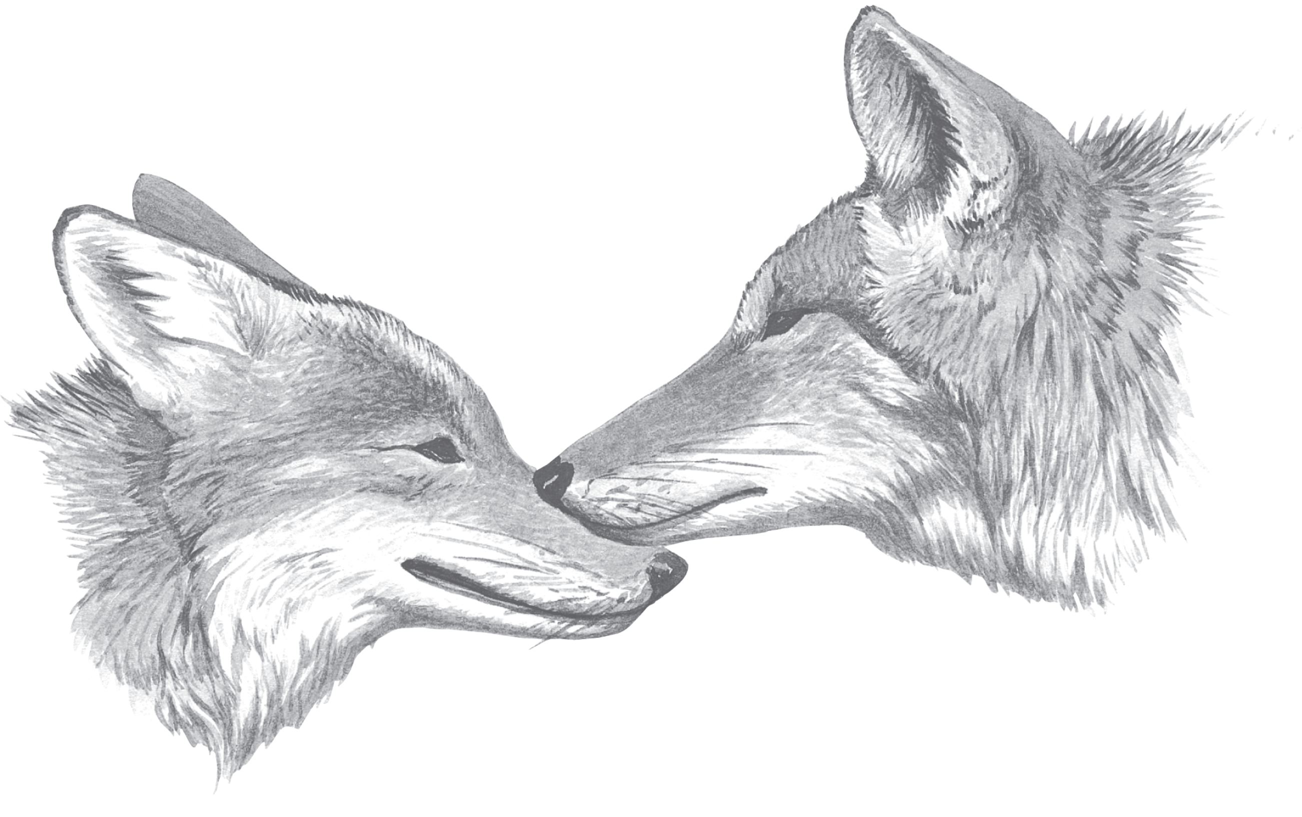
CHAPTER

1

Introduction



CHAPTER OUTLINE

These are exciting times for people interested in the study of mammals. Since the first edition of *Mammal Species of the World* was published in 1982, nearly 760 new mammal species have been described. Of those, over 400 mammal species were discovered since 1993 (Ceballos & Ehrlich 2009). These discoveries were the result of recent explorations in remote parts of the world, taxonomic revisions of problematic groups, and evaluation of DNA evidence for **cryptic species**. Indeed, the cumulative number of new mammal species is still on the rise. Recently discovered fossils continue to change the landscape of mammalian evolution. In addition, new tools from the field of molecular biology are helping to address questions in animal behavior and mammalian phylogeny. The study of mammalian relationships is being revolutionized by molecular data that suggest new hypotheses that remain to be tested (Murphy et al. 2001; Springer et al. 2007). Advances in radiotelemetry and the use of satellites to track far-ranging mammals increase our understanding of the life histories of many secretive species. The use of radioisotopes to measure field metabolic rates is changing the way mammalogists think about mammalian physiology. New computer models that simulate changes in populations allow mammalogists to generate testable predictions that would be impossible to formulate without such software. And now as in the past, careful, patient observations and experiments in the field are contributing to our understanding of mammals.

Although our scientific knowledge is increasing dramatically, numerous important questions remain to be answered by future generations of mammalogists. The advances described above have yielded new and exciting results. For example, the discovery that elephants can communicate using infrasound, or that kangaroo rats use foot-drumming as a form of seismic communication, has opened new areas of research on these well-studied mammals. Indeed, a combination of technological advances and innovative thinking on the part of many mammalogists has contributed to the development of entirely new areas of research. The fields of functional genomics, landscape ecology, and conservation medicine are three examples. Modern mammalogy is a dynamic and exciting field in need of curious minds (**Box 1-1**).

