CHAPTER 3

Mammals as Evolutionary Partners

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INTRODUCTION

Mammals have been available as potential hosts for parasites for approximately 190 million years. Although we know very little about the parasites that might have occurred on early mammals, we do know that both hosts

Table 3.1 The Geological Time Scale and Major Phylogenetic Events in Mammals

Age in Millions of Years: 0, 1, 2, 4, 6, 8, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 250

ERA	PERIOD		EPOCH	MAJOR PHYLOGENETIC EVENTS
CENOZOIC	Quarternary		Pleistocene	Modern species evolved; many extinctions
	1.8 mya			
	Tertiary	Neogene	Pliocene	MODERN GENERA EVOLVED
			12 mya	
			Miocene	
			25	
		Paleogene	Oligocene	MOST MODERN FAMILIES EXTANT Pholidota Macroscelidea, Hyracoidea
			37	
			Eocene	Cetacea, Proboscidea Sirenia Chiroptera Artiodactyla Perissodactyla MOST MODERN ORDERS PRESENT
			55	
			Paleocene	Lagomorpha, Tubulidentata, Dermoptera, Rodentia, Edentata, Fissipedia RAPID EVOLUTION OF MAMMALS
	65 mya			
MESOZOIC	Cretaceous		Late (Upper)	Insectivora, Primates, Carnivora, Scandentia (?)
			Middle	
			Early (Lower)	DIVERGENCE OF PLACENTALS AND MARSUPIALS
	140 mya			
	Jurassic		Late	Multituberculata
			Middle	Pantotheria Triconodonta
			Early	Monotremata (?)
	190 mya			
	Triassic		Rhaetic	EARLY MAMMALS AROSE
			200 mya	
			Middle	Therapsid reptiles present
			Early	
	230 mya			
PALEOZOIC (Not considered)				

and parasites underwent a tremendous radiation. Mammals have evolved to occupy a wide variety of niches and are found on all land masses and throughout the oceans and freshwaters. Concurrently, arthropods have evolved to occupy a wide array of niches available on the mammalian body. The radiation of mammals was paralleled by a corresponding radiation of the parasitic arthropods, both in morphological and taxonomic diversity, a process referred to as *coevolution*.

Coevolution is a popular term in widespread use in today's biological literature, and has been invoked to describe a variety of observed phenomena. However, in many cases the term has been undefined and used loosely. The prefix "co-," meaning "with" or "together" added to the base word evolution implies that two (or more) organisms are evolving together or with one another. Janzen (1980:611) defined coevolution as "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first." Although Janzen's article is aimed primarily at plant–animal interactions, his contention is that the current use of the term coevolution is misleading in many instances. He suggests that we adopt the strict definition of coevolution in which both organisms have evolved responses to each other. Brooks (1979) described *coevolution* in host–parasite systems as encompassing two phenomena, which he termed *co-accommodation* and *co-speciation*. He defined co-accommodation as a "mutual adaptation of a given parasite species and its host(s) through time [which] includes such parameters as pathogenicity, host specificity, and synchrony of life cycles stages," and co-speciation as "cladogenesis of an ancestral parasite species as a result of, or concomitant with, host cladogenesis" (Brooks 1979:300). He viewed co-speciation as an outcome of allopatric speciation and the vicariance biogeography model.

Coevolution between a host and parasite, in its strictest sense, occurs as a result of each exerting a selective force on the other. Such an interaction is difficult to demonstrate, and in many host–parasite systems, coevolution in the strict sense may not occur. Often the host exerts selective pressure on the parasite, but the parasite does not have a corresponding effect on the host. Descriptions of host–parasite systems often use the term coevolution, whereas co-speciation or co-accommodation may more accurately describe the situation. Previously used terms such as "interactions," "symbiosis," "mutualism," and "animal–plant interactions" are not synonymous with coevolution and perhaps better describe many of the interactions observed (Janzen 1980).

An example of co-speciation of host and parasite where the parasite exhibits an evolutionary response to the host but the host exhibits no counterevolutionary response is found in pocket gophers (*Geomys*) and their parasitic lice (*Geomydoecus*) (Timm 1979, 1983; Timm and Price 1980).

Population levels of lice, *Geomydoecus* (Mallophaga: Trichodectidae), were found to vary seasonally on pocket gophers of the genus *Geomys* (Rodentia: Geomyidae). In the northern pocket gophers, there was an average of 500 lice per individual gopher during the summer months, with some individual pocket gophers harboring as many as 2000 lice. All stages of the lice are found on the host; the eggs are glued individually to the base of the hair shaft. First, second, and third instars each last for approximately 10 days, and the adults probably overwinter. All stages of lice occur most abundantly on the back of the head and nape of the neck, presumably because these are the most difficult areas for the gopher to reach while grooming (Timm 1983). That the lice have adapted or evolved specializations to their hosts is obvious from their morphology (extreme dorsoventrally flattened bodies, tarsal claws to grasp individual hairs, posteriorly projecting setae), and from their success as parasites measured in terms of both individual populations and taxonomic diversity. Every one of several thousand pocket gophers examined had high numbers of lice, and to date some 102 specific and subspecific taxa of *Geomydoecus* have been recognized. As pocket gophers are solitary, dispersal of lice from one host to another presents additional problems. A young pocket gopher captured just after dispersal from the natal tunnel system (probably within the preceding 24 hours) already had a population of 350 lice. Additionally, the lice appear to be cueing their reproduction to the reproductive cycle of their hosts (Timm 1983). Close, parallel responses of lice and their hosts suggests that the lice have evolved "traits" in response to their hosts.

However, have the pocket gophers undergone an evolutionary change in response to their parasitic lice? Here the answer is probably no. In work with both captive and wild hosts there was no indication that the lice (even as many as 2000 on a single pocket gopher) had any impact upon their hosts. Lice of the genus *Geomydoecus* feed on dead tissue, probably scrapings of skin, and thus incur no direct cost to the host while feeding. They apparently transmit neither diseases nor endoparasites to their hosts.

The one behavior pattern of the host that affects the lice is grooming. But we cannot say that grooming by pocket gophers evolved in response to their harboring Mallophaga. Grooming probably reflects a need to keep the fur clean from dirt, or else may be a direct response to the larger bloodsucking parasites such as fleas or mesostigmatid mites. The fact that grooming by pocket gophers is the main factor controlling louse populations is an incidental by-product of host grooming behavior that is not directed toward the lice.

It can be argued that additional grooming would be a cost to the host in terms of energy expenditure. Increased grooming could make any host more vulnerable to predation, either while grooming or while spending additional time foraging to compensate for the increased energy expenditure. However, it is likely that *Geomys* does not spend more time grooming in response to a high louse population (personal observation). Even if there was an increase in time spent grooming, it probably would have little negative effect on the pocket gophers because they live entirely within an enclosed tunnel system. Both grooming and foraging take place well below the surface. The major predators on an adult *Geomys* are sit-and-wait predators like badgers (*Taxidea taxus*) that open the tunnel and wait for the pocket gopher to repair the damage, or long-tailed weasels (*Mustela frenata*) and snakes that can enter a tunnel system opened by a gopher actively working on it. Weasels and snakes cannot open a closed tunnel system. Pocket gophers on the surface, especially young dispersing animals, are susceptible to predation by raptors, but this is quite independent of louse populations. Further, during the period of highest louse populations (early summer and late fall), most populations of pocket gophers have unlimited supplies of food. Any additional energy expenditure caused by the parasites would be insignificant.

Thus at this time we must conclude that lice of the genus *Geomydoecus*, although they are considered parasitic and their populations may be high, have no effect upon their host. The selective pressure has been exerted on only one member of the system, and therefore coevolution is not an appropriate term. The concordant patterns of speciation between gophers and their lice (Heaney and Timm 1983; Timm 1983) are best thought of in the sense of co-speciation or co-accommodation, which is not synonymous with coevolution.

Documenting coevolution in nature is no trivial task, especially if we use increased or decreased reproductive success by both host and parasite as our measure. Coevolution measured in terms of maximized reproductive output in both host and parasite has been demonstrated for bot flies (Diptera: Cuterebridae) of the genus *Cuterebra* and their rodent hosts. Cuterebrids are subcutaneous parasites commonly found on North American cricetine and sciuromorph rodents.

Bot flies are relatively large in proportion to their hosts; a mature larvae may be 30–35 mm on a white-footed mouse, *Peromyscus*, whose body length is 80–90 mm. It has been demonstrated that excessive numbers of bots artificially inflicted on a host can kill it (Timm and Lee 1981). Smith (1978) demonstrated that deer mice (*Peromyscus maniculatus*) with multiple infestations of bot flies (*Cuterebra approximata*) were more vulnerable to predation by short-tailed weasels (*Mustela erminea*) than were mice with one or no bots. He concluded that "*Peromyscus maniculatus* infected with single *C. approximata* larvae did not appear to be any more vulnerable to shorttail weasel predation than did uninfected control mice" (Smith 1978:47). Additionally, he was able to quantify the cost of bot fly parasitism to the host in terms of calories. During its developmental period, a single bot fly larva consumed 27 kcal, two bots consumed 47 kcal, and three bots consumed 61 kcal of energy (Smith 1975). Larvae from multiple infestations received proportionally less energy than those in single infestations and hence were significantly smaller than those found singly. Immature larvae on a host that either died or was killed by a predator would not survive.

The egg-laying strategy of female bots also suggests an evolved response. Female bots lay 1000–3000 eggs, but scatter them widely so that the infestation rate per individual mouse averages only one or two. Thus there is a definite cost to the host infected with bot flies and a reciprocal cost to the bots if the host is too heavily infected. Bots of larger body size probably have an advantage in overwintering and in successfully mating the following summer.

Timm and Cook (1979) showed that white-footed mice (*Peromyscus leucopus*) have evolved a tolerance for bot fly parasitism. One or two larvae had no effect on the breeding condition of adult male mice, and adult females showed no decrease in number of embryos, corpora lutea, or placental scars (see also Timm and Lee 1981). That this tolerance is evolved is suggested by the fact that Old World hosts, not normally exposed to New World cuterebrids, may be killed if infected with bot fly larvae (Catts 1982). Thus a host–parasite system has "coevolved" adaptations by both the host and parasite to maximize reproductive output.

Other perspectives on coevolution, co-accommodation, co-adaptation, and co-speciation can be found in Price (1980), Thompson (1982), Futuyma and Slatkin (1983), and Nitecki (1983).

MAMMALS AS HABITAT

Hair

The presence of hair is a unique characteristic of mammals, and all mammals have at least some hairs during their development. Hair provides mammals with protection in the form of insulation, antiabrasion, and defense (e.g., quills of porcupines). Specialized hairs are used as tactile organs (vibrissae) and for communication. The hair itself is of epidermal origin, the follicle invaginates the dermis as the hair arises. A typical hair is composed of numerous tightly compacted, keratinized cells forming three distinct layers: an inner medulla consists of the cornified remnants of epithelial cells; the cortex, which is formed of keratinized cells fused into a hyaline mass, comprises the main constituent of the hair shaft and contains most of the pigment; and the cuticle, which may comprise numerous scales that wrap around the hair shaft, forms a thin outer protective layer composed of heavily keratinized cells. The body of most mammals is covered with two main types of hair: stiff guard hairs which provide protection, and softer underfur which primarily serves as insulation. Hairs are typically associated with a variety of sebaceous and sudoriferous glands, and the surface of the hair is often oily. One or more sebaceous glands are found within each hair follicle.

In a few mammalian groups adults are essentially devoid of hair. This is especially true in the Cetacea, but is also true in one species of east African rodent, the naked mole rat (*Heterocephalus glaber*), and in one genus of southeast Asian molossid bats that is represented by two species, both referred to as naked or hairless bats (*Cheiromeles*). Hairlessness must be considered a secondarily derived condition.

For ectoparasitic arthropods, hair provides concealment and in some cases food. However, hair presents its own unique set of problems to the parasite. It is a stiff proteinaceous structure whose rigidity is provided by disulfide bonds. Its composition may be difficult for arthropods both to ingest and digest, and hair is probably not a highly nutritious resource. The stiff, dense nature of hair on the mammalian body creates a forest that can hinder an arthropod's ability to maneuver across the skin. The laterally compressed bodies of fleas and the dorsoventrally compressed bodies of lice are adaptations in response to intense selection pressure. The ability to move rapidly through hair is necessary to avoid dislodgement while the host is grooming. Another problem with hair is that it is an ephemeral resource shed (lost) on a routine basis. This hair loss-replacement pattern is termed molt. In some mammals (for example, carnivores), hair loss and replacement involves individual hairs scattered over the body surface. In most rodents the molting pattern starts as a small patch and sweeps across the entire body within a few weeks. Molt may occur seasonally or annually. Arthropod eggs glued to hairs that are being shed will be lost, as would instars or adults firmly attached to individual hairs. Molt patterns, however, are triggered by environmental cues such as changing day length, and thus are predictable. The normal molt pattern may be delayed if the animal is in poor body condition, or, as in the case of pregnant females, when energy reserves are stressed.

