1 Introduction: primates in evolutionary time

A major goal of this book is to show that fossil primates (including fossil humans) fit within evolutionary patterns seen among other mammals. What is a mammal? Mammals are a class of animals. That is, they are technically arranged in the zoological Class Mammalia, which is formally characterized by a number of distinctive traits. With the exception of birds, most of the animals with which we are most familiar are mammals. There are about 5,000 living mammal species, although they comprise only about 5 percent of all known animal species. The term "crown species" is often used to refer to living species, in contrast to fossil species, because the living animals appear at the top or crown of an evolutionary tree. Mammals have a very ancient and complicated evolutionary history. Figure 1.1 presents a simplified version of this evolutionary past. A complete and continuous fossil record documents the transition from first reptiles to first mammals. Although a number of "mammal-like reptile" or proto-mammal groups independently evolved mammalian traits, the first creatures identified as true mammals emerge about 200 mya (million years ago). Living mammals occur in three main groups: the ancient monotreme mammals of Australasia, and the closely related placental and marsupial mammals, whose origins are much more recent.

Mammals are animals that have backbones or spinal (vertebral) columns, composed of individual vertebrae or vertebral bones. They are thus members of a major division of animals called vertebrates (Subphylum Vertebrata). Most mammals, the placental and marsupial mammals, give birth to live young. The exceptions are the monotreme mammals, the duck-billed platypus and the echidnas, or spiny anteaters. These monotreme mammals lay eggs. Mammals nurse their young, or lactate with milk produced from mammary glands, which are modified sweat glands. In monotremes, milk oozes through to the surface of a mother's fur, where it is licked up by the young. In other mammals, the young actively suckle milk, as they latch onto a discrete nipple or teat. Mammal hearts are four-chambered, and completely divided vertically into right and left halves. Mammals are endothermic, using physiology to maintain a stable internal body temperature, despite the changing ambient temperature. They possess hair, usually of different types (a fine undercoat and a longer outer coat), and specialized sensory hairs or whiskers (vibrissae) on the head. *Megaconus*, a mammal-like fossil from 165–164 mya, preserves a halo of guard hairs and denser undercoat hairs in fine sediments immediately surrounding the skeleton, although the middle ear and ankle region resemble those of mammal-like reptiles (Zhou *et al.*, 2013).

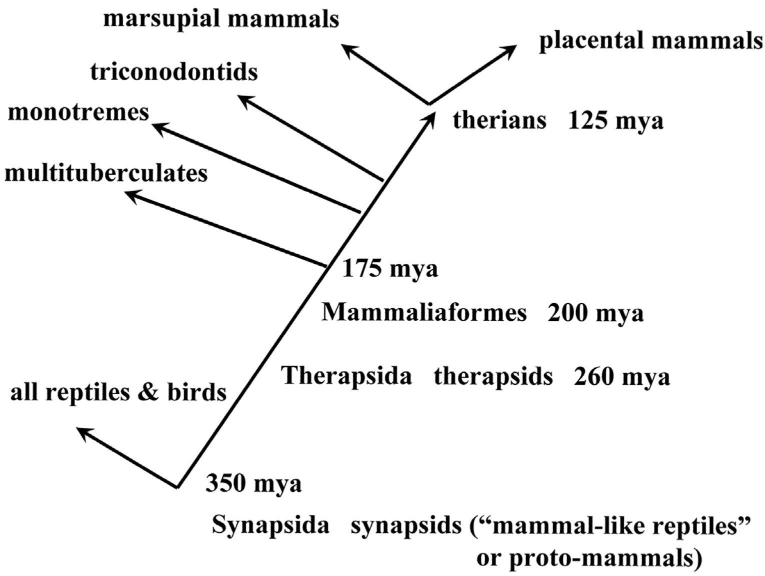

Figure 1.1. Mammal evolution. This figure illustrates the evolution of mammals from synapsids, and the origin of major mammal groups.

