

## 4. Mammals Take Over

### Reptiles become Mammals

Mammals are animals that nourish their young with milk that females produce in modified sweat glands called mammary glands, which give the whole mammal group its name. Mammals are separated into three classes according to their method of giving birth: monotremes, which lay eggs; marsupials, which give birth to very underdeveloped young that complete their development in a pouch usually located on the female's stomach; and placental mammals that give birth to fully developed young. The term "placental mammals" that's often used for mammals that give birth to fully developed young is a little misleading; those mammals are properly called Eutheria. It's misleading because marsupials also have rudimentary placentae although the marsupials' placenta is more of a glorified yolk sac and doesn't make as much of a contribution to fetal nourishment as the placenta of Eutheria. Marsupials are properly called Metatheria; Eutheria and Metatheria together are called theria, which make up 99.9% of all mammals.

The signature feature of mammals, mammary glands, are soft tissue that doesn't fossilize after an animal dies and are, therefore, impossible to use to trace the evolution of mammals. Fortunately, all mammals have distinctive teeth and bone structures that do fossilize and can mark our evolution. Teeth are the hardest part of a mammal's body and fossilize better than any other part. In fact, some species of extinct mammals are known only from their teeth. Mammalian teeth are unique in several respects. We have four types of teeth in our set (incisors, canines, premolars, and molars) each specialized for a specific purpose, but our reptilian ancestors only had uncrowned points. We replace our teeth only once, but our reptilian ancestors continuously replaced theirs. Our molars have multiple roots and cusps, but our reptilian ancestors had only one root and no cusps (uncrowned points instead) for each tooth. The evolution of our teeth is one of the interesting stories of the evolution of mammals.

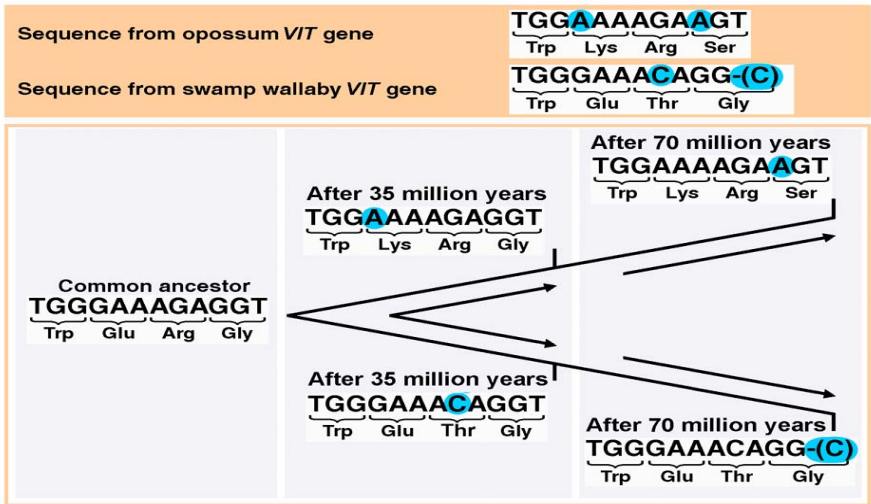
Early fossil hunters usually identified mammals solely by their teeth, but many new finds since the 1980s have enabled paleontologists to accumulate significant data on bone structure too. There are several bone structures that are different between mammals and our reptilian ancestors. Our lumbar region (lower back) has no ribs, but our reptilian ancestors had ribs there. The lack of ribs in our lower torso makes room at the bottom of the rib cage for our diaphragm, which significantly improves our breathing com-

pared to animals without one. Our fingers and toes have bones that number 2-3-3-3-3 (thumb to little finger or big toe to little toe), but our reptilian ancestors have 2-3-4-5-4 number of bones in corresponding digits. Our lower jaw is made of only one bone, but our reptilian ancestors' jaws were made of several bones. Our reptilian ancestors had a different jaw joint structure than we mammals do. We have bone, called the secondary palate, that forms the roof of our mouth to separate our nasal and oral cavities so we can breathe while we chew, but our reptilian ancestors didn't have a bony secondary palate. Only mammals have the collection of small bones in the middle ear commonly called hammer, anvil, and stirrup whereas our reptilian ancestors had only the stirrup. The transformation of two bones in the reptilian jaw joint into our hammer and anvil is another interesting story in the evolution of mammals.

## Molecular Clock

The evolution of our teeth and bones from our reptilian ancestors to our present form has traditionally been measured by the fossil record. Since around 1980, this fossil record has been increasingly supported by molecular analysis of DNA, RNA, and proteins. The idea that DNA is a sort of "molecular clock" that could be used to date evolutionary changes first occurred to Emile Zuckerkandl and Linus Pauling, who noticed in 1962 that the number of amino acid differences in hemoglobin changes with evolutionary time as estimated by fossil evidence. They compared human, gorilla, horse, and chicken hemoglobin and discovered that there is less difference between human and gorilla hemoglobin than between human/gorilla and horse, and there is more difference still between human/gorilla/horse hemoglobin and that of chicken. The further away from human they looked in terms of evolutionary development (and, therefore, time), the greater the difference in hemoglobin. The idea that this seeming relationship between evolutionary time and number of changes in DNA became especially intriguing after improvements in DNA sequencing were made around the turn of the third millennium. All that is needed is to calibrate the average rate of change in DNA (the number of changes per million years in other words) with physical changes in plants or animals, either in their form or the functioning of their systems, such as their hemoglobin.

The molecular clock is certainly a natural method of tracing evolution because mutations in DNA of sperm and egg cells (gametes) are what drives changes in form and function that natural selection weeds out as being least adapted to the environment and food chain existing at any particular time, in other words, what drives evolution. As the environment and food chain change over time, forms and functions that had become disadvantageous at one time might become advantageous at another. Thus, the fossil evidence reveals that sometimes a few forms and functions that existed in critters that had become extinct reappear later in species which were successful because those new (later) environmental conditions made those forms and functions favorable again.



### A Molecular Clock Example

Consider, for example, a tiny segment of the Virginia opossum's *VIT* gene, which is involved with producing egg yolk, that has the DNA sequence **TGGAAAAGAAGT**. Assuming the code sequence begins with the first "T", this segment of DNA codes for the amino acid sequence triptophan, lysine, arginine, and serine that are part of a vitellogenin protein. Compare that segment with the corresponding segment of a related marsupial species (swamp wallaby), which has the corresponding DNA sequence **TGGGAAACAGG-(C)** and codes for the amino acid sequence triptophan, glutamic acid, threonine, and glycine. The **-(C)** indicates that a base was deleted and the adjacent base, "C", moved over to take its place. Comparison with their common ancestor from the fossil record indicates that this tiny DNA sequence undergoes one mutation every 35 million years, and this clock rate can be used to calculate how far back in time the species separated from their common ancestor. The corresponding DNA sequence of the common ancestor, then, is **TGGGAAAGAGGT**. Not all mutations make dramatic changes in the amino acid sequence; in the bottom mutation sequence, the "T" in the common ancestor mutated to a "C" 70 million years after the common ancestor, but both **GGT** and **GGC** code for glycine.