As a discipline, mammalogy occupies the efforts of a diverse group of scientists. Vertebrate zoologists study such aspects as the structure, **taxonomy**, distribution, and life histories of mammals, physiologists consider mammalian hibernation and water metabolism, physicists and engineers study mammalian echolocation and locomotion, vertebrate paleontologists and molecular biologists outline the patterns of mammalian evolution, and ecologists and behaviorists consider where and how mammals live and adapt to changing environments. In addition, perceptive observers without formal zoological training contribute a wealth of information.

Mammals are worthy of study for many reasons. Practical aspects of mammalogy attract some. By studying various kinds of laboratory mammals, we gain practical knowledge about mammalian histology and about the effects of diseases and drugs. Work on domesticated breeds of mammals improves meat production, and research on game species shows how sustained yields of these animals may be achieved through appropriate management techniques. To most students and researchers, however, practical applications are not foremost. Because we human primates are mammals, we are fascinated by our relatives. Mammals are beautiful and fascinating creatures that show physiological, structural, and behavioral adaptations to an amazing array of lifestyles. Thus, living mammals in their natural settings are the focal point of interest. The adaptations themselves, how they evolve, how they enable mammals efficiently to exploit demanding environmental conditions, and the interaction between mammals and their environment are all fascinating lines of inquiry. The most productive studies are the result of the intense interest of researchers in a biological relationship rather than their preoccupation with solving a practical problem. In this book, we deal primarily with the impressive literature on mammals that results from such basic research. Far from being impractical, the perspective gained from such work must guide our decisions affecting the recovery and survival of threatened species of mammals and, indeed, of entire ecosystems.

Basic research during the last half century has expanded our knowledge of mammalian biology tremendously. Echolocation (animal sonar) has been intensively studied in bats and marine mammals. The remarkable ability of some mammals to live in conditions of extreme aridity with no drinking water has been partially explained. Experiments on the circulatory and metabolic adaptations associated with temperature regulation and metabolic economy have been tested. Adaptations to deep diving in marine mammals have been examined. Hibernation and migration and the mechanisms that influence them have

BOX 1-1 New Methods for Studying Mammals

In recent years mammalogists have increasingly adopted new methods in their fieldwork and research. Some methods draw on varied technological improvements in video, molecular chemistry, DNA sequencing, and geochronology. In particular, several new (and some old low-technology) noninvasive methods save time, money, and equipment, relative to radiocollaring and radiotracking methods.

Numerous noninvasive or minimally intrusive techniques have been very widely adopted globally in the study of wild mammals (Evans & Yablokov 2004; Long et al. 2008). One of the most popular has been **camera-trapping**, placing automatic cameras along animal trails or grids to capture still photos or stop-action videos of mammals unmolested by the presence of humans (**Fig. 1-1**). The photos are analogous to museum specimens that provide vouchers and are especially valuable for nocturnal, rare, and wide-ranging species such as carnivores (Kays & Slauson 2008; Rowcliffe et al. 2008). Some cameras capable of taking short bursts of sequential photos can even provide videos useful for studying behavior (Kays et al. 2009a, 2009b). More high-technology methods use thermal-imaging cameras and night-vision devices. In a reversal of who is taking the photos, "crittercams," animal-borne video systems, harness the animals with minicameras to provide data potentially pertinent to biological studies (Moll et al. 2007). An ancient method, following and identifying mammal tracks and signs, has seen a great resurgence in the last few years as a noninvasive research technique (Elbroch 2003; Liebenberg 1990; CyberTracker software: www.cybertracker.org/). These kinds of tracking data will soon be compiled in a new web repository called Movebank (www.movebank.org) for data sharing. "Signs" such as mammal scats and hair samples, collected at scent posts, can provide samples of bile acids, DNA, or stable isotopes, that will lead to individual recognition of such secretive animals as wolverines. These methods are especially popular with mammalogists who receive help from enthusiastic students and the public (**citizen scientists;** Silvertown 2009).

Advances in computing, molecular extraction, amplification, analysis, automation, and DNA sequencing methods, combined with improvements in data sharing and transfer (e.g., GenBank, Morphobank) and phylogenetic analysis software, have revolutionized and sped up our ways of reconstructing mammal phylogeny. Even recovery of fragmentary DNA from fossils and subfossils (e.g., Australian Centre for Ancient DNA: http://www.adelaide.edu.au/acad/) together with improved geochronometry (dating of fossils and rocks) and biochronology (placement of fossils in geological time) has increased our understanding of extinct mammal relationships and timing of divergence of lineages as well as phenomena such as mammal domestication. **Stable isotopes** found in various tissues of mammals have been used recently in the study of mammal migrations and diets (Herrera et al. 2001; Hobson & Wassenaar 2008). Using the Global Positioning System satellites to track mammals carrying transmitters facilitated research on long-distance movements of marine or land mammals.