Most arthropods broadly lumped into the category of mammalian ectoparasites spend at least some portion of their life cycle within the hair; however, few species actually consume the hair itself. Perhaps the only insects to feed on hair are the parasitic beetles *Catopidius* (Leiodidae), *Loberopsyllus* (Languriidae), and *Leptinus* (Leptinidae) (Marshall 1981; Peck 1982). Although it was commonly believed that chewing lice (Mallophaga) fed upon the hair of their hosts, Marshall (1981:129) states unequivocally, "There is no evidence that lice feed upon hair." However, many species of Ischnocera on birds feed partially or exclusively on feathers. Perhaps feathers are a more nutritious food source than hair. Certainly, feathers offer a more structurally diverse environment for ectoparasites than does hair. Another conspicuous difference in the utilization of feathers and hair by arthropods is that several families of mites and lice have colonized the air space or hollow interior of the feather shaft, whereas no arthropods have been able to utilize the hollow hair shafts found in a few species of mammals. The mammalian hair shaft has no umbilicus as does the feather shaft, thus there is no easy entrance point in hair.

Skin

Skin is the protective layer that covers the body surface of mammals. It serves a primary function in thermoregulation, to prevent desiccation, and to provide protection (Sokolov 1982). The glands within the skin function in excretion, and the nerves receive stimuli from the environment. Mammalian skin, like that in other vertebrates, is composed of two discrete layers, the epidermis and the dermis. The surface layer, the epidermis, is composed of epithelial tissue, called stratified epithelium, divided into four layers. The outermost, that exposed to the surface and parasitic arthropods, consists of dead hardened cells that are compressed into a cornified layer termed the stratum corneum. Immediately beneath the stratum corneum is a thin, clear layer, the stratum lucidum, comprising several layers of flattened compacted cells. Beneath that is a layer termed the stratum granulosum, which is actually composed of three to five distinct layers of living epithelial cells ranging from cuboidal to columnar in shape. The innermost layer, the stratum malpighii, is the only layer that contains actively dividing cells undergoing mitosis. Skin (epithelial) cells are formed in the stratum malpighii and are pushed outward by additional actively dividing cells; as they migrate outward, they undergo a complex process called keratinization. All the cell organelles, including the nuclei, disappear, and the cells flatten and fill with granules of keratohyalin. The resulting tissue forms a dense, tough, outer protective layer that wears away, and is continuously replaced. There are no blood vessels found within the epidermis. The dermis, lying beneath the epidermis, is composed of connective tissue, muscles, fat deposits, and vascular and nervous tissue. Beneath the dermis is a layer of loose connective and adipose tissue. Arthropods seeking a blood meal must be able to penetrate through the epidermis to reach the rich supply of blood vessels found within the dermis.

Of all the parasitic arthropods that live on the skin of mammals, relatively few feed directly upon the skin itself. These include insects of the orders Dermaptera (families Arixeniidae and Hemimeridae), Coleoptera (Leiodidae, Leptinidae, Platypsyllidae, Staphylinidae, Languriidae, and Scarabaeidae), Amblycera, and Ischnocera; and mites of the family Psoroptidae.

Glands

A wide variety of glands having diverse functions are found within the skin of mammals, but they fall basically within two types: the sebaceous glands (oil glands) and the sudoriferous glands (sweat glands). Glands serve a variety of functions, including excretion of metabolic wastes, evaporative cooling, communication, and nourishment of young.

Sebaceous glands lie in the dermis and function primarily in lubrication, protection of the skin surface, and reduction of water loss. The secretion from sebaceous glands is produced by the breakdown of the glandular epithelial cells and includes both cell debris and lipids (Montagna 1974). All hair follicles in mammalian skin have sebaceous glands associated with them that open directly into the follicle and whose secretions protect the hair from becoming dry and brittle. Sebaceous glands are also important to mammals in scent marking, both for intra- and interspecific recognition and territoriality. The location of these scent glands varies among the different groups of mammals. For example, shrews (*Blarina, Cryptotis,* and *Sorex*) have midventral and lateral scent glands (Bee et al. 1980); kangaroo rats (*Dipodomys*) have an enlarged scent gland along the midline of the back (Quay 1953); some species of voles (*Microtus*) have lateral scent glands called hip glands (Jannett 1975; Quay 1968; and Tamarin 1981); and many carnivores have an enlarged anal gland for scent marking. Anal glands are prominently developed in the Mustelidae (skunks), Canidae (dogs), and Viverridae (civets). The Meibomian glands lying within the eyelids are modified sebaceous glands that lubricate the eye.

Sudoriferous glands (sweat glands) also lie within the dermis and are found throughout the body surface on many species of mammals. However, they are not known to occur in several groups of mammals, notably the edentates, pinnipeds, and cetaceans. Sudoriferous glands are of two basic types: apocrine glands that are usually located adjacent to hair follicles, and eccrine glands that open directly to the skin surface, independent of hair follicles. The secretions from sudoriferous glands are a product of cellular metabolism, and not a result of cellular decomposition as in sebaceous glands. These secretions often include water, salts, and fatty substances, and their function is generally thermoregulation. Many of the types of glands found in mammals have no counterparts in other vertebrates; for example, mammary glands, highly modified sudoriferous glands, are unique to mammals. Mammary glands are thought to have evolved from sudoriferous glands. The most primitive mammary glands are found in the most primitive mammals, the monotremes, and consist of roughly 100 lobules within the skin that open directly to the ventral surface. Each lobule is associated with a stiff hair and the young lick the milk off the hairs. Bats have perhaps the most diverse array of both sudoriferous and sebaceous glands found within the Mammalia. Glands are found throughout much of the skin surface on the lips, face, throat, chest, and wing membranes (Quay 1970). In recent years, this rich diversity of glands has been found to harbor a diverse fauna of associated mites. A recent review of scent glands in mammals and their functions was provided by Müller-Schwarze (1983).

A few groups of mites, especially demodicids, have been able to successfully invade hair follicles and the sebaceous and sudoriferous glands. *Demodex* punctures the cells of the glands and hair follicles with its stylet chelicerae and feeds upon cell contents. Although demodicids may occur in extremely high numbers, there seldom is any major tissue destruction (Nutting 1965; Nutting and Woolley 1965). Apparently no insects have invaded the glands of mammals.

Respiratory Tract

The respiratory tract of mammals includes the nasal cavity, pharynx, larynx, trachea, and bronchi. These organs are basically tubes for the passage of air from the external environment to the lungs. The respiratory tract of mammals is warm, moist, and has rich supplies of blood and oxygen. The respiratory system can be entered easily through the open external nares, and the first tissue encountered by invading parasites is the soft nasal mucosa.

The nasal chamber of mammals is composed of thin bone (turbinates), cartilage, muscles, connective tissue, and a passageway for air. Sebaceous glands, especially those secreting mucus, are large and well developed. A rich supply of blood vessels is associated with the olfactory epithelial cells. The primary function of this complex arrangement, in addition to olfaction, is the conservation of heat and water during respiratory exchange. There is a distinct temperature gradient within the nose, with the tip approaching ambient temperature. The nasal region is warm and moist, and has a rich supply of oxygen continuously moving across it. The mucosa is easy for an arthropod to burrow through. The turbinal bones provide support as do other parts of the skeletal system, yet because of their extreme thinness do not prohibit arthropod burrowing. Thus the nasal region can provide an ideal environment for development of soft-bodied arthropods. Nasal mites generally are found within the mucous membranes and either feed on blood or the nasal mucosa.

Several families represented by numerous genera of mites and at least three genera of bot flies are known to occur in mammalian nasal passages. Mites parasitic within the nasal mucosa include the following families and genera: Ereynetidae (*Neospeleognathopsis, Paraspeleognathopsis, Speleognathus,* and *Speleorodens*) (Fain 1962, 1963); Gastronyssidae (*Mycteronyssus, Opsonyssus, Rodhainyssus, Sciuracarus,* and *Yunkeracarus*) (Fain 1964a); Halarachnidae (*Halarachne, Orthohalarachne, Pneumonyssoides, Pneumonyssus,* and *Rhinophaga*); Lemurnyssidae (*Lemurnyssus* and *Mortelmansia*) (Fain 1964b); and Trombiculidae (*Alexfainia, Asoschoengastia, Blix, Crotonasis, Doloisia, Euschoengastia, Gahrliepia, Kymocta, Leptotrombidium, Microtrombicula, Myxacarus, Nasicola, Rhinibius, Schoutedenichia, Traubacarus, Vergrandia,* and *Whartonia*).

Nasal mites of the genus *Orthohalarachne* (Halarachnidae) are found in the mucosa of eared seals (Otariidae) and walruses (Odobenidae); the genus *Halarachne* is found in the earless seals (Phocidae) and in sea otters (*Enhydra lutris*) (Fay and Furman 1982). Generally, the impact of parasitic arthropods has been thought to be insignificant to the health of marine mammals. However, in northern fur seals (*Callorhinus ursinus*), Kim et al. (1980:45) reported that all subadult and adult seals examined ($N = 81$) contained high populations of both *Orthohalarachne attenuata* and *O. diminuata* and that "The heavy infestation with these mites appeared to result in impairment of respiration in fur seals, and could also cause lesions in the lungs and secondary alveolar emphysema, predispose to more serious diseases, or even kill the host animal." Additionally, Kenyon et al. (1965:960) reported a captive sea otter harbored "over 3000 *H*[*alarachne*] *miroungae*" and that "The nasal passages were crowded with mites and the mucosa showed severe reddening. Also, the turbinates had been destroyed, leaving a nearly unobstructed void from external nares to posterior nasal passages." Other species of nasal mites apparently cause little or no damage to their hosts.

The nasal bot and warble flies found in the nasal fossae, frontal sinuses, and in the nasopharyngeal pouches of mammals include two genera of Oestridae: *Cephenemyia* on cervids and *Oestrus* on bovids.

Several species of mites in the genera *Pneumocoptes* (Pneumocoptidae), *Orthohalarachne* and *Pneumonyssus* (Halarachnidae), and *Lemurnyssus* and *Mortelmansia* (Lemurnyssidae) are known as pulmonary mites and live within the lungs, bronchi, and trachea of the upper respiratory system in mammals. When found, they are generally abundant, but do little damage to the host. Most species feed directly upon blood.

Subcuticular Layer

The subcuticular niche within the mammalian body has not been colonized by very many groups of arthropods. Some conditions necessary for arthropod development are ideal in this environment: warm constant temperature, moisture, and a rich nutrient supply. However, free oxygen levels are low. Penetration of both the epidermis and dermis to form a direct link with the surface is necessary if the parasite's waste products are extensive and a rich oxygen supply is necessary. Bot flies, blow flies, and flesh flies of the families Calliphoridae, Cuterebridae, Oestridae, and Sarcophagidae are the only insects that are found in this niche. Perhaps because of their larger body size, insects have been more successful than other groups of arthropods in penetrating the epidermis and dermis. Most species do not burrow directly through the skin to obtain access to the subcuticular regions, but rather enter through preexisting openings, such as the eyes, nose, mouth, and hair follicles. In the calliphorid flies, especially *Cochliomyia*, the female deposits her eggs on an open wound in the host where the epidermal and dermal layers have already been broken. The human bot (*Dermatobia hominis*) apparently burrows through the dermal layers within a hole originally made by a female mosquito. Mites of the family Cloacaridae (*Epimyodex*) have been found subcutaneously in the fascia in the lower back region of moles and several other species of small mammals (Fain and Orts 1969). It is believed that they enter the host's body through the genitalia and then migrate to this position, rather than penetrate the skin directly.

Other Organs

Mites of several families have proven successful in invading a wide array of mammalian organs. Within the digestive tract, two genera of Demodicidae (*Rhinodex* and *Stomatodex*) and two genera of Sarcoptidae (*Chirnyssus* and *Nycteridocoptes*) are found within the oral cavity of bats and lemurs. In bats *Stomatodex* is often found inside the lips, beneath the tongue, and near the epiglottis. Phillips et al. (1969:1368) reported that the long-nosed bat, *Leptonycteris nivalis* (Phyllostomidae), harbored high populations of mites, *Radfordiella* (Macronyssidae), within the oral mucosa, and that "Osteolysis of hard palate and odontolysis of teeth result from infestations of mites adjacent to the upper premolars and molars." Interestingly, neither mites nor the associated bone damage were found in the closely related and sympatric species, *Leptonycteris sanborni.*

Gastronyssus bakeri (Gastronyssidae) lives within the epithelial lining of the stomach and intestines of megachiropterans (Fain 1955). *Paraspinturnix globosus* (Spinturnicidae) has been described only from within the anus of North American vespertilionid bats of the genus *Myotis* (Rudnick 1960), but may represent an overwintering stage of a more typical spinturnicid.

Demodex canis (Demodicidae) is known from the spleen, kidney, blood, tongue muscles, urine, bladder, liver, intestinal wall, and thyroid glands of dogs, in addition to being found in the skin and associated glands.

A few species of mites live on the surface of the skin and feed on the secretions of the eye; several species of *Demodex* live within the Meibomian glands of the eyelid (Lombert et al. 1983); and *Opsonyssus* (Gastronyssidae) lives within the orbit of the eye itself. Ocular secretions of large mammals are fed on by a few species of tropical and subtropical Lepidoptera of the families Geometridae, Noctuidae, and Pyralidae.