A furry pelt thus originated long before the true mammals appear. Unlike fish or reptiles, mammals have a distinct and restricted period of growth. They do not continue growing as long as they live.

Mammal teeth have a core of bone-like dentine encased in a fabulously hard coat of enamel. Enamel, which is largely calcium phosphate, is one of the toughest of organic materials. When the root cavity of a tooth seals up from the bottom, the tooth then stops growing. Some mammals, such as rodents, have teeth that grow throughout life. Mammals develop only two sets of teeth—a milk or deciduous set that is lost during juvenile life, and an adult or permanent set. Unlike the teeth of fish or reptiles, the teeth of mammals are heterodont. They have four different shapes, depending on their position within the jaws. From the front of the jaw to the back, these teeth are respectively called incisors, canines, premolars, and molars. Molar teeth are never replaced—they do not have deciduous versions. Milk or deciduous molars are, in fact, premolars. These different types of teeth perform different functions. Every mammal species has a characteristic number of teeth of each type. These numbers are summarized by a dental formula, which lists the number of teeth of each type in one half of the head. The basic placental dental formula is

$$\frac{\mathrm{I3.C1.P4.M3}}{\mathrm{I3.C1.P4.M3}}$$

where I stands for incisor, C for canine, P for premolar, and M for molar. Each tooth is numbered from front to back. A deciduous incisor tooth is indicated by the following convention: dI. Isolated teeth are identified by superscripts or subscripts. Thus, P^4 refers to the last upper premolar; P_4 refers to the last lower premolar.

The upper and lower molar teeth of mammals meet together or occlude. As a result, these molars can tear, crush, or chew or masticate food, depending on the shape of the molars.[1] As seen in Figure 1.1, marsupial and placental mammals are identified as therians. The ancestral therian possessed a distinctive form of molar tooth: a tribosphenic molar in which both upper and lower molars have three principal cusps, and the lower molar has a distinctive posterior talonid basin which occludes with the principal cusp, the protocone, of the upper molar. This molar shape allows therians both to crush food inside the talonid basin, and to shear food along the anterior vertical face of the basin. Figure 1.2 illustrates the basic therian molar pattern, from which the molar teeth of all marsupial and placental mammals are derived.

Mammals develop a secondary palate, a plate of bone that grows in from the edges of the upper jaws, and envelopes the original synapsid palate in a cylinder. The internal air passage opens at the back of the throat. Mammals can therefore eat and breathe at the same time. This is important, because mammals have a high metabolic rate—they need to process food quickly, in order to survive. They cannot hold their breath for a long time, while trying to ingest struggling, intractable prey, or a large bolus of food. The mammalian lower jaw is formed by a separate dentary bone in each half of the lower jaw, joined together by a symphysis in the middle. Alternatively, the symphysis may be fused, and the lower jaw is then a single, complete bone, called a mandible. The jaw joint is formed by an articulation between the dentary bone in the mandible and the squamosal bone in the cranium. There is a cheek bone (zygomatic arch), and ancient ribs in the neck region (cervical ribs) are lost or reduced. The ball joint (occipital condyle) that attaches the cranium to the first neck vertebra becomes a double ball joint in mammals, allowing the head to be more flexible and mobile.

Mammalian limb structure is entirely reorganized. The shoulder or pectoral girdle becomes stronger and more flexible, as does the pelvic girdle, which has more vertebrae fused to the hip bones. In therian mammals (marsupials and placentals), the separate coracoid bone of the shoulder girdle becomes fused to the shoulder blade to form the coracoid process. In addition, the ankle joint of therians is formed only between the tibia bone and the astragulus bone. There is no contact between the calcaneus ankle bone and the tibia. The limbs of mammals are held vertically under the body; they do not sprawl out to either side. Each digit of the extremities (hands and feet) has a characteristic number of phalangeal bones or phalanges. Some mammals walk with their feet flat on the ground, but most walk up on their toes or digits. In any case, the digits are shortened, and do not splay out sideways. Ribs are lost in mammals, until only an anterior rib cage

[1] There is a website on mammalian teeth that contains a large database of both living and extinct mammal species. It is accessible via the downloadable Morphobrowser web interface. This allows for 3D visualization, rotation, and scaling of tooth images, as well as allowing for the import and export of dental data. This website can be accessed via the following URL: http://www.biocenter.helsinki.fi/bi/evodevo/morphobrowser/.