Adapted from a figure on the University of California, Berkeley Web site <http://evolution.berkeley.edu/evosite/evo101/IIIE1cMolecularclocks.shtml> (Retrieved March 2009)

Although the molecular clock is a promising method of analyzing evolution, it's in its infancy and suffers from several drawbacks at this time. The molecular clock is currently considered to depend only on time because many mutations in sperm and egg cells are random and can therefore be measured as an average number of mutations over a time period. On the other hand, the molecular clock more properly should be a function, at least partly, of generations rather than solely of time. Mutations enter the general population through generations of young, and short life spans lead to a rapid turnover of generations and a more rapid permanent establishment (called "fixing") of a mutation in the general population. Time, then, is a somewhat poor proxy for generations. If ancient species have short lifetimes (rapid generation turnover) and the mutation average is based on contemporary animals with long life spans, extrapolating average DNA change

rate back hundreds of millions of years could erroneously predict the first appearance of species much earlier in geologic time than their true first appearance. And the Molecular Clock sometimes estimate the earliest occurrence of animals to be further back in time than fossil evidence does. Moreover, using an average rate of change in DNA is questionable because it implies changes are steady, which is unproven. Mutations in DNA may, in fact, come in bunches between extended periods without changes. What's more, each gene in the DNA seems to mutate at its own rate, and each must be calibrated with fossils that have dates well established from the fossil record.

Another drawback with the Molecular Clock is its assumption that the first appearance of a gene in an animal's DNA automatically means that the gene is active (expressed). The expression of a gene is controlled by a system called the epigenome. Scientists only became aware of the epigenome's existence early in the third millennium, so the keepers of the Molecular Clock haven't yet been able to consider it. Just because a gene is present doesn't mean that the epigenome is also ready to use it. As of 2010, no one knows whether or not the epigenome evolves at the same time as the genome, or after.

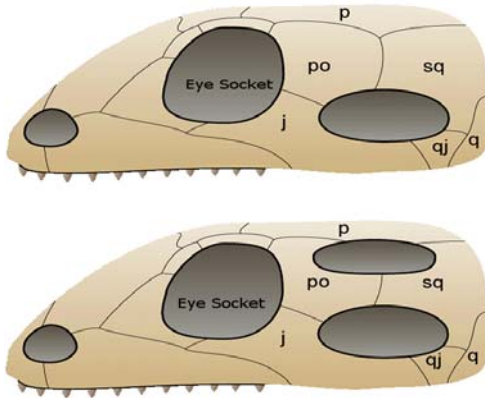
## **Mammals Come into Being**

By the end of the twenty-first century, the molecular clock might become the best method of determining the correct times when all our ancestors first appeared and where all animals lie on the branches of the evolutionary tree, but until the bugs are worked out, the fossil record will continue to be the standard. Although, as Richard Cifelli of the Oklahoma Museum of Natural History has pointed out, the fossil record is notoriously incomplete, it's hard evidence.

Fossils demonstrating the evolution of mammals have been difficult to tease out of ancient rock partly because the first mammals were usually creatures that were small enough (cat-sized or smaller) to escape the notice of the predators of the time, the dinosaurs. Between 1764 (when the first mammal fossil was found) and 1979, scientists discovered 116 types of ancient mammals. But between 1980 and 2007, around 200 more have been found, almost twice as many as in the first 215 years of hunting mammalian fossils. The opening of new fossil beds, such as the extremely rich ones in Mongolia, led to discovery of a wealth of new mammal fossils.

In the 1980s, paleontologists began to put their accumulated information into a data base and eventually developed software that could use information in the data base to make detailed comparisons of every tooth and bone in mammals' bodies. The expanding data base and diagnostic software has enabled paleontologists to trace the evolution of mammals more accurately than ever before. And bones, especially the jaw bone and the three small bones of the middle ear, have been extremely important in tracing mammalian evolution and identifying the various mammalian lineages.

Our ancestors split away from other amniotes (animals whose reproductive embryo is enclosed by a protective water-tight, fluid-filled sac called



### Synapsid and Diapsid Skulls

Synapsid skulls have one opening behind the eye socket; mammals descended from ancient synapsids. Diapsid skulls have two openings; reptiles like dinosaurs and crocodiles descended from ancient diapsids. Some skull bones are identified: **p** is the parietal bone, **po** the postorbital (behind the eye), **sq** is squamosal, **j** is jugal, **qj** is quadratojugal, and **q** is quadrate.

Adapted from Wikipedia

the amnion) in the Carboniferous Period when they developed a special opening (temporal fenestra) in the sides of their skull behind their eye sockets. This opening is characteristic of the class of animals called Synapsida (from which mammals evolved), made their skulls lighter, and created a better arrangement for attaching jaw muscles, giving them a superior bite. This evolutionary advantage over other reptiles permitted them to spread widely (paleontologists say "they radiated") during the late Carboniferous. Other reptiles (called Anapsida) at the time had solid skulls, which were, therefore, heavier than those of our ancestor Synapsida. The only surviving anapsids are the turtles. Just before the end of the Carboniferous, about 300 million years ago, another group of reptiles (called Diapsida) developed two holes on each side of their skull behind their eye sockets. This gave the diapsids as significant an advantage as the synapsids, so they were able to proliferate too, becoming dinosaurs, crocodilians, and lizards.

As of the beginning of the third millennium, *Archaeothyris florensis*, which lived in what is now North America during the late Carboniferous (around 310 to 404 million years ago), is the earliest known synapsid. Its teeth were all the same shape (sharp and pointed) but were of different sizes, thus exhibiting a small degree of mammalian type of differentiation. *A. florensis* was only 50 centimeters (19 inches) from the end of its nose to the tip of its tail. There probably were synapsids several millions of years before *A. florensis*, but their remains are likely lost for all time. We only get to see the occasional glimpse of the great epic of evolution, so no one knows whether or not *A. florensis* is our direct ancestor. It's probably a cousin, but *A. florensis* and its relatives mark the beginning of the synapsid line, which is the line from which we came.

*Dimetrodon*, shown on page 68, was another synapsid cousin. It first appeared in what is now North America and Europe just after the beginning of the Permian Period, around 290 million years ago, and some species thrived until around 260 million years ago, near the end of the Period. The word "*Dimetrodon*" means "two measures of teeth" from the (Anglicized) Greek "di" (meaning "two"), "metron" ("measure"), and "don" ("tooth") because it had two kinds of teeth: shearing teeth and canine teeth. *Dimetrodon*



was the top predator throughout the first half of the Permian. Its competitors were the diapsid reptiles, which were much smaller during that time, and carnivorous amphibians such as *Eryops megacephalus*, which were limited by their need to stay close to water. *Dimetrodon* with its splayed legs and lizard-like gait certainly looked much more like a reptile than a mammal, but it and its relatives began the differentiation of teeth that all mammals have. *Dimetrodon* or one of its cousins is an ancestor of all mammals.

