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What is a mammal?

At first sight, this is not a difficult question. Every child is able to identify an animal as a mammal. Since its earliest age it can identify what is a cat, dog, rabbit, bear, fox, wolf, monkey, deer, mouse, or pig and soon experiences that with anyone who lacks such a knowledge there would be little chance to communicate about other things as well. To identify an animal as a mammal is indeed easy. But by which characteristics? The child would perhaps explain: *Mammals are hairy four-legged animals with faces.*

A child answers: A hairy four-legged animal with a face

Against expectation, the three characteristics reported by this naive description express almost everything that is most essential about mammals.

Hair, or fur, probably the most obvious mammalian feature, is a structure unique to that group, and unlike the feathers of birds is not related to the dermal scales of reptiles. A mammal has several types of hairs that comprise the pelage. Specialized hairs, called vibrissae, mostly concentrated in the facial region of the head, perform a tactile function. Pelage is seasonally replaced in most mammals, usually once or twice a year by the process called molting. In some mammals, such as ermines, the brown summer camouflage can be changed to a white coat in winter. In others, such as humans, elephants, rhinoceroses, naked mole rats, and aardvarks, and in particular the aquatic mammals such as walruses, hippopotami, sirenia, or cetaceans, the hair coat is secondarily reduced (though only in the latter group is it absent completely, including vibrissae). In the aquatic mammals (but not only in them), the role of the pelage is performed by a thick layer of subcutaneous adipose tissue by which the surface of body is almost completely isolated from its warm core and the effect of a cold ambient environment is substantially reduced. Thanks to this tissue, some mammals can forage even in cold arctic waters and, as a seal does, rest on ice without risk of freezing to it. In short, the essential role of the subcutaneous adipose layer and pelage is in thermal isolation, in preventing loss of body heat. Mammals, like birds, are *endotherms* (heat is generated from inside of the body by continuous metabolic processes) and *homeotherms* (the body temperature is maintained within a narrow constant range).

The body temperature of mammals, about 98.6°F (37°C), is optimal for most enzymatic reactions. A broad variety of functions are, therefore, kept ready for an immediate triggering or ad hoc mutual coupling. All this also increases the versatility of various complex functions such as locomotion, defensive reactions, and sensory performances or neural processing of sensory information and its association analysis. The constant body temperature permits, among other things, a high level of activity at night and year-round colonization of the low temperature regions and habitats that are not accessible to the ectothermic vertebrates. In short, endothermy has a number of both advantages and problems. Endothermy is very expensive and the high metabolic rate of mammals requires quite a large energetic intake. In response, mammals developed a large number of very effective feeding adaptations and foraging strategies, enabling them to exploit an extreme variety of food resources from insects and small vertebrates (a basic diet for many groups) to green plants (a widely accessible but indigestible substance for most non-mammals). At the same time, mammals have also developed diverse ways to efficiently control energy expenditure.

Besides structural adaptations such as hair, mammals have also developed diverse physiological and behavioral means to prevent heat and water loss, such as burrowing into underground dens; seasonal migrations or heterothermy; and the controlled drop of body temperature and metabolic expenditure during part of the day, or even the year (hibernation in temperate bats, bears, and rodents as well as summer estivation in some desert mammals). So, considerable adaptive effort in both directions increases foraging efficiency and energy expenditure control. When integrated with morphological, physiological, behavioral, and social aspects, it is an essential feature of mammalian evolution and has contributed to the appearance of the mammalian character in many respects.

Four legs, each with five toes, are common not only to many mammals, but to all terrestrial vertebrates (amphibians, reptiles, birds, and mammals), a clade called Tetrapoda. Nevertheless, in the arrangement of limbs and the modes of locomotion that it promotes, mammals differ extensively from the remaining groups. The difference is so clear that it allows us to identify a moving animal in a distance as a mammal even in one blink of an eye. In contrast to the "splayed" reptilian
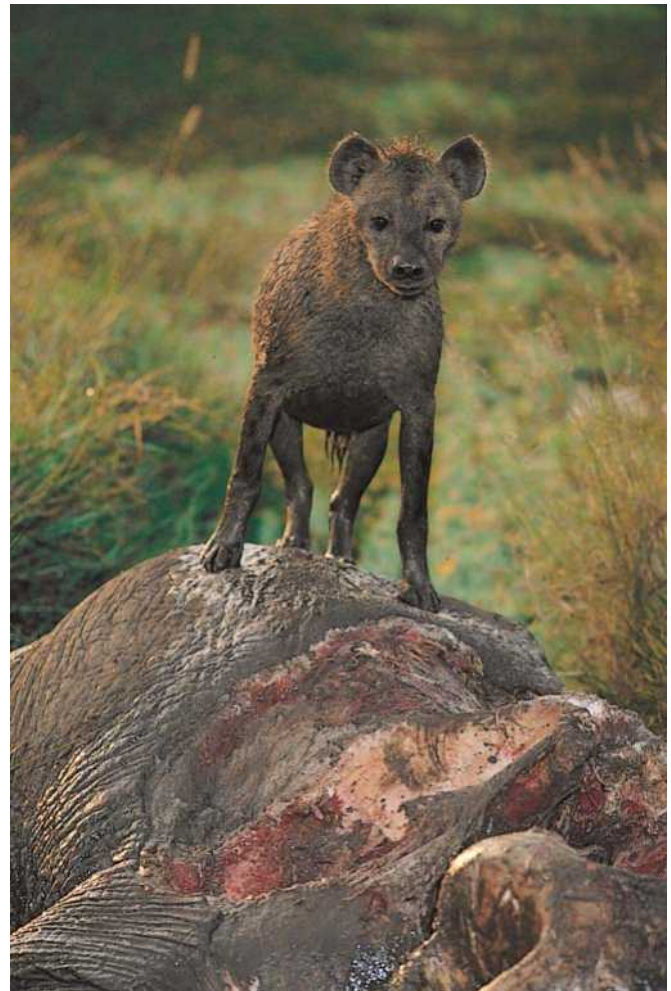
Red kangaroos (*Macropus rufus*) on the move. (Photo by Animals Animals ©Gerard Lacz. Reproduced by permission.)

groups. The presence of sophisticated mechanisms of social integration and an enlarged role in interindividual discrimination and social signaling are broadly characteristic of mammals. Nevertheless, each isolated component contributing to the complex image of the mammalian face says something important regarding the nature of the mammalian constitution, and, moreover, they are actually unique characters of the group. This is particularly valid for fleshy cheeks and lips, the muscular belt surrounding the opening of a mouth. The lips and the spacious pocket behind them between the cheeks and teeth (the *vestibulum oris*) are closely related to feeding, and not only in that they enlarge the versatility of food processing in an adult mammal. The lips, cheeks and *vestibulum oris* are completely developed at the time of birth and since that time have engaged in the first behavioral skill performed by a mammal. Synergetic contraction of lip and cheek muscles producing a low pressure in the *vestibulum oris* is the key component of the suckling reflex, the elementary feeding adaptation of a newborn mammal. All mammals, without exception, nourish their young with milk and all female mammals have large paired apocrine glands specialized for this role—the mammary glands, or mammae. Nevertheless, not