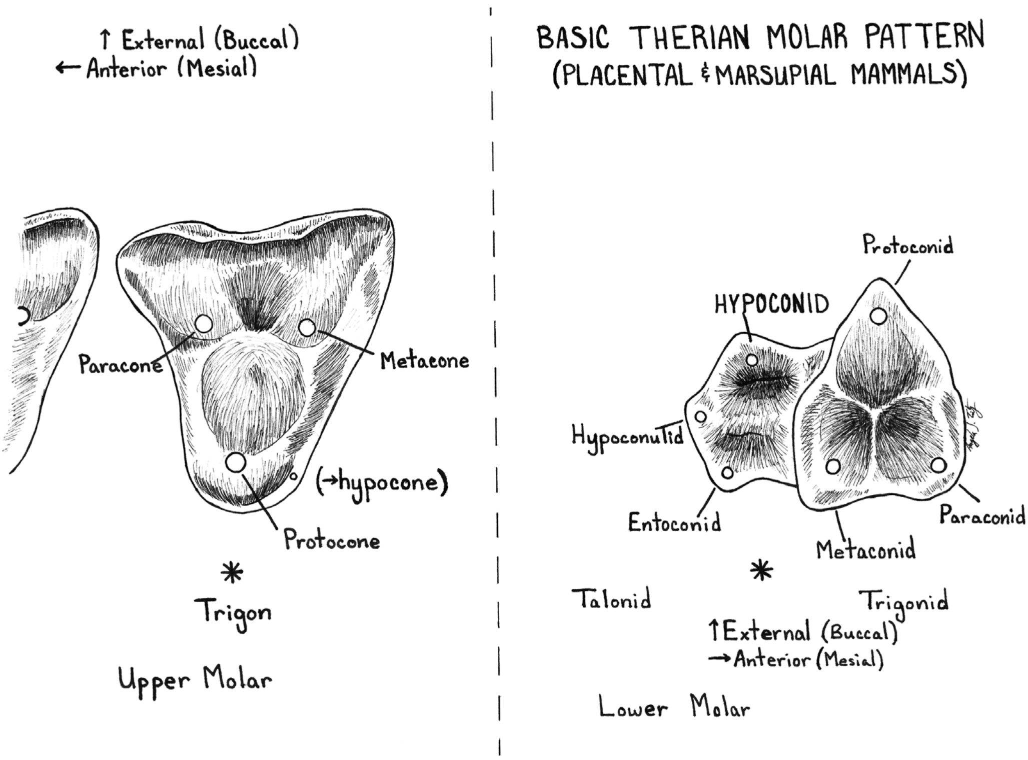

Figure 1.2. The basic therian molar tooth pattern. Note that the upper and lower molars are reversed. Photocopy this figure. Then fold it along the center line, hold it up to the light, and approximate the two stars in each half of the figure. The figure will then illustrate occlusion between the upper and lower molar teeth. Note that the principal cusp of the upper molar (the protocone) fits into the posterior basin (the talonid basin) of the lower molar. Illustration by Angela J. Tritz.

remains. The remaining ribs are locked together, forming a rather rigid thorax. Unlike the ribs of reptiles, mammalian ribs do not markedly expand and contract. Mammals therefore breathe in an entirely different fashion. They use a muscular wall (the diaphragm) that separates the lung and abdominal cavities to pump air in and out of the lungs through muscular effort. Figure 1.3 shows a familiar living mammal.