FIGURE 1-1 Photograph of a coyote from a camera trap in New York.

been studied. There have been important contributions to our knowledge of mammalian population cycles and the factors that may control them. Studies of functional morphology have increased our understanding of mammalian terrestrial, aquatic, and aerial locomotion. Probably no field has been slower to develop than that of conservation biology. This field, however, has advanced rapidly, perhaps in response to the belated realization that time is growing short for the study of particular species in their natural environments. Studies of behavior and population genetics have contributed tremendously to our appreciation of how finely tuned mammals are to their environments. There is no doubt that mammals play vital roles in shaping regional and global ecosystems.

Mammalogists were quick to recognize that pristine ecosystems, including many of their favorite study sites, were in peril. Global **biodiversity**, the result of millions of years of evolution, is declining because of the cumulative impact of more than a quarter million new people added to the planet each day. Worldwide extinction of plant and animal species is accelerating at an alarming rate, primarily because of the fragmentation or outright loss of habitat (Cardilio et al. 2006; Davies et al. 2008). Many large or highly specialized mammals are now threatened with extinction. Since the last edition of this book was published in 2000, however, several new mammalian genera and species (including primates, rodents, and ungulates) have been discovered living in remote or poorly explored parts of the world. Ironically, these discoveries were made by mammalogists attempting to describe and conserve the remaining biodiversity before it disappears.

Classification

In any careful study, one of the vital early steps is the organization and naming of objects. As stated by Simpson (1945) with reference to animals, "It is impossible to examine their relationships to each other and their places among the vast, incredibly complex phenomena of the universe, in short to treat them scientifically, without putting them into some sort of formal arrangement." The arrangement of organisms is the substance of taxonomy, but modern taxonomists, perhaps better termed systematists, are less interested in identifying and classifying animals than in studying their evolution. These systematists bring information from such fields as genetics, ecology, behavior, and paleontology to bear on the subjects of their research. They attempt to base their classifications on the most reliable evidence of evolutionary relationships. Excellent discussions of the importance of **systematics** to our knowledge of animal evolution are given by Mayr (1963), McKenna and Bell (1997), Nei and Kumar (2000), Hall (2007), and Simpson (1945).

Because of difficulties that arise when a single kind of animal or plant is given different common names by people in different areas or by many common names by people in one area, scientists more than 200 years ago adopted a system of naming organisms that would be recognized by biologists throughout the world. Each known kind of organism has been given a binomial (two-part) scientific name. The first, the generic name, may be applied to a number of related kinds, but the second name refers to a specific kind, a **species**. As an example, the blacktail jackrabbit of the western United States is *Lepus californicus.* To the genus *Lepus* belongs a number of similar, but distinct, long-legged species of hares, such as *L. othos* of Alaska, *L. europaeus* of Europe, and *L. capensis* of Africa. Because considerable geographic variation frequently occurs within a species, a third name is often added to designate **subspecies**. Thus, the large-eared and pale-colored subspecies of *L. californicus* that lives in the deserts of the western United States is *L. c. deserticola*; the smaller-eared and dark-colored subspecies from coastal California is *L. c. californicus.*

The species is the basic unit of classification. A once widely accepted definition of species was given by Mayr (1942): "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Each species is generally separated from all other species by a "reproductive gap," but within each species, there is the possibility for gene exchange. According to Dobzhansky (1950), all members of a species "share a common gene pool."

The hierarchy of classification, based on the starting point of the species, has been developed to express degrees of **phylogenetic relationship** among species and groups of species. The taxonomic scheme includes a series of categories, each category more inclusive than the one below it. Using our example of the hares, many long-legged species are included in *Lepus.* This genus and other genera containing rabbit-like mammals form the Leporidae; this family and the Ochotonidae (the pikas) share certain structural features not possessed by the other mammals and belong to the order Lagomorpha. This order and all other mammalian orders form the class Mammalia, members of which differ from all other animals in the possession of hair, mammary glands, and many other features. Mammals, birds, reptiles, amphibians, and fish all possess a bony or cartilaginous endoskeleton, and these groups (in addition to some others) form the phylum Chordata. All of the phyla of animals (Porifera, Cnidaria, Platyhelminthes, and so forth) are united in the animal kingdom. The classification of our jackrabbit can be outlined as follows:

Kingdom Animalia
    Phylum Chordata
        Class Mammalia
            Order Lagomorpha
                Family Leporidae
                    Genus *Lepus*
                        Species *Lepus californicus*
                            Subspecies *Lepus californicus deserticola*

Further subdivision of this classification scheme may result from the recognition of additional intermediate categories, such as subclass, superorder, or subfamily. Most ordinal names end in –a, as in Carnivora; all family names end in –idae, and all subfamily names end in –inae. In this book, contractions of the names of orders, families, or subfamilies are often used as adjectives for the sake of convenience: leporid will refer to Leporidae, leporine to Leporinae, lagomorph to Lagomorpha, and so on.

Some similarities between different kinds of animals are due to **parallelism** or to **convergence**, two forms of the more general concept of **homoplasy**. Parallelism occurs when two closely related kinds of animals pursued similar modes of life and evolved similar structural adaptations. The similar specializations of the skull and dentition (elongate snouts and reduced number of teeth) that occur in a number of genera of nectar-feeding Neotropical bats are examples of parallelism. Convergence involves the development of similar adaptations to similar (or occasionally nearly identical) styles of life by species in different orders. The golden moles of Africa and the "marsupial moles" of Australia are convergently evolved. These animals belong to different mammalian infraclasses (Eutheria and Metatheria, respectively; see Table 4-1), and their lineages have been separate for more than 70 million years. Their habits are much the same, however, and structurally they resemble each other in many ways.