stance (i.e. horizontal from the body and parallel to the ground), the limbs of mammals are held directly beneath the body and move in a plane parallel to the long axis of the body. In contrast to reptiles, whose locomotion is mostly restricted to the lateral undulation of the trunk, mammals flex their vertebrate column vertically during locomotion. This arrangement enables a powered directional movement, such as sustained running or galloping, very effective for escaping from a predator, chasing mobile prey, or exploring spatially dispersed food resources. The respective rearrangements also bring another effect. By strengthening the vertebral column against lateral movement, the thoracic cavity can be considerably enlarged and the thoracic muscles released from a locomotory engagement, promoting changes to the effective volume of the thoracic cavity. With a synergetic support from another strictly mammalian structure, a muscular diaphragm separating the thoracic and visceral cavity, the volume of the thoracic cavity can change during a breathing cycle much more than with any other vertebrates. With the alveolar lungs, typical for mammals, that are designed to respond to volume changes, breathing performance enormously increases. This enables a mammal to not only keep its basal metabolic rate at a very high level (a prerequisite for endothermy) but, in particular, to increase it considerably during locomotion. In this connection, it should be stressed that the biomechanics of mammalian locomotion not only allow a perfect synchronization of limb movements and breathing cycles but, with the vertical flex of the vertebral column, are synergetic to the breathing movements and support it directly. As a result, the instantly high locomotory activity that characterizes a mammal increases metabolic requirements but at the same time helps to respond to them.

The face is the essential source of intra-group social information not only for humans but for many other mammal

A spotted hyena (*Crocuta crocuta*) stands on its meal of a baby elephant. (Photo by Harald Schütz. Reproduced by permission.)

Some mammals, such as this goat, have rather dramatic antlers or horns. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

all mammalian newborns actually suck the milk. In the egg-lying monotremes (the Australian duck-billed platypus and spiny anteaters), mammary glands lack the common milk ducts and nipples, so young do not suck but instead lick the milk using their tongue. All other mammals, both marsupials and eutherians, together denoted as Theria, bear a distinctive structure supporting suckling—the paired mammary nipples. The nipples originate independently from mammary glands, they are present both in males and females, and their number and position is an important character of individual clades. The therian mammals are all viviparous. For the most vulnerable period of their lives they are protected first by the intrauterine development with placental attachment of the embryo and then by prolonged postnatal parental care. A milk diet during the latter stage postpones the strict functional control on jaws and dentition and enables postnatal growth, the essential factor for the feeding efficiency of an adult mammal. At the same time this provides extra time for development of other advanced and often greatly specialized mammalian characteristics: an evolving brain and the refinement of motor capacities and behavioral skills. Thanks to the extended parental investment that mammalian offspring have at the beginning of their independent life, they enjoy a much higher chance for post-weaning survival than the offspring of most other vertebrates. The enormous cost of the parental investment places, of course, a significant limit upon the number of offspring that can be produced. Despite the great variation in reproductive strategies among individual mammalian

clades, in comparison to other vertebrates (excepting elasmobranchians and birds), the mammals are clearly the K-strategists (producing few; but well-cared for, offspring) in general.

The other components of the mammalian face provide correspondingly significant information on the nature of these animals. The vivid eyes with movable eyelids, external auricles, nose, and last but not least long whiskers (vibrissae, the hairs specialized for tactile functions), show that a mammal is a sensory animal. Most extant mammals are noctural or crepuscular and this was almost certainly also the case with their ancestors. In contrast to other tetrapods, which are mostly diurnal and perceive almost all spatial information from vision, mammals were forced to build up a sensory image of the world from a combination of different sources, in particular olfaction and hearing. Nevertheless, vision is well developed in most mammals and is capable of very fine structural and color discrimination, and some mammals are secondarily just optical animals. For example, primates exhibit a greatly enlarged capability for stereoscopic vision. In any case, all mammals have structurally complete eyes, though the eyes may be cov-
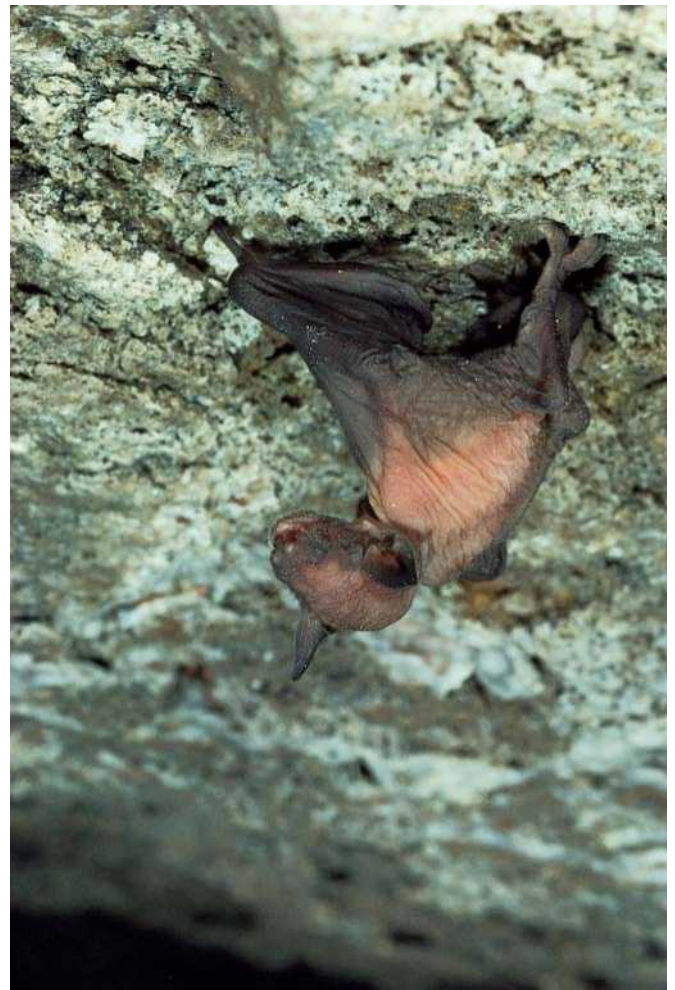
A baby gray bat (*Myotis grisescens*). (Photo by Merlin D. Tuttle/Bat Conservation International/Photo Researchers, Inc. Reproduced by permission.)

Near Kilimanjaro, a giraffe (*Giraffa camelopardalis*) pauses to survey for predators. Giraffes are the tallest extant mammals, males reaching 18 ft (5.5 m) in height. (Photo by Harald Schütz. Reproduced by permission.)

ered by skin in some fossorial mammals (such as blind mole rats, or marsupial moles) or their performance may be reduced in some respect. In comparison with other vertebrates, the performance of vision is particularly high under low light intensities, and the eyes are quite mobile. The latter character may compensate for a reduced ability of head rotation in mammals due to the bicondylous occipital joint contrasting to a monocondylous joint in birds or reptiles. The eyes are covered by movable eyelids (not appearing in reptiles), significant both in protecting the eyes and in social signaling. The remaining two structures—nose and auricles—are particularly unique for mammals and are related to the senses that are especially important for mammals: olfaction and hearing. Not only the nose and auricles themselves, but also the other structures associated with the senses of smell and hearing feature many traits unique to mammals.