Around midway through the Permian, the preeminence of *Dimetrodon* and its close relatives (together called pelycosaurs) began to wane as another group, the therapsids (sometimes called protomammals), began to grow in importance. Therapsids had split from other pelycosaurs many millions of years earlier. The several species of *Cynognathus* (which was about the size of a large dog) from South Africa were typical therapsids. Therapsids' jaws were more powerful, and their teeth were more differentiated (incisors, large canines, and cheek teeth) than those of pelycosaurs. The number of bones in therapsids' fingers and toes had the mammalian 2-3-3-3-3 formula (thumb to little finger or big toe to little toe), and their legs were oriented more vertically beneath their bodies than were the sprawling legs of pelycosaurs and reptiles although therapsids still walked basically like lizards. *Pristerognathus* also had the beginnings of the mammalian secondary palate (roof of the mouth) that enable mammals to chew and breathe at the same time. Earlier critters didn't have a secondary palate, so they couldn't chew and breathe at the same time and just swallowed mouthfuls whole. Chewing aids digestion. By the time of The Great Dying at the end of the Permian, the pelycosaurs had been gone for many millions of years, and therapsids were the apex predators and primary herbivores.



*Pristerognathus minor*

*Pristerognathus* was a dog-sized predator of the late Permian that had teeth, a partial secondary palate, and jaw bones that were intermediate between us and our reptilian ancestors. Large canine teeth like those of *Pristerognathus* evolved in many animals over time. The illustrations of prehistoric animals in these pages are artist's representations and are scientifically accurate only in the animal's size and bulk (i.e., hefty or gracile).

A few therapsids survived The Great Dying to carry their kind into the Triassic, and chief among the survivors was a group of therapsids called the cynodonts ("dog teeth"). What was probably one of their first members, *Charassognathus gracilis*, had appeared just before The Great Dying. What bad timing! Nevertheless, cynodonts like *Cynognathus* (230 to 225 million years ago), which left remains over most of the world, became the primary herbivores and predators for the first half of the Triassic. Some cynodont species were herbivores whereas others were predators. *Cynognathus* itself was a predator about the size of a wolf, and it probably walked like one. Its lower jaw was almost entirely one bone like ours is, and this tooth-bearing (dentary) bone held three kinds of teeth (incisors for cutting, canines for stabbing, and cheek teeth for shearing food into small pieces). The bones at the back of the jaw that formed its reptilian jaw joint were smaller than those of its predecessors, which was an important part of their transformation to mammalian middle ear bones. *Cynognathus* had a secondary palate, suggesting that it could breathe and chew simultaneously. Its lack of ribs in the area of its stomach implies that it had a diaphragm, which greatly improved breathing compared with animals without one. *Cynognathus* and other cynodonts were probably the first warm-blooded animals in our line, and they might have also been furry. One of *Cynognathus*'s relatives is a far distant ancestor of ours.

Although cynodonts like *Cynognathus* ruled the early Triassic time, they were overwhelmed by the dinosaurs, which were newly evolved, aggressive, and better adapted to the hot, dry climate of Triassic Pangaea. So cynodonts were driven by competition to become smaller than their ancestors (and probably nocturnal). They also began to look and act more like mammals than their predecessors, so paleontologists have given these new cynodonts their own name: Mammaliaformes. Most early mammaliaformes such as the inch long *Morganucodon* (late Triassic, around 205 million years ago) were small, furry, rodent-like creatures that had our highly specialized, cusped molars for grinding food. Small animals like *Morganucodon* and modern shrews have more surface area relative to their volume (high surface-to-volume ratio) than larger ones. (The area of a sphere, for example, increases by the square of its radius whereas the volume increases by the cube of its radius. So as the sphere gets larger, the volume increases faster than the area, and the area-to-volume ratio gets smaller.) This high surface area for heat loss relative to body volume for heat generation means that smaller animals lose body heat faster than larger ones, and they have to eat more to survive. Any development like good teeth that improves feeding strategy is highly prized by smaller critters.

*Morganucodon*, had two jaw joints (as did the earlier *Probainognathus jenseni*): the old reptilian joint plus a new mammalian one. The bones of the old reptilian jaw joint were beginning to be freed up to become our middle ear bones. As inferred from fossils of mammaliaform braincases, their brains were also undergoing a reorganization and expansion: the portions (bulbs) associated with hearing and smelling were enlarging. They probably lived in

burrows by day, coming out at night and using their relatively keen senses of hearing and smell to hunt insects and small reptiles.

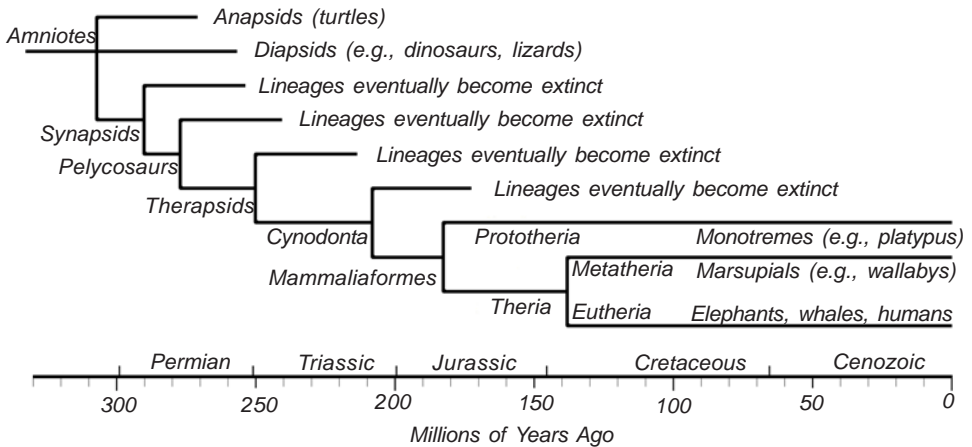
The kinds of mammaliaformes greatly expanded during the Jurassic. The new forms such as *Megazostrodon* (200 million years ago) and *Hadrocodium wui* (195 million years ago) were still small, shrew-like nocturnal insectivores, but they had a full mammalian jaw joint, called the temporomandibular joint, or the TMJ for short. (Some people suffer chronic inflammation of their temporomandibular joint. This condition is sometimes confusingly called TMJ, which actually refers to the joint itself and not its pathology, which should more properly be called TMJ syndrome or temporomandibular joint disorder, abbreviated as TMJD.) They had a much larger brain case for their size than other contemporary mammaliaformes, and much of this larger brain was devoted to scent and hearing. To complete its improved hearing ability, *Hadrocodium* also had a full mammalian middle ear of hammer, anvil, and stirrup. Although the bones would move around a little in the millions of years to follow, the transformation of the reptilian jaw bones to the mammalian middle ear was then essentially complete. It had taken over 100 million years.

This separate development of the mammalian hammer and anvil to join the ancient reptilian stirrup and the transformation of the reptiles' jaw bones into the hammer and anvil is mirrored in the development of a mammalian embryo. In an embryo, the stirrup comes from a collection of cells called the hyoid arch, but the hammer and anvil both come from a different collection of cells called the mandibular arch which also forms the lower jaw. As the embryo develops, bone forms in the mandibular arch region, and later in development, the hammer and anvil bones leave the jaw region and migrate to the middle ear area just as they did during that 100 million years in the distant past.

Some Jurassic mammaliaformes found niches that were relatively safe from dinosaur predation and were thus able to grow a little larger than *Megazostrodon* and its brethren. *Castorocauda lutrasimilis* mentioned on page 80 (China, 164 million years ago), called the "Jurassic beaver," is a prime example. *Castorocauda* lived in burrows on the banks of lakes or streams and ate fish. It was the largest mammaliaform of the Jurassic, weighing probably between 500 and 800 grams (1 to almost 2 pounds) and growing to 42.5 cm (17 inches) or more in length. One *Castorocauda* fossil was so well preserved that evidence of guard hairs and underfur is clear.