Chapter 4 provides an outline of the classification of mammals used in this book. It is based largely on the classification by Wilson and Reeder in 2005. We wish to stress that no universal agreement has been reached on the classification of mammals. Our knowledge of many groups of mammals is incomplete, and future study may demonstrate that some of the families listed here can be discarded because they contain animals best included in another family. Other species and families are yet to be described. The present classification, then, is not used by all mammalogists, and it is by no means immutable.

Phylogeny Reconstruction

Since the 18th century, taxonomists have based their systems of classification on overall similarity among organisms. In the 1960s, Willi Hennig proposed a more objective method to make the classification reflect the actual evolutionary history of the group. This system came to be known as phylogenetic systematics or **cladistics** (Wiley 1981). In biology, therefore, the subdiscipline of systematics primarily deals with the classification and **phylogeny** of organisms. Classification is simply a way of ordering species into hierarchical groups and giving names to them so that they can be recognized and discussed. In phylogenetics, researchers develop hypotheses to reconstruct the evolutionary history or relatedness among species. In recent decades classifiers of organisms have incorporated phylogenetic information into classification schemes so that the named groups comprise evolutionarily related species. This is much easier said than done. There are also increasing efforts to use and integrate data from a variety of sources, including molecular, paleontological, morphological, biogeographic, ecological, and behavioral studies into phylogenetic hypotheses. Molecular data in particular are revolutionizing the way we view relationships and classify mammals, and even changing our concept of species (Baker & Bradley 2006; Riddle et al. 2008).

Methods used to infer phylogenetic relationships are explained in Kitching et al. (1998), Nei and Kumar (2000), and Swofford (1998). Detailed descriptions of the theory and practice of classifying mammals and reconstructing their evolutionary relationships are beyond the scope of this book, but we give a few brief notes, including some of the technical jargon. Establishing the pattern of relationships among mammals or any other group of organisms is often referred to as phylogeny reconstruction. The reconstruction of a phylogeny usually involves cladistics as a technique of analysis (**Box 1-2**). The goal of cladistic analysis is to produce a hypothesis of phylogenetic relationships of a group of organisms. The hypothesis is presented as a **cladogram** (such as that in **Fig. 1-2**), a branching, tree-like diagram in which the ends of the branches represent species or **taxa** and the branching points or **nodes** indicate the point at which species separated from one another to follow their own evolutionary pathways. A cladogram may show the relationships of species of mammals within a group to one another, or it may show the relationships of a group of mammals to other living organisms. The data used to produce a cladogram of mammals are called **characters** and usually consist of morphological features or molecules such as DNA or proteins.

The most important feature of cladistics is its reliance on shared derived characters (called **synapomorphies**) to establish relationships instead of overall similarity. In building a cladogram or phylogeny, the characters can have various **character states** (e.g., in the character "number

Taxa	Sequence data	Trait X	Trait Y
H	AAA GCT ACT	yes	no
G	AAA GCT ACT	yes	no
F	AAA GGT ACT	yes	no
E	CAA GGT ACT	yes	no
D	CAA GGT ACT	yes	no
C	CAA GGT ACG	yes	yes
B	CAA GGT ACG	yes	yes
A	CAA GGT ACG	yes	yes