Mammals construct much of their spatial information with the sole aid of olfactory, acoustic, or tactile stimuli combined with information from low-intensity vision. This task necessitated not only a considerable increase in the capacity and sensory versatility of the respective organs, but also the refinement of the semantic analysis of the information they provide. As a result, the brain structures responsible for these tasks are greatly enlarged in mammals. The tectum mesen-

cephali, a center for semantic analysis of optical information, bi-lobed in other vertebrates, is supplemented by a distinct center of acoustic analysis by which the tectum of mammals becomes a four-lobed structure, the corpora quadrigemina. The forebrain or telencephalon, a structure related to olfactory analysis, is by far the largest part of the mammalian brain. Its enlargement is particularly due to the enlarging of the neocortex, a multi-layered surface structure of the brain, which further channels inputs from other brain structures and plays the role of a superposed integrative center for all sensory, sensory-motor, and social information.

A zoologist answers: A highly derived amniote

Many of the characters common to mammals do not appear in other animals. Some of them, of course, can be observed also in birds—a very high (in respect to both maximum and mean values) metabolic rate and activity level or complexity of particular adaptations such as advanced parental care and social life, increased sensory capacities, and new pathways of processing sensory information or enormous ecological versatility. Fine differences between birds and mammals suggest that the respective adaptations are homoplasies—that is, they evolved in both groups independently.
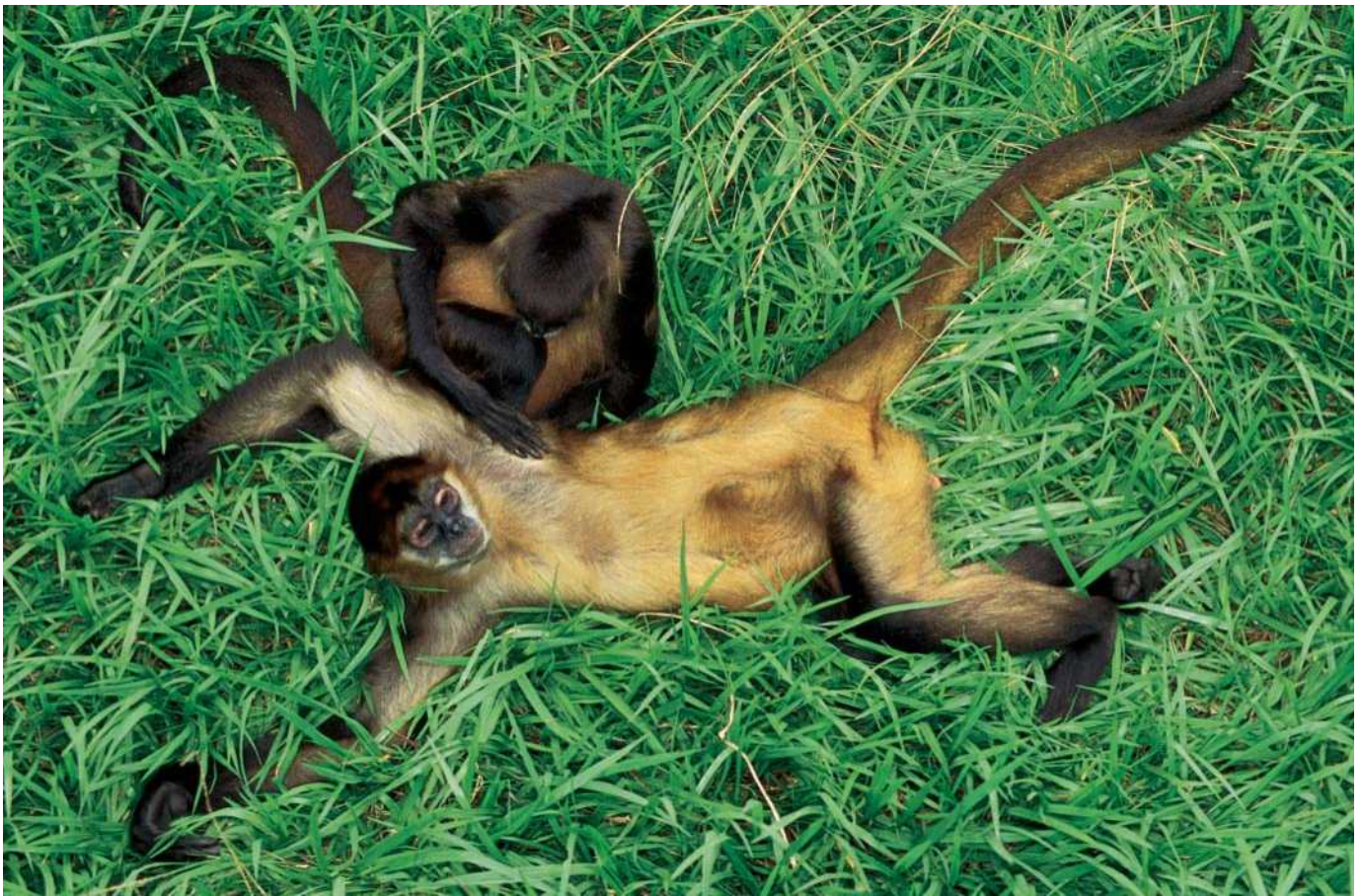
Black-handed spider monkeys (*Ateles geoffroyi*) grooming. (Photo by Gail M. Shumway. Bruce Coleman, Inc. Reproduced by permission.)

Other mammalian characteristics are synapomorphies of Amniota, the characteristics shared because of common ancestry. The amniotes, a group including reptiles, birds, and mammals, are the terrestrial vertebrates in which embryonic development takes place under the protection of fetal membranes (amnion, chorion, allantois). As in other amniotes, mammals are further characterized by an increased role of parental investment, internal fertilization, keratinized skin derivatives, an advanced type of kidney (metanephros) with a specific ureter, an advanced type of lung respiration, and the decisive role of dermal bones in skull morphology. Of course, at the same time, mammals share a large number of characteristics with all other vertebrates, including the general body plan, solid inner skeleton, the design of homeostatic mechanisms (including pathways of neural and humoral regulation), and functional integration of particular developmental modules. Mammals also share with other vertebrates the patterns of segmentation of trunk skeleton and muscles and the specific arrangements of the homeobox genes organizing the body segmentation as well as a lack of their expression in the head region, etc. These characters are synapomorphies of vertebrates, which are at least partly retained not only in some amniotes but throughout all other vertebrate clades. With respect to mammals, these are symplesiomorphies, the primitive characters that do not reveal closer relations of the class but on its broadest phylogenetic context.

