

# 1

J. DAVID ARCHIBALD  
AND KENNETH D. ROSE

## WOMB WITH A VIEW: THE RISE OF PLACENTALS

**A**LTHOUGH EVOLUTIONARY SUCCESS IS A difficult if not impossible concept to define, we believe we know it when we see it. This is the case with the extant placentals, the clade of mammals to which we belong. Living placentals include only 1,050 genera and some 4,400 species (Wilson and Reeder, 1993)—compare this to just one of the other tetrapod clades, the birds, which has more than 9,000 species. Nevertheless, placentals range tremendously in their ecological diversity, from tiny shrews to the gargantuan blue whale, from pinnipeds swimming the frigid high-latitude oceans to the golden moles swimming the hot sands of southern Africa.

The evolutionary success of mammals is one of the few in evolutionary history for which we can offer an explanation. First, there is what Gould (1989) popularized as historical contingencies. For placental mammals, these were mode of reproduction, level of metabolism, and an ancestral, generalized quadrupedal stance (Archibald, 2001). Euviviparity, which includes lengthy *in utero* development of the embryo, requires that all support and sustenance come from the mother through the chorio-allantoic placenta. This mode of reproduction is unique to placentals. It allows the mother to continue normal activities while pregnant. Placentals, like other mammals, are endothermic, producing their heat through metabolic means. In small mammals, such as most rodents, between 80% and 90% of food goes toward maintaining endothermy (Vaughan et al., 2000). The common ancestor of all mammals, as well as that leading to eutherians, was a small, insectivorous quadruped that retained five digits on all four limbs. Such a generalized pattern permitted a wide

diversity of stance and locomotion in later eutherians. For example, placentals have limbs modified for greatly varied activities, including swimming, flight, digging, running, hopping, climbing, brachiation, and capture of prey.

Second, placentals had spread to all continents except Australia and possibly Antarctica by the time dinosaurs became extinct some 65 million years ago. Thus, they were serendipitously poised to inherit the ecological space vacated by dinosaurs. They began almost immediately to speciate, although it was millions of years before placentals gained in size and ecological diversity (Kirchner and Weil, 2001). But even by about 10–15 million years after the Cretaceous/Tertiary (K/T) boundary, the vast majority of major placental clades that we call orders are recognizable.

The study of the evolutionary history of mammals, or any other taxon, requires a well-established, testable argument for the relationship of the included species. As with many plants and animals, our current ideas of systematic relationships for mammals trace their beginnings to Linnaeus (1758). Table 1.1 shows a sampling of some better-known, higher-level classifications emphasizing the ordinal-level trends in classification starting with Linnaeus. This table focuses on placentals, but as early classifications had not yet realized the higher relationships of placentals, marsupials, and monotremes, the last two taxa were confounded with placentals in earlier classifications. One obvious trend since Linnaeus is the increase in recognized placental orders (or equivalents). From eight extant orders recognized by Linnaeus in 1758 and Cuvier in 1817, the number has increased to 18 today (Wilson and Reeder, 1993; McKenna and Bell, 1997; Murphy et al., 2001). Unquestionably, what has been meant by an order has changed over time. Even accounting for this, mammals that originally had been grouped solely on a shared body plan were often recognized as lineages or clades once evolution was widely accepted in the mid-nineteenth century.

Although Simpson (1945) provided one of the best reviews of the various higher taxa of mammals, Gregory's (1910) older treatment remains a superlative narrative of the history of mammalian systematics, even though it was published almost a century ago. Gregory (1910: 87) pointed to a number of modifications that changed and improved our understanding of mammalian systematics. Three stand out: "The anthropocentric classification . . . gives way to the evolutionary classification," "[d]iscovery and development of the principles of the evolution of the feet . . . and of the teeth," and "[r]eunion and integration of results of mammalogy, comparative anatomy, embryology, paleontology." The first of these changes placed humans with other primates rather than in a separate order (Cuvier's *Bimana* for humans disappears). The second of these differentiated homologies from homoplasies found among mammalian teeth and feet (e.g., there are groups of "even-toed" and "odd-toed" ungulates). The third saw the better integration of "soft" and "hard" anatomy (e.g., monotremes and marsupials are recognized to be only distantly related to placentals).