The ear canal has been invaded by a few species of Astigmata and Mesostigmata: *Otodectes* in carnivores (Sweatman 1958a); *Psoroptes* in ungulates (Sweatman 1958b); and *Noteodres* in the dwarf galago, *Galago demidovi,* and a single species of laelapid, *Raillietia hopkins,* in the ears of cattle, sheep, goats, and some African antelope. *Demodex marsupiali* recently was described from the pilocerumen gland complex in the opossum, *Didelphis marsupialis.* Nutting et al. (1980:83) reported that "Pathogenesis is limited to epithelial cell destruction, minor orifice occlusion, and some keratinization . . . mites occasionally penetrate into the dermis, without host cellular response."

EVOLUTION OF MAMMALS

Origins

The first mammals appeared on earth during the late Triassic period (Rhaetic) of the Mesozoic era (see Table 3.1), approximately 190 million years ago. These early mammals evolved from the extinct mammal-like reptiles of the subclass Synapsida, order Therapsida. The exact mammalian ancestor within this group of reptiles is not known. It has been suggested that mammals evolved from several related lines of therapsids (Olson 1959). Such a polyphyletic origin is suggested by the fact that several groups of therapsids possessed mammalian characteristics. A monophyletic origin of the class Mammalia is supported by many authors, based on differing interpretations of the fossil record. Hopson (1967) concluded that mammals probably arose from only one group of advanced late Triassic cynodont therapsids. This view of a monophyletic origin was independently arrived at by Parrington (1967) and Crompton and Jenkins (1973) further supported this view and stated that, although many of the therapsids showed parallel evolution of mammal-like traits, only a single family of cynodonts gave rise to all mammals. Three types of cynodonts possess many mammalian characteristics and may be sister groups to the early mammals: *Probainognathus*, the Tritheledontidae, and the Tritylodontidae (Kemp 1982). Current evidence supports this theory, and a monophyletic origin is now widely accepted (Clemens 1970; Crompton and Jenkins 1973).

The continent on which mammals evolved remains unknown. The oldest known fossils commonly accepted as "good" mammals are from the late Triassic period of western Europe (Clemens et al. 1979). The only earlier fossil that might be mammalian is from the early late Triassic period in southern Brazil. Named *Therioherpeton*, it is either a very reptile-like mammal or a mammal-like reptile (Bonaparte and Barberena 1975). However, given the fragmentary nature of the fossil record, it is not possible to denote a specific location for the origin of mammals. Late Triassic and early Jurassic fossil mammals are also known from Africa, Asia, and North America, indicating that early primitive mammals were widespread and morphologically diverse (Clemens et al. 1979; Jenkins et al. 1983).

Early mammals were small, and most were probably insectivores or carnivores. Although the fossil evidence is sparse, it appears that little radiation occurred, at least in terms of fossilized hard structures, until late in the Mesozoic era. A period of great mammalian radiation began in the late Cretaceous (late Mesozoic) period and continued on into the Paleocene (early Cenozoic) epoch. During this time, many of the modern mammalian orders first appeared. This radiation continued throughout the Cenozoic era, and by the Oligocene epoch the majority of modern families had developed. Many modern genera were present as early as the Pliocene epoch. Modern species or their direct ancestors appeared during the Pleistocene epoch. For excellent and more detailed reviews of this subject, see Crompton and Jenkins (1979) and Kemp (1982).

Mesozoic Era

From the time of their first appearance in the late Triassic period (Rhaetic) until the end of the Mesozoic era, a period of approximately 120 million years, mammals formed only a small fraction of the earth's terrestrial fauna. All Mesozoic mammals so far discovered have been small in size and rather similar in body form. However, during this period several major evolutionary changes occurred. During the Mesozoic era the two major modern mammalian infraclasses, the Eutheria (placentals) and Metatheria (marsupials), originated.

By the end of the Triassic period, mammals had diverged into three major families: the Haramiyidae, the Morganucodontidae, and the Kuehneotheriidae (Clemens 1970; Crompton and Jenkins 1973, 1979; Hopson and Crompton 1969; McKenna 1969).

The Haramiyidae is a poorly known family of uncertain affinities. It appeared in the fossil record earlier than the morganucodontids or kuehneotheriids, having similarities to primitive multituberculates that may indeed be considered ancestral to that group. The Morganucodontidae were ancestral to the non-therian mammals, including the early triconodonts and docodonts and possibly the multituberculates. Although the monotremes do not appear in the fossil record until the Miocene epoch (Clemens 1979), they have similarities with the Morganucodontidae and may have arisen from this group. The Kuehneotheriidae gave rise to therian mammals, including the symmetrodonts, pantotheres, marsupials, and eutherian mammals. Figure 3.1 shows the major groups of Mesozoic mammals; also see the review by Crompton and Jenkins (1979).

Cenozoic Era

The beginning of the Cenozoic era, approximately 65 million years ago, marks the start of the great radiation of mammals. At the end of the Mesozoic era, global climates changed, primarily expressed as major cooling trends (Savin 1977; Lillegraven et al. 1979). During this time the dominant reptilian group, the dinosaurs, became extinct. Such cooling trends may have favored the homeothermic mammals over their reptilian counterparts, and with the extinction of the dinosaurs mammals radiated into niches they had not previously occupied. A tremendous explosion in terms of rapid evolution of new forms occurred during the 65 million years of the Cenozoic era as compared to the previous 125 million years of the Mesozoic after mammals first evolved, even though the Cenozoic covers a time span only half as long. Although they were evolving rapidly, mammals were still not a dominant group in the Paleocene epoch, and all were

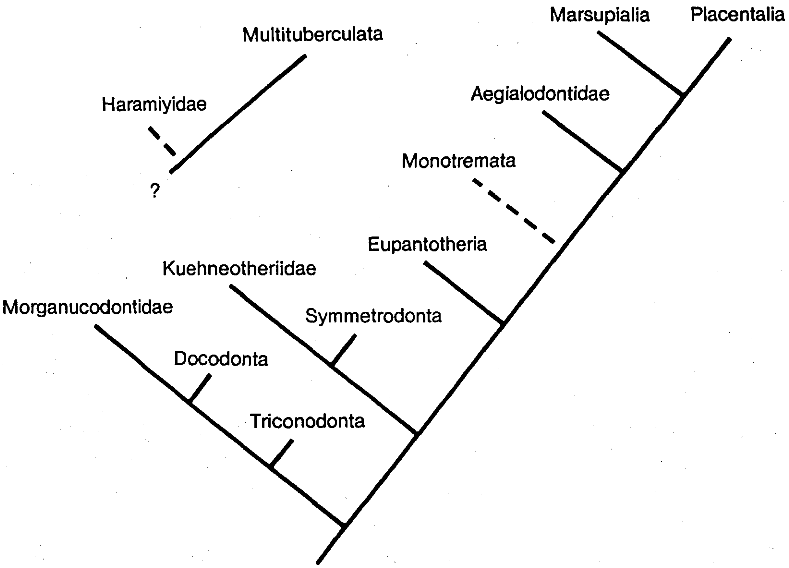

Figure 3.1 A phylogenetic tree for early mammals. (From T. S. Kemp, *Mammal-Like Reptiles and the Origin of Mammals*. Academic Press, London, 1982.)

small in size. By the late Paleocene and early Eocene epochs there was a dramatic increase in overall numbers of orders, and during this time nearly all extant mammalian orders evolved (Kurtén 1972). A period of stability in terms of numbers of orders present at any given time occurred during the Eocene, Oligocene, Miocene, and Pliocene epochs. This was a period of diversification, with new groups evolving as others became extinct. There was a slight decrease in the total number of different types of mammals at the end of the Pleistocene epoch due to the widespread extinction of many large mammals without ecological replacement.

Plate Tectonics and the Geographic Radiation of Mammals

The face of the earth has undergone dramatic changes during the 190 million years since the mammals first arose from reptiles, through the processes of continental drift and plate tectonics. Changes in the locations and configurations of the land masses affected the distribution of the earth's flora and fauna. Populations were split and isolated, local climates changed, and migration and gene flow of populations between continents either prevented or initiated. Thus continental drift had a great effect on the distribution of extant mammals through its effect on their ancestors (Cracraft 1974; Lillegraven et al. 1979).

During the Triassic period the major land masses were joined into one large supercontinent called Pangaea (Fig. 3.2). In the early Jurassic period,

Figure 3.2 Continents at the Rhaetic-late Triassic period, 200 million years ago.

Pangaea began to split into a northern land mass, Laurasia, composed of the North American and Eurasian continental plates, and a southern land mass, Gondwanaland, made up of the South American, African, Indian, Australian, and Antarctic plates (Fig. 3.3). At approximately the same time, Gondwanaland also began to split into an eastern section (Antarctica and Australia) and a western section (South America and Africa). The South American and African plates began to separate from one another by the late Jurassic period and were well separated by the early to mid-Cretaceous period (Fig. 3.4). India had separated from Australia–Antarctica, and Madagascar was free from Africa by the late Cretaceous period. By the end of the Paleocene epoch, eastern North America and western Europe were no longer joined (Fig. 3.5). Australia and Antarctica became separated by the late Paleocene or early Eocene epoch. By the Oligocene or early Miocene epoch, India had moved into its present position against the southern part of the Eurasian plate (Fig. 3.6); the impact of the collision and

Figure 3.3 The breakup of the world land masses at the mid-Jurassic period, 160 million years ago.

continued northward movement of India created the Himalaya mountains. By the late Miocene epoch the continents had more or less assumed their present positions (Fig. 3.7). There is some disagreement among authors as to exact continental configurations and times of separations, but the general positions and plate movements are widely accepted (see Smith and Briden 1979 for more details).

Another factor affecting the dispersal and distribution of organisms during this long time span was the existence, at various times and in various places, of huge epicontinental seas (Lillegraven et al. 1979). These large bodies of water could effectively prevent the migration of species from one area of a continent to another, and thence on to another continental plate. High mountain ranges would have had a similar effect on dispersal.

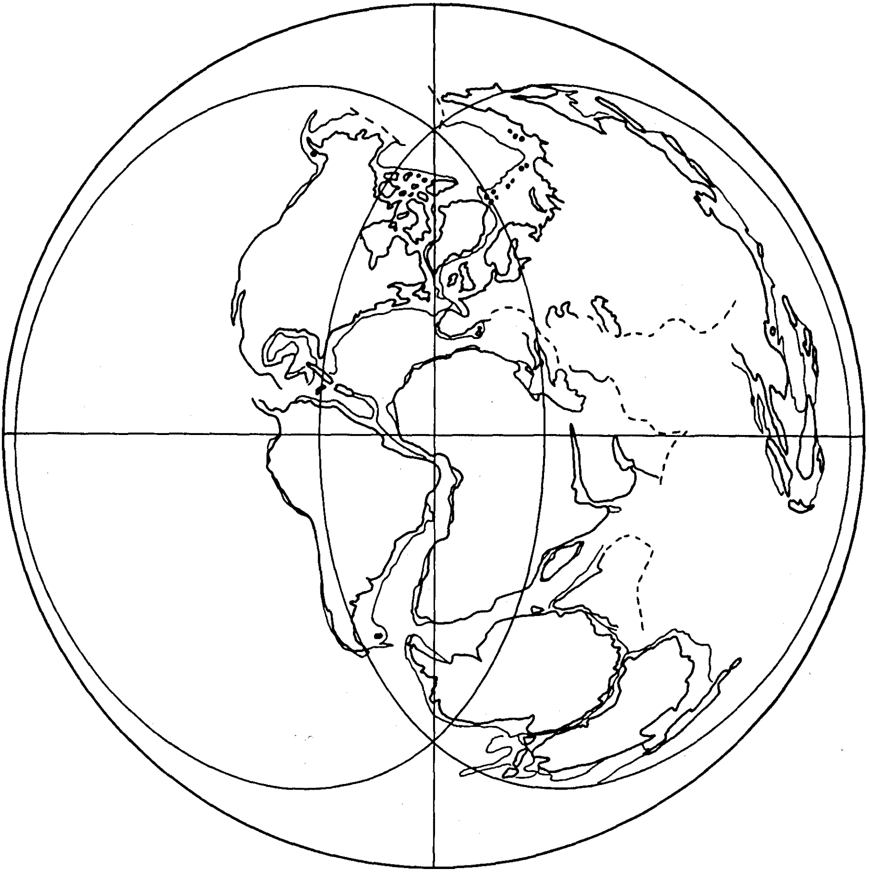

Figure 3.4 Continents at the early Cretaceous period, 120 million years ago.