Mammals also exhibit a large number of qualities that are fully unique to them, the autapomorphies. The autapomorphies are the characteristics by which a taxon can be clearly distinguished and diagnosed. Thus, though many characteristics of mammals are not specific just to them, answering the question "what is a mammal?" means first demonstrating the autapomorphies of that group. A simplified list of them includes:

(1) *The young are nourished with milk* produced by (2) *mammary glands*. These glands appear in all female mammals, and are the structure from which the class Mammalia got its name. (3) *Obligatory vivipary* (in Theria, i.e., marsupials and placentals) is the reproductive mode with a specialized organ interconnecting the embryo and maternal tissues, the *chorioallantoic placenta* (in Eutheria, i.e., placentals). (4) *Hairs*, covering the body, grow from deep invaginations of the germinal layer of epidermis called *follicles*. Similar to other amniotes, the hair is composed of keratin and pigments, but its structure is unique for mammals. (5) *Skin* is rich in various glands. Most mammals have sweat glands (contributing to water balance and cooling the body surface), scent glands, and sebaceous glands. (6) The *specific integumental derivatives*, characteristic of particular groups of mammals, are composed either exclusively of keratin (such as claws, nails, and hoofs, which protect the terminal phalanx of the digits and adapt them to a

A silverback jackal (*Canis mesomelas*) and an African elephant (*Loxodonta africana*) at a watering hole in Chobe National Park, Botswana. (Photo by © Theo Allofs/Corbis. Reproduced by permission.)

specific way of locomotion or foraging) or of keratin in combination with dermal bone structures (horns of bovids and antlers of cervid artiodactyls, which play a considerable role in social signaling). A large variety of integumental derivatives are included in defensive adaptations: dermal armors of armadillos or keratinized scales of pangolins, spines modified from hairs in echidnas, hedgehogs, tenrecs, porcupines, or spiny mice, or the accumulations of hairlike fibers keratinized into a horn structure in rhinoceroses. (7) *Limb position and function* are modified to support specific locomotory modes of mammals such as jumping, galloping, or sustained running and can be specifically rearranged. The extreme rearrangements are seen in bats, which fly using a forelimb wing, and in specialized marine mammals, pinnipedian carnivores, cetaceans, and sirenia, whose forelimbs take the shape of a fin (the external hind limbs are absent in the latter two groups). (8) *Pectoral girdle is simplified* in comparison to the non-mammalian state: coracoid, precoracoid and interclavicle bones are lost (except for monotremes, which retain them) or partly included in the scapula. Also the clavicle, the last skeletal element that fixes the limb to the axial and thoracic skeleton, is

lost in many groups. With these rearrangements the forelimbs get new locomotory qualities (such as extensive protraction), supporting abilities such as climbing and fine limb movements and providing a new spectrum of manipulative functions from cleaning hair to a variety of prey manipulations. (9) *The bones of the pelvic girdle are fused into a single bone*, with enlarged and horizontally prolonged ilium.

(10) A great degree of *regional differentiation of the vertebral column*. All mammals (except some edentates and manatees) have seven cervical vertebrae with the first two (atlas and axis) specifically rearranged to support powered head movements. (11) *The vertebral column is strengthened against lateral movements* but is greatly disposed to the vertical flexion. This is seen first of all in the lumbar section, whose vertebrae, in contrast to the non-mammalian ancestors, lack ribs. (12) The mammalian *skull is bicondylous* (the first vertebra, atlas, joints the skull via paired occipital condyles located on the lateral sides of the large occipital foramen), with (13) *an enlarged braincase*, (14) *massive zygomatic arches* (formed by the jugale and squamosum bones), and (15) a spacious *nasal cavity with a labyrith of nasal turbinalia* covered by vascularized tissue important both for olfaction (ethmoidal turbinalia) and/or heat and water exchange during breathing (maxillary turbinalia). (16) The nostrils open at a common structure called the *nose*, obviously the most prominent point of the head. The ancestral form of the nose, the *rhinarium*, is a hairless field of densely circular-patterned skin surrounding the nostril openings. The rhinarium is particularly large in macrosmatic (highly developed sense of smell) mammals (such as carnivores or artiodactyls), in lagomorphs, some rodents, and bats. In strepsirhine primates it is incised by a central groove, the phlitrum, while in some other groups such as in macroscelids or in elephants, the nose is prolonged and attains a number of supplementary functions. In contrast, all these structures are absent in cetaceans in which the nasal cavity is reduced and the nostrils (or a single nostril opening in Odontoceti) appear at the top of the head and their function is restricted to respiration. (17) Left and right maxillary and palatal bones are fused in early development and form the *secondary bony palate*, which is further extended by a fleshy soft palate. These structures provide a complete separation of the respiratory and alimentary tracts. The early appearance of such a separation is one of the essential prerequisites for suckling milk by a newborn and, hence, it seems probable that the secondary palate first appeared simply as an adaptation for this. (18) The *heart* is a large *four-chambered organ* (as in birds) with the *left aorta persistent* (not the right one, as in birds). (19) *Erythrocytes, the red blood cells, are biconcave and lack nuclei*. Thrombocytes are transformed to nonnucleated blood platelets.

(20) *Lungs have an alveolar structure*, ventilated by volume changes performed by the counteraction of two independent muscular systems, and a (21) *muscular diaphragm*, unique for mammals. (22) The *voice organ in the larynx*, with several pairs of membranous muscles, is unique for mammals. It is capable of very specialized functions such as the production of various communicative signals or high-frequency echolocation calls in bats and cetaceans. (23) There are *three ossicles in the middle ear* (malleus, incus, stapes). The former two are unique to mammals and are derived from the elements of the pri-

mary mandibular joint—articulare and quadratum—which still retain their original function in the immediate mammalian ancestors. The third bone of the primary mandibular joint, the angulare, changes in mammals into the tympanic bone, which fixes the tympanic membrane and finally enlarges into a bony cover of the middle ear—the bulae tympani. (24) The *sound receptor (Corti´s organ of the inner ear) is quite long and spirally coiled* in mammals (except for monotremes) and surrounded by *petrosum*, a very compact bone created by a fusion of several elements. (25) With an enlarged braincase, the middle ear and tympanic membrane are thus located deeper in the head and open to the external environment by a *long auditory meatus* terminating with (26) a *large movable external auricle*. Auricles (pinnae) are specifically shaped in particular clades and contribute to the lateral discrimination of the auditory stimuli and directionality of hearing. They may be absent in some aquatic mammals (cetaceans, sirenia, walruses), while they are extremely pronounced and diversified in other groups such as bats, for which the acoustic stimuli (echoes of the ultrasonic calls they emit) are by far the most important source of spatial information. (27) In contrast to other amniotes, *the lower jaw, or mandible, is composed of a single bone*, dentary or dentale, which directly articulates with the temporal bone of the skull at the (28) *dentary-squamosal joint*. This arrangement not only fastens the jaw joint to resist the forces exerted during strong biting but also simplifies the functional rearrangements of jaw morphology responding to different demands of particular feeding specializations. (29) In all mammals, the posterior part of the mandible extends dorsally into the *ramus mandibulae*, which provides an area of attachment for the massive temporal muscles responsible for the powered adduction of the mandible.

(30) Essentially, all mammals have *large teeth* despite considerable variation in number, shape, and function in particular groups and/or the fact that some mammals secondarily lack any teeth at all (anteaters of different groups, and the platypus). Teeth are deep-rooted in bony sockets called alveoles. Only three bones host the teeth in mammals: the premaxilla and maxilla in the upper jaw and the dentary in the lower jaw. (31) Mammalian *dentition is generally heterodont (of different size, shape, etc.)*. Besides the conical or unicuspidate teeth (incisors and a single pair of canines in each jaw) mammals also have large complex multicuspidate molars (three in placentals, four in marsupials, in each jaw quadrant) and premolars situated between canines and molars whose shape and number varies considerably among particular groups. The latter two teeth types are sometimes called "postcanines" or "cheek teeth." (32) *The molars* are unique to mammals. The basic molar type ancestral to all particular groups of mammals is called tribosphenic. It consists of three sharp cones connected with sharp blades. In combination with the deep compression chambers between blades, such an arrangement provides an excellent tool both for shearing soft tissues and crushing insect exoskeletons. This type of molar is retained in all groups feeding on insects, such as many marsupials, tenrecs, macroscelids, true insectivores such as moles, shrews or hedgehogs, bats, tree shrews, and prosimian primates, but the design of the molar teeth is often extensively rearranged in other groups. The multicuspidate structure of molars bears enormous potential for morphogenetic and functional re-