From the time of Simpson's classification in 1945 onward, there was the general perception that orders represented

true evolutionary lineages or clades. The orders Macroscelidea (Butler, 1956) and Scandentia (Butler, 1972) were the last two to be recognized at the ordinal level, resulting in the standard 18 anatomically based orders of placental mammals as listed by Wilson and Reeder (1993): Xenarthra, Insectivora, Scandentia, Dermoptera, Chiroptera, Primates, Carnivora, Cetacea, Sirenia, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla, Pholidota, Rodentia, Lagomorpha, and Macroscelidea. Although there were many studies that tried to link various orders based on anatomical data and to find the origins of these orders, few well-supported results were forthcoming. In other words, with a few possible exceptions (see below), these 18 orders were the most inclusive groups of placental mammals for which we had good evidence for monophyly. In some ways, little had changed since the time of Gregory. In 1910, he noted that Linnaeus' classifications of 1758 and 1766 were "really an attempt to express relationship between distinct orders (as they are now accepted), an attempt that was certainly premature in Linné's time, since even now when the content of mammalogy is a hundred times greater, the interordinal connections are still either wholly unsettled or at best more a matter of probability than of demonstrated certainty" (Gregory, 1910: 30).

There are four superordinal groupings, however, that have long had anatomical support (Table 1.1). The oldest and generally most consistent is the grouping of rodents and lagomorphs under some common name, the most familiar being Glires, a name dating back to Linnaeus in 1758 (first used as an order). With the exception of the classification of McKenna and Bell (1997), it is still commonly accepted. The next oldest superordinal grouping of extant placentals that has had consistent support is Gregory's (1910) Archonta. Although two of the original members, macroscelidids and chiropterans, are now removed, primates, tupaiids, and dermopterans remain. The third is Simpson's (1945) proposed Paenungulata, whose extant members are the proboscideans, hyraxes, and sirenians. This name has found wide acceptance, again with the exception of McKenna and Bell (1997), who used the name *Uranotheria* for the same grouping. The fourth and final is Xenarthra, which has been recognized as a superordinal clade since 1975 by McKenna, although he referred to it as *Edentata*. This usage continued with McKenna and Bell (1997) and in various molecular studies (e.g., Murphy et al., 2001). With this consistent history, it should be no surprise that four chapters of the present volume deal with these four superordinal groupings.

A major change in mammalian systematics since Simpson (1945) has been the advent of powerful techniques that enable the study of ever-increasing portions of the genome. It is impossible to point to any one study that brought these techniques to maturity, but certainly the research of Murphy et al. (2001) demonstrates the trend. Such studies have provided strong evidence for four superordinal clades: Afrotheria, Xenarthra, Euarchontoglires, and Laurasiatheria (Table 1.1). Particularly notable is the recognition of an African clade, Afrotheria, including six previously recognized groups. Of these six groups, five were traditional orders, whereas



the sixth, Tenrecoidea (McDowell, 1958), has been part of the established Lipotyphla. Its transfer to the African clade was not predicted based upon anatomy, but molecular evidence indicates that tenrecoids shared a more recent ancestor with elephants than they did with shrews, hedgehogs, or moles. The other three molecularly based superordinal clades held fewer surprises. In fact, the four anatomically based superordinal clades discussed earlier—Glires, Archonta (with the removal of Chiroptera), Paenungulata, and Xenarthra—are now supported by molecular evidence (e.g., Murphy et al., 2001). The greatest contribution of mammalian molecular systematic studies has been the strong support of superordinal clades that have not been recovered with any certainty based on anatomy. At the ordinal level, where the anatomical and molecular studies agree on 16 of 18 orders, the changes were less profound. Aside from the breakup of Lipotyphla, the most striking revision concerns Cetacea. As some anatomical studies had already showed, cetaceans were at least the sister taxon of artiodactyls, but the molecules are more radical in nesting Cetacea within Artiodactyla.

Before outlining the history and organization of this book on placental mammals, it is worthwhile to define what we mean by this term. By and large throughout this book, Placentalia is defined as the taxon including all extant placentals and their most recent common ancestor. A more inclusive taxon, Eutheria, is here retained to include all extinct mammals that share a more recent common ancestor than they do with Metatheria (including Marsupialia; Rougier et al., 1998).