Plio-Pleistocene Epoch

The Pleistocene epoch began approximately 1.8 million years before the present and ended approximately 8000 years ago (Kurtén and Anderson 1980; Savage and Russell 1983). During this epoch most modern species or their direct ancestors appeared. It was during the late Pliocene epoch that North and South America became connected by the Panamanian land bridge at approximately 3.0 million years before the present (Marshall et al. 1982), allowing a major faunal interchange between the two continents. Prior to the formation of this land bridge, between what is now Panama and Colombia, some interchange between the two continents had occurred by waif dispersal. Early immigrants from North America into South America include the caviomorph rodents in the mid-Tertiary and procyonid carnivores in the late Tertiary periods (Kurtén and Anderson 1980;

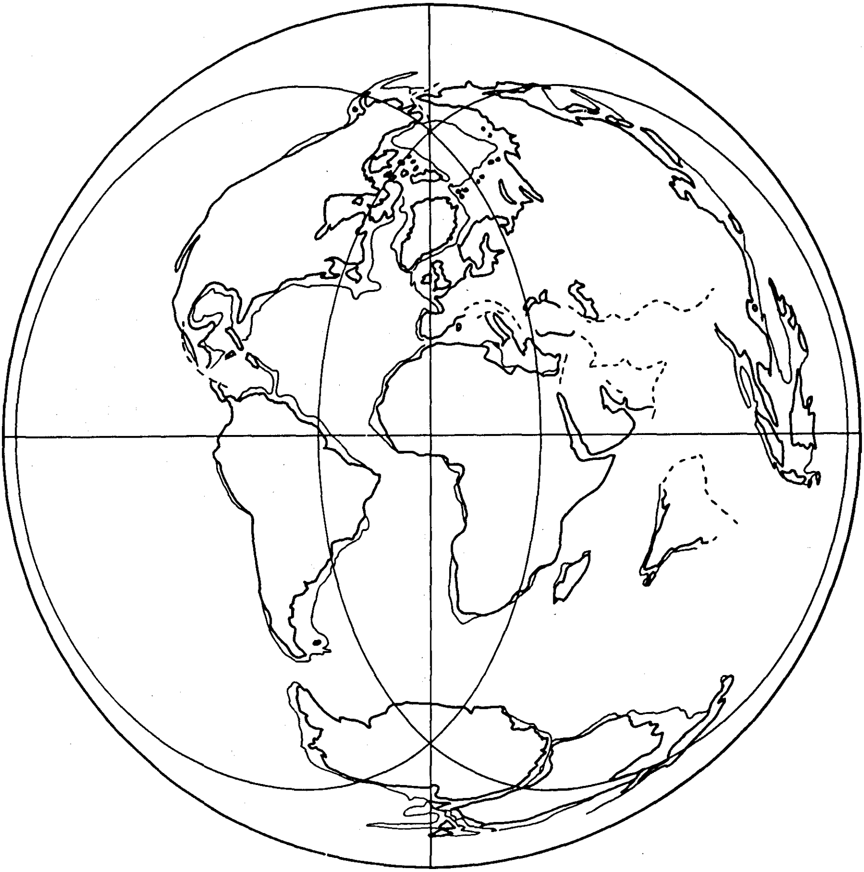

Figure 3.5 Continents at the Paleocene epoch, 60 million years ago.

Marshall 1980; Simpson 1980). There were also faunal exchanges between Eurasia and North America during the Plio-Pleistocene epoch by way of the Beringian land bridge (Hopkins et al. 1982). These exchanges occurred in several episodes at approximately 3.5, 1.8, and 0.08 million years before the present (Kurtén and Anderson 1980) owing to opening and closing of the land connection by glacially controlled eustatic fluctuations (Hopkins 1967).

The Pleistocene epoch was a time of widespread extinction, resulting in a decrease in overall numbers of species of mammals, due to lack of ecological replacement. These extinctions occurred throughout the Pleistocene and affected both large and small mammals, although the extinction of the megafauna has received more attention. Some entire families that became extinct on one continent survived on other continents. Many causes for these extinctions have been proposed. Early Pleistocene extinctions in

Figure 3.6 Continents at the early Miocene epoch, 20 million years ago.

North America seem largely due to increasing aridity and the subsequent vegetational changes (Dort and Jones 1970). Late Pleistocene extinctions have been attributed both to climatic changes and (for the megafauna) to hunting pressure by humans (Martin 1982; Mosimann and Martin 1975). However, recent evidence seems to indicate that overkill by human hunters was not the major cause of extinctions (Gillespie et al. 1978; MacNeish 1976). Kurtén and Anderson (1980:363) attribute these extinctions to a variety of local conditions, stating that "Extinction did not occur uniformly across the continent. Local conditions affected local populations. No one cause can account for it; rather, a mosaic of adverse conditions prevailed. We believe that changes in vegetation, sudden storms, droughts, loss of habitat, interspecific competition, low reproduction rates, and overspecialization . . . reduced or weakened populations, making them vulnerable to environmental pressures, including man."

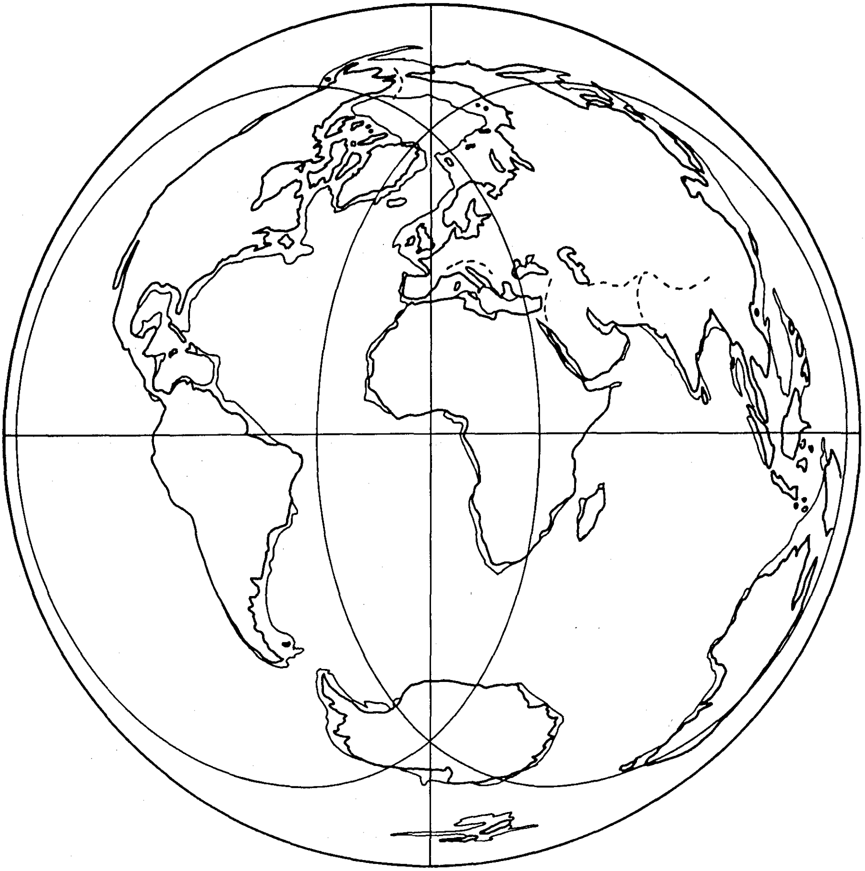

Figure 3.7 Present continents.

DIVERSITY AND DISTRIBUTION OF MAMMALS

Subclass Prototheria

Order Monotremata

The prototherians, the duckbilled platypus and the echidnas, are the most primitive of all mammals. Three genera of modern-day monotremes are recognized. The single species of duckbilled platypus, *Ornithorhynchus anatinus*, represents a monotypic family, the Ornithorhynchidae. Three species of Recent echidnas are known, belonging to two genera and representing the family Tachyglossidae. The monotremes inhabit Australia, New Guinea, and Tasmania. The fossil record of the three genera is well represented in Pleistocene deposits of Australia; however, earlier monotreme fossils consist of only two isolated teeth from the middle Miocene epoch of South Australia. The only modern-day monotreme to possess even rudiments of teeth is the duckbilled platypus, which has a few premolars and molars that are lost early in development. The Miocene teeth have been assigned to the Ornithorhynchidae, although they shed little light on the evolution of the modern monotremes. Clemens (1979:309) summarized the three groups of hypotheses concerning the origin of monotremes as follows: "The first includes those that recognize a basic evolutionary dichotomy subdividing the Mammalia into nontherian and therian lineages and allocate the monotremes to the nontherians without nominating a known Mesozoic order as their ancestral stock. Another group of hypotheses also recognizes the fundamental dichotomy between therian and nontherian mammals and allocates the monotremes to the nontherian group . . . indicating that among nontherian orders monotremes are most . . . closely related to multituberculates. . . . The third group of hypotheses suggests a special phylogenetic relationship between monotremes and marsupials."

There is very little support today for associating monotremes and marsupials. Thus all we can say about the evolution of the monotremes is that they are an old group of uncertain ancestry. Using a cladistic analysis of a wide array of characters, Marshall (1979:369) demonstrated that "the most basic division of the Mammalia is the dichotomy into the subclasses Prototheria (including Monotremata, Multituberculata, Triconodonta, Docodonta) and Theria (including Metatheria, Eutheria, Pantotheria and Symmetrodonta). Two major groups exist among living viviparous mammals, the Metatheria and Eutheria; in a cladistic framework these are sister-groups. It is demonstrated that there is no special (sister-group) relationship between monotremes and marsupials, and there is no justification for placing them in a group Marsupionta." Excellent summaries of the biology of monotremes may be found in Griffiths (1968, 1978).

Subclass Theria

Infraclass Metatheria

Marsupials. The marsupials are an old group, the marsupial/placental dichotomy having taken place in the early Cretaceous period (Lillegraven 1974). Mid- and late Cretaceous fossils, mostly isolated teeth, are especially abundant in North American faunas until the Paleocene epoch (Clemens 1979). Today the marsupials are found in two areas: the Australian region, including Australia, New Guinea, Tasmania, and nearby islands; and the Neotropics, with one species, *Didelphis virginiana*, now found as far north as the northern United States.

The continent on which marsupials originated continues to be a matter of debate that can only be settled with the discovery of additional fossil material. G. G. Simpson earlier argued that marsupials originated in North America and then migrated to South America, Europe, and Australia; however, recently (Simpson 1980) he conceded that a South American origin is also possible. Most recent authors believe the marsupials evolved in South America or the larger Gondwanaland land mass and then colonized North America, Europe, and finally Australia through Antarctica. Fossil marsupials recently were discovered from the Eocene epoch of Antarctica by Woodburne and Zinsmeister (1982), who suggested that the new fossils support the theory that marsupials originated in South America and migrated across Antarctica to Australia while the three continents were still joined together (prior to 56 million years ago). In North America, marsupial remains are abundant in early Cretaceous formations; the earliest South American fossils are from the late Cretaceous period of southwestern Bolivia.

The classification of the marsupials has been relatively stable at the generic and family level for some time, although the classification at the ordinal level is currently in a state of flux. Historically, all have been classified as a single order, the Marsupialia, and many recent authors still treat them as such (i.e., Honacki et al. 1982). However, in 1959, Cain (1959:214) stated that "Because of their peculiar features [marsupials] are always ranked as a single order of mammals within a separate class, although the briefest inspection is enough to show that there is at least as much difference between a kangaroo and a dasyure (for example) as between an insectivore and a rodent, let alone a rodent and a lagomorph." In studying both fossil and Recent marsupials, Ride (1964) proposed recognizing four orders of Marsupialia: the Marsupicarnivora, the Paucituberculata, the Peramelina, and the Diprotodonta, with the two species of marsupial moles, *Notoryctes* (Notoryctidae), remaining *incertae sedis.* Ride (1964:125) said of the marsupial mole, "*Notoryctes,* the marsupial mole, is unknown as a fossil and it is so highly specialized in dentition, skull structure, and limb structure that arguments as to its affinities which are based upon these features can only produce tentative results." Kirsch (1977a, b) and Marshall (1981) provided reviews of the previous classifications of both fossil and Recent marsupials, with Kirsch recognizing only three orders of marsupials. Recently Szalay (1982) also proposed that four orders of Recent and fossil marsupials be recognized, two New World and two Australian; however, his arrangement of families within those orders differs from that proposed by Ride. Szalay organized the four orders into two newly described cohorts, the Ameridelphia and the Australidelphia. The Ameridelphia are entirely New World in distribution, and the Australidelphia are distributed throughout Australia (and adjacent areas), except for the south temperate *Dromiciops australis.* Kirsch and Archer (1982) however, stated that the serological and dental data align *Dromiciops* with the American didelphids.

The classification of marsupials used here (Table 3.2) includes the four orders recognized by Ride (1964); however, the Notoryctidae are here included as a family within the order Marsupicarnivora. Two orders, Diprotodontia (107 Recent species) and Peramelina (19 Recent species) are restricted to the Australian region. The order Paucituberculata (7 Recent species) is restricted to the Neotropics. The order Marsupicarnivora (130 Recent species) is found both in the Australian and Neotropical regions.

The marsupials are not the primitive form from which eutherians evolved, but rather a separate and equally highly evolved lineage. Of this distinction Kirsch (1977c:900) concluded "In summary, marsupials and placentals probably represent two different solutions to some of the problems of being a mammal; as is usually the case, both solutions have advantages as well as disadvantages. Metatherians and eutherians represent a true bifurcation of the Theria and not respectively sequential adaptive stopping-points on the lineage."