But the most prolific Jurassic mammaliaformes, the multituberculata, were small like *Megazostrodon* and *Hadrocodium wui*. Multituberculata, sometimes called the "rodents of the Mesozoic," first appeared 160 million years ago, during the middle Jurassic, in what are now the northern continents. They survived the mass extinction at the end of the Cretaceous, finally becoming extinct only 35 million years ago. They get their name from the many cusps, or tubercles, (hence "multituberculates") set in rows on their molar teeth. Like modern rodents, they had a single pair of lower incisors and no canines although the early, Jurassic forms had them. Little is known about early multituberculata because most Jurassic and Cretaceous forms





### Splits in Early Mammal Lineage

The split times of mammaliaformes into Prototheria and Theria and of Theria into Metatheria and Eutheria are averages of estimates from several sources published in *Science* and *Nature*. Earlier splits reflect the first occurrence of the particular fossil. The actual split was probably somewhat earlier than that shown.

are known only from their teeth, but a few like *Sinobaatar lingyuanensis* have left complete skeletons.

Sometime around the end of the Jurassic or early Cretaceous, a few mammals split from the ancient lineage by developing the ability to gestate their young internally (Theria) instead of laying eggs like *Megazostrodon* and *Hadrocodium wui* did. One of the earliest known Theria is *Sinodelphys szalayi*, which was found in the 125 million year old Yixian Formation in Liaoning Province, China. During the early Cretaceous, what is now the Liaoning Province was a basin formed by a geologic fault. The basin contained a shallow lake and was flanked by volcanoes, which were the key to the exquisite preservation of fossils. Eruptions of the volcanoes buried animals under fine volcanic ash in the same way Mount Vesuvius buried Pompeii and Herculaneum under 60 feet of ash and pumice in 79 CE. Yixian fossils couldn't decay before they were encased in their volcanic tombs, so even traces of *Sinodelphys's* hair was preserved. Several characteristics of *Sinodelphys's* teeth and bones suggest that it was a metatherian like modern marsupials, perhaps even a close ancestor. The structure of its ankles and feet indicates that it was adept at climbing trees like the modern opossum.

Not all Cretaceous mammals were small. *Repenomamus giganticus*, also from the Yixian Formation and the larger of the two species of the *Repenomamus* genus, was the size of a small dog, about 1 meter (39 inches) long and weighed around 12 to 14 kg (26 to 31 lb). A specimen of the smaller species, *Repenomamus robustus*, was discovered with the fragmentary skeleton of a juvenile dinosaur, *Psittacosaurus*, preserved in its stomach.

In 2008, David Brawand, Walter Wahli, and Henrik Kaessmann of the University of Lausanne, Lausanne, Switzerland, published results of their study of the influence DNA mutations had on mammals' transition from laying eggs like *Hadrocodium wui* to bearing live (albeit underdeveloped) young like *Sinodelphys szalaii*. They studied the genomes of a human, dog, armadillo, North American opossum, tammar wallaby, swamp wallaby, chicken, and Platypus to see how the genes that supply vitellogenin proteins to an egg yolk and the genes that make casein, the primary protein in milk, evolved over time. Their study illustrated the interplay between gene mutations and natural selection that drives the natural process we call evolution.

They found that some genes had developed favorable mutations and became capable of producing casein millions of years before *Hadrocodium* showed up in the fossil record, but whether the genes were expressed at that time is unknown. Some time after *Hadrocodium* appeared, maybe 20 million years or so, the three genes that supply vitellogenin proteins that are vital to an egg yolk began to accumulate mutations and become corrupted to the point that, one by one over the course of nearly 100 million years, they became inactive pseudogenes in all but the monotreme Platypus. Platypus retains one uncorrupted vitellogenin gene (*VIT*), and the fact that Platypus has only one uncorrupted vitellogenin gene explains why its eggs are yolk poor compared with a chicken, which has three active vitellogenin genes.

Our ancestors could tolerate mutations in and subsequent inactivation of their vitellogenin genes because they had developed casein genes and could supplement poor embryo development with milk protein after it was born. Cousins of our casein-producing ancestors who didn't develop casein genes probably also developed deleterious mutations in their vitellogenin genes, but their line became extinct because they hadn't evolved an alternate way of augmenting deficient egg yolk proteins. Evolution is the result of mutations in genes, either the substitution, insertion, or deletion of a new base pair. As it turns out, substitutions might not alter the sequence of amino acids that make up the protein that the gene codes for. But insertions and deletions shift everything, so the amino acid sequence is often changed, making a different protein. If the change does no harm, the animal lives to pass the mutation on to its young; if the change gives the animal a small advantage in the daily struggle to eat and avoid being eaten, its offspring proliferate.

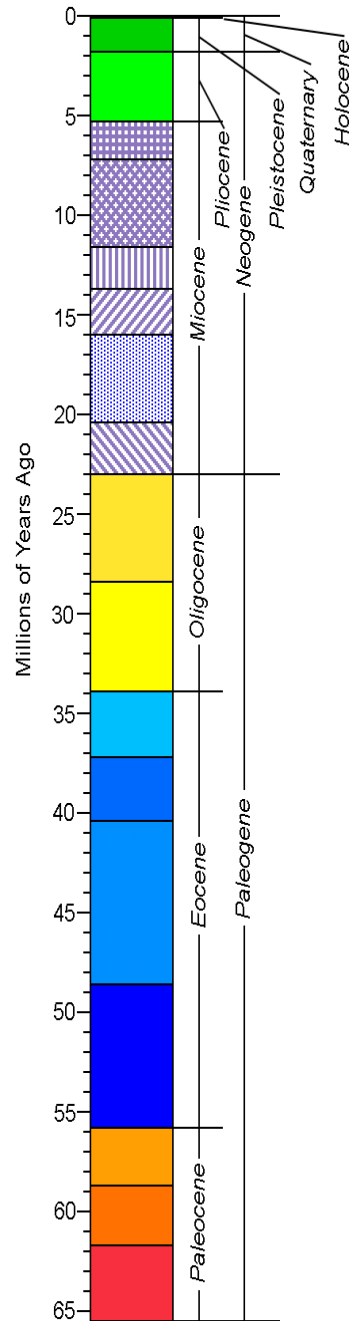
By the time the great Chicxulub meteor hit the Earth, theria had split from their egg-laying cousins (prototheria) and had, in turn, split into what would become modern Metatheria (marsupials) and Eutheria (bearing fully-developed young). The egg-laying prototheria would evolve into modern monotremes. "Monotreme" means "one opening" in Greek, and monotremes like the modern Platypus and echidnas use the same orifice for urination, defecation, and reproduction. Marsupials use one opening for both urination and defecation but have a separate orifice for reproduction. Eutheria have

separate openings for each function. All things considered, monotremes could be considered an “elementary” mammal, marsupials “more advanced,” and Eutheria the “most advanced.” There are very few late Cretaceous monotreme fossils found, but late Cretaceous Metatheria like *Didelphodon* and Eutheria like *Maelestes gobiensis* left a rich legacy for the Cenozoic Period.

