (1997) update of Simpson (1945). Even after the radical reorganisation of the mammalian family tree heralded by the use of molecular phylogenetic techniques (Springer *et al.*, 1997; Stanhope *et al.*, 1998), the concept of the group Glires containing

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the separate, but closely related, orders of Rodentia and Lagomorpha has remained. Druzinsky (this volume, Chapter 12) notes a number of morphological synapomorphies uniting the Glires including: loss of the first and fourth incisors and the canines in the upper and lower jaws; loss of the lower third incisor; ever-growing upper and lower second incisors; loss of the lingual enamel on the second incisors; a diastema between the incisors and cheek teeth; and loss of the post-glenoid ridge.

Aside from the lagomorphs, the relationship of rodents to other extant mammals has been highly uncertain until relatively recent times. Linnaeus (1758) placed rodents in a larger grouping of clawed mammals, named 'Unguiculata', an alliance that included primates, flying lemurs, bats, lipotyphlan insectivores, carnivorans and edentates (the modern orders Xenarthra, Pholidota and Tubulidentata). This association is also found in the classifications of Scopoli (1777), Lacépède (1799), Cuvier (1800) and Cope (1891). Similar groupings involving some or all of these mammalian orders were also erected on the basis of brain morphology (Bonaparte, 1837; Owen, 1868) and placental anatomy (Huxley, 1872). Gregory (1910) maintained the concept of 'Unguiculata' but removed rodents from it and, following this approach, few subsequent classifications attempted to ally the rodents with these 'unguiculate' orders. However, it should be noted that some of the first mammalian phylogenies constructed using molecular techniques recovered a group not unlike Linnaeus's Unguiculata albeit minus the edentates (Shoshani *et al.*, 1985).

Towards the later part of the twentieth century, several classifications linked the rodents (and lagomorphs) with the Macroscelidea, within the larger Anagalida (Novacek, 1986; McKenna and Bell, 1997). However, this association was not supported by later molecular analyses that completely rearranged the mammalian family tree and placed the elephant-shrews in the grouping of endemic African mammals, the Afrotheria (Springer *et al.*, 1997; Stanhope *et al.*, 1998). These molecular phylogenies, and many of those that followed (e.g. Madsen *et al.*, 2001; Murphy *et al.*, 2001a,b; Amrine-Madsen *et al.*, 2003; Springer *et al.*, 2003; Bininda-Emonds *et al.*, 2007; Meredith *et al.*, 2011), have largely agreed with one another regarding the interrelationships of the eutherian orders. These studies indicate that rodents and rabbits are indeed closely related and form the sister-group to primates, tree-shrews and colugos ('Euarchonta' i.e. the Archonta of Gregory (1910) without bats), within the descriptively (if unaesthetically) named superorder 'Euarchontoglires'. This position of rodents within the mammalian family tree, prefigured to some degree by early sequence analysis of eye lens proteins (de Jong, 1985), has been stable for a number of years now and appears to signify a consensus amongst mammalian systematists.

The search for relatives of rodents amongst fossil groups has naturally concentrated, in many instances, on groups showing some degree of incisor enlargement. Thus, potential candidates for the ancestors or sister-group to rodents have included multituberculates (Major, 1893), tillodonts and taeniodonts (Cope, 1888) and mixodectids (Osborn, 1902). Early primates, such as plesiadapiforms, were suggested as possible rodent relatives by several authors (Wood, 1962; McKenna, 1969; Van Valen, 1971). However, it was noted that this would be a relationship based on homoplasy, as

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the enlarged teeth of rodents are the retained deciduous second incisors, whereas they are believed to be the first incisors in plesiadapiforms (Luckett, 1985). McKenna (1969) alternatively proposed a relationship between rodents and leptictids; this was supported by Szalay (1985), based on postcranial morphology. A close affinity between rodents and the Palaeocene eurymylids of Asia has had support from a number of researchers (Li and Ting, 1985; Meng and Wyss, 2001; Meng *et al.*, 2003) based on similarities of the dentition. The most recent analyses suggest that the Eurymylidae are indeed the sister-group to Rodentia, and that these two clades together (Simplicidentata) form the sister-group to the Duplicidentata (Lagomorpha plus stem fossil forms) within a monophyletic Glires (Meng and Wyss, 2005).

Thirty years of rodentology: what's next? Past, present and future analyses of rodent phylogeny

Writing this volume gave us a unique opportunity to look back over rodentologist shoulders to see where the rodent research has been, what was accomplished in 30 years, and what will happen next.