Infraclass Eutheria

Order Edentata (Xenarthra). The edentates are a highly specialized group of five Recent families of some 32 species. All are New World in distribution, most being found in the Neotropical region, although a few species are now found in the southern Nearctic. There is little doubt that the center of evolution of this group was in South America, where they remained isolated from perhaps the late Cretaceous through the Pleistocene period. It is thought that the edentates evolved from the primitive suborder Palaeanodonta in North America and migrated to South America by the late Cretaceous period or early Paleocene epoch, or that they arose in South America during the early Paleocene epoch. The Edentata (*sensu lato*) are thought to have been the first lineage to split from the Eutheria in the Cretaceous period. The Recent edentates include the Central and South American anteaters, armadillos, and tree sloths. Two-toed sloths (*Choloepus*) originally were included with the three-toed forms (*Bradypus*) in the family Bradypodidae. Recently it has been suggested that *Choloepus* is most closely related to the extinct giant ground sloths of the North American Pleistocene epoch, and should be considered a member of the family Megalonychidae (Webb in press). Recent reviews on ecology, systematics, and evolution of edentates were provided by Montgomery (in press) and Wetzel (1982).

Order Insectivora. The Insectivora are a diverse group of small mammals sharing many primitive characters. There has been much debate as to the relationships between families. In the past many families of uncertain affinity were placed in the order Insectivora. Historically, the Tupaiidae (tree shrews) and Macroscelididae (elephant shrews) were classified as

Table 3.2 Diversity and Geographical Distribution of Recent Mammals[a]

	Region								
Order and Family	Neotropical	Nearctic	Palearctic	Ethiopian	Oriental	Australian	Oceanic	Recent Genera	Recent Species
Order Monotremata						X		3	3
Family Tachyglossidae						X		2	2
Ornithorynchidae						X		1	1
Order Diprotodontia						X		32	107
Family Burramyidae						X		4	7
Macropodidae						X		16	57
Phalangeridae						X		3	15
Phascolarctidae						X		1	1
Petauridae						X		5	23
Tarsipedidae						X		1	1
Vombatidae						X		2	3
Order Peramelina						X		8	19
Family Peramelidae						X		7	17
Thylacomyidae						X		1	2
Order Marsupicarnivora	X	X				X		28	130
Family Dasyuridae						X		13	50
Didelphidae	X	X						11	76
Microbiotheriidae	X							1	1
Myrmecobiidae						X		1	1
Notoryctidae						X		1	1
Thylacinidae						X		1	1
Order Paucituberculata	X							3	7
Family Caenolestidae	X							3	7
Order Edentata (Xenarthra)	X	X						16	32
Family Myrmecophagidae	X							3	4
Bradypodidae	X							1	3
Choloepidae	X							1	2
Megalonychidae (extinct)	X							3	3
Dasypodidae	X	X						8	20
Order Insectivora	X	X	X	X	X	O		66	396
Family Solenodontidae	X							1	2
Nesophontidae	X							1	6
Tenrecidae				X				12	33
Chrysochloridae				X				7	18

Table 3.2 (Continued)

Order and Family	Region Neotropical	Nearctic	Palearctic	Ethiopian	Oriental	Australian	Oceanic	Recent Genera	Recent Species
Erinaceidae			X	X	X			9	18
Soricidae	O	X	X	X	X	O		21	288
Talpidae		X	X		X			15	31
Order Macroscelidea			O	X				4	15
Family Macroscelididae			O	X				4	15
Order Scandentia					X			5	16
Family Tupaiidae					X			5	16
Order Dermoptera					X			1	2
Family Cynocephalidae					X			1	2
Order Chiroptera	X	X	X	X	X	X	X	176	917
Family Pteropodidae			O	X	X	X	O	42	160
Rhinopomatidae			X	X	X			1	3
Emballonuridae	X		O	X	X	X	O	12	48
Craseonycteridae					X			1	1
Nycteridae			O	X	X	O		1	14
Megadermatidae				X	X	X		4	5
Rhinolophidae (incl. Hipposiderinae)			X	X	X	X	O	10	127
Noctilionidae	X							1	2
Mormoopidae	X							2	8
Phyllostomidae (incl. Desmodontinae)	X	O						48	138
Natalidae	X							1	5
Furipteridae	X							2	2
Thyropteridae	X							1	2
Myzopodidae				X				1	1
Vespertilionidae	X	X	X	X	X	X	O	36	315
Mystacinidae							X	1	1
Molossidae	X	X	X	X	X	X	O	12	86
Order Primates	X	X	X	X	X	X	X	54	181
Family Cheirogaleidae				X				4	7
Lemuridae				X				4	16
Indriidae				X				3	4
Daubentoniidae				X				1	1

Table 3.2 (Continued)

Order and Family	Neotropical	Nearctic	Palearctic	Ethiopian	Oriental	Australian	Oceanic	Recent Genera	Recent Species
Lorisidae				X	X			4	5
Galagidae				X				2	8
Tarsiidae					X	O		1	3
Callithricidae	X							4	15
Callimiconidae	X							1	1
Cebidae	X							11	31
Cercopithecidae			O	X	X	O		11	76
Hylobatidae					X			1	9
Pongidae				X	X			3	4
Hominidae	X	X	X	X	X	X	X	1	1
Order Rodentia	X	X	X	X	X	X	O	385	1728
Family Aplodontidae		X						1	1
Sciuridae	X	X	X	X	X	O		49	261
Geomyidae	X	X						5	38
Heteromyidae	X	X						5	63
Castoridae		X	X					1	2
Anomaluridae				X				3	7
Pedetidae				X				1	1
Cricetidae	X	X	X	X	X			105	530
Spalacidae			X					1	3
Rhizomyidae			X	X	X			3	6
Arvicolidae		X	X					20	128
Muridae			X	X	X	X	O	108	437
Gliridae			X	X				7	15
Seleviniidae			X					1	1
Zapodidae		X	X					4	14
Dipodidae			X	O				11	30
Hystricidae			X	X	X	O		4	11
Erethizontidae	X	X						5	12
Caviidae	X							5	14
Hydrochaeridae	X							1	1
Heptaxodontidae (extinct)	X							2	2
Dinomyidae	X							1	1

Table 3.2 (Continued)

Order and Family	Region							Recent Genera	Recent Species
	Neotropical	Nearctic	Palearctic	Ethiopian	Oriental	Australian	Oceanic		
Agoutidae	X							1	2
Dasyproctidae	X							2	13
Chinchillidae	X							3	6
Capromyidae	X							4	13
Myocastoridae	X							1	1
Octodontidae	X							5	8
Ctenomyidae	X							1	33
Abrocomidae	X							1	2
Echimyidae	X							13	55
Thryonomyidae				X				1	2
Petromyidae				X				1	1
Bathyergidae				X				5	9
Ctenodactylidae				X				4	5
Order Lagomorpha	X	X	X	X	X			12	65
Family Ochotonidae		X	X					2	19
Leporidae	X	X	X	X	X			10	45
Order Carnivora (incl. Pinnipedia)	X	X	X	X	X	X	X	108	271
Family Canidae	X	X	X	X	X	X		11	35
Ursidae (incl. *Ailuropoda*)	X	X	X		X			5	9
Procyonidae (incl. *Ailurus*)	X	X	X					7	19
Mustelidae	X	X	X	X	X		O	23	63
Viverridae				X	X			19	34
Herpestidae			X	X	X			17	36
Protelidae				X				1	1
Hyaenidae			X	X	X			2	3
Felidae	X	X	X	X	X			5	37
Otariidae							X	7	14
Odobenidae							X	1	1
Phocidae			O				X	10	19
Order Cetacea								39	77
Family Platanistidae	X		O		X		O	4	5
Delphinidae					O		X	17	33
Phocoenidae			O				X	3	6

Table 3.2 (Continued)

Order and Family	Neotropical	Nearctic	Palearctic	Ethiopian	Oriental	Australian	Oceanic	Recent Genera	Recent Species
Monodontidae		O	O				X	2	2
Physeteridae							X	2	3
Ziphiidae							X	6	18
Eschrichtidae							X	1	1
Balaenopteridae							X	2	6
Balaenidae							X	2	3
Order Sirenia	X	O	O	X	O	O	X	3	5
Family Dugongidae			O	O	O	O	X	2	2
Trichechidae	X	O		X			O	1	3
Order Proboscidea				X	X			2	2
Family Elephantidae				X	X			2	2
Order Perissodactyla	X		X	X	X			6	18
Family Equidae			X	X	O			1	9
Tapiridae	X				X			1	4
Rhinocerotidae				X	X			4	5
Order Hyracoidea			O	X				3	7
Family Procaviidae			O	X				3	7
Order Tubulidentata				X				1	1
Family Orycteropodidae				X				1	1
Order Artiodactyla	X	X	X	X	X	O		77	187
Family Suidae			X	X	X	O		5	8
Tayassuidae	X	O						2	3
Hippopotamidae			O	X				2	2
Camelidae	X		X					3	6
Tragulidae				X	X			2	4
Cervidae (incl. Moschinae)	X	X	X		X	O		15	38
Giraffidae				X				2	2
Bovidae (incl. Antilocaprinae)		X	X	X	X	O		46	124
Order Pholidota				X	X			1	7
Family Manidae				X	X			1	7

Region spans the columns Neotropical to Oceanic.

[a] X indicates region of principal distribution; O indicates region of secondary, minor distribution.

families of Insectivora. In this scheme the Tupaiidae and Macroscelididae were grouped together as a suborder, the Menotyphla, with the remaining families forming the suborder Lipotyphla.

Recent attempts to clarify the relationships have produced a variety of classifications (see Findley 1967; McKenna 1975; Van Valen 1967). The classification given here is that presented by Honacki et al. (1982), and includes the families Solenodontidae, Nesophontidae, Tenrecidae, Chrysochloridae, Erinaceidae, Soricidae, and Talpidae. In this system the Tupaiidae and Macroscelididae are treated as separate orders.

The Solenodontidae, or solenodons, are restricted to the islands of Cuba and Hispaniola. A single Recent genus (*Solenodon*) represented by two species is known. A summary of what little is known of the biology of these species is presented by Nowak and Paradiso (1983). The fossil record dates back only to the late Pleistocene epoch.

The Nesophontidae is known from a single Recent genus, *Nesophontes*, and six species, originally found on several West Indian islands; however, it is now extinct. It is thought that their extinction followed shortly after the arrival of the Spanish to the New World. Habitat destruction and the introduction of rats and cats to the islands perhaps led to extinction of these insectivores. Findley (1967) considered the genus *Nesophontes* a member of the family Solenodontidae.

The Tenrecidae, or tenrecs and otter shrews, are an old and diverse group of 12 Recent genera and 33 species in 3 subfamilies. The otter shrews, two genera and three species, are found in equatorial Africa. Many authors regard the otter shrews as a distinct family, the Potamogalidae. The tenrecs are all restricted to the island of Madagascar except for introductions to several islands in the Indian Ocean. Three species of tenrecs are known from the early Miocene epoch of Africa. The only known fossil tenrecs from Madagascar are from the Pleistocene, although the group undoubtedly existed on the island before it separated from the African mainland. Of their relationships Butler (1978:63) stated, "Whatever their relationships may be, it is not disputed that the Tenrecidae are an ancient, isolated group. Though unknown before the Miocene, it is very likely that they formed part of the Paleocene African fauna. In the Miocene there were three very distinct genera, implying an earlier radiation." An excellent study of tenrec behavior was presented by Eisenberg and Gould (1970).

The Chrysochloridae, or golden moles, consists of 7 genera and 18 species of small fossorial insectivores. They are confined to central and southeastern Africa. The oldest known fossils are from the early Miocene of Africa.

The Erinaceidae, or hedgehogs and gymnures, include 9 Recent genera and 18 species. Today the family is found throughout the Ethiopian, Oriental, and Palearctic faunal regions. Fossil hedgehogs are known from the Eocene to early Pliocene epochs of North America, late Eocene of Europe, Miocene of Africa, and Oligocene of Africa.

The Soricidae, or shrews, includes some of the smallest mammals. They are widely distributed throughout most habitat types in the northern hemisphere and Africa. They are found on all continents, but the greatest diversity is in the Nearctic, Ethiopian, and Palearctic faunal regions; there are 21 Recent genera and some 288 species. The systematics of many species in the two largest genera (*Crocidura* and *Sorex*) are poorly understood. The oldest known fossils are from the late Eocene epoch of Europe and early Oligocene of North America.

The Talpidae, or moles and desmans, are fossorial or semiaquatic insectivores of the northern hemispheres. Twelve Recent genera and 27 species are known. The oldest known fossils are from the late Eocene epoch of Europe and the middle Oligocene of North America.

Order Macroscelidea. The elephant shrews comprise a single family, Macroscelididae, of 15 species in 4 genera restricted to the African continent; one species is found in Morocco and Algeria and the remaining species in central, eastern, and southern Africa. The fossil record is poor and entirely restricted to Africa (Patterson 1965). Fossil elephant shrews are known from the early Oligocene, Miocene, and Pliocene epochs. Elephant shrews have often been considered a subfamily of Insectivora (Le Gros Clark 1932; Patterson 1957); however, recent evidence suggests that the Macroscelidea are best considered a distinct order (Butler 1956; Patterson 1965; McKenna 1975). Romer (1971:211) stated that "They appear to be an isolated African offshoot from some primitive insectivore stock." This family was reviewed by Corbet and Hanks (1968).