The authors recount what we currently know of the initial radiation and ordinal relationships of placental mammals, primarily focusing on the anatomical evidence. The most recent volume in English dealing with an overview of the placental radiation was published more than 10 years ago (Szalay et al., 1993). Much has transpired since that time, most notably, a greater exchange between molecular and the more traditional anatomically based systematics. In this volume, 11 chapters examine all major clades or orders of extant placentals. Two chapters provide a wider and deeper perspective of the molecular and morphological evidence for placental origins and diversification. In addition, a chapter recounts George Gaylord Simpson's seminal contributions to the study of placentals.

Rather than charging the contributing authors with providing new data or new phylogenetic analyses, we asked them to summarize objectively the current state of knowledge and views about the origin and relationships of placental clades, presenting consensual views when possible, and recognizing significant minority viewpoints when not. Except for the overview chapter on molecular systematics, the authors were asked to focus on the morphological evidence and to note major points of agreement or discrepancy with molecular data. Although we are certainly not unbiased ourselves, we feel that the authors have admirably fulfilled our request.

The inception of this volume dates from the 2001 annual meeting of the Society of Vertebrate Paleontology in Bozeman, Montana, when the editors found they shared a mutual interest in hosting a symposium on the subject of placental evolution. David's interests are in the timing, biogeography, and relationships of stem placentals, whereas Ken's are more related to the question of the origin of extant placental orders. The dovetailing of our interests helped to bring this symposium to fruition at the annual meeting of the Society of Vertebrate Paleontology in Norman, Oklahoma, in 2002. This also coincided with the centenary of the birth of one of the greatest twentieth-century paleontologists, George Gaylord Simpson, who devoted much of his career to elucidating the early evolution and relationships of placental mammals. Thus, it was an easy choice to dedicate the symposium and its companion volume to this important scientific figure.

The chapters of this book, although generally based on the symposium, are more current, more comprehensive, and more detailed. Manuscripts were received in the spring or summer of 2003 and each was externally reviewed by at least two individuals. The authors then revised and returned final manuscripts in the autumn of 2003.

In chapter 2, Simpson biographer Léo Laporte recounts the major themes of G. G. Simpson's career, including the introduction of quantitative techniques to vertebrate paleontology and his influential use of paleontology in contributing to the Modern Synthesis of evolution. Laporte points out in a quote from Philip Gingerich that Simpson wrote about twice as many papers on systematics (mostly on mammals) than on broader evolutionary themes, although he is more widely known for the latter. It is practically impossible for mammalian paleobiologists to investigate any group of early mammals without referring to Simpson's work.

The next two chapters provide, respectively, anatomical and molecular overviews of what we know concerning earlier segments of eutherian evolution. In the past five to 10 years, there has been an explosion of new Cretaceous fossils and molecular studies dealing with the eutherian radiation. Chapter 3, by John Wible, Guillermo Rougier, and Michael Novacek, begins by providing a morphological characterization of eutherians based on dental, cranial, and postcranial anatomy. This discussion includes not only placentals, but more basal eutherians, as well as more distant outgroups. The authors next examine the interrelationships of Cretaceous eutherians and possible relationships to extant placental clades. The authors find no consensus among paleontologists on whether such taxa as the Cretaceous "zhelestids" and the zambdalestids are closely related to extant superordinal placental clades. Issues surrounding the timing of the origin and initial radiation of placental mammals are also examined: here there is agreement that the origin and diversification of extant placental orders did not occur until after the K/T boundary.

In chapter 4, the second contribution on higher relationships, Mark Springer, William Murphy, Eduardo Eizirik, and

Stephen O'Brien examine the molecular evidence. They find that the current interpretation of the timing of the origin of extant placental orders, as deduced from molecular data, now shows more concordance with paleontological data than it has in the past. Of the 18 orders these authors recognize, eight appear after the K/T boundary, whereas 10 predate it by as much as 18 million years. Although this may at first seem a large difference between anatomy and molecules, the authors note that earlier molecular studies placed rodent origins well over 100 million years ago. Nonetheless, Springer et al. find that the molecular evidence supports a Cretaceous super- or interordinal radiation of placental mammals, which Wible and his coauthors (chapter 3) find problematic based on fossil evidence.