Mammal brain evolution has been studied in detail.[2] Because the first mammals were nocturnal, both the sense of touch and the sense of smell were accentuated, rather than vision. Each of the sensory vibrissae on a mammal's snout can move

[2] A website devoted to mammalian brain anatomy and evolution contains photos, atlases, and descriptions of the brains of more than 175 species of living mammals. These include the brains of living non-human primates. It can be found at the following URL: http://www.brainmuseum.org/.

(a)

Figure 1.3. This domesticated dog illustrates several traits that are characteristic of mammals. (a) Besides the normal hair of the pelt, vibrissae on the snout function for the sense of touch or the tactile sense. The importance of olfaction is shown by the long snout and the moist, naked nose or rhinarium. The teeth are heterodont. (b) The legs are vertical, and are placed directly under the body. As is true of many mammals, the dog is standing up on its toes or digits, illustrating a form of posture or locomotion called digitigrady. Digitigrady increases stride length, and therefore minimizes the cost of locomotion.

independently of the others, and, when an individual whisker touches an object, a mammal's brain records the location of the object and the pressure that it exerts on the whisker. The brain then integrates information from the array of whiskers to unveil the shape of the unknown object (Towal *et al.*, 2011). When the first mammals emerge 200 mya, their brains already contain relatively large olfactory lobes—areas of the brain devoted to the processing of olfactory information. Improved smell and tactile abilities occur concomitantly with superior coordination, and are followed by a further enhancement of olfaction (Rowe *et al.*, 2011). The ancestors of living mammals experience a third pulse in olfactory ability, along with an expansion of epithelial tissue lining delicate, scrolled turbinal bones in the snout. Reflecting the primacy of the sense of smell, olfactory receptor genes in living mammals comprise a major portion of the genome. In fact, the general augmentation of the mammal brain relative to body size is a gift of the olfactory sense (Rowe *et al.*, 2011:Fig. 3).

(b)

Figure 1.3. (*cont.*)

Mammals evolve from synapsids. In synapsids, the lower jaw is formed by multiple small bones. Two of these bones (the articular and quadrate) ultimately end up in the middle ear region of mammals, becoming the incus and malleus, respectively. This transformation is shown not only in fossils, but also during embryonic development. Thus, these cartilaginous embryonic jaw bones become bones of the middle ear in living mammals. The evidence of mammal evolution is seen not only in fossils, but also in embryology.

Multiple lineages or clades of synapsids independently acquired characteristic mammal traits. They acquired these traits in a mosaic fashion, not as a complete suite of traits that arrive all at once. Thus, during a particular point in geological time, a number of different synapsid lineages were experimenting with a mammal-like way of life. The living monotreme mammals seem to be the descendants of a separate lineage of animals that crossed over the threshold into mammal status. This is shown by paleontology, which demonstrates the different way in which bones of the monotreme middle ear are derived from bones of the synapsid lower jaw (Rich *et al.*, 2005). Thus, a key trait for mammals evolves independently between monotremes and other mammals. This trait is the transformation of bones in the synapsid jaw into the incus and malleus bones of the middle ear. It is likely that this separation from the lower jaw of bones that now function in mammalian hearing occurred independently in a number of other extinct lineages. A 120 mya fossil triconodont from China has a middle ear that is still not completely free from the lower jaw. This discovery implies that the definitive mammalian middle ear, fully separated from the lower jaw, evolved independently in three mammal lineages—the monotremes, the extinct multituberculates, and the therian mammals (Meng *et al.*, 2011:Fig. 4).