Traditionally, the first part of the Cenozoic Era has been called the Tertiary. That’s why the Chicxulub meteor impact event is called the Cretaceous-Tertiary (K-T) boundary. The Tertiary was, in turn, divided into the Paleogene (composed of the Paleocene, Eocene, and Oligocene) and Neogene (composed of the Miocene and Pliocene). The second part of the Cenozoic was called the Quaternary, which covered only the last 1.8 million years and was composed of the Pleistocene and Holocene (our current epoch). Those designations are a holdover from the eighteenth and nineteenth centuries when organizing geologic time began.

In the late twentieth century, geologists began, with only limited success, to reorganize the Cenozoic by eliminating the terms “Tertiary” and “Quaternary”, dividing it instead into the Paleogene (encompassing the Paleocene, Eocene, and Oligocene as before) and the Neogene (composed of the Miocene, Pliocene, Pleistocene, and Holocene). Some researchers have adopted this organization by calling the Chicxulub meteor impact event the Cretaceous-Paleogene (K-Pg) extinction instead of the Cretaceous-Tertiary (K-T) event.

The International Union for Quaternary Research has balked at eliminating the Quaternary, citing the unique climate issues of the last 2 million years, and the disagreement remains unresolved. This chapter will divide the Cenozoic into the Paleogene (encompassing the Paleocene, Eocene, and Oligocene as before) and the Neogene (Miocene, Pliocene, Pleistocene, and Holocene), which will doubtless annoy everyone.



**Cenozoic Timeline**

A timeline to scale of the Cenozoic Era.

## Paleogene

The K-Pg event killed a vast amount of photosynthesizing life, which is the source of all biomass, on land and in the sea. So the plant-based food chain collapsed as herbivores died out when their food source disappeared, and carnivores died when their prey did. The K-Pg event wiped out all dinosaurs (technically, just the non-avian dinosaurs) on the land, the last remaining Cretaceous pterosaur family in the air, and mosasaurs and plesiosaurs in the sea.

The Chicxulub survivors formed a food chain based on carrion or on the detritus of photosynthesizing life that died from the K-Pg impact. After the event, worms and insects fed on the vast quantities of decaying plant debris and animal carcasses, and mammals and birds fed on the worms and insects. The small size of most mammals during the Cretaceous thus became a big advantage for surviving the K-Pg event. Crocodilians and croc-like champsosaurs fed on the dead dinosaurs, and the crocs' slow, cold-blooded metabolisms also allowed them to go long periods of time without eating. So it was crocodilians, birds, monotremes, marsupials, multituberculates, and Eutheria that greeted the devastated new world of the Paleogene.

The Paleogene Period has a lot in common with the Triassic Period. They both cover almost the same length of time (Triassic's 52 million years compared with 42.5 million years for the Paleogene), and they both are periods of recovery and faunal changeover following a major mass extinction. As best we understand the Triassic, it was fairly uniformly warm, but the Paleogene began about as warm as the Cretaceous, then warmed up even more, finally cooling down toward the end. The breakup of Pangea was complete, and the separate land masses moved toward their present positions, sailing on the magma seas of Earth's mantle.

## Paleocene (65.5 to 55.8 million years ago)

The Paleocene, which means "ancient recent life", is the geologic epoch of the Paleogene Period that immediately followed the K-Pg mass extinction event. North America was particularly devastated by the Chicxulub meteor because of its proximity to the impact site. The reestablishment of the vital plant-based food chain began with the widespread appearance of ferns (a "fern spike"), which are the customary first plants to colonize a devastated land. For example, ferns were the first plants to return to Krakatoa and Mt. St. Helens after they erupted. Flowering plants (angiosperms) soon followed, and the uniformly warm world-wide climate allowed conifers and deciduous trees to ultimately grow all the way to the poles. Cacti and palms appeared, and tropical palm forests grew as far north as northern Wyoming.

In geologic terms, Cenozoic fossils are recently deposited, so they're more accessible than those of any previous time. A good place for Paleocene fossils of sea life is Nye Klov in Denmark. Good places for fossils of land dwellers are Montana, North Dakota, South Dakota, Wyoming, and New Mexico in the western United States although, after the end of Mao Zedong's

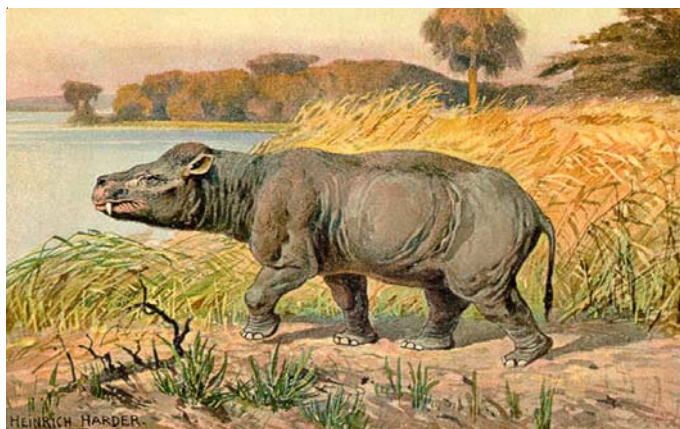
Cultural Revolution, Chinese scientists became free to open Paleocene fossil beds in China that have been very productive.

The Hell Creek formation in Montana and parts of North Dakota, South Dakota, and Wyoming is a particularly well-studied area for K-Pg animal fossils, and the iridium-rich K-Pg boundary separating the Cretaceous from the Cenozoic is a distinct, thin sedimentary layer near the top of the formation. Dinosaur bones are found below the iridium-rich K-Pg boundary but not above. Ten kinds of marsupials, eleven kinds of multituberculates, and six kinds of eutherians have been found in the Cretaceous rocks below the boundary. One kind of marsupial, a handful of multituberculates, and thirteen eutherians (but no dinosaurs) have been found in the Paleocene rocks above the boundary. The mammalian takeover, especially by eutherians (giving birth to fully developed young), had begun.

Cretaceous multituberculates were rather small, around the size of a squirrel or smaller, but the Cenozoic critters grew larger. *Taeniolabis taoensis*, found in New Mexico, Wyoming, and Saskatchewan, was the largest known multi-tuberculate, weighing as much as 30 kg (66 pounds), about the size of a large beaver. *Taeniolabis lamberti* from Montana, though hefty, was not quite as large as *T. taoensis*. China and Mongolia also boast several stout Paleocene multituberculates such as *Lambdopsalis bulla*, *Prionessus lucifer*, *Sphenopsalis nobilis*, and seven species of *Catopsalis*.

Pantodonts are a group of Paleocene Eutheria from North America, Asia, and South America. Like all the K-Pg survivors, they followed the same path of development that many animal groups had trod in the previous hundreds of millions of years, especially after a major mass extinction: Early members were small, and later members grew progressively larger. The most primitive Pantodonts were about the size of a large house cat (less than 10 kilograms, or 22 lbs) and probably survived by eating anything they could (omnivores). By the middle of the Paleocene, The plant-based food chain was reestablished well enough that the group could specialize as strictly herbivores, and members such as the three species of *Pantolambda* (Montana, Wyoming, and New Mexico) were the size of sheep. Later members such as the three species of *Barylambda* were the size of ponies. The last members, six species of *Coryphodon*, were around 1 meter (3.3 feet) at the shoulder and 2.25 meters (7.4 feet) long, and were the world's first large browsing mammal at the time. *Coryphodon* survived into the Eocene, at which time the whole Pantodont group died out.