Back to the past

Unquestionably, the inspiration for this book was *Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis* (Luckett and Hartenberger, 1985a). However, our book is not modelled on that volume because the whole face of rodent research has changed considerably over the past 30 years, and the same was true in the years preceding the original publication of *Evolutionary Relationships*: 'during the past 30 years, greater emphasis has been placed on the classification of rodents than on the reconstruction of their phylogeny. Such classifications have focused almost entirely on the relative merits of different components of the masticatory apparatus [. . .] as key features for understanding the major pathways of rodent evolution' (Luckett and Hartenberger, 1985b, p. 685). In *Evolutionary Relationships*, considerable space was devoted to deciphering relationships both within the order Rodentia and between rodents and other eutherian orders: 'semantic disagreements over the "best" approaches to phylogenetic analysis were kept to a minimum perhaps because most participants were anxious to learn about any evidence that might shed light on the uncertainties surrounding the possible evolutionary relationships among the 50 families of extant and fossil rodents' (Luckett and Hartenberger, 1985b, p. 685). At that time, the sister-group relationships of Rodentia was still an open question and the burning concept of the Glires had not yet reached a consensus. The Glires concept is now put forward as an example for phylogeneticists because it succeeds in reconciling morphological data with molecular results.

The Luckett and Hartenberger book (1985a) has massively influenced the past three decades of rodentology. It is difficult to think of a single article on rodent cranial morphology that does not reference one or more of its chapters, as in fact do 13 chapters of this volume. We are particularly pleased, in this volume, to include two chapters authored by contributors to *Evolutionary Relationships* (Christiane Denys in Chapter 7 and Monique Vianey-Liaud in Chapter 20), as well as a preface from its editors, Patrick Luckett and Jean-Louis Hartenberger. A quick online search clearly highlights the popularity of their book. Over the past 30 years, *Evolutionary Relationships Among Rodents* has been cited more than 1400 times. It is also interesting to note that the most cited chapters are: 'Rodent macromolecular systematics' by Vincent Sarich; 'The order Rodentia: major questions on their evolutionary origin, relationships and suprafamilial systematics' by Jean-Louis Hartenberger; and 'Superordinal and intraordinal affinities of rodents: developmental evidence from the dentition and placentation' by Patrick Luckett. The success of these three chapters reflects the increased interest of rodentologists in molecular, palaeontological and developmental data. In their concluding chapter, Luckett and Hartenberger (1985b) proposed seven important areas for future investigations of rodent research, all of which are linked to phylogeny: cranial morphology and development; postcranial morphology; incisor enamel structure; molecular evolution and proteins; foetal membrane development; structural, functional and developmental studies of dentition; palaeontology and the stratigraphic framework. We do not have space here to review all the work that has been done in those different areas over the past 30 years; however, we can confidently affirm that, apart from the postcranial morphology, these topics have received extensive attention. References to these works can be found scattered across all chapters of the present volume: 'cranial morphology and development' is addressed in Chapters 5, 8, 10, 11, 13 and 14; 'postcranial morphology' in Chapters 19 and 20; 'incisor enamel structure' in Chapter 16; 'molecular evolution and proteins' in Chapter 2; 'structural, functional and developmental studies of the dentition' in Chapters 15 – 18; and 'palaeontology and the stratigraphic framework' in Chapters 3 – 9.

Present volume

Recent developments have emphasised the need to integrate the tools and data from molecular biology into morphological analyses, for example the use of gene circuits to help understand the evolution and development of rodent teeth and skeletal structure. In *Evolutionary Relationships Among Rodents*, Luckett and Hartenberger (1985a) stated that: 'Other problems of systematic relationships remain to be clarified, and it is our hope that future investigations will attempt to resolve these controversies by multidisciplinary analyses. If future research on rodent evolution is accomplished by collaborative efforts between paleontologists and neontologists, then one of the main goals of this [. . .] volume will have been attained' (p. ix). We believe that Luckett and Hartenberger's hope has been realised. With this new edited volume on rodent biology, we aim to highlight how interdisciplinary synergy is addressing the major challenge of understanding rodent evolutionary success. The full title of this book is *Evolution of the Rodents: Advances in Phylogeny, Functional Morphology and Development* but this is not intended to suggest that the three fields listed in the subtitle are treated in isolation in different chapters. Indeed, most chapters deal with all of these topics to varying degrees. For this reason we have not grouped the chapters into subsections as no arrangement could ever be a perfect fit for all chapters. That said, there is some logic to the order of the contributions in this volume. Chapter 2 (Fabre *et al.*) sets the scene by reviewing the phylogeny of the Rodentia as revealed by molecular analyses. The next seven chapters examine evolution and diversity in a number of selected rodent taxa, namely early sciurognaths (Dawson, Chapter 3), Tertiary phiomorphs (Barbière and Marivaux, Chapter 4), octodontoids (Verzi *et al.*, Chapter 5), dinomyids (Rinderknecht and Blanco, Chapter 6), African murids (Denys and Winkler, Chapter 7), sciurids (Roth and Mercer, Chapter 8), and marmots (Polly *et al.*, Chapter 9). These taxa are not chosen to give coverage to the entirety of Rodentia (that would require a very long book), but to highlight rodent groups that have been the subject of significant and interesting research in recent years. The two subsequent chapters (Hautier *et al.*, Chapter 10; Renaud *et al.* Chapter 11) highlight the use of a tool that has been particularly important for assessing morphological variability in rodents, namely geometric morphometrics. Following these contributions, the remaining nine chapters are directed at particular parts of the rodent anatomy: the masticatory apparatus (Druzinsky, Chapter 12; Cox and Jeffery, Chapter 13), the middle ears (Mason, Chapter 14), the teeth (Charles and Viriot, Chapter 15; Gomes Rodrigues, Chapter 16; Lazzari *et al.*, Chapter 17; Renvoisé and Montuire, Chapter 18), and the postcranium (Wilson and Geiger, Chapter 19; Vianey-Liaud *et al.*, Chapter 20).