The live-bearing, therian mammals (marsupials and placentals) are clearly distinct from the egg-laying monotreme mammals. The extinct multituberculates, the longest lived of any mammal group (Figure 1.1, Chapter 8), also appear to have given birth to live young, in contrast to the monotremes. Multituberculates had epipubic bones that supported a pouch, as in living marsupials (Jenkins & Krause, 1983:Fig. 2). Genome analysis further illustrates the distinct nature of monotreme mammals. The genome of the platypus, a monotreme, has its own unique traits. It has major differences from the genomes of both placental and marsupial mammals, and also shares some genetic features with reptiles and birds (Warren *et al.*, 2008). At the genetic level, the platypus is as much a composite as its body is. Yet, genetic analysis reveals what fossils cannot: endothermy and lactation were acquired before other mammalian traits.

As mammals evolve, they demonstrate patterns in time and space that relate to origin, extinction, competition, and dispersion. Mammals respond to alterations in geography, global sea level, and climatic fluctuations. Through time, continents show a succession of faunas and floras. Some of these are distinctive and virtually unique; others are admixtures formed by the dispersal of species from separate areas of origin. Fossil primates are no different from other mammals. They conform to patterns of origin and extinction that characterize other mammals.

There are over 20 orders or major, formal zoological groups of living mammals. Among the orders of mammals is the Order Primates: the First or Top Animals, when this word is translated from Latin. This name reflects an old idea that humans are not only the natural end point of Nature, but they are the very reason why Nature exists. This idea argued that Nature is subordinate to humans, and only exists to fulfill human needs. Humans are outside, and above, Nature. Living and fossil humans are members of the Order Primates. Other members of this order are ape-like or monkey-like animals, or animals less well defined in the popular mind, such as the lemurs, lorises, and tarsiers. If humans are the nearest approach to perfection in the natural world, then animals resembling humans in either anatomy or behavior must also be of the utmost importance. This is one approach to the non-human primates—to consider them an inherently interesting and charming group of creatures whose study may illuminate questions about the origins of human anatomy, behavior, intelligence, and morality. The civilizations of India, China, and Japan have traditionally taken this approach. This is enhanced by the Hindu and Buddhist religions, which minimize the differences between human and animal. Thus, the macaque monkeys native to Japan (*Macaca fuscata*) appear in countless depictions that illustrate the Buddhist moral teaching to "See no evil, hear no evil, speak no evil."