The largest group of Paleocene mammals were the Condylarthra, which is actually a catchall group with few common traits among its members. Paleontologists call Condylarthra a "wastebasket" taxon, but the term "wastebasket" implies they're throwing them away, which is not true although they are in the process of discarding the name "Condylarthra". *Protungulatum* ("first ungulate") was a K-Pg survivor from Montana and the first known member of the condylarth group. Its teeth suggest that it or a close relative was the first common ancestor of all hoofed mammals (ungulates) such as the odd-toed ungulate horses and even-toed ungulate cattle. Many



### *Coryphodon*

This painting (circa 1920) of the pantodont *Coryphodon* was one of several paintings that German landscape artist Heinrich Harder did for collector cards of various prehistoric animals. With a brain weighing just 90 grams (3.2 oz) and a body weight of around 500 kilograms (1,100 lb), it had the dubious honor of having the smallest brain/body weight ratio of any mammal, extant or extinct.

condylarths like the sheep-sized herbivore *Ectoconus* had toes that ended in hooves rather than claws, and some such as *Phenacodus* walked on their toes like the modern tapir. Other condylarths like the omnivores *Arctocyon* (about the size of a Shetland Sheepdog but without the Sheltie's heavy coat) and *Chriacus*, which was about 1 meter (3.3 ft) long and weighed around 7 kilograms (15 lb), had claws and walked on the soles of their feet. These types of creatures formed the basis for further radiation of hoofed mammals in the Eocene Epoch.

Except for the first members of the group, which were omnivorous by necessity, most condylarths were herbivores, and the animal groups that preyed on them were the creodonts, miacids, and mesonychids. Early in the Cenozoic, creodonts like the late Paleocene *Oxyaena* were the top predators of North America, Eurasia, and Africa, but a different group (the carnivores) gradually replaced them as the Cenozoic wore on. The last creodont genus, *Dissopsalis*, died out in Pakistan about eight million years ago. *Oxyaena* lived in what is now the Rocky Mountain region of North America although, in *Oxyaena*'s time, the mountain range had yet to rise up. It was a rather cat-like animal about 1 meter (3.3 feet) long.

Both creodonts and miacids probably derived from the same Cretaceous ancestor: *Cimolestes* or its close kin. Both creodonts and miacids had 44 teeth including carnassial cheek teeth that modern carnivores use to shear meat. When a dog chews on a bone, it turns its head to the side and uses its strong carnassial cheek teeth to crush the bone or shear meat from it. Miacids such as *Miacis* were primitive carnivores that lived in North America and Eurasia during the Paleocene and Eocene Epochs. They were about the size of a weasel, had retractable claws, and had brains that were relatively



larger for their body size than those of the creodonts, which suggests they were probably more intelligent than creodonts. Miacids were probably forest dwellers adept at climbing trees and preying on small mammals, reptiles, and birds, and they might have included eggs and fruits in their diet. Miacids probably evolved into modern carnivores.

Competing with creodonts and miacids were the mesonychids from Asia, where the most primitive mesonychid (the early Paleocene, weasel-like *Yangtanglestes*) was found. Like the herbivorous condylarths *Ectoconus* and *Phenacodus*, mesonychids had toes that ended in hooves (They're sometimes called "wolves on hooves".) rather than claws, which is unusual for a meat eater. By the Late Paleocene, mesonychid species like the coyote-sized *Dissacus* had spread to North America and Europe. In general, mesonychids were larger than most creodonts and miacids; the largest mesonychid, New Mexico's *Ankalagon*, grew to be as large as a bear. However, mesonychids lacked true carnassial teeth, which was a disadvantage in their competition with the other predatory mammals, creodonts and miacids.

Mammals weren't the only predators, however. There were several kinds of crocodiles, though their need to stay close to water limited their influence somewhat. Large flightless birds such as the three Paleocene species of *Gastornis*, called "terror cranes", were perhaps the most feared predators. *Gastornis* grew up to 2 meters (6.6 feet) tall and had a huge beak and powerful legs with taloned feet. Some paleontologists argue that *Gastornis*'s North American cousin, called *Diatryma*, had more characteristics of a herbivore than of a predator, and others argue that *Gastornis* and *Diatryma* are the same beast. As of 2010, the jury is still out on this one.

More than 30 primate genera comprising at least 80 species have been recovered from Paleocene rocks, and at least one of our ancestors is probably among their number. But paleontologists disagree about how all these archaic primates relate to one another and to us humans, how they subsisted, and whether some of them are really primates at all. Of course, there are always disagreements when data are scarce, and most of these Paleocene forms are known only by their teeth. (Paleontologists recognize primate teeth by their low, rounded cusps on premolars and molars, as contrasted with the ridges or high, pointed cusps of other Eutherians.) Few complete skulls such as those of *Dryomomys szalaii* and *Plesiadapis tricuspidens* are found, and fewer still are even partial skeletons found with skulls such as *Carpolestes simpsoni*. Conditions that enable survival of fossils as complete as Eocene's *Darwinius* from the Germany's Messel Pit are extremely rare.

*Purgatorius*, first found on Purgatory Hill in Montana's Hell Creek Formation and described by Van Valen and Sloan in a 1965 issue of *Science*, is generally accepted as the first recognizable primate, although *Pandemonium* has been found in Montana rocks of about the same age. Numerous teeth from *Purgatorius* have been found in formations that are between 64.75 and 64.11 million years old. It was a very small critter, perhaps 15 centimeters (6 inches) long and weighing around 159 grams (5.61 oz). Such

a small size was typical of Paleocene primates. For example, the lower jaw of *Ignacius clarkforkensis* would fit on your thumb nail, but its molars when magnified clearly reveal their low, rounded primate cusps. Ninety-five percent of the primates that first appeared before 60 million years ago were from North America.

During the Paleocene, primates acquired some of their unique characteristics such as grasping "hands" and "feet" (*Carpolestes* and *Dryomomys*, for example) with nails instead of claws (*Carpolestes* had a nail on its "big toe"). Claws are advantageous for climbing large diameter objects; however, when compared with claws, nails improve the ability to manipulate objects and to grasp small diameter tree stems where grew the fruit on which many early primates fed as part of their diet and where predators, being heavier than the diminutive primates, dared not come. After all, the prime directive of evolution is to eat and not be eaten.

The evolution of our forward facing eyes was slow, probably because their advantage for survival, though definite, was subtle; they were simply an improvement in an array of abilities that were already working pretty well. Paleontologists have a lively debate about the characteristics of forward facing eyes that make them a desirable trait. The advantage of depth perception for finding food and for leaping is the most often cited, but a new idea that two forward facing eyes allow a clearer view of objects through intervening foliage (called "X-ray vision", which is a bit of an exaggeration) has also been proposed. All Paleocene primates, such as *Carpolestes* and *Plesiadapis*, probably had eyes that faced more or less to the side. *Carpolestes* had neither binocular vision nor skeletal adaptations for leaping from tree to tree, so it was probably simply a climber.