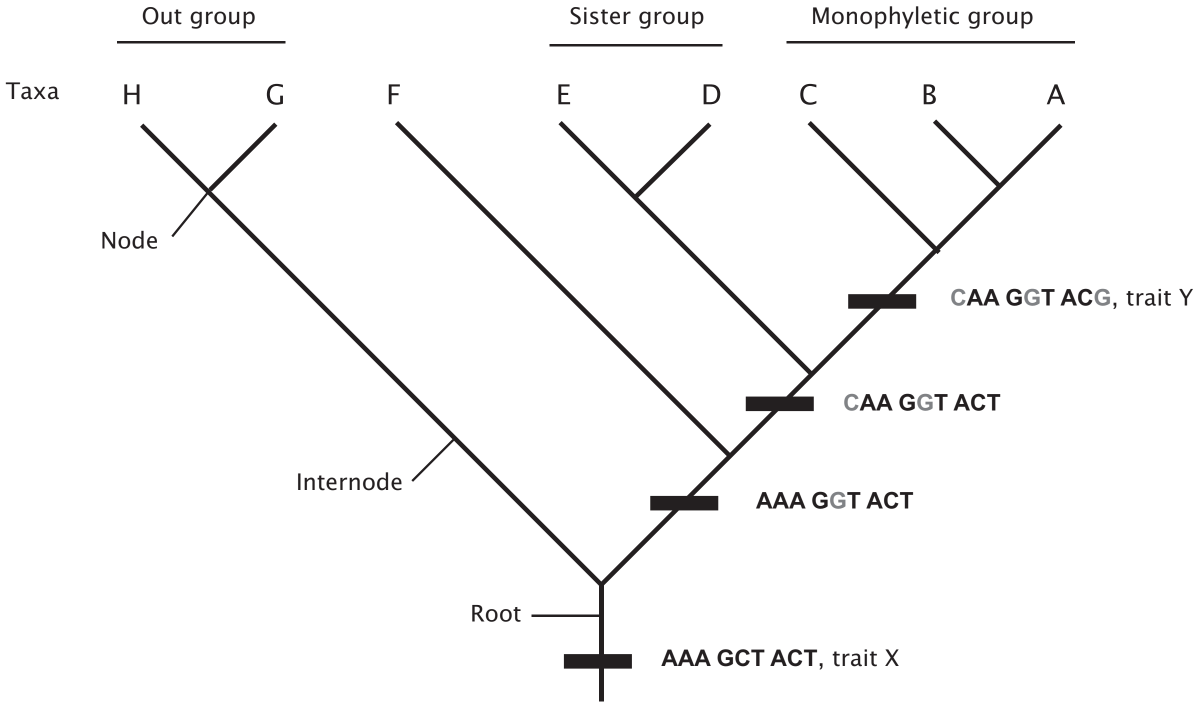


FIGURE 1-2 A phylogeny of eight taxa A through H based on DNA sequence data and two morphological traits (X and Y). The character matrix for the sequence data and the morphological traits is given above an example of one phylogenetic hypothesis. In the cladogram shown, Taxa A, B, and C form a monophyletic group. Taxa A through E also form a monophyletic group; however, a grouping of taxa E, D, C, and B would be paraphyletic. A node represents a speciation event where two lineages diverge from each other. An outgroup is a group of taxa that serves as a reference for determining the relationships of other taxa. A sister group is a group of taxa that is the most closely related to the ingroup.

of toes on hind feet," the possible character states might be "five toes" or "four toes" or "two toes"). The various character states must be analyzed, and their **polarity** (direction of evolutionary transformation) must be determined. In this example, the trend is toward reduction from five digits, the primitive number of toes in mammals and other terrestrial vertebrates, to fewer than five digits. The best way to determine character polarity is by including in the analysis an **outgroup**, consisting of a lineage that is closely related but outside of the **ingroup** (the group being studied). The underlying assumption is that if an outgroup itself is not too **derived**, it will tend to share **ancestral** (**plesiomorphic**) but not derived (**apomorphic**) features with the ingroup, thereby indicating which are ancestral character states.

Primitive or ancestral features shared by the outgroup and ingroup are called **symplesiomorphies** and provide no information about phylogenetic relationships. Because all mammals have hair, for example, this shared primitive characteristic would be of no use in understanding the evolutionary relationships of rodents (or any other mammalian group). Strict application of cladistics requires that only shared derived features (synapomorphies) be used to construct a hypothesis of relationships. The presence of a small pair of peg-like upper incisors immediately behind the first pair of incisors, therefore, is a synapomorphy of lagomorphs that clearly distinguishes them from rodents. Synapomorphies indicate a close relationship unless a character state arises by convergent evolution in an unrelated species. Ideally, synapomorphic character

BOX 1-2 Using Molecules to Construct Phylogenies

Phylogenetic systematics is a field that seeks to reconstruct the evolutionary history of groups of organisms. Because all life on Earth is related, like a family tree, there can only be one true history of descent from the first living organism that appeared some 3.8 billion years ago. Obviously, that true history was not observed and recorded, but it did leave behind tangible clues that biologists can use to reconstruct the evolutionary history of particular groups of organisms. Biologists have two major lines of evidence: morphology and molecules.

Fossils and living species have long been studied to yield morphological characteristics useful for constructing phylogenies (evolutionary trees). The use of molecules (DNA, RNA, proteins) is relatively new. By comparing homologous molecules from different organisms, it is possible to establish their evolutionary relationships. The basic premise behind molecular phylogenies is that all life uses the same DNA code, many of the genes are homologous across diverse taxa, and the DNA code is modified over time by mutations. Thus, species that diverged from each other relatively recently should have few such mutations, whereas those that diverged long ago will have accumulated many changes.

Molecular systematists begin by extracting DNA or proteins from several taxa of interest. They determine the sequence of DNA or amino acids for a specific region of the gene(s) or protein(s), and using a variety of sophisticated tools, they align those sequences for all the taxa (Fig. 1-2). The changes that have accumulated in those sequences are now apparent, and the goal is to find the evolutionary tree that best explains the sequences changes (using computer-assisted phylogenetic analysis software with appropriate assumptions). For example, in the hypothetical phylogeny illustrated here, the common ancestor of taxa A, B, C, D, E, F, G, and H, all share the ancestral DNA sequence (AAA GCT ACT) and morphological trait X (symplesiomorphies). The clade including taxa A through F accumulated one mutation in their DNA for this gene (C becomes G at position 5), and this character is a synapomorphy for the clade A–F. Another mutation occurs in position 1 (A becomes C) after lineage F diverges from the clade A–E. Finally, a third mutation (T becomes G in position 9) occurs in the common ancestor of taxa A, B, and C, and these taxa also evolve a new morphological trait Y. If we assumed that taxon C was more closely related to taxa E and D, then it would have required trait Y and the third mutation in the DNA sequence to evolve twice in two separate lineages—a highly unlikely event. Combining molecular and morphological evidence is useful where one type of evidence alone leads to ambiguous results. Many of the phylogenies in this text are based on combinations of molecular and morphological data.