Future of rodentology and of rodents through a conservation lens

To understand probable future research trends in rodentology, it is helpful to see how rodentology has evolved over the past 60 years. Before *Evolutionary Relationships*, research efforts tended to focus on classification rather than phylogeny. Then, following *Evolutionary Relationships*, more emphasis was placed on evaluating evolutionary intraordinal affinities using multidisciplinary analyses. Nowadays, thanks to the rise of molecular systematics, we can confidently affirm that we are working within a stable phylogenetical framework, and this opens up exciting opportunities to study morphological evolution from new perspectives. Like hamsters on a spinning wheel, rodentologists seemed to have gone around in circles by first using morphological characters to reconstruct phylogenetic relationships among rodents, and then phylogeny to understand morphological evolution. While early workers feared homoplasies, we are now in a position to try to assess the evolution of morphological variation in the framework of the phylogeny using multidisciplinary synergy in order to understand the core of convergent evolutionary processes.

Of course, not all parts of the rodent phylogeny are understood and a lot of work still needs to be completed to solve the puzzle of the rodent tree of life. However, this gap might be filled in the future through old museum specimen sequencing and fieldwork efforts. In fact, rodent systematicians are still in the age of taxonomic discoveries and several more decades will probably be required to uncover the full extent of the full

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extent of the outstanding biodiversity; there remains a tremendous amount of systematic work that needs to be done in the field and in museums. Additional mitochondrial and nuclear DNA investigations coupled to morpho-anatomical studies are required to shed light on some cryptic branches, especially in the mouse-related clade, as well as to better understand their complex evolution. In future, new molecular dating approaches will allow refinement of the way the evolutionary rate variations are described along the tree branches (see Chapter 2). The introduction of Next-Generation Sequencing (NGS) technology and new ancient DNA extraction methods represents a decisive step towards extracting genetic information from extant and extinct biological systems. There is no doubt that the use of this method on the whole Rodentia order will lead to a number of important breakthroughs in the very near future.

The study of the fossil record will remain one of the keys to interpreting the evolution of morphological features as it plays a vital role in enabling researchers to build a richer picture of the diversity achieved by rodents. By grouping substantial amounts of phylogenetic data, it is now possible to compare rates of morphological and molecular evolution. However, only phylogenetic methods that rely on the analysis of anatomical characteristics can take both fossil and extant species into account and still remain applicable to the entire Rodentia order. Moreover, only a detailed knowledge of the phylogeny of the Rodentia makes it conceivable to study phenomena of geographic dispersion for the group. Studying palaeontological data on its own will improve our understanding of the evolutionary and palaeobiogeographic history of the group and help to resolve any ambiguities, such as the controversy around their enigmatic arrival in South America (Antoine *et al.*, 2012).

If homoplasies are indeed more common in rodents than in other mammalian orders as is often suggested, then understanding function will be key to identifying the underlying causes of this convergence. Functional morphology is currently a vibrant research field, producing many new insights each year, and this is as true of rodents as of other taxa. Advances in technology are driving a great deal of this research, particularly in the areas of imaging science and functional simulation. The resolution that can be achieved by micro-computed tomography (microCT) is increasing year on year, enabling ever-greater detail to be visualised in osteological specimens (see e.g. Chapters 12–14). Furthermore, for even smaller specimens such as individual teeth, synchrotron facilities are becoming more accessible (e.g. Chapter 16). Yet, despite the wide use of imaging technology to study bone, soft tissues are far less frequently considered. It is our prediction that the study of musculature and other soft tissues will become increasingly important in the coming years for the understanding of function. This will involve alternative imaging techniques, such as MRI, or the use of histochemical stains to enable the visualisation of soft tissues with microCT. Much headway has been made in this area recently with the use of iodine potassium iodide to reveal rodent masticatory and cardiac musculature (Cox and Jeffery, 2011; Jeffery *et al.*, 2011; Stephenson *et al.*, 2012; Baverstock *et al.*, 2013), and experiments are ongoing to test the efficacy of other stains such as phosphomolybdic acid. State-of-the-art *in vivo* scanning techniques are also likely to play an important role in future rodent research, with *in vivo* CT, positron