Order Scandentia. The tree shrews comprise a single family, Tupaiidae, of 16 species in five genera, that is restricted to the Oriental region. This family occurs throughout eastern Asia, on the mainland from India and China, through the Malay Peninsula, Borneo, and the Philippines. Tree shrews have been variously classified as a family of Insectivora (Romer 1971; Van Valen 1982), Primates (Le Gros Clark 1932; Simpson 1945), and most recently as a separate order, the Scandentia (Butler 1972; McKenna 1975). The genera within the family Tupaiidae form a coherent grouping, possessing several primitive characters that perhaps place them closest to the ancestral stock of all placental mammals (Campbell 1974). An extensive bibliography of the tree shrews, including parasites, was provided by Elliot (1971). Luckett (1980) reviewed evidence assessing relationships. There is no fossil record for the family Tupaiidae.

In describing a new species of *Psorergates* (Psorergatidae) from *Tupaia dorsalis* and reviewing the mites found on tupaiids, Giesen and Lukoschus (1982:266) stated, "These data on the distribution of parasitic mite taxa confirm neither a relation to Primates nor to Insectivora. Aberrant species and monotypic genera on Tupaiidae seem to support the hypothesis of an unique phylogenetic evolution for the Scandentia."

Order Dermoptera. The Recent flying lemurs, or colugos, comprise a single family with two species in a single genus (*Cynocephalus*) that occurs in Southeast Asia and the Philippines. The only fossils known, tentatively identified as dermopterans, are from the late Paleocene and early Eocene epochs of North America. Van Valen (1967) considered the Dermoptera a suborder of the Insectivora; however, most recent authors consider the group to represent a distinct order. The general consensus, expressed by Patterson (1957:24), is "that dermopterans derive from the general insectivore stock from which chiropterans and primates also arose."

Order Chiroptera. Bats occur on all land masses with the exception of a few isolated oceanic islands and the polar caps. Most remote oceanic islands have endemic populations of bats. Recent bats are divided into two suborders: the Megachiroptera and the Microchiroptera. Megachiropterans are strictly Old World in distribution; microchiropterans are found worldwide. The oldest known fossil bat, *Icaronycteris index* of the early Eocene epoch of Wyoming (Jepsen 1966, 1970), has been assigned to the Microchiroptera, although it and several other early genera may best be considered a distinct suborder, the Eochiroptera. Fossil megachiropterans are known from a few specimens of the Oligocene and Miocene epochs of Europe. Well-developed bats, not dissimilar from modern-day microchiropterans, are known from middle Eocene deposits in both North America and Europe. By the beginning of the Oligocene epoch, at least six extant families of bats and several extant genera were already established. A diphyletic origin to the two major groups of bats, the mega- and microchiropterans, has been postulated (Smith 1976; Smith and Madkour 1980); however, most workers concur that the group is monophyletic (Van Valen 1979). Bats undoubtedly arose from an insectivoran-like ancestor. Excellent recent reviews of the ecology of parasitic insects on bats were provided by Marshall (1981, 1982). A review of the arthropods parasitic on the Neotropical family Phyllostomidae may be found in Webb and Loomis (1977).

Order Primates. The Primates are a diverse group of some 181 species in 54 genera found mostly in tropical and subtropical areas. Currently, 14 families are recognized. The Recent primates are divided into two or three distinct suborders. The more primitive group is the suborder Strepsirhini, which includes the lemurs, indrids, lorises, and galagos, all of which are Old World in distribution. The suborder Haplorhini includes two infraorders: the Platyrrhini, the cebids and marmosets of the New World tropics, and the infraorder Catarrhini, the cercopithecids, hylobatids, pongids, and hominids of the Old World tropics and subtropics. A few species of cercopithecids extend into the southern Palearctic, and the one extant hominid, *Homo sapiens*, is now worldwide in distribution. The tarsiers have been included at various times either in the Strepsirhini (then called the

Prosimi), the Haplorhini, or most recently, as a distinct suborder, the Tarsii.

Precisely where the Primates originated and the routes of dispersal is a subject that has been hotly debated in recent years (see Ciochon and Chiarelli 1980; Luckett and Szalay 1975). *Purgatorius* of the late Cretaceous period of North America has been described as the earliest known primate fossil (Van Valen and Sloan 1965); however, its affinities to the primates is debatable. The earliest unquestioned primate fossils are from the early Paleocene epoch of North America. Late Paleocene primates are abundant in both North American and European faunas. The oldest known primate fossils from South America and Africa are from the Oligocene epoch (Hershkovitz 1974, 1977; Simons et al. 1978; Simons and Kay 1983). The consensus is now that the Primates evolved in Africa, although there is a paucity of early African fossils. Other models for the origin of primates include those of Asian origin (Delson and Rosenberger 1980; Gingerich 1980), North American origin (Simpson 1945), and South American origin. African and Asian models are currently being debated (see Ciochon and Chiarelli 1980).

Concerning the phylogeny of tarsiers, Cartmill (1982:279) wrote: "There are currently three principal schools of thought concerning the phylogenetic affinities of the genus *Tarsius*. One school regards *Tarsius* as the most distant living primate relative of the Simiiformes; the second school regards *Tarsius* plus the extinct Omomyidae as constituting the phyletic sister group of Simiiformes; and the third school holds that *Tarsius* itself is the sister group of the Simiiformes. Oddly, all three schools contend that comparative otic anatomy provides crucial evidence for their favorite phylogenetic schemes." Gingerich (1980:133) concluded that "There is disagreement regarding the major phyletic relationships of Tarsiiformes, Lemuriformes, and Simiiformes, with different results depending on whether one attempts to trace phyletic groups through the fossil record or to infer history from the comparative anatomy of living forms. . . . Parallelisms and reversals are common evolutionary phenomena. . . . This means . . . that our evidence regarding primate phylogeny is still far from complete . . . and that we need to take a more critical look at different methods being used to reconstruct primate history."

Within the suborder Strepsirhini, four families are restricted entirely to Madagascar: the Lemuridae (16 Recent species), the Cheirogaleidae (7 Recent species), the Indriidae (4 Recent species), and the Daubentoniidae (1 Recent species). The Galagidae (8 Recent species) is found only in sub-Saharan Africa; the Lorisidae (5 Recent species) is found in Southeast Asia and west-central Africa; and the Tarsiidae (3 Recent species) is Southeast Asian in distribution and is usually considered a distinct suborder, Tarsii.

Four families comprise the infraorder Catarrhini (suborder Haplorhini), and all were originally Old World in distribution: the Cercopithecidae (76 Recent species) are found in the Ethiopian, Palearctic, and Oriental faunal regions; the Hylobatidae, or gibbons (9 Recent species), are restricted to southeast Asia; the Pongidae, or great apes (4 Recent species), are found in the Ethiopian and Oriental faunal regions; the Hominidae, or man (1 Recent species), are now worldwide in distribution. The earliest known hominid, *Australopithecus afarensis*, is approximately 3.0 million years old. As early as 1945, Simpson (1945:187) stated, "Most students now believe that the gibbons, apes, and man form a natural unit." The Hominidae is recognized as a distinct family, primarily on the basis of intellectual development. There is little biochemical justification for regarding the Hominidae as a family distinct from the Pongidae (see King and Wilson 1975; Yunis et al. 1980). Three families comprise the infraorder Platyrrhini (suborder Haplorhini), all Neotropical in distribution: the Callimiconidae (1 Recent species), the Callithricidae (15 Recent species), and the Cebidae (some 31+ Recent species).

Order Rodentia. The order Rodentia is the largest and most diverse order of mammals, including some 37 families and 1728+ Recent species. Rodents are the most successful of all living mammals; the order Rodentia has more species, genera, and families than any other mammalian order. Rodents occupy a wide range of niches including arboreal, terrestrial, semiaquatic, and subterranean, and have the widest geographic distribution of any order. They are found worldwide except for Antarctica and some oceanic islands. Rodents often exceed other mammals in local diversity and abundance. Most are small in size (rat sized), although the range is from 5 grams in the Old World harvest mouse, *Micromys minutus*, to 79 kilograms in the South American capybara, *Hydrochoerus hydrochaeris*.

The relationships of the rodents to the other orders of mammals are poorly understood. Historically, the rodents and lagomorphs have been considered together as suborders of the order Rodentia. All recent authors consider the two groups as distinct orders of separate ancestory. It has been suggested that the rodents are most closely related to the Primates (McKenna 1961), Insectivora (Wood 1962), or the Carnivora (Szalay and Decker 1974). McKenna (1975) in a recent classification of the Mammalia, listed the order Rodentia as *incertae sedis*. Romer (1971:303) stated that "The origin of the rodents is obscure. When they first appear, in the late Paleocene, in the genus *Paramys*, we are already dealing with a typical, if rather primitive, true rodent, with the definitive ordinal characters well developed. Presumably, of course, they had arisen from some basal, insectivorous, placental stock; but no transitional forms are known. To perfect the dental and other features of the order, a considerable period of time—perhaps the whole extent of the Paleocene—seems necessary. But in what region or environment this occurred, we do not know." A complex of some five genera of true rodents is now known from the latest Paleocene epoch (Clarkforkian) of the western United States, representing the earliest known rodents (Savage and Russell 1983).

Traditionally, three suborders of Rodentia are recognized, although there is considerable disagreement as to the relationships of the suborders and to the placement of families within the groups: the Sciuromorpha, including the squirrel-like rodents of the families Anomaluridae, Aplodontidae, Castoridae, Geomyidae, Heteromyidae, Pedetidae, and Sciuridae; the Myomorpha or rat and mouse-like rodents of the families Arvicolidae, Cricetidae, Dipodidae, Gliridae, Muridae, Rhizomyidae, Seleviniidae, Spalacidae, and Zapodidae; and the Hystricomorpha or porcupine-like rodents of the families Abrocomidae, Agoutidae, Bathyergidae, Capromyidae, Caviidae, Chinchillidae, Ctenodactylidae, Ctenomyidae, Dasyproctidae, Dinomyidae, Echimyidae, Erethizontidae, Heptaxodontidae, Hydrochaeridae, Hystricidae, Myocastoridae, Octodontidae, Petromyidae, and Thryonomyidae (see Vaughan 1978; Eisenberg 1981; Nowak and Paradiso 1983; Woods 1982; and references therein).

Romer (1971) recognizes three suborders, the Sciuromorpha, Myomorpha, and Caviomorpha, but lists three superfamilies (Castoroidea, Theridomyoidea, and Thryonomyoidea) and four families (Anomaluridae, Ctenodactylidae, Hystricidae, and Pedetidae) as not assigned to either superfamily or suborder. The relict family Aplodontidae was assigned by Wood (1965), along with several extinct families, to the suborder Protrogomorpha. Several recent authors have questioned the value of continuing to recognize suborders within the Rodentia. A review of the problems and classifications of rodent suborders may be found in Anderson (1967).

The Anomaluridae, or scaly-tailed squirrels, are found in central and western Africa in both tropical and subtropical forests; no fossils of this family are known (Kingdon 1974). The Aplodontidae, the mountain beaver or sewellel, is now represented by the single species, *Aplodontia rufa*, which is restricted to the Pacific Northwest. It is the sole surviving member of a once widespread family whose fossils are known from the late Eocene of North America, Oligocene of Europe, and Pliocene epoch of Asia. The Castoridae, or beavers, are Holarctic in distribution, among the largest of rodents (weighing up to 40 kilograms), and semiaquatic. Fossils are known from the early Oligocene of North America and the late Oligocene of Europe.

The Geomyidae, or pocket gophers, are endemic to North America and are found from southern Canada to extreme Northwestern Colombia. Pocket gophers are fossorial; the earliest fossils are from the latest Oligocene. The Heteromyidae, or pocket mice, are the sister group of the geomyids and also are distributed from southern Canada to northern South America; the habitats occupied range from arid deserts to humid tropical forests (Genoways 1973). The earliest fossils are from the early Oligocene epoch. The Pedetidae, or springhaas, are represented by a single living species, *Pedetes capensis*, which occurs in arid areas of the southern Ethiopian region; the earliest fossils are from the Miocene epoch of Africa.

The Sciuridae, or squirrels, marmots, chipmunks, and prairie dogs, are found in all zoogeographic regions except for the Australian; this is a large and diverse family occupying a wide array of habitats. The earliest fossils are from the Oligocene epoch of Europe and North America. The Arvicolidae, or lemmings, muskrats, and voles, are Holarctic and primarily found in forests and prairies; the muskrats are semiaquatic. The earliest fossils are from the Oligocene.

The Cricetidae, or gerbils, hamsters, mice, and rats, are widely distributed in numerous habitats in both the New and Old World; the earliest fossils are Oligocene (Carleton 1980). The Arvicolidae and Cricetidae, along with the murid rodents, are considered by some authors to belong to a single family, the Muridae. The Dipodidae, or jerboas, are arid-adapted jumping rodents of the southern Palearctic; the earliest fossils are from the Pliocene epoch of Asia. The Gliridae, or dormice, are found in the Ethiopian, Oriental, and Palearctic regions; the earliest fossils are from the middle Oligocene epoch of Europe. The Muridae, or rats and mice, are now found worldwide, although they were originally restricted to the Old World; the greatest species diversity is found in southeast Asia; the earliest fossils are from the Pliocene epoch of Europe and Asia.