It is important to remember that cladistic analysis generates an evolutionary tree, which represents a hypothesis of relationships among the organisms supported by the data analyzed; but, new data could emerge in support of a different hypothesis. In general, the more homologous characters used, the more robust the hypothesis.

states represent **homologous** not **analogous** features, but convergent evolution of characters is very difficult to discern and frequently causes problems for systematists. Old World jerboas and New World kangaroo rats independently evolved elongate hindlimbs and bipedal hopping, a particularly good example of convergent evolution. Barring any convergent characters in other species or groups under study, a group that exclusively shares derived characters is said to be **monophyletic** and to form a **clade**. A monophyletic clade is a phylogenetic lineage that arose from a single ancestor and includes only the ancestor and all of its descendants. The clade or branch of a cladogram nearest to a monophyletic clade is termed the **sister group** (Fig. 1-2).

A cladogram indicates only the relative timing of separation of species or lineages, but often it is desirable to know the numerical timing of divergence of lineages. For this, the cladogram must be linked with the geologic time scale. When the morphological data and resultant cladogram are combined with independent **geochronological** data from the rocks in which the fossils were buried, it is possible to estimate the time of appearance of fossil species and produce an evolutionary tree that is calibrated to the geologic time scale.

Many molecular geneticists use DNA and other molecules to construct cladograms or a **molecular phylogeny** of a group of mammals (Box 1-2). By using the so-called **molecular clock** (**Box 1-3**), they can also link a time scale to the phylogeny. Instead of measuring the time of first appearance of a recognizable member of a certain mammalian group in the fossil record, molecular systematists are able to estimate the time of divergence or lineage splitting of two species or lineages of mammals before the lineages may have become well differentiated morphologically. Often the molecular and morphological data agree, giving greater confidence in the accuracy of the phylogenetic hypothesis. The phylogenetic information, in turn, can be linked to biogeographic data and aspects of geological history, such as the past positions of the continents, islands, or tectonic plates and the timing of their collision or separation. When morphological and molecular phylogenies and various aspects of geological history are combined, the result can be an eclectic, robust model for the evolutionary history of a mammalian group.

Virtually all systematists agree that named taxa should share a common evolutionary origin. Naming taxa based on cladistic hypotheses is an entirely different problem from determining phylogenetic relationships, and one that is intractable and controversial. Some **cladists** prefer to name only monophyletic groups (at their nodes in a cladogram), but in practice, this can result in a proliferation of names and taxa of unequivalent ranks that fall between the standard categories of Class, Order, Family, and so on. To reconcile this problem, many systematists informally name nodes but do not provide them with a rank or category. Others name **crown groups**, which consist of the hypothetical ancestors of all the living members of a group and all its descendants, extinct and extant. For Mammalia, for example, this would include the common ancestor of Monotremata, Metatheria, and Eutheria and all of the common ancestor's descendants (Rowe 1988; Rowe & Gauthier 1992).

In addition to these works cited, students are referred to Wilson and Reeder (2005) and McKenna and Bell (1997). As an entry into the vast literature about the phylogeny of mammals, see Rose and Archibald (2005), Szalay et al. (1993a, 1993b), Honeycutt and Adkins (1993), Novacek (1992a), and also "The Tree of Life" web site that deals with mammals and their extinct relatives (http://tolweb.org/Mammalia).

BOX 1-3 The Molecular Clock—Does It Run on Time?

The molecular clock is a concept that assumes that the time that two species diverged from one another can be calculated by measuring the number of molecular differences between the species' DNA sequences or proteins. Instead of measuring time, the molecular clock measures the number of silent mutations (those that do not result in amino acid sequence changes) that accumulate in the gene sequences of different species over time (**Fig. 1-3**). Evolutionary biologists use this information to estimate the date when two species diverged on the geologic timeline.

In 1962, Zuckerkandl and Pauling recognized that the number of amino acid differences in the protein hemoglobin was random and occurred at a constant rate. This led to the proposal that the number of mutations in a given stretch of DNA could be used as a measure of time since two or more species diverged. Like all clocks, however, the "molecular clock" has to be calibrated. This is accomplished by using known dates from the fossil record for the taxa being studied. Thus, if the mutation rate for a specific nonfunctional gene is 3 mutations per million years (r) and there are 21 mutations in the DNA sequences between two species (d), the estimated time (t) those two species began to diverge is calculated as $t = d/2r$, or approximately 3.5 million years ago.

Later research showed that different genes evolve at different rates. Functionally important genes are more often conserved and mutate more slowly than genes with less vital functions. Consequently, more recent speciation events are dated using genes with higher mutation rates, and slow evolving genes are used to date more ancient divergence events.

The molecular clock hypothesis has certain limitations. As Ayala (1999, 2000) pointed out, the molecular clock is unlikely to give accurate divergence dates if (1) the species being compared have different generation times; (2) population sizes of the species differ by orders of magnitude (e.g., comparing small isolated mole-rat populations with those of the nearly cosmopolitan *Rattus* sp.); (3) the species differ markedly in metabolism, evolutionary history, or life history traits; (4) the intensity of natural selection changes dramatically over time; or (5) the function of the protein or gene being used is altered over time.