Many young mammals practice skills needed for survival. These lion cubs practice hunting in the grass. (Photo by K. Ammann. Bruce Coleman, Inc. Reproduced by permission.)

arrangements, one of the prerequisites of the large diversity of feeding adaptations in mammals. (33) Mammalian dentition is *diphyodont*. This means that there are two generations at each tooth position (except for molars): the milk or deciduous teeth of the young and the permanent teeth of an adult mammal. Diphyodonty solves a functional-morphological dilemma: the size of teeth, an essential factor in feeding efficiency, is limited by the size of the jaws. While the jaws can grow extensively, the posteruption size of the teeth cannot be changed due to the rigidity of their enamel cover, which is the essential quality of a tooth. With diphyodonty, the size of the late erupting permanent teeth can be maximized and adapted to adult jaw size while the deciduous dentition provides a corresponding solution for the postweaning period. Dental morphology and the patterns of tooth replacement are specifically modified in some clades. In marsupials, only one milk tooth—the last premolar—comes in eruption, while the others are resorbed prior to eruption. Dolphins, aardvarks, and armadillos have a homodont dentition without any tooth replacement. No tooth replacement occurs in small and short-living mammals with greatly specialized dentition, such as shrews or muroid rodents (deciduous teeth are resorbed instead of eruption), while in some large herbivores tooth replacement can become a continuous process by which the tooth row enlarges gradually by subsequent eruption of still larger molar teeth in the posterior part of the jaws. In elephants and manatees, this process includes a horizontal shift of the erupting tooth, which thus replaces the preceding cheek tooth. All these processes are well synchronized with the growth of jaws, the course of tooth wear, and subsequent prolonging of time available for tooth development. (34) A general *enlargement of the brain* related perhaps not only to an increase in the amount of sensory information and/or a need to integrate sensory information from different sources, but also to more locomotory activity, high versatility in locomo-

A cheetah (*Acinonyx jubatus*) chases a Thomson's gazelle (*Gazella thomsonii*). The cheetah is the fastest land animal and can reach speeds of 70 mph (113 kph). (Photo by Tom Brakefield. Bruce Coleman, Inc. Reproduced by permission.)

tory functions, a greatly diversified social life, and a considerably expanded role for social and individual learning. (38) The extended spectrum of behavioral reactions and their interconnections with an increased capacity of social and individual learning and interindividual discrimination should also be mentioned. In fact, this characteristic is very significant for mammals, as are the following two: (39) *Growth is terminated* both by hormonal control and structural factors. The most influential structural aspect of body growth is the appearance of *cartilaginous epiphyseal discs separating diaphyses and epiphyses* of long bones. With completed ossification, the discs disappear and growth is finished. Corresponding mechanisms determine the size of the skull (except in cetaceans, which have a telescoped skull in which the posterior bones of the cranium overlap each other). (40) Sex is determined by chromosomal constitution *(XY system, heterogametic sex is a male)*.

Almost all of these (and other) characteristics undergo significant variations and their modifications are often largely specific for particular clades of mammals. What is common for all is perhaps that in mammals all the characters are more densely interrelated than in other groups (except for birds). The morphological adaptations related to locomotion or feeding are often also integrated for social signaling, physiological regulation, or reproductive strategy, and often are controlled by quite distant and non-apparent factors. Thus, the excessive structures of ruminant artiodactyls, such as the horns of bovids and antlers of deer, are undoubtedly significant in social signaling, in courtship and display behavior, and frequently are discussed as excessive products of sexual selection. However, the proximate factor of these structures, the hereditary disposition for excessive production of mineralized bone tissue, can actually be selected rather by its much less

obvious effect in a female: her ability to produce a large, extremely precocial newborn with highly mineralized long bones that enable it to walk immediately after parturition. The female preference for the excessive state of the correlated characters in a male, his large body size and display qualities, possibly supported by social learning, supplement the mechanisms of the selection in quite a non-trivial way. Such a multi-layered arrangement of different factors included in a particular adaptation is indeed something very mammalian.

A paleontologist answers: The product of the earliest divergence of amniotes and index fossils of the Cenozoic

Mammals are the only extant descendants of the synapsids—the first well-established group of amniotes, named after a rounded temporal opening behind the orbit bordered by the jugale and squamosum bones. Since the beginning of amniotes, evolution of synapsids proceeded separately from the other amniotes, which later diversified in particular reptile lineages including dinosaurs and birds. The first amniotes recorded from the middle Carboniferous (320 million years ago) were just synapsids and just this clade predominated in the fossil record of the terrestrial vertebrates until the early Triassic. A large number of taxa appearing among early synapsids represented at least two different clades: Eupelycosauria and Caseasauria. The former included large carnivorous forms and the latter were generalized small- or medium-sized omnivores. Since the middle Permian (260 mya), another group of synapsids called Therapsida dominated the terrestrial record. In comparison with pelycosaurs, therapsids had much larger temporal openings, a single pair of large canines,

and clear functional and shape differences between the anterior and the posterior teeth. Two lineages of that group, Dicynodontia and Cynodontia, survived the mass extinction at the Permian/Triassic boundary (248 mya).

Immediate ancestors of mammals are found among the cynodonts. Mammals are closely related to cynodont groups called tritylodontids and trithelodontids, which first appeared during the late Triassic. All three groups, including mammals, had additional cusps on posterior teeth, a well-developed ramus mandibulae, and a complete secondary palate. In some of them (*Diarthrognathus*), the jaw joint was formed both by the original articulation (articulare-quadratum) and by the mammal-like process (dentary-squamosal). In the oldest true mammals, the former jaw articulation is abandoned and removed in the middle ear. These characters are the index diagnostic features of a mammal in the fossil record (no. 23, 26, 27 of the above list).

The oldest mammals, *Sinoconodon*, *Adelobasileus*, *Kuehneotherium*, or *Morganucodon* (about 200–225 million years old), were all very small, with long heterodont dentition and a triangular arrangement of molar cusps designed for shearing. They were most probably quite agile night creatures resembling today's insectivores. The relative brain volume in the earliest mammals was close to that found in extant insectivores and about three times higher than in cynodonts. Of course, they still differed from the modern mammals in many respects. The derived characters of modern mammals (as reviewed in the preceding text) did not evolve together but were subsequently accumulated during the long history of synapsid evolution.

In contrast to the medium- to large-sized diurnal dinosaurs, birds, and other reptiles that had dominated the terrestrial habitats, the early mammals were quite small, nocturnal creatures. Nevertheless, since the Jurassic period they grew in greatly diversified groups and at least four lineages of that radiation survived the mass extinction at the Cretaceous/Tertiary boundary (65 mya). Three of these groups, monotremes, marsupials, and placentals, are extant; the fourth group, multituberculates, survived until the end of Oligocene. Multituberculates resembled rodents in design of dentition (two pairs of prominent incisors separated from a series of cheek teeth by a toothless diastema), but their cheek teeth and skull morphology were quite different from those in any other groups of mammals.