Unquestionably, the greatest contribution of these molecular studies has been the apparent untangling of superordinal relationships, which have eluded anatomical evidence for more than 100 years. As mentioned earlier, molecular studies have revealed four reasonably well-substantiated superordinal clades—Afrotheria, Xenarthra, Laurasiatheria, and Euarchontoglires. The most surprising of these is Afrotheria, which clusters previously disparate groups of largely African-centered taxa. Less surprising is Paenungulata (hyraxes, elephants, and sirenians), which both molecules and anatomy recover, albeit in differing combinations of included orders. The biogeography of these four clades is also discussed by Springer and his coauthors, with molecules usually supporting a Gondwanan center for placental origins and fossils supporting a Laurasian origin.

The next 11 chapters approximately follow the superordinal clades as recognized by molecular studies. The chapters deal with clusters of higher taxa conventionally considered "orders" of placental mammals. This hierarchical level is one of the more interesting in the history of the study of mammalian evolution (see Table 1.1). Until the advent of widespread molecular studies, all major taxa seemed to have a taxonomic rank that served as a barrier, beyond which one could not clearly argue for monophyly. Because such ranks are not biologically meaningful from one major taxon to another, it is not surprising that the rank of this barrier varies from taxon to taxon. For mammals—in particular, placental mammals—the barrier falls at the rank of the order.

Chapter 5, by Robert Asher, is the first of the chapters dealing with either superordinal- or ordinal-level groupings. Asher addresses the issue of what, if anything, are insectivores? More than any other group of placentals, insectivores, in any taxonomic guise, have had a checkered history. With the dissolution and exclusion of Menotyphla (tree and elephant shrews) from Insectivora more than 50 years ago, the latter term and Lipotyphla (hedgehogs, shrews, moles, *Solenodon*, *Nesophontes*, golden moles, and tenrecs) have often been used interchangeably. Asher explores a number of characters and character complexes that have been considered important in insectivoran systematics. Even when golden moles and tenrecs are removed, as argued by molecular data, the remaining Lipotyphla defies easy characteriza-

tion, especially when sometimes incomplete fossil taxa are included in analyses. With the current allocation of insectivoran taxa to at least two (if not more) major clades of Placentalia, Asher notes that the older and now often rejected idea of insectivorans as basal placentals may in some form be correct.

In chapter 6, Patricia Holroyd and Jason Mussell tackle two of the least diverse but most enigmatic placental orders, Macroscelidea and Tubulidentata. Elephant shrews were first placed within or aligned with various insectivores. Their recognition as an ordinal-level clade did not occur until the 1950s. Holroyd and Mussell discuss four major hypotheses of macroscelidean relationships. For tubulidentates, the authors recognize three prevailing hypotheses of relationship. They could find no clear consensus on the origins of either of these two orders, but some of the hypotheses are more consistent with one another. First, a condylarthan/tethythere origin based on anatomical data is more consistent with an afrothere clade, which is recognized in molecular studies. Second, a close relationship of macroscelideans and tubulidentates with other, largely African, lineages fits the biogeographic picture for these taxa. As these authors note, however, there remain many problems with these hypotheses.

In chapter 7, Emmanuel Gheerbrant, Daryl Domning, and Pascal Tassy examine the superordinal placental clade Paenungulata—named in 1945 by George Gaylord Simpson. In addition to the extant Proboscidea, Hyracoidea, and Sirenia, various extinct taxa have been included in the clade. Molecular analyses strongly support this clade, although relationships within Paenungulata based on molecules have varied. Although Paenungulata is often supported on the basis of anatomical studies, the authors note the competing issue of possible hyracoid-perissodactyl relationships. The poor resolution may be the result of the lack of appropriate fossil African taxa of afrotheres. Recent fossil discoveries support an African origin of proboscideans and hyracoidea by at least the late Paleocene, whereas the earliest known sirenian is an early Eocene terrestrial quadruped from the Western Hemisphere.

Kenneth Rose, Robert Emry, Timothy Gaudin, and Gerhard Storch in chapter 8 examine two orders that have often been linked, xenarthrans and pholidotans. They deem the evidence for a monophyletic Xenarthra, including sloths, armadillos, anteaters, and such extinct relatives as glyptodonts, to be compelling. As the name implies, all xenarthrans are characterized (except in quite derived taxa, such as glyptodonts) by having accessory articulations in parts of their vertebral column. The authors find little compelling morphological or molecular evidence for the more inclusive Edentata, which has included the extant orders Xenarthra and Pholidota (pangolins), often with a variety of extinct taxa as well. They find rather meager anatomical evidence linking Pholidota with Carnivora, a relationship more strongly supported by molecules. The best-known but most enigmatic taxa involved in the question of Edentata are the extinct palaeonodonts. Most of the anatomical evidence



supports a palaeodont and pangolin clade, but some is sufficiently equivocal to permit a possible xenarthran tie.