The Rhizomyidae, or bamboo rats, are found in west-central Africa and Southeast Asia; the earliest fossils are from the late Oligocene of Europe. The Seleviniidae, or desert dormouse, is known from a single species, *Selevinia betpakdalensis*, found in a restricted desert region of the USSR; there are no known fossils (Nowak and Paradiso 1983). The Spalacidae, or mole rats, are found in the southern Palearctic; as the name implies, mole rats are fossorial. The earliest fossils are from the latest Pliocene. The Zapodidae, or jumping mice, are a Holarctic group of small mice generally found in forests, meadows, and marshes; the earliest fossils are from the Oligocene of Europe and the early Miocene of North America (Wrigley 1972).

The Abrocomidae, or chinchilla rats and chinchillones, contain a single genus, *Abrocoma*, with two species that are found at higher elevations in west-central South America; the earliest fossils are from the late Miocene of South America. The family Agoutidae, or pacas, contains a single genus, *Agouti*, with two species, found from east-central Mexico to Paraguay; they are moderate-sized, nocturnal, forest animals (Collett 1981). The pacas are often considered a subfamily of Dasyproctidae. The Dasyproctidae, or agoutis and acouchis, includes two genera of moderate-sized forest rodents that occur from southern Mexico throughout much of South America; the earliest fossils are from the Oligocene of South America (Smythe 1978).

The Bathyergidae, or African mole-rats, occur south of the Sahara Desert in Africa (Kingdon 1974). They are highly adapted to a fossorial existence; fossils are known from the Miocene of Africa and Oligocene of Mongolia. The Capromyidae, or hutias, include several large, nocturnal rodents restricted to the Antilles; the earliest fossils are from the late Pleistocene of the West Indies (Anderson et al. 1983). The Caviidae, or cavies, cuis, and guinea pigs, occur over much of South America; caviids generally are found at higher elevations, rocky outcrops, and savannahs (Rood 1972; Lacher 1981). The earliest fossils are from the middle Miocene of South America. The Chinchillidae, or chinchillas and viscachas, are medium-sized rodents of the South American Andes and pampas; the earliest fossils are from the early Oligocene of South America.

The Ctenodactylidae, or gundis, are restricted to North Africa; they are medium-sized rodents of arid areas (George 1974). The earliest fossils are from the Oligocene of Asia. The Ctenomyidae, or tuco-tucos, are a highly fossorial complex of species belonging to a single genus *Ctenomys*, found in the southern half of South America (Weir 1974). The earliest fossils are from the Pliocene. The Dinomyidae, or pacarana, are represented by a single living species, *Dinomys branickii* from the Andean highlands of central South America. The earliest fossils are from the Miocene. The Echimyidae, or spiny rats, are found in forested regions throughout the northern half of South America and southern Central America. The earliest fossils are from the late Oligocene.

The Erethizontidae, or New World porcupines, include several large-bodied, spiny rodents distributed across the United States and Canada and through much of Central and South America; fossil porcupines are known from the Oligocene of South America and the late Pliocene of North America. The Heptaxodontidae are an extinct family of large-bodied rodents known only from Pleistocene and Recent fossils found in cave deposits in the West Indies. This family undoubtedly became extinct through the activity of man. The Hydrochaeridae, or capybara, is represented by a single living species, *Hydrochaeris hydrochaeris,* the largest of all rodents. Capybaras are found throughout eastern South America and Panama; the earliest fossils are from the early Pliocene of South America. The Hystricidae, or Old World porcupines, are large-bodied, spiny rodents found throughout all of Africa and much of southern Asia. The fossil record dates back to the Oligocene of Europe, middle Pliocene of Asia, and Pleistocene of Africa.

The Myocastoridae, the nutria of coypu, is represented by a single living species, *Myocastor coypus,* a large-bodied, semiaquatic rodent originally found throughout southern South America, and now widely distributed in Europe and the southern and northwestern United States, where they were introduced for the fur industry (Lowery 1974). The earliest fossils are from the early Miocene of South America. The Octodontidae, or octodonts, are rat-sized rodents found in the Andean mountains, foothills, and adjacent coastal areas of South America; the earliest fossils are from the early Oligocene (Woods and Boraker 1975). The Petromyidae, or dassie rat, is known from a single species, *Petromus typicus,* found in arid areas of southwestern Africa; there are no known fossils. The Thryonomyidae, or cane rats, are represented by a single Recent genus, *Thryonomys* with two species, and are found throughout the southern half of Africa; the earliest fossils are from the Miocene (Kingdon 1974).

Order Lagomorpha. The Lagomorpha, the rabbits, hares, and pikas, are an old group, although extant species show little variation in body form. Lagomorphs are native to all continents except Australia and Antarctica; none were endemic to the Australian faunal region, however, they have been introduced onto many of the islands by man in recent years. There are two Recent families in the order: the Leporidae, which includes the rabbits and hares (45 Recent species), is widely distributed and now widely introduced, and the Ochotonidae, or pikas (19 Recent species), which are Holarctic in distribution. McKenna (1982:213) stated that "The order [Lagomorpha] almost certainly originated in Asia, spreading from there to other continents at various times in the Cenozoic." The oldest known lagomorph is *Mimotona* from the Paleocene of Asia. Wilson (1960) suggested that the ochotonids and leporids diverged from a common ancestor during the Oligocene. Europe and Asia seem to have been the center of evolution and diversification for the ochotonids; they reached their greatest diversity and distribution in the Miocene and have declined since. The leporids spread to other continents early on. The order Lagomorpha has no clear relationship to any other mammalian order. Over the years, the systematic position of lagomorphs has varied considerably. Older classifications considered the group a suborder, the Duplicidentata, of the Rodentia. Using amino acid sequence information, Dene et al. (1982) suggested that the Lagomorpha, Scandentia (tree shrews), and Carnivora were a monophyletic group.

Order Carnivora. The Carnivora are a widespread and successful group that includes a diverse array of body forms. Today carnivores are found on all land masses and in the oceans. In recent years several species have been successfully introduced by man onto continents not previously occupied. This is especially true for domestic dogs (*Canis familiaris*), cats (*Felis catus*), and mongooses (*Herpestes*). The Recent Carnivora include some 12 families and 271 species. The number of families and even orders included in this group remains controversial.

The Phocidae, or earless seals, and the Otariidae, the sea lions and fur seals, are often considered together as a distinct order, the Pinnipedia, or as a distinct suborder, the Fissipedia. However, recent evidence indicates that this grouping is artificial and based on convergence; pinnipeds as such are a polyphyletic group, having been derived from separate terrestrial ancestors (McLaren 1960; Tedford 1976). The Phocidae are now thought to have originated from mustelid stock in the North Atlantic; the earliest fossils are mid-Miocene (Ray 1976). The Otariidae are believed to have originated from canoid stock in the north Pacific. Repenning (1976) considers the walruses (Odobenidae) and the Otariidae to have evolved from an extinct aquatic family, the Enaliarctidae, which was derived from the canoid carnivores. He included the two families together in a separate order, the Otarioidea.

Two suborders of Carnivora are often recognized: Caniformia which includes the families Canidae, Ursidae, Odobenidae, Otariidae, Procyonidae, Mustelidae, and Phocidae; and Feliformia which includes the Viverridae, Herpestidae, Protelidae, Hyaenidae, and Felidae. The suborder Caniformia is sometimes grouped into three superfamilies: Canoidea, including only the family Canidae; Arctoidea, including the Ursidae, Otariidae, Odobenidae, and Procyonidae; and Musteloidea, including the Mustelidae and Phocidae.

The Canidae, or wolves, dogs, jackals, and foxes, include some 11 Recent genera and 35 species; they are worldwide in distribution. Canid fossils are known from the Pliocene in Africa (Savage 1978), the late Eocene of North America and Europe, early Oligocene in Asia, and early Pleistocene in South America. A review of the systematics and ecology of the wild canids may be found in Fox (1975).

The Ursidae, or bears and giant panda, includes five Recent genera and nine species. Fossil bears are known from the Pliocene of North America and Asia; they reached the South American and African continents during the Pleistocene (Savage 1978). Although the number of recognized species of bears has remained fairly constant, the number of genera recognized by various authors fluctuates, as does the number of subfamilies (Mondolfi 1983).

The relationships of the giant panda (*Ailuropoda melanoleuca*) and the lesser (or red) panda (*Ailurus fulgens*) to the other carnivores has been problematic for some time and remains so today. Giant pandas and lesser pandas historically have been placed in monotypic families, Ailuropodidae and Ailuridae, respectively, or together as a subfamily of the Procyonidae (Ewer 1973). Excellent reviews of the giant panda which place them as a subfamily of bears may be found in Davis (1964) and Chorn and Hoffmann (1978). Lesser pandas are most often considered members of the procyonids; however, Ginsburg (1982) recently reiterated that *Ailurus* is most closely related to the bears and otariid seals and must be considered a monotypic family, Ailuridae.

The Procyonidae, or raccoons, coatis, and allies, include 7 Recent genera and 19 species. All except the lesser panda are Neotropical or Nearctic in distribution; most are omnivorous, highly opportunistic predators. Fossil procyonids are known from the late Oligocene to Recent in North America, from the late Miocene to the late Pliocene in Europe; they reached South America during the Pliocene. A review of the ecology and systematics of the procyonids can be found in Ewer (1973).

The family Mustelidae is a diverse group of some 23 Recent genera and

63 species, and includes the weasels, martens, skunks, badgers, and otters. Mustelids are found in all faunal regions except the Australian. The distribution of the family is basically Holarctic, and many individual species or species complexes are Holarctic. Ecologically they are replaced in the tropical Old World by the viverrids and herpestids. The geological range of the Mustelidae is early Oligocene to Recent in North America, Europe, and Asia; late Miocene to Recent in Africa; and Pliocene to Recent in South America. Recently, Muizon (1982:259) suggested that the Mustelidae "represents a paraphyletic grouping and the genera *Enhydra* [sea otters] and *Enhydriodon* . . . constitute the sister group of the Phocidae."

The family Viverridae has traditionally included a diverse grouping of six subfamilies; however, C. Wozencraft (in Honacki et al. 1982) recently suggested that the mongooses merit recognition as a distinct family, the Herpestidae. The Viverridae (*sensu stricto*) would thus include the genets, civets, and palm civets, some 19 Recent genera and 34 species restricted to the Ethiopian and Oriental faunal regions. On the origin of the viverrids (*sensu lato*), Savage (1978:257) wrote, "The family is ancient, originating from the Miacidae probably in late Eocene times in Eurasia. On dental characters alone, it is impossible to distinguish late viverravine miacids from early viverrids. . . . There are no known miacids in Africa and the first migrants, probably in earliest Miocene, were already viverrids." Savage also suggested that the viverrids colonized the island of Madagascar "sporadically from Miocene times onward." The viverrids apparently reached Madagascar by rafting, and there were probably at least two separate colonizations.

The family Protelidae contains a single Recent genus and species, *Proteles cristatus*, the aardwolf. Aardwolves are restricted to eastern and southern Africa. They are often considered members of the family Hyaenidae; however, they also have been placed within the Viverridae (Savage 1978). The families Protelidae and Hyaenidae are thought to have evolved from a branch of the Viverridae. There is no fossil record of aardwolves. Aardwolves feed primarily on termites. A review of the biology of *Proteles* may be found in Kingdon (1977).

The Hyaenidae, or hyaenas, contains two Recent genera and three species. Hyaenids are found in the Ethiopian, Oriental, and Palaearctic faunal regions. Hyaenas are highly specialized for carrion feeding, although the spotted hyaena, *Crocuta crocuta* is an effective predator on big game. The oldest known fossils are from the late Miocene of Eurasia, and most are restricted to the Old World; however, one genus crossed the Beringian land bridge and was found in North America during the Pleistocene epoch. Hyaenids reached their peak diversity in the Pleistocene. The family Hyaenidae is thought to be a direct descendent of the Viverridae. A review of hyaenid evolution was provided by Thenius (1966). Reviews of the biology of individual species may be found in Mills (1982) and Kruuk (1972).

The family Felidae, or cats, contains some four or five Recent genera and 37 species. There is little consensus on the number of genera or relationships between species, although there is little disagreement of the number of species recognized. The number of genera recognized by various authors ranges from two to 15 (Hemmer 1978). The family is worldwide in distribution, except for the Australian and Oceanic regions. Cats are the most specialized and predaceous of the carnivores, and are fairly uniform in body structure. Fossils are known from the late Eocene in North America and Eurasia, Miocene of Africa, and Pleistocene of South America. Savage (1977:243) suggested that the "felids and viverrids have independent origins from miacids." Reviews of the Recent species of cats may be found in Eaton (1973) and Guggisberg (1975).

Most Carnivora are flesh eaters, although a few are insectivorous (aardwolves and meerkats) or herbivorous (giant pandas and binturongs). Carnivores are generally medium to large sized and have a complex social behavior. An excellent review of the ecology, systematics, and evolution of the Carnivora was presented by Ewer (1973), and a recent review of behavior in carnivores was presented by Macdonald (1983).