The major radiation of mammals appeared at the beginning of Tertiary, in the Paleocene. That radiation produced many groups that are now extinct (including nine extinct orders) as well as almost all the orders of modern mammals. During the Paleocene and Eocene, other groups occupied the niches of current mammalian groups. In Eurasia and North America it was Dinocerata, Taeniodonta, and Tillodontia as herbivores and Pantodonta and Creodonta as their predators. All these are extinct lineages not related to any of the recent orders. The most isolated situation was in Australia, which had been cut-off from the other continents since the Cretaceous and was not influenced by the intervention of the eutherian mammals. The mammalian evolution in South America after its separation from Africa at the early Paleocene was equally

isolated. Besides the marsupials (clade of Ameridelphia) and edentates with giant glyptodonts, mylodonts, and megalonychids, whose relatives survived until recently, a great variety of strange eutherians appeared here during the Paleocene and Eocene. This includes the large herbivores of the orders Notoungulata, Astrapotheria, Litopterna, and Xenungulata, as well as the Pyrotheria (resembling proboscideans) and their giant marsupial predators, such as *Thylacosmilus*, resembling the large saber-toothed cats. The mammalian fauna of South America was further supplemented by special clades of hystricognathe rodents, haplorhine primates, and several clades of bats, particularly the leaf-nosed bats. These groups probably entered South America during the Paleocene or Eocene by rafting from Africa. The evolution in splendid isolation of South America terminated with the appearance of a land bridge with North America some 3 mya, which heavily impacted the fauna of both continents. The impact of African and Asian fauna on the European mammalian evolution by the end of Eocene was of a similar significance.

It is important to remember that the fossil record of mammals, including detailed pathways of evolutionary divergences and/or the stories of particular clades, is much more complete and rich in information than in any other group of vertebrates. This is due to the fact that the massive bones of mammals, and in particular their teeth, which provide most information on both the relationship and feeding adaptation of a taxon, are particularly well suited to be preserved in fossil deposits. Due to this factor, the fossil record of mammals is perhaps the most complete among the vertebrates. Also, during the late Cenozoic, Neogene, and Quaternary, the fossil record of some mammalian groups (such as rodents, insectivores, and ungulates) is so rich that the phylogeny of many clades can be traced in surprisingly great detail by the respective fossil record. For the same reason, some of these fossils (e.g., voles in the Quaternary period) are the most important terrestrial index fossils and are of key significance not only for local biostratigraphies and precise dating of the late Cenozoic deposits, but also for large-scale paleobiogeography and even for intercontinental correlations. The late Cenozoic period is characterized by gradually increasing effects of climatic oscillations, including repeated periods of cold and dry climate—glacials—followed by the evolution of grass and the treeless grassland country. Many clades of mammals responded to these changes and produced the extreme specialists in food resources of the glacial habitats, such as mammoths, woolly rhinos, lemmings, cave bears, and cave lions.

The most diversified animals

There are about 4,600 species of mammals. This is a relatively small number compared to the 9,600 species of birds or 35,000 fish species and almost nothing in comparison to about 100,000 species of mollusks or some 10,000,000 species of crustaceans and insects. Even such groups as extant reptiles (with 6,000 species) and frogs (with about 5,200 species) are more diversified at the species level. Nevertheless, in diversity of body sizes, locomotory types, habitat adaptations, or feeding strategies, the mammals greatly exceed all that is common in other classes.

Only birds and arthropods may approach such variety. However, at least in diversity of body size, the mammals clearly surpass even them. The body mass of the largest extant terrestial mammal—the African elephant *Loxodonta africana*— with shoulder height of 11.5 ft (3.5 m), reaches to 6.6 tons (6,000 kg). The extinct rhinocerotid *Baluchitherium* was about 18 ft (5.5 m) and 20 tons (18,000 kg), respectively. The largest animal to ever appear—the blue whale (*Balaenoptera musculus*)—with up to 98 ft (30 m) in length, reaches 220 tons (200,000 kg). In contrast to dinosaurs or elesmobranchians, which also produced quite large forms, the average mammal is a small animal the size of a rat, and the smallest mammals such as a pygmy white-toothed shrew (*Suncus etruscus)* or Kitti's hog-nosed bat (*Craseonycteris thonglongyai*) have a body length of just 1.2–1.6 in (3–4 cm) and weigh only 0.05-0.07 oz (1.5–2 g).

Mammals colonized almost all habitats and regions on the Earth. They now feed on flying insects hundreds of meters above the ground; jump through foliage in the canopy of a tropical forest; graze in lowland savannas and high mountain alpine meadows; hunt for fish under the ice cover of arctic seas; burrow the underground labyrinths to feed on diverse plant roots, bulbs, or insects; cruise the world's oceans, or dive there to depths of 1.8 mi (3 km) in the hunt for giant squid. Some even sit by a computer and write articles like this.

About 4,600 species of mammals are arranged in approximately 1,300 genera, 135 families, and 25 orders. Rodents with 1,820 species, 426 genera and 29 families are far the largest order, while in contrast, 8 orders include less than 10 species, and four of them are even monotypic (Microbiotheria, Notoryctemorphia, Tubulidentata, Dermoptera). Although interrelationship among individual orders is still the subject of a vivid debate, three major clades of mammals are quite clear: monotremes (2 families, 3 genera, 3 species), marsupials (7 orders, 16 families, 78 genera and 280 spp.), and eutherian or placentals (17 orders, 117 families, 1,220 genera, 4,300 spp.), the latter two clades are together denoted as Theria.

The essential differences among the three major clades of mammals are in mode of their reproduction and patterns of embryonic development. Monotremes (platypus and echidnas), restricted to the Australian region, show only little difference from their ancestral amniote conditions. They deliver eggs rich in yolk, and incubate them for 10 to 11 days. Young hatch from the egg in a manner similar to birds. Monotremes also retain the reptile conditions in the morphology of the reproductive system: the ovary is large and short oviducts come via paired uteri to a broad vagina, which opens with the urinary bladder and rectum into a common cloaca. Except for monotremes, all mammals are viviparous with intrauterine embryonic development and have quite small eggs, poor in yolk (particularly in eutherians).

There are essential differences between marsupials and eutherians in the earliest stages of embryonic development, as well as in many other characteristics. The reproductive tract in a female marsupial is bifurcated (with two vaginas), and also the tip of the penis in a male marsupial is bifurcated. Many marsupials have a marsupium, the abdominal pouch for rearing young, supported with the marsupial epipubic bones that are present in both sexes. The marsupial intrauterine development is very short and the embryo is attached to the uterine endometrium by the choriovitelline (yolk) placenta that lacks the villi penetrating deeper in the wall of uterus (except in bandicoots). The marsupial newborns are very small and little developed, and birth is nontraumatic. In contrast, the lactation period is much longer than in eutherians (only bats and some primates have proportionally long lactation periods). Nevertheless, the mother's total investment by the time of weaning young is roughly equal in both clades, but its distribution is different. The marsupial strategy is much less stressful for a mother and allows an extensive variation in tactics of reproduction. For instance, in the kangaroo, a mother can have three generations of young at one time: the young baby returning to drink low-protein but high-fat milk, the embryo-like young attached to a nipple nourished with high-protein but low-fat milk, and an embryo in the uterus for which development is delayed until the second-stage young is released.