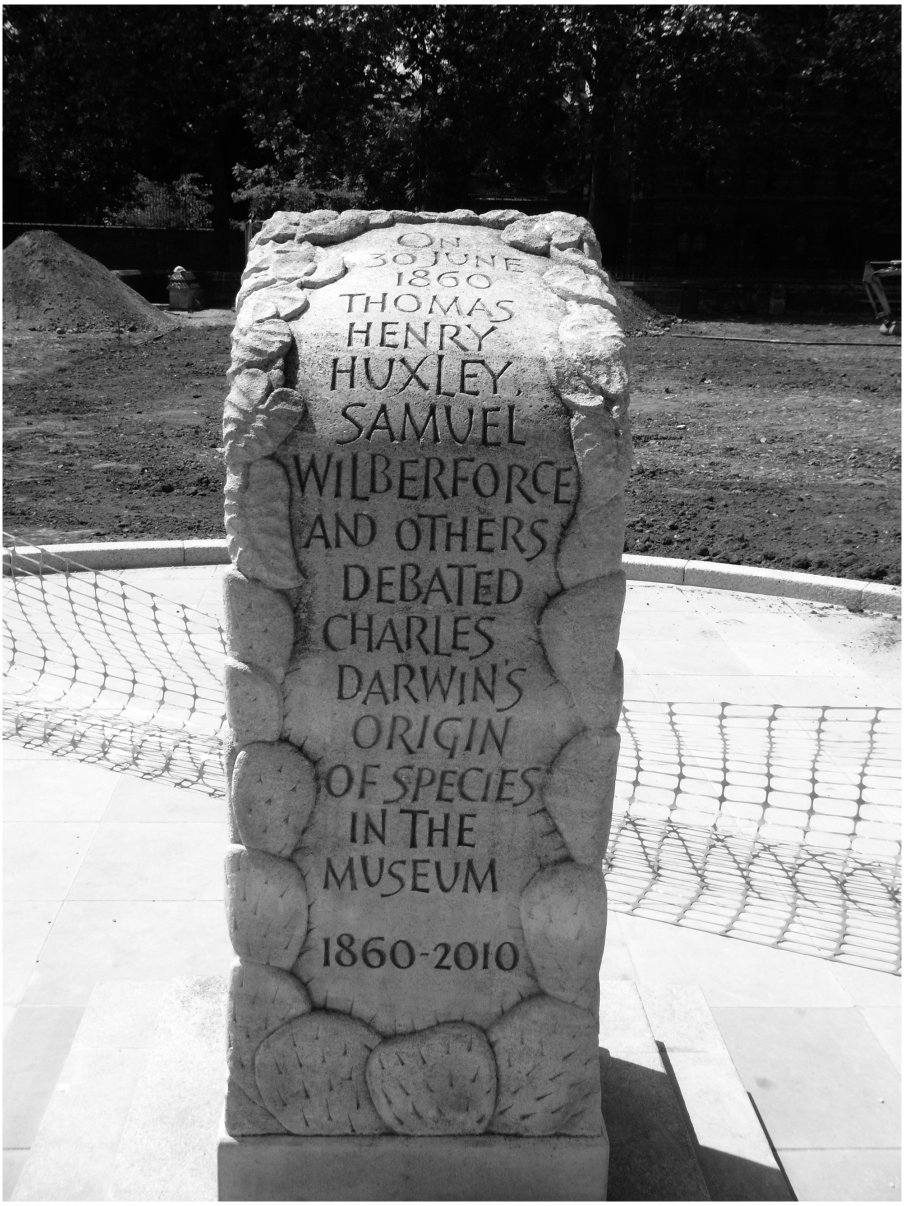

Figure 1.4. Stela at the entrance of the Museum of Natural History, Oxford, memorializing the famous June 30, 1860 debate that took place there between Thomas Henry Huxley, Bishop Wilberforce and others on Darwin's *Origin of Species*.

There is an alternative viewpoint. In Western Civilization, primates were often considered to be tainted or ruined creatures precisely because their resemblance to humans appeared to mock the human condition. This view is ancient in the West, where the Greek word *pithekos* or "trickster" was applied to Barbary macaques and baboons, called “apes” by the old Greek scholars. Because the human mind and body were considered the zenith of the natural world—the gods themselves being merely exaggerated versions of mortal humans—human-like animals were especially revolting. This view of primates as ruined animals that mocked the human condition was continued in the Bestiaries written by Medieval Christian scholars, as well as in the traditional folklore of European nations. If non-human primates were peculiarly degraded animals, one might then regard them in the same way that the eighteenth-century English novelist Jonathan Swift used his invented creatures, the Yahoos, to depict the unique corruptions of humans. This view of non-human primates ultimately hindered the easy acceptance of the idea of human evolution for many people. They experienced a visceral disgust at the notion of being related to apes and monkeys. Thus, when a great public debate on evolution took place in Oxford, England, in June 1860, Bishop Samuel Wilberforce mockingly inquired of Thomas Henry Huxley whether he had apes on his grandfather’s or his grandmother’s side of the family. Huxley replied that he would rather have “a miserable ape for a grandfather,” rather than an intelligent and influential man who subverted scientific discussion through the use of ridicule (Desmond, 1997:279). This retort (and Huxley had many others like it) effectively silenced the bishop and many other critics of evolution (Figure 1.4).