Chapter 9, by Mary Silcox, Jonathan Bloch, Eric Sargis, and Douglas Boyer, examines the superordinal clade Archonta, or Euarchonta, as they prefer. Archonta was named by Gregory (1910) for the orders we now recognize as Scandentia, Macroscelidea, Dermoptera, Chiroptera, and Primates. Acceptance of such a clade (in various guises) did not become widespread until the 1970s. The authors note that within Archonta, the clade Volitantia (for Dermoptera and Chiroptera) was strongly supported by anatomical data. Although their phylogenetic analysis supported Volitantia within Archonta, removal of bats does not alter the remaining topology, including a Scandentia and Dermoptera clade. Most recently, molecular studies remove Chiroptera from Archonta, but strongly retain a clade including Dermoptera, Scandentia, and Primates. It is this revised clade (Euarchonta) that concerns much of the chapter. Although the fossil record of scandentians in the early Tertiary remains poor, and that for dermopterans is not much better, the primate fossil record is quite good. The fossil record provides evidence bearing on the timing and place of origin of archontans. For both Dermoptera *sensu lato* and Primates *sensu lato*, the earliest representatives are known from the early Paleocene of North America, with primates, at least, in Asia and Africa by the late Paleocene. A discrepancy still remains between the timing of the origin of archontans based on fossils, which place it near the K/T boundary, versus that based on molecules, which place it about 85 million years ago.

In chapter 10, Jin Meng and André Wyss deal with the superordinal clade Glires, which includes the two extant orders Rodentia and Lagomorpha. As these authors point out, the question of whether Rodentia and Lagomorpha form a clade has been long enduring. Although this debate was, until recently, based only on anatomical studies, even with the advent of molecular studies, the question of gliran monophyly remained equivocal. This question now appears to be near resolution. Members of Glires share a number of specializations in the anterior dentition; notably, reduction to one pair of upper and lower incisors in rodents and two pairs of upper and one pair of lower incisors in lagomorphs. These incisors are evergrowing and have enamel restricted more or less to the anterior surface. Accompanying these modifications is the development of a large diastema between the incisors and cheek teeth. Although some other mammals show similar changes, modifications of the cheek teeth in basal rodents and lagomorphs further argue for their forming a clade. In addition, molecular studies now strongly support a Glires clade, with this clade being sister to Archonta (Euarchontoglires). There is now considerable confidence that the stem taxa of both rodents and lagomorphs can be traced to the early Paleocene, thus arguing that Glires dates back at least to the K/T boundary. Even the most recent molecular dates, however, still place this split at slightly more than 80 million years ago. Meng and Wyss do

not support recent paleontological studies arguing that stem glirans are known from some 85 million years ago.

Nancy Simmons reviews the most recent ideas on the evolutionary history of Chiroptera in chapter 11. Bats appear in the early Eocene fully volant and capable of echolocation. They clearly spread rapidly after their origin, as they are known from the early Eocene of North America, Europe, Africa, and Australia, and in the last case, are the earliest definite placentals known from that continent. Although bat monophyly has been questioned in the past, evidence from numerous organ systems, as well as molecular studies, now make it one of the most strongly supported ordinal clades of placentals. The same cannot be said for within-Chiroptera relationships. The idea of a megachiropteran clade and a microchiropteran clade has been the standard, based largely on anatomical evidence from fossil and recent forms. Microchiropteran monophyly has been challenged, however, mostly from molecular studies, which link some microchiropteran families with megachiropterans. This suggests that echolocation evolved in basal bats only to be lost in megachiropterans. One of the most intriguing results discussed by Simmons is that the diversification of extant families of bats occurred mostly in the Eocene, certainly one of the earliest such radiations among placental clades.