Instead of abandoning the molecular clock entirely, the assumptions of the molecular clock have been relaxed, allowing the mutation rate to vary across the branches of the evolutionary tree. Nevertheless, it is important to remember that even relaxed-clock methods need to be calibrated using the absolute age of some evolutionary divergence event from the fossil record.

Carefully calculated and calibrated, the molecular clock can provide important date estimates, especially for fossil-poor taxa, and it remains an important tool in evolutionary biology (**Fig. 1-4**; Kumar 2005). In addition, as Ho (2008) pointed out, "With the rapid accumulation of new genetic data, particularly as a result of the many genomic sequencing projects that are currently underway, it seems that the molecular clock will continue to shed light on the tempo and time scale of evolution for years to come." With respect to mammals, Baker & Bradley (2006) suggested that changing from a morphological species concept to a genetic species concept could reveal as many as 2,000 additional "genetic species" of mammals hidden among the 5,400 known by their morphology.

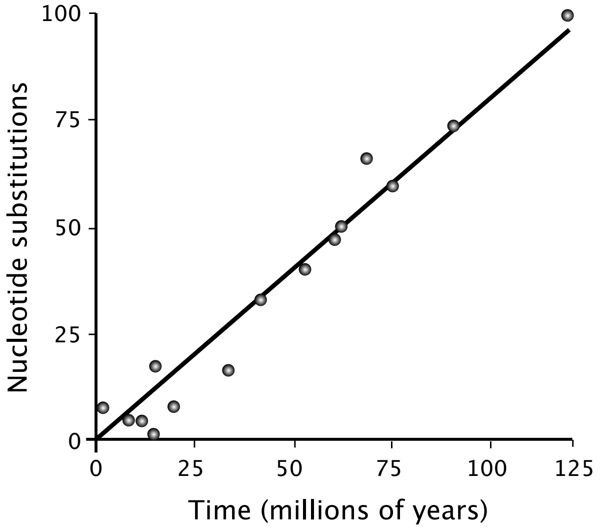


FIGURE 1-3 A graph of the combined number of nucleotide substitutions from 7 proteins and the species divergence time for 15 pairs of mammalian species. (Modified from Fitch WM. 1976. Molecular evolutionary clocks, pgs. 160-178, in *Molecular Evolution* (FJ Ayala, ed.) Sinauer Associates, Sunderland, MA.)