Order Cetacea. The cetaceans, or whales, are found throughout all oceans of the world, and a few species of dolphins are now secondarily found in fresh water. The Recent members of the order Cetacea are generally divided into two distinct suborders: the Mysticeti, or baleen whales, and the Odontoceti, or toothed whales. A third suborder, the Archaeoceti includes the extinct primitive whales. A few authors regard the suborders as separate orders: the Mysticeta, Odontoceta, and Archaeoceta (i.e., DeBlase 1982). This discrepancy results from the problem of whether the whales had a monophyletic or a polyphyletic origin.

The oldest and most primitive cetaceans, the archaeocetes from the Eocene, Oligocene, and Miocene, are thought to have evolved from primitive, carnivorous condylarths. The earliest archaeocete known is *Pakicetus* from the early Eocene of Pakistan (Gingerich et al. 1983); middle Eocene whales are known from formations in North America, Africa, and Asia. The earliest Mysticeti are from the middle Oligocene of Europe, and the oldest Odontoceti are from the late Eocene of North America.

All cetaceans are extremely specialized for an aquatic mode of life; adaptations include fusiform body shape, modification of the anterior limbs into flippers, a lack of external hind limbs, and an essentially hairless body. Ectoparasites of cetaceans include acarids, diatoms, amphipods, ciliates, cirripeds, copepods, isopods, lampreys, and remoras (Arvy 1982). A recent review of the evolution, zoogeography, and ecology of the Cetacea may be found in Gaskin (1982).

Order Sirenia. The order Sirenia includes the manatees, dugongs, and sea cows; all are large bodied, fully aquatic herbivores. The order contains two Recent families: the Dugongidae with two monotypic genera, *Dugong* and *Hydrodamalis*; and Trichechidae with one genus, *Trichechus*, and three species. The extant species are tropical or subtropical in distribution. Stellar's sea cow (*Hydrodamalis gigas*) was confined to the shallow waters around Bering and Copper Islands in the Bering Sea but was hunted to extinction by Russian whaling crews only 27 years after its discovery in the mid-1700s. The most primitive sirenian known is *Prorastomus* of the middle Eocene of Jamaica (Savage 1976). Domning (1982:599) wrote concerning the relationships of *Prorastomus* that "the tooth formula of *Prorastomus* is in fact typical of primitive sirenians, including dugongids, and that its geographic occurrence likewise represents the primeval 'Tethyan' distribution of the order. It may be regarded as a good structural ancestor for all later sirenians. . . ." Late Eocene genera are known from Europe and North Africa. The sirenians reached their peak diversity in the Miocene and Pliocene epochs. It is thought that the Sirenia and Proboscidea evolved from a common condylarth ancestor. Reviews of the biology and evolution of Sirenia may be found in Domning (1976, 1978, 1982), Forsten and Youngman (1982), Hartman (1979), and Husar (1977).

Order Proboscidea. Recent elephants include only two species: the African elephant, *Loxodonta africana*, and the Indian elephant, *Elephas maximus*. Both belong to the single family Elephantidae. *Loxodonta* was until recently found throughout sub-Saharan Africa, and *Elephas* throughout much of south Asia. The order Proboscidea evolved in Africa, the oldest true proboscidean being *Palaeomastodon*, a tapir-sized animal of the late Eocene epoch of northern Africa. The Proboscidea underwent a rapid radiation during the later Cenozoic era. Fossil elephants include a diverse array of forms now categorized into four families and perhaps representing 100 species. By the late Miocene epoch proboscideans had reached North and South America and Eurasia. Several forms became extinct during the Pleistocene epoch; only the family Elephantidae remains extant today. Reviews of the evolution and origin of the elephants may be found in Aguirre (1969) and Maglio (1973).

Order Perissodactyla. The Recent members of the order Perissodactyla comprise three distinct families: the Equidae, the horses, zebras, and asses (nine species); the Tapiridae, the tapirs (four species); and the Rhinocerotidae, the rhinoceroses (five species). The Perissodactyla evolved from the order Condylarthra; the initial radiation probably stemmed from the phenacodontid condylarths during the late Paleocene epoch of Eurasia. By the early Eocene, three superfamilies of perissodactyls were already present: the equoids, tapiroids, and chalicotherioids. The rhinocerotoids appeared at the "beginning of the late Eocene, apparently derived from secondary radiations of tapiroids" (Radinsky 1969:308). The order underwent a tremendous adaptive radiation in the Eocene epoch such that shortly after its emergence some 14 families had evolved. The horses and rhinoceroses flourished until the Pleistocene in both the Old and New World; late Pleistocene extinctions drastically reduced their ranges. Before recent introductions by man, the equids were restricted to Africa and Eurasia; rhinoceroses are restricted to the southern half of Africa and south Asia; tapirs are restricted to the northern Neotropics and southeast Asia. The Recent perissodactyls are all herbivorous.

Order Hyracoidea. The Recent Hyracoidea, variously called hyraxes, conies, or dassies, constitute a single family, Procaviidae, with three genera and seven species. All three genera are Ethiopian in distribution, with one species, *Procavia capensis*, extending north along the Nile River, the eastern Mediterranean, and the southeastern Arabian peninsula. The oldest known hyrax fossils are from the upper Eocene-lower Oligocene of Egypt and are little differentiated from modern hyraxes (Meyer 1978). Africa was undoubtedly the center of origin for the order. The relationships of the Hyracoidea to the other orders of mammals are obscure. They have been variously associated with the Perissodactyla (McKenna 1975) and the Proboscidea and Sirenia as subungulates (Romer 1971; Simpson 1945). Dubrovo (1978:380) stated, "they most probably originated from Cretaceous mammals which may also possibly have given rise to the ancestral forms of condylarths, the Proboscidea, the Sirenia, and some other mammalian orders." Hyraxes are herbivorous and live in colonies that are isolated from neighboring colonies by varying distances. The Hyracoidea are unique within the Mammalia in harboring a complex fauna of lice that includes several species of both anoplurans and mallophagans (Hopkins 1949). Reviews of the biology of hyraxes may be found in Olds and Shoshani (1982) and Kingdon (1971).

Order Tubulidentata. The Recent aardvarks include only one family, Orycteropodidae, composed of a single species, *Orycteropus afer*. Aardvarks are now restricted to the Ethiopian faunal region, sub-Sahara Africa. It is believed that the aardvarks evolved in Africa from the extinct order Condylarthra, perhaps during the Paleocene epoch (Patterson 1975). Pliocene *Orycteropus* are known from Asia and Europe. Fossil aardvarks are also known from Madagascar. Aardvarks are insectivorous, semifossorial, solitary, and nocturnal (Melton 1976).

Order Artiodactyla. The Artiodactyla, or even-toed ungulates, are one of the most successful orders of mammals in terms of diversity, adaptive radiation, distribution, and numbers of species. Artiodactyls are found in all biogeographic regions except the Australian and Oceanic. The order includes eight Recent families: the Suidae, or pigs (eight species); Tayassuidae, or peccaries (three species); Hippopotamidae, or hippopotamuses (two species); Camelidae, or camels, llamas, guanacos, and vicuñas (six species); Tragulidae, the chevrotains or mouse deer (four species); Cervidae, or deer (38 species); Giraffidae, giraffes and okapis (two species); and Bovidae, the cattle and antelope (124 species).

The Suidae probably arose in either Europe or Asia during the Oligocene and reached Africa by the early Miocene where they evolved into a wide variety of types. Today they are found throughout the southern half of Eurasia and all of Africa. The Tayassuidae seems to have arisen in North America during the Oligocene epoch; Oligocene and Miocene fossils are known from Europe, Pliocene fossils from Asia, and Pleistocene fossils from Africa and South America (Cooke and Wilkinson 1978). Today they are found throughout the northern three-fourths of South America, all of Central America, Mexico, and the extreme southwestern United States. The Hippopotamidae probably arose in sub-Saharan Africa during the early Miocene epoch and then entered north Africa and Europe in the early Pleistocene (Coryndon 1978). Today they are restricted to sub-Saharan Africa and the Nile River. The Camelidae probably arose during the late Eocene in North America, and dispersed to Asia across the Beringian land bridge during the Pliocene. Today two distinct groups are found, the true camels across north Africa and central Asia and the llamas, guanacos, and vicuñas in the highlands of southern Peru, south through Bolivia and Chile. The latter groups reached South America during the Pleistocene epoch. The Tragulidae are known from the Miocene epoch of Africa, Asia, and Europe. Today the chevrotains are restricted to west Africa, southern India, and Southeast Asia. The Cervidae first appeared in the early Oligocene epoch of Asia, and reached North America across Beringia in the early Miocene. Today the cervids are widely distributed in both the Old and New World. The Giraffidae first appeared in the early Miocene of northern Africa (Churcher 1978), and fossil giraffids are known from India. Today the family is restricted to sub-Saharan Africa.

The Bovidae first appeared in Europe in the early Miocene epoch and underwent a tremendous radiation during the Pliocene. The North American pronghorn, *Antilocapra americana*, was until recently considered a monotypic family, Antilocapridae; however, O'Gara and Matson (1975) demonstrated that it best be considered a subfamily of the Bovidae. Bovids are widespread in the Nearctic, Palearctic, Ethiopian, and Oriental faunal regions.

The enormous Plio-Pleistocene radiation of the artiodactyls corresponds to the decline of the equids, which were perhaps ecological competitors (although see Cifelli 1981). Most artiodactyls are herbivorous and live in groups of varying sizes; the pigs and peccaries are omnivorous. Excellent reviews of the biology of selected species may be found in Clutton-Brock et al. (1982), Gauthier-Pilters and Dagg (1981), Leuthold (1977), and Sinclair (1977).

Order Pholidota. The order Pholidota, the pangolins or scaly anteaters, contains a single family, Manidae, with one extant genus, *Manis*, and seven Recent species. Pangolins are found in tropical and subtropical Africa and Southeast Asia. Four species occur in sub-Saharan Africa and three in Asia, including the islands of the Philippines, Sumatra, Java, and Borneo. The fossil record of the Pholidota is poor, however, pangolins are known from the Oligocene and Miocene epochs of Europe. Historically the pangolins have been included within the order Edentata, however, they are now treated as a distinct order. Of the relationship between the Pholidota and Edentata, Patterson (1978:270) stated that they "had a common ancestry in the later Cretaceous . . . that radiated during the Cenozoic with varying degrees of success in South America, North America, and the Old World. Whether one regards these groups as distinct orders or as suborders of an order Edentata is of minor moment." Pangolins are nocturnal and insectivorous; ants and termites comprise the bulk of the diet for most species. A review of the biology of the African species may be found in Kingdon (1971).

Additional reviews of the Mammalia include Grzimek (1975), Vaughan (1978), Eisenberg (1981), DeBlase (1982), and Anderson and Jones (1984); those with especial reference to parasites include Hoffstetter (1982) and Patterson (1957).

SUMMARY

The symbiotic association of mammals and arthropods perhaps spans more than 190 million years. As mammals evolved to occupy a wide variety of niches on all land masses, arthropods evolved to invade and colonize a wide array of habitats and niches on the mammalian body.

Coevolution between a host and parasite is difficult to demonstrate, and in many host–parasite systems coevolution (*sensu stricto*) may not occur. As the pocket gophers (*Geomys*) and their chewing lice (*Geomydoecus*) show, co-speciation often occurs between host and parasite, where the parasite exhibits an evolutionary response to the host but the host shows no counterevolutionary response (Timm 1983; Timm and Price 1980). Both the host and parasite may also develop coevolved adaptations to maximize reproductive output, as white-footed mice (*Peromyscus leucopus*) evolved a tolerance for cuterebrid parasitism (Timm and Cook 1979).

Mammals provide habitats for parasitic arthropods that include the subcuticular layer, hair, skin, glands, respiratory tract, and various other organs; the parasites may be highly adapted to their specific habitats.

The first mammals appeared on earth during the late Triassic period (Rhaetic) of the Mesozoic era, approximately 190 million years ago. They must have evolved from the mammal-like reptiles of the synapsid Therapsida, although the exact mammalian ancestor within this group of reptiles is unknown. Mammals are commonly considered to have a monophyletic origin, perhaps derived from a single family of cynodonts.

The oldest known mammalian fossils are from the late Triassic period of western Europe (Clemens et al. 1979), although the original continent where mammals evolved is not known. The only earlier fossil is from the early Triassic period of southern Brazil. A period of great mammalian radiation began in the late Cretaceous period (late Mesozoic) and continued on into the Paleocene epoch. During this time many of the Recent mammalian orders first appeared (Table 3.1). This radiation continued throughout the Cenozoic era. By the Oligocene epoch the majority of modern family taxa had developed, and many modern genus taxa appeared as early as the Pliocene epoch. The distribution of extant mammals was affected by continental drift.

Diversity and distribution of mammals are discussed by orders: Monotremata, Marsupialia, Edentata, Insectivora, Macroscelidea, Scandentia, Dermoptera, Chiroptera, Primates, Rodentia, Lagomorpha, Carnivora, Cetacea, Sirenia, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla, and Pholidota (Table 3.2).

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