In chapter 12, the evolutionary history of Carnivora is reviewed by John Flynn and Gina Wesley-Hunt. Until relatively recently, any eutherian exhibiting a carnassial pair formed by the last upper premolar and first lower molar was considered to belong to Carnivora. Later analyses suggest that extant or crown-group Carnivora forms a clade to the exclusion of the more basal stem taxa, Viverravidae and some Miacidae, which also have this carnassial pair. The more inclusive Carnivoramorpha, which includes all of these taxa, is first seen in the early Paleocene of North America. Within crown-group Carnivora, molecular or combined data sets find strong support for all major clades except Viverridae and Mustelidae. Flynn and Wesley-Hunt also discuss the possible relationship of various creodonts to carnivoramorphan. Although the authors support the general view that creodonts may be sister to Carnivoramorpha, they find little evidence that creodonts form a monophyletic clade. They note that possible relations of Carnivora to other placentals based on morphology remain sketchy. A link between Carnivora and Pholidota has weak morphological but stronger molecular support.

In chapter 13, on Perissodactyla, Jeremy Hooker notes that there is unanimous agreement regarding the three extant clades (rhinos + tapirs and horses). There is, however, no overall consensus on the higher-level relationships among extant and extinct perissodactyls when the extinct chalicotherioids and brontotherioids are included. Hooker finds that some anatomical studies still conclude that there is a close relationship between perissodactyls and hyracoids, whereas molecular studies place these taxa far apart, the former in Laurasiatheria and the latter in Afrotheria. The

question of the origins of Perissodactyla is, as for other placental orders, not confidently resolved, although phenacodontid condylarths are usually implicated. When more recently recognized Asian phenacodonts and perissodactyls are included in the phylogenetic analysis, a picture emerges in which brontotheres, not horses or tapiroids, are most basal in the order.

Artiodactyla has always seemed to be one of the most clearly delimited placental orders, characterized by its double-trochleated astragalus, which was long thought to be unique to the order. Similarly, within Artiodactyla, the tripartite groups of suiforms, tylopods, and ruminants appeared to be relatively stable. If recent molecular results continue to be supported, however, the monophyly of Artiodactyla can no longer be maintained, unless whales are included, the oldest of which are now known to have had a similar double-trochleated astragalus. Nor would suiforms be monophyletic, and the interrelationships of the three artiodactyl clades would change radically. In chapter 14, Jessica Theodor, Kenneth Rose, and Jörg Erfurt examine the traditional, anatomically based concept of Artiodactyla and also explore the ramifications of the changes argued by the molecules. They note that the issue of discerning the time and place of origin of artiodactyls remains ambiguous, as the oldest representatives first appear in North America, Europe, and southern Asia almost simultaneously in the earliest Eocene, without a clear ancestor or sister taxon. An archaic ungulate (condylarth) is implicated, but the possible candidates include arctocyonids, hyopsodontids, mioclaenids, or mesonychians. Moreover, some anatomically based analyses argue that whales are the sister taxon to artiodactyls rather than belonging within Artiodactyla. These studies suggest that the most likely ancestor for both artiodactyls and whales is an arctocyonid, but the evidence for this is not very strong. Artiodactyls and whales first appear in the fossil record within a few million years of each other—55 and 53.5 million years ago, respectively. Such similar dates seem concordant; however, if hippopotamids, which are first known from 15–16 million years ago, are the sister taxon to whales (as indicated by molecular data), then there is a gap in the fossil record of more than 37 million years between the first whales and hippopotamids.

No less than Charles Darwin in *Origin of Species* (1859) commented on the possible origin of cetaceans, speculating that they could have arisen from an aquatic bearlike creature snapping at insects in the water. Ridicule of this off-hand remark led to its exclusion in all later editions of this landmark volume. As Philip Gingerich recounts in chapter 15, the enigmatic origin of cetaceans has prompted considerable speculation. He reviews how the very rapid accumulation of data from both anatomical and molecular studies has resolved this enigma. Cetaceans are now clearly recognized at least as the sister taxon to Artiodactyla, if not sister to hippopotamids. Gingerich expands on the discussion begun in chapter 14, which suggests that if the anthracotheres are the closest extinct group to hippopotamids, then the former

are the possible sister taxon to cetaceans. The author concludes with a discussion of the environmental context of the origin and diversification of cetaceans, arguing that the origin not only of Cetacea but of many other orders of mammals that appear near the Paleocene-Eocene boundary is correlated with a thermal maximum. Cetaceans appeared along the shores of the warm Tethys Sea at about this time. These early forms, the archaeocetes, probably did not, however, survive the cooling event at the Eocene-Oligocene boundary. This is the earliest likely time for the origin of the two major extant cetacean clades, Odontoceti and Mysticeti.