Primates among the mammals

Living primates are subject to intense scrutiny and interest, not only from scholars, but also from members of the general public. At the present time, much of this examination concerns conservation and the fate of endangered species. A continually updated database of all the living primates is maintained at the following website: http://alltheworldsprimates.org. Although the focus of the website is conservation, the website includes descriptions, photographs, and aerial satellite and normal road maps showing the ranges of all known primate species and subspecies identified by formal taxonomic and common names, as well as video and audio clips for about 16 percent of them. The database is relational, which allows for different modes of searching for information. However, users need to join Primate Conservation, Inc., and pay a steep fee in order to log on to the website, although institutional memberships exist.[3]

As the nineteenth century drew to a close, it became clear to most scholars that evolution was real, that human evolution had occurred, and that humans were certainly a member of the Order Primates. Yet, what is the relationship of this order to other orders of mammals? The traits that define primates, both living and fossil, will be discussed in Chapter 7. This definition is problematic, because primates appear to possess no unique keystone or signature features that ineluctably allow

[3] As an example of the kind of data that can be retrieved from this primate database, detailed information about time spent feeding, time spent feeding on different food types, and the nutritional

scholars to identify them. This is true even when living species are examined. Thus, within the twentieth century, tree-shrews (Order Scandentia), elephant-shrews (Order Macroscelidea), colugos (Order Dermoptera), and fruit bats (a subgroup of Order Chiroptera) have been identified as primates by eminent scholars. Yet, how can gliding colugos, flying bats, and tree-climbing primates be grouped together? The answer lies in convergent evolution, the independent origin of traits among lineages that are distant in ancestry. Thus, as discussed above, the middle ear of monotremes is convergent to that of placental and marsupial mammals. The close evolutionary relationship between tree-shrews, colugos, and primates is often now recognized by a taxonomic category called Euarchonta. A Grandorder Archonta may also include bats. Figures 1.5 and 1.6 illustrate two distinguished attempts to define the relationships of primates and other placental mammals. Figure 1.5 is based on an analysis of morphology (Novacek *et al.*, 1988). Figure 1.6 is based on an analysis of molecular evidence (Murphy *et al.*, 2001). Note in Figure 1.6 that elephant-shrews and bats are no longer considered to be closely affiliated to primates. Also, note that DNA and molecular evidence currently indicate that colugos are the closest living relatives of primates (Janečka *et al.*, 2007; Perelman *et al.*, 2011). I will not use subordinal distinctions between primates of modern aspect (euprimates) and the extinct plesiadapiform primates for two reasons: we cannot retrieve ancient DNA or molecular evidence from the plesiadapiform primates; and accumulating fossil evidence (Chapter 8) indicates that some plesiadapiform species had acquired traits characteristic of euprimates.

The controversy surrounding primate definition becomes even more intense when fossils are studied, because no soft-tissue traits are present, and bones and teeth may be fragmentary. Another factor is that the earliest primates were apparently adapted for ecological niches now occupied by rodents, and they therefore possess many traits not seen in living primates (Chapter 8). Major changes in niche structure therefore affect primate traits through evolutionary time.

It is nevertheless clear that primates, far from being the First Animals—a literal translation of the Latin word *Primates*—are not specialized. They are generalized in dentition and body form. One need only consider kangaroos, elephants, moles, sloths, and whales to realize that this statement is true. All of these animals have radically transformed their dentition and body plan to reflect highly specialized lifeways. On the contrary, primates have very generalized teeth and skeletons, and they even retain bones like the collarbone or clavicle that are otherwise lost in most other mammals. Primates in the distant geological past (Deep Time) are also closer

breakdown of these food types is available for some species. This allows a researcher to examine and compare dietary quality in these species. It is regrettable that access to this database is not free. This is not true for similar databases for fossil mammals (e.g. NOW—the Neogene Mammal Database [http://www.helsinki.fi/science/now/]) or mammalian anatomy (e.g. Comparative Mammalian Brain Collections [http://www.brainmuseum.org]). The database for All the World's Primates justifies its fees by arguing that the dire problems of primate conservation make it necessary to charge fees. However, fund-raising for conservation never seems to end, and worthwhile research is thwarted by high fees.