As has been true of other animals that have existed over the past 600 million years, some Paleocene primate genera were more successful than others. Some, such as France's *Berruvius* and *Sarnacius*, Utah's *Draconodus*, and Wyoming's *Pandemonium*, had only one species and lived for only a couple million years in a relatively small area. *Plesiadapis*, on the other hand, first appeared in the western United States perhaps 63 million years ago. Then *Plesiadapis walbeckensis* appeared in Germany, possibly as early as 61 million years ago. More than a dozen more species appeared in western North America and Europe before the end of the Paleocene. Finally, *Plesiadapis russelli* was the last representative of the successful genus, living in what is now France during the early Eocene, around 50 million years ago.

Of course, animal life was far, far more abundant in the Paleocene ecosystem than described here. Primitive members of most modern major animal groups roamed the great forests of the several continents, although much less is known about Africa, South America, and Australia than about North America and Eurasia. What we know about South American and Australian fauna indicates that marsupials made up more than half of all their mammal species. Many, like South American *Pucadelphys*, were omnivores because being able to eat anything is a big advantage, or were insectivores like tiny South American *Minusculodelphis* because there will always be

insects. South American marsupial omnivores and insectivores also had their share of marsupial predators such as *Mayulestes*.

The abundance of Paleocene animals might be better understood by noting that there were 62 known species of birds alone, including three species of owls: *Ogygoptynx wetmorei* from North America and two species of *Berruornis* from Europe. There were two species of *Presbyornis*, a duck-like or goose-like waterbird from North America, and two species of *Waimanu*, a penguin-like bird from New Zealand. By the end of the Paleocene, the world's ecosystem was again rich and complex.

The transition from the Paleocene to the Eocene was marked by the most significant climate change of the Cenozoic Era, a rapid rise in global temperatures called the Paleocene-Eocene Thermal Maximum (PETM). As reported in a 2005 issue of *Science*, the sea surface temperature rose 5° C (9° F) in the tropics and 9° C (16° F) at high latitudes in a space of only 1000 years, and they slowly rose for another 30,000 years before they reached their maximum. The current best explanation of this sudden temperature rise is that the gradual warming of the late Paleocene reached the point where methane hydrate stored in ocean and deep freshwater sediments began to release its methane. Methane hydrate is a form of water ice in which large amounts of methane are trapped within the ice's crystal structure. The methane comes from both the reduction of CO<sub>2</sub> by ocean floor microbes and the decomposition of organic matter. Methane is a greenhouse gas that's 10 times more effective than carbon dioxide at causing climate warming although it has a short atmospheric half life of 7 years. Large amounts of methane are currently stored as hydrates in the ocean's continental shelves and in deep freshwater lakes, and recent estimates suggest the global inventory is between 500 and 2500 gigatonnes carbon. By comparison, the current total carbon as carbon dioxide in the atmosphere is around 700 gigatons carbon. The release of methane from methane hydrates is, perhaps, the greatest threat of global warming.

## **Eocene (55.8 to 33.9 million years ago)**

Climate, which is the average of weather over long periods of time, was rather uniform the world over during the Eocene with little seasonal change in the weather although average global temperature slowly declined as the Period wore on. The temperature difference between equatorial regions and the poles was about half of what it is today. Temperate forests extended to the poles, and areas as far north as Red Lodge, Montana, experienced rainy tropical climates.

The long mid-Atlantic rift that had sundered part of Pangea continued to push North and South America away from Europe and Africa; however, Greenland hadn't moved very far at that time, leaving an occasional land bridge between Europe and North America. As North America moved west during the late Cretaceous and the Paleocene, the Western Interior Seaway that ran inside North America's west coast was gradually closed, uniting the eastern part of the continent with scattered islands that now form the

exotic terranes of the western part. In the process, the Rocky Mountains were uplifted along the western edge of the Seaway in what is called the Laramide orogeny, which ended during the Eocene. This was the third uplift for the Rockies, the first occurring during the creation of Rodinia and the second during the formation of Pangaea. The subduction zone created by North America's continued thrusting against and riding up over the Juan de Fuca plate (east of the north part of the Pacific plate) formed the Cascade Volcanic Arc, which first appeared during the Eocene 36 million years ago. The 22 volcanoes of the Cascade Volcanic Arc were vigorously active until a few thousand years ago, but now peaks such as Mount St. Helens, Mount Rainier, Mount Mazama (Crater Lake), Mount Shasta, and Mount Hood (informally considered dormant) are only infrequently active. South America had been pushing up over the Nazca plate and uplifting the Andes Mountains since the Jurassic Period.

The mid-Atlantic rift continued around the southern tip of Africa and was pushing Africa north into Europe and the Middle East, which were a hodgepodge of various sized islands. The movement of Africa into Europe began to lift the Alps aided by the usual subduction zone volcanism, which is still evident today as Stromboli, Vesuvius, and Etna. India, which had separated from Gondwanaland 100 million years earlier, was beginning to push into Asia and lift up the Himalayas. Australia had separated from Antarctica and was beginning to move northeast toward its present position. The world was taking its present form.

The high temperatures and warm oceans of the early Eocene, the warmest time of the entire Cenozoic Era, encouraged forests to spread from pole to pole. Fossils and actual preserved (not fossilized) pieces of Eocene trees such as swamp cypress and dawn redwood have been found on Ellesmere Island in the Arctic, and fossils of Eocene subtropical and tropical trees such as palms have been found in Greenland, northern Europe, and Alaska. Antarctica began the Eocene with a warm temperate to sub-tropical rainforest of southern beech along its shores.

Around the middle of the Epoch, the Earth began to cool, which introduced seasonal changes to the weather, and deciduous trees began to replace tropical species. By the end of the period, deciduous forests covered large parts of Antarctica and the northern continents. Rain forests continued to hold sway only in equatorial regions of South America, Africa, India, and Australia. Some of interior Antarctica was covered with tundra. Grasses had newly evolved but were still confined to river banks and lake shores and had not yet expanded into plains and savannas. Until the beginning of the third millennium, grasses were thought to have evolved around 55 million years ago, based on fossil records. However, recent findings of 65-million-year-old phytoliths (rigid microscopic forms that occur in many plants) resembling those in grass (including ancestors of rice and bamboo) in Cretaceous dinosaur coprolites (fossilized dung), may place the appearance of grasses to an earlier date. As of 2010, the book is not closed on that.

Mammalian diversity previewed during the Paleocene began to dress for

their parts during the Eocene as direct evolutionary ancestors of a dozen major modern eutherian animal groups joined the marsupials and monotremes on the world's great stage. The new players were primitive Pholidota (pangolins), Erinaceomorpha (hedgehogs and their relatives), Chiroptera (bats), Lagomorpha (rabbits and their relatives), Rodentia (rodents), Hyracoidea (hyraxes), Sirenia (manatees and dugongs), Proboscidea (elephants and tapirs), Perissodactyla (odd-toed ungulates such as horses), Artiodactyla (even-toed ungulates such as cattle), Cetacea (whales and dolphins), and Carnivora (cats and dogs).

The first pangolin, or scaly anteater, *Eomanis*, was unearthed from the middle Eocene (about 40 million years ago) of Europe. *Eomanis* was 50 centimeters (20 inches) long, and its preserved stomach contents tell us it ate plants as well as insects. Unlike modern pangolins, *Eomanis* didn't have scales on its legs or tail. *Metacheiromys*, a middle Eocene mammal from Wyoming, didn't seem to have scales either, but it's still generally considered to be a primitive pangolin. Modern pangolins live in tropical areas of Asia and Africa and are between 30 and 100 centimeters (12 to 39 inches) long excluding their tail. Their scales are made of keratin, the same substance fingernails are made of. When threatened, they can roll into a ball like an armadillo and emit a noxious stench like a skunk's from the entire surface of their skin.