A key agent of eutherian reproduction is the highly specialized organ supporting a prolonged embryonic development—the chorioallantoic placenta. Eutherian newborns are large and despite considerable variation over particular clades, are potentially capable of an independent life soon after birth. Large herbivores such as elephants, perissodactyls, and artiodactyls, as well as cetaceans, sirenians, hyraxes, and some primates, deliver single, fully developed newborns with open eyes, ears, and even the ability to walk immediately after birth. Such a newborn is called precocial in contrast to the altricial newborns of insectivores, bats, rodents, or carnivores, which are hairless, blind, and fully dependent on intensive mother's care. Both developmental strategies may, of course, appear within one clade as in lagomorphs (large litters and altricial young in a rabbit versus small litters and precocial young in a hare). Variations in reproductive strategies are closely interconnected with numerous behavioral adaptations and adaptations in social organization and population dynamics, all of which contribute significantly to mammalian diversity.

Recent molecular data strongly support the essential role of geographic factors in phylogenetic history and in taxonomic diversity of mammals. Thus, there is very strong support for the African clade Afrotheria, which is composed of the tenrecid and potamogalid insectivores, golden moles, macroscelids, aardvark, hyraxes, proboscideans, and sirenia. Also, the extensive covergences between Australian marsupials and particular eutherian clades and/or the paleontological data on mammalian evolution on particular continents suggest that on each continent, the adaptive radiation produced quite similar life forms: small to medium sized insectivores, rodent-like herbivores, large herbivores, and their predators. The niche of large herbivores seems to be particularly attractive (at least 18 different clades attained it) but at the same time, it is perhaps the most dangerous (13 of them are extinct).

Nearly one fourth of all mammals fly. This is pertinent to a number of species, the number of genera, and perhaps for the number of individuals as well. Bats, with more than 1,000 species in 265 genera, are the most common mammals in

The manatee (*Trichechus manatus*) is primarily herbivorous. Here a mother nurses her young. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

many tropical and subtropical habitats. Mostly active at night, bats hunt for various kinds of aerial prey (a basic strategy of the clade) or feed on fruit, nectar, or pollen. Some bats feed on frogs, reptiles, or other bats, and in the tropics of South America, the total biomass of bats exceeds that of all other mammals. Several Old World bats, such as false vampires, feed on small vertebrates, while others feed on fish plucked from the water surface. Frugivorous and nectarivorous bats are the essential agents for pollination and seed dispersal of many tropical plants, including banana and mango. Bats are often very social and form large colonies, including the largest assemblies known in mammals, such as the maternity colony of about 36 million Mexican free-tailed bats in Bracken Cave in Texas.

However, most of the extant mammals (nearly a half of all genera) maintain the basic mammalian niche. They are terrestrial, mostly nocturnal or crepuscular, and forage for different food resources that are available on the ground. In a tropical forest this may be seeds and fruits falling down from the canopy and the invertebrate or vertebrate animals feeding on them. In the subtropics and temperate regions, the significance of this habitat increases as the soil surface becomes the most significant crossroads of ecosystem metabolism. In a temperate ecosystem, the soil is the major conveyer of the energetic flow and an important source of free

energy that is available in a variety of food resources. It is no wonder that in the temperate regions terrestrial mammals form more than half of the local mammalian taxa (while it is one third or less in the tropics) and that their densities exceed those of all remaining mammalian species. Among them we find the groups that are the most progressive and most rapidly diversifying clades of the extant mammals (such as shrews or muroid rodents). Terrestrial mammals are, as a rule, quite small animals, and are often the r-strategists. They have short life spans, large litter sizes, several litters per year, and rapidly attain sexual maturity, sometimes even a few weeks after birth. Most of the small ground mammals dig underground burrows for resting. This reduces not only the risk of predation, but due to stable microclimatic conditions of the underground habitat, it also reduces metabolic stress by ambient temperature or by daytime changes in other weather conditions. Many mammals also tend to spend a considerable part of their active life underground, including food gathering. Those that combine it with terrestrial foraging are called semifossorial—most of the 57 genera of semifossorial mammals are rodents. Those that are entirely adapted to an underground way of life and often do not come above ground at all are called fossorial. The fossorial adaptations, which make them all quite similar in general appearance, are seen in 35 genera of 13 different clades and evolved convergently in all major geographic regions (Australian marsupial mole,

Holoarctic true moles, the African golden moles, and 10 groups of rodents in Holoarctic, Ethiopian, and Neotropical regions). Compared to their relatives, the fossorial mammals are all the K-strategists, some with pronounced tendencies to complex organization (mole rats).

The mammals also evolved another way to inhabit terrestrial habitats. It is called scansorial adaptation and is typical of large herbivores with an enormous locomotory capacity, enabling them to exploit distant patches of optimal resources and react actively to seasonal changes in them. In many instances these are social animals living in large nomadic herds. Kangaroos, the large macropodid marsupials of Australia, exhibit this scansorial adaptation. They move rapidly around their terrestrial habitat by hopping bipedally on their long, powerful hind legs, using their long tails for balance.

Locomotory modes are entirely different in the 156 genera of mammals that forage in arboreal habitats. Essentially arboricolous are primates, dermopterans, and tree shrews, as well as many marsupials, rodents, bats, and some edentates and carnivores. Typical for most of them are long forelimbs and a long tail, often prehensile. Other arboricolous mammals have a haired membrane between their legs, enabling them to glide between tree trunks. The mammals equipped for such gliding flight include flying lemurs (Dermoptera), several groups of rodents (flying squirrels, African anomalurids), and three genera of marsupials.

Roughly 107 genera and 170 species are aquatic or semi-aquatic and mostly fish-eating. Three grades can be distinguished here: (1) terrestrial animals that enter aquatic habitats only temporarily for feeding only (African otter shrews, Old World water shrews, desmans, water opossum, more clades of rodents, including large rodents such as beaver and capybara, and several clades of carnivores, particularly otters); (2) marine mammals that spend most of their life in aquatic habitats but come to shore for breeding (all pinnipedian carnivores, such as seals, sea lions and walruses, and sea otters); and (3) the exclusively aquatic mammals incapable of surviving outside of the aquatic environment—sirenians and cetaceans. The latter group is quite diversified, and includes 78 species in 41 genera that can be subdivided into two major clades: Mysticeti, whales that filter marine plankton with baleen plates hanging from roof of the mouth cavity, and Odontoceti, dolphins and toothed whales, which echolocate and feed on fish or squid (including the giant deep-sea architeuthids as in the sperm whale). Cetaceans evolved various sophisticated adapatations for prolonged diving into deep oceanic waters, such very economic ways of gas exchange that include a reduced heart rate during diving and more oxygen-binding hemoglobin and myoglobin in blood than in other mammals. Cetaceans, though closely related to non-ruminant artiodactyls and recently included together with them in a common order, Cetartiodactyla, diverge from the common picture of "what is a mammal?" perhaps most of all.

The extreme diversity in feeding adaptations is among the most prominent characteristics of mammals. Feeding specializations such as grazing grass or herbal foliage, palynovory (eating pollen of plants), myrmecophagy (specialized feeding on ants and termites), and sanguivory (feeding on blood of birds and mammals, in five species of true vampires) are not known from any other vertebrates. At the same time, all the feeding adaptations occurring in other vertebrate clades occur also among mammals.