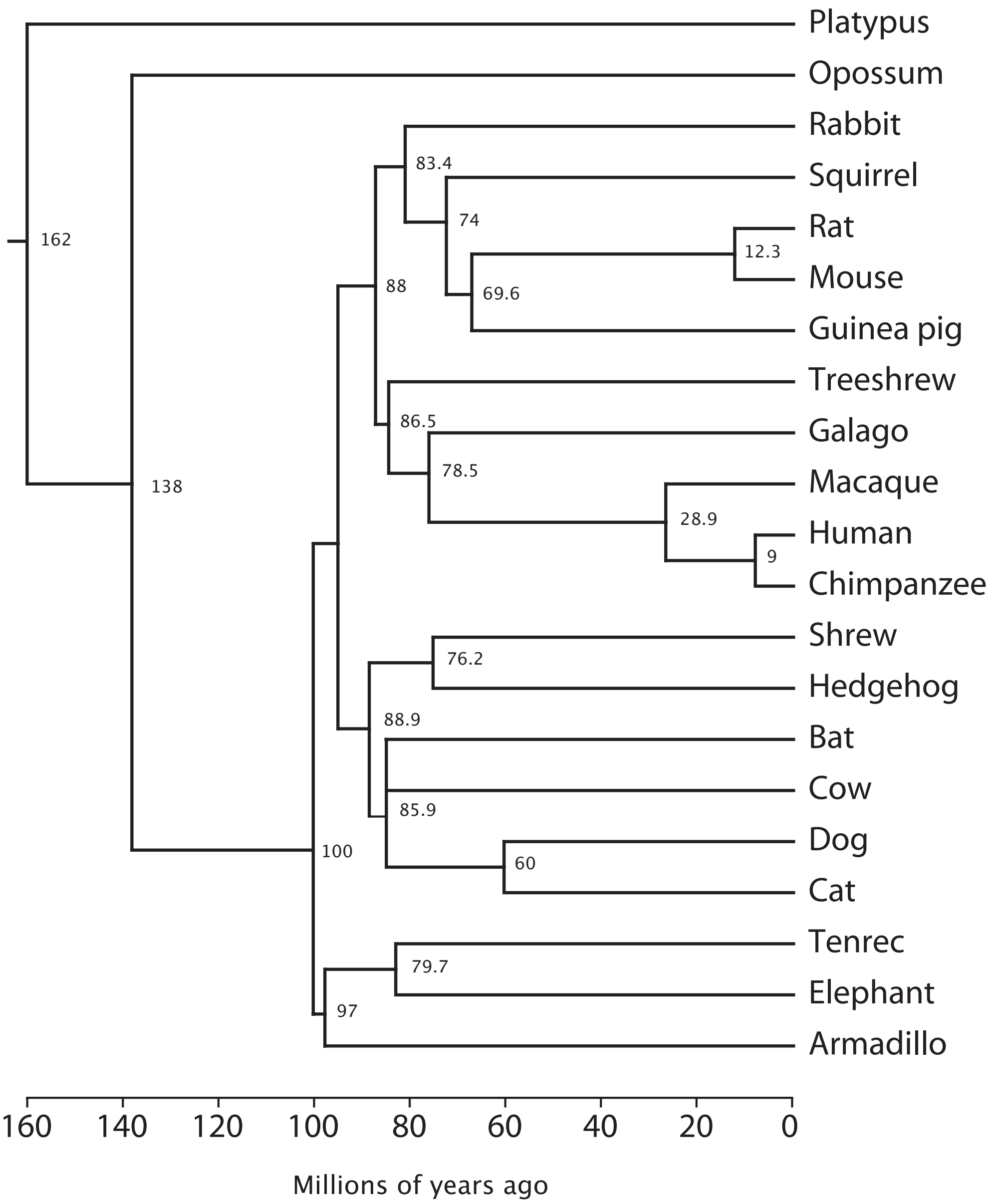


FIGURE 1-4 A molecular phylogeny of mammals showing estimated divergence times (millions of years ago) based on analysis of 3,012 genes (2,844,615 nucleotides) from a total of 22 species. (Adapted from Hallström, BM and A Janke, *BMC Evolutionary Biology* 8 (2008): 1-13.)

SUMMARY

These are exciting times for people interested in the study of mammals. Over 400 mammal species were discovered since 1993 as a result of recent explorations in remote parts of the world, taxonomic revisions of problematic groups, and the evaluation of DNA evidence for cryptic species. Indeed, the cumulative number of new mammal species is still increasing. Recently discovered fossils also continue to reshape the landscape of mammalian evolution. In addition, new tools from the field of molecular biology are helping to address questions in mammalian behavior, phylogeny, and other fields. Although our scientific knowledge is increasing dramatically, numerous important questions remain to be answered by the next generation of mammalogists. Among the most important are questions that address the causes and repercussions of mammalian extinctions. Many mammals are now threatened with extinction primarily by human activities, even as we struggle to catalog and conserve species. In recent years, mammalogists have increasingly studied wild mammals by using noninvasive techniques such as camera- and video-trapping, thermal imaging, satellite tracking, and identification of tracks and signs. Laboratory analyses used in modern studies include the recovery of bile acids, DNA, stable isotopes, or other evidence from mammal scats and hair samples and extracting and sequencing fragments of ancient DNA from fossils and subfossils. Contributions during fieldwork by enthusiastic students and the public as citizen scientists are important also.

The classification of mammals, must be based on evolutionary relationships. Each known kind of organism is given a binomial scientific name. The first, or generic name, may be applied to a number of related kinds, but the second name refers to a specific kind, a species. Each species shares a common gene pool and is generally separated from all other species by a "reproductive gap." A classification that expresses the true evolution of mammals uses a series of categories, each category more inclusive than the one below it in the classification hierarchy. The present classification, proposed by Wilson and Reeder in 2005, will continue to change as the study of mammals advances.

Researchers develop hypotheses to reconstruct the evolutionary history or relatedness among species using phylogenetic information. The hypothesis is presented as a phylogeny or cladogram, a branching, tree-like diagram in which the ends of the branches represent species or higher level taxa, and the branching points or nodes indicate the point at which species separated from one another to follow their own evolutionary pathways. The data used to produce a phylogeny are shared characters and usually consist of morphological features and molecular ones, such as DNA sequences. Systematists strive to use only shared derived features (synapomorphies) to construct a hypothesis of relationships. When a cladogram is combined with independent geochronological data from fossil-bearing rocks, it can indicate the timing of evolutionary events. Molecular geneticists use DNA and other molecules to construct cladograms or molecular phylogenies, and use the molecular clock to link a time scale to the phylogeny.

The fifth edition of this text represents a significant change from the previous edition, published in 2000. Although the basic framework remains intact, we needed to incorporate more than a decade of new research. All of the chapters were extensively rewritten and updated. In the first part of this book (Chapters 1 through 4), we define mammals and summarize their origins. In the second part (Chapters 5 to 19), we present the orders and families of mammals in detail. In the third part (Chapters 20 to 26), we treat special topics such as mammalian echolocation, physiology, behavior, ecology, and zoogeography. From this coverage, students can gain a general understanding and an appreciation of the form and function of mammals. Two additional new chapters, Chapter 27, Domesticated Mammals and Chapter 28, Mammalian Disease and Zoonoses, are available on the web site that accompanies the text.

KEY TERMS

Analogous
Ancestral
Apomorphy
Biodiversity
Camera trap
Character states
Characters
Citizen science
Clade
Cladist
Cladistics
Cladogram
Convergence
Crown group
Cryptic species
Derived
Geochronological
Homologous
Homoplasy
Ingroup
Molecular clock
Molecular phylogeny
Monophyletic
Nodes
Outgroup
Parallelism
Phylogenetic relationship
Phylogeny
Plesiomorphy
Polarity
Sister group
Species
Stable isotope
Subspecies
Symplesiomorphy
Synapomorphy
Systematics
Taxa
Taxonomy

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