As this collection of papers demonstrates, there is a consensus that nearly all of the 18 conventional placental orders are compellingly monophyletic. The only exceptions are Lipotyphla and Artiodactyla as commonly conceived, for which both morphological and molecular evidence now challenge the traditional taxonomic arrangements. Despite these findings, it must be admitted that we generally lack fossil evidence of the precise phylogenetic origins of the orders. In most cases, we can at best point to a family of archaic eutherians as a likely source (e.g., cimolestids for Carnivora, or more precisely, Carnivoramorpha; phenacodontids for Perissodactyla; arctocyonids for Artiodactyla). With regard to higher level relationships, the morphological evidence supports the monophyly of Glires, Archonta (or Euarchonta), Artiodactyla (or Cetartiodactyla, including whales), Tethytheria, and, to a lesser extent, Paenungulata and a Carnivora + Pholidota clade. The oldest fossils that can be definitively allocated to any of the 18 orders postdate the K/T boundary and in many cases (particularly crown groups) are no older than Eocene. In almost all cases, the authors conclude that the orders most likely did not originate until after the K/T boundary. Thus although probable divergence dates based on molecular evidence are becoming more compatible with those based on morphological evidence (e.g., for perissodactyls, artiodactyls, bats, crown-group Carnivora, and paenungulates), there remains significant discrepancies between molecular and morphological estimates for some other groups (e.g., primates, rodents, Glires).

## REFERENCES

- Archibald, J. D. 2001. Eutheria; pp. 1–4 in *Encyclopedia of Life Sciences*. www.els.net. Macmillan Publishers, Nature Publishing Group, London.
- . 2003. Timing and biogeography of the eutherian radiation: Fossils and molecules compared. *Molecular Phylogeny and Evolution* 28: 350–359.
- Butler, P. M. 1956. The skull of *Ictops* and the classification of the Insectivora. *Proceedings of the Zoological Society, London* 126: 453–481.
- . 1972. The problem of insectivore classification; pp. 253–265 in K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*. Winchester Press, New York.

- Cuvier, G. 1817. La règne animal distribué d'après son organisation, pour servir de base l'histoire naturelle des animaux et d'introduction l'anatomie comparée. Les mammifères. Deterville, Paris.
- Darwin, C. R. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.
- Flower, W. H. 1883. On the arrangement of the orders and families. Proceedings of the Zoological Society, London 1883: 178–186.
- Gould, S. J. 1989. Wonderful Life: The Burgess Shale and the Nature of History. W. W. Norton, New York.
- Gregory, W. K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History 27: 1–524.
- Kirchner, J. W., and A. Weil. 2001. Delayed biological recovery from extinctions throughout the fossil record. Nature 404: 177–179.
- Linnaeus, C. 1758. Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tenth edition. Impensis Direct, Salvius, Stockholm.
- . 1766. Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Twelfth edition. Impensis Direct, Salvius, Stockholm.
- McDowell, S. B., Jr. 1958. The Greater Antillean insectivores. Bulletin of the American Museum of Natural History 115: 113–214.
- McKenna, M. C. 1975. Toward a phylogenetic classification of Mammalia; pp. 21–46 in W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Primates: A Multidisciplinary Approach. Plenum, New York.
- McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals above the Species Level. Columbia University Press, New York.
- Murphy, W. J., E. Eizirik, S. J. O'Brien, O. Madsen, M. Scally, C. J. Douady, E. Teeling, O. A. Ryder, M. J. Stanhope, W. W. de Jong, and M. S. Springer. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294: 2348–2351.
- Rougier, G. W., J. R. Wible, and M. J. Novacek. 1998. Implications of *Deltatheridium* specimens for early marsupial history. Nature 396: 459–463.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: 1–350.
- Szalay, F. S., M. J. Novacek, and M. C. McKenna (eds.). 1993. Mammal Phylogeny: Placentals. Springer-Verlag, New York.
- Vaughn, T. A., J. M. Ryan, and N. J. Czaplewski. 2000. Mammalogy. Fourth edition. Saunders College Publishing, Fort Worth.
- Wilson D. E., and D. M. Reeder. 1993. Mammal Species of the World: A Taxonomic and Geographic Reference. Second edition. Smithsonian Institution Press, Washington D.C.