In all mammals, the efficiency of a feeding specialization depends upon the appropriate morphological, physiological, and behavioral adaptations. First, it concerns the design of the teeth and dentition. The generalized heterodont dentition and the tribosphenic molar teeth designed for an insectivorous diet (as retained in various marsupials, insectivores, tree shrews, prosimian primates, and bats) can be easily modified to the carnivorous diet. A carnivorous diet further demands enlarging the size of the canines and arrangements that increase the shearing effect of cheek teeth. A lower position of the jaw joint increases the powered action of temporal muscles at the anterior part of dentition, and in extremely specialized carnivores such as cats, the dentition is then considerably shortened and reduced except for canines and the carnasial cheek teeth (the last upper premolar and the first lower molar, generally the largest teeth of carnivores). There is no problem with digesting the tissues of vertebrates and thus no special arrangements of the alimentary tract are needed.

In contrast, herbivores, especially those specialized in feeding on green plant mass, require a modified jaw design. This kind of food is everywhere and easily accessible as a rule, but it is extremely difficult to digest for several reasons. One is that this diet is very poor in nutritive content and must be consumed in very large volumes; it must also be broken down mechanically into small particles. Hence, the dentition is overburdened by wear of occluding teeth and their abrasion with hard plant tissue. Efficiency of feeding depends directly on the design of the tooth crown, on the size of total area for effective occlusion, and the efficiency of masticatory action. Large teeth with flat surfaces and high crowns resistant to intensive wear are particularly required.

The major problem with a diet of plants is that mammals (as well as other animals) do not produce enzymes that break down cellulose. They must rely on symbiotic microorganisms residing in their alimentary tract, evolve an appropriate housing for them, and ensure a sufficient time for proper food fermentation. The mammals evolved several ways to fulfill these requirements. One is the foregut fermentation (digastric digestion system) characteristic of ruminant artiodactyls (bovids, cervids), kangaroos, and colobus monkeys. The fermentation chambers are situated in spacious folds of the stomach; from these fermentation chambers the partially fermented food can be regurgitated and chewed during a rest period, which also prolongs the movement of food through the gut. The microorganisms detoxify alkaloids by which growing plants defend against herbivores prior to digestion, but are very sensitive to tanins contained in the dry plant tissues. The foregut fermenters avoid dry plants but feed on growing parts of plants, selectively cut with the tongue and lips (ruminants even lack the upper incisors).

Perissodactyls, rodents, lagomorphs, hyraxes, and elephants evolved hindgut fermentation (monogastric digestion system), where fermenting microorganisms are housed in the caecum and large intestine. Food is not regurgitated and all mechan-

ical disintegration of food must be performed at one mastication event. Except for caeca, the passage of food through the gut is almost twice as fast as in the foregut fermenters. Hindgut fermenters can survive on a very low-quality food, if it is available in large quantity. They can effectively separate the tanins and dry plant mass, both of which decrease the efficiency of the foregut fermenting. Correspondingly, the foregut and hindgut fermenters prefer different parts of plants and can both forage in the same habitats without any actual competition. The latter are, of course, under more intense pressure to evolve further adaptations to compensate for the energetic disadvantages of their digestion. One of them is extreme enlargement of caeca (as in rodents); another is considerable increase in the height of cheek teeth (maximized in several clades of lagomorphs and rodents, in which cheek teeth are hypselodont, or permanently growing). The third way is an increase in body size. This enlarges the length of the alimentary tract and prolongs the passage of food through it, while at the same time it reduces the rate of metabolism. The behavioral reduction of metabolic rate by a general decrease of activity level as in foliovore (leaf-eating) sloths or the koala produces the same results.

The gradual increase in body size is a feature of mammalian evolutionary dynamics, as it was repeatedly demonstrated by the fossil record of many clades. This is seen in most eutherians (not only in the herbivorous clades), but is much less apparent in marsupials. It seems that in addition to the common factors promoting a larger body size (a reduced basal metabolic rate, smaller ratio of surface area to body mass, and smaller heat transfer with ambient environment), something else comes into play, something which has to do with the essential differences of both the clades. This is the enormous stress of the eutherian way of reproduction. While intrauterine development is short and a litter weight is less than 1% of the mother body mass in a marsupial, the eutherian female must endure a very long pregnancy and the traumatic birth of a litter that in small eutherians such as insectivores, rodents, or bats, may weigh 50% of the mother's body mass.

With enlarging body size, the stress of pregnancy and parturition is reduced as the size of a newborn is relatively smaller (compared with 3-5% of a mother's mass in large mammals and 10-20% in smaller mammals). With a reduction of litter size, it further provides a chance to refine the female investment and deliver fully developed precocial young, as in ungulates or cetaceans. This aspect of mammalian adaptation and diversity should remind us that perhaps the ways in which a female does manage the stress of eutherian reproduction (the factor that magnified the strength of selection pressure) became the most influential source of viability of our clade.

Neighbors, competitors, and friends

Mammals and humans have been the closest relatives and nearest neighbors throughout the entire history of humankind. Mammals contribute essentially to our diet and we keep billions of domesticated mammals solely for that purpose. Hunting mammals for protein-rich meat became an essential background factor in human evolution several million years ago. More recently, the discovery of how to get such animal protein in another way started the Neolithic revolution some 10,000 years ago. The symbiotic coexistence with herds of large herbivores—which included taking part in their reproduction and consuming their milk and offspring—ensured the energetic base for a considerable increase in the human population of that time and became one of the most important developments in human history. Moreover, the other essential component of the Neolithic revolution may be related to mammals. Feeding on seeds of grass and storing them in the form of a seasonal food reserve could hardly have been discovered without inspiration from the steppe harvesting mouse (*Mus spicilegus)* and its huge corn stores or kurgans, containing up to 110 lb (50 kg) of corn. The theory that humans borrowed the idea of grain storage from a mouse is supported by the fact that the storage pits of Neolithic people were exact copies of the mouse kurgans. Mammals have even been engaged in the industrial and technological revolutions. Prior to the steam engine and for a long time in parallel with it, draft animals such as oxen, donkeys, and horses were a predominant source of power not only for agriculture, transport, and trade, but also for mining and early industry. Indeed, our civilization arose on the backs of an endless row of draft mammals.

At the same time, many wild mammals have been considered dangerous enemies of humans: predators, sources of epizootic infections, or competitors for the prey monopolized by humans. Many mammals were killed for these reasons, while some were killed merely because we could kill them. As a result, many species of wild mammal were drastically reduced in numbers leading to their local or global extinctions. The case of the giant sea cow (*Hydrodamalis stelleri)* is particularly illustrative here, but the situation with many other large mammals, including whales, is not much different. The introduction of cats, rats, rabbits, and other commensal species to regions colonized by humans has badly impacted the native fauna many times, and the industrial pollution and other impacts of recent economic activity act in a similar way on a global scale. About 20% of extant mammalian species may be endangered by extinction, mostly due to the destruction of tropical forest.

However, since the Paleolithic, humans also have kept mammals as pets and companions. Even now, the small carnivores or rodents that share our houses bring us a great deal of pleasure from physical and mental contact with something that, despite its apparent differences, can communicate with us and provide what often is not available from our human neighbors—spontaneous interest and heartfelt love. Contact with a pet mammal may remind us of something that is almost forgotten in the modern age: that humans are not the exclusive inhabitants of this planet, and that learning from the animals may teach us something essential about the true nature of the world and the deep nature of human beings as well.

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