Primitive hedgehogs have been found in North America (*Macrocranion junnei*, *M. nitens*, and *M. robinson*) and Europe (*M. tupaiodon*, *M. tenerum*, *M. vandeboeki*, and *Pholidocercus hassiacus*). Like modern hedgehogs, *P. hassiacus* was covered with thin spines, but unlike modern hedgehogs it had scales on its head and a long scaly tail. *P. hassiacus* and *Macrocranion tupaiodon* were found in the Messel Pit in Germany, and the excellent preservation of fossil's stomach contents in the pit tells us that they ate insects, fruits, and leaves.

The Messel Pit is a quarry near the village of Messel, southeast of Frankfurt am Main, Germany, where oil shale has been strip-mined. During the Eocene, the area was somewhat volcanic because of Africa's push into the collection of islands that was Europe at the time, and the pit was probably a volcanic lake similar to Lake Nyos in Cameroon. Its water column was highly stratified, and the bottom became devoid of oxygen. This prevented bacteria that decompose the dead from accumulating, thus preserving whatever fell into the lake and was buried in its silty bottom. Undecomposed microorganisms that accumulated in the sediment were converted by the pressure of overlying layers of sediment into oil, and the sediment itself formed shale. The larger than expected number of land animals such as *P. hassiacus* and *Eomanis* found in the shale likely was the result of mass die-offs from occasional releases of carbon dioxide and hydrogen sulfide from the lake. A similar gas release from Lake Nyos in 1986 suffocated 1,700 people and 3,500 livestock in nearby villages.

The oldest known echolocating bat, *Icaronycteris index*, was found in the 52 million year old Green River Formation in Wyoming. The creature was about 14 centimeters (5.5 inches) long and had a 37 centimeter (15 inch)

wingspan. It closely resembled modern bats, but its tail was longer and not connected to the hind legs with a skin membrane like modern bats. Its anatomy suggests that it slept while hanging upside down. *Onychonycteris finneyi*, another bat, was found in the same geologic formation as *Icaronycteris*, so was probably contemporaneous. But *Onychonycteris*, like modern fruit bats, was not able to echolocate. Specimens of *Icaronycteris* and *Onychonycteris* are a bit more complete than their Australian contemporary *Australonycteris clarkae*. Like *Icaronycteris*, *Australonycteris* could echolocate, suggesting that it too fed on insects. *Palaeochiropteryx tupaiodon* is another specimen from the Messel Pit. This bat lived around 44 million years ago and had relatively broad, short wings, indicative of adaptation for slow, highly maneuverable flight rather typical of many modern bats. Weighing a little under a half pound, *Witwatia* (two species) from the Fayum in Egypt is one of the largest fossil bats ever discovered. It lived around 35 million years ago.

*Gomphos elkema*, the oldest member of the rabbit family ever to be found, was uncovered in Mongolia. Although, like modern rabbits, *Gomphos* had a foot more than twice as long as its hand, it had a rather long tail, and some of its teeth were more squirrel-like than rabbit-like. *Gomphos* lived around 50 million years ago.

During the Eocene, rodents began that great proliferation that would make them one of the ubiquitous members of the modern biosphere. *Birbalomys* (four species) from Asia is one of the earliest rodents found, and some paleontologists consider it to be the most primitive true rodent, related to the ancestors of all members of the order Rodentia. *Ischyromys* is an extinct genus of rodent from North America. The 60 cm (2 ft) long creature is another of the oldest rodents known. It resembled a mouse and already had characteristic rodent incisors. *Ischyromys*'s hind legs were longer than the forelegs and might have had other uses than simply walking. Unlike most other mammals of its time, *Ischyromys* was probably arboreal (along with its relative *Paramys*). It was a well-adapted climber that gradually beat out competition from rodent-like arboreal plesiadapiform primates.

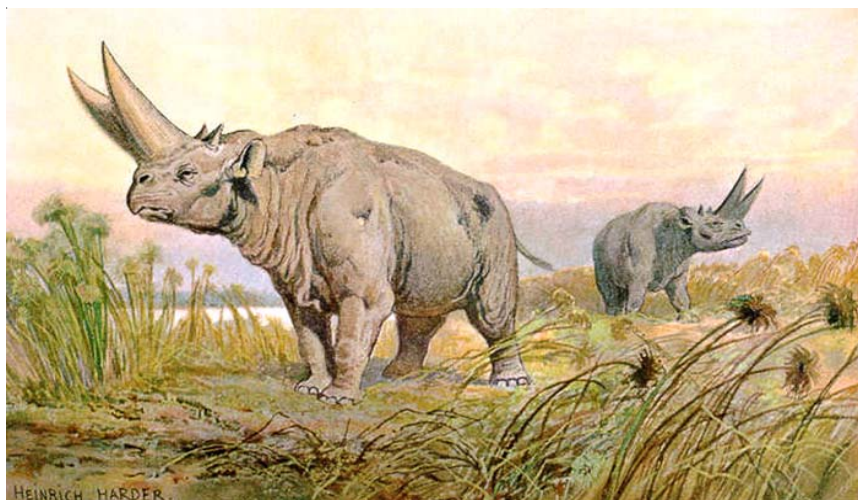
Eocene hyraxes, like their modern descendants, were primarily African herbivores. Modern hyraxes are furry critters, 30 to 70 centimeters (12 to 27 inches) long and weighing between 2 and 5 kilograms (4.4 to 11 pounds), about the size and appearance of a woodchuck. They have padded feet with small hooves on their toes like elephants do. Their Eocene ancestors were generally larger and were Africa's primary herbivores at the time. The first known true hyrax is probably *Seggeurius amourensis* from early Eocene deposits in Algeria, which are possibly as much as 50 million year old. Around 44 million years ago, *Microhyrax* and a couple of species of *Megalohyrax* joined *Seggeurius* in Algeria. Around 38 million years ago, *Thyrohyrax* showed up in Egypt. By the end of the Eocene, several species of *Saghatherium*, *Bunohyrax*, and *Titanohyrax*, which was the size of a small rhinoceros, had joined *Thyrohyrax*.

*Prorastomus sirenoides* is earliest primitive manatee (which live in both fresh and salt water) discovered so far, but only the skull and a few verte-



bra have been found. It was discovered in Jamaica and lived in the early Eocene sometime between 55.8 and 40.4 million years ago. *Pezosiren portelli* is another Jamaican manatee fossil, but unlike *Prorastomus*, enough remains have been found to make a complete skeleton. *Pezosiren* was a form that was somewhere in the manatee's transition from land to water because it had the same skull and basic skeletal features of modern manatees but also had four limbs capable of walking on land. It lived around 48.6 to 40.4 million years ago. *Protosiren* (five species) is the manatee-like dugong genus from which all dugongs (which live exclusively in salt water) are thought to have descended. Fossils have been found in the United States, Egypt, France, Hungary, India, and Pakistan. *Protosiren* was likely another transition genus because it had small hind limbs. Although its hind limbs were well-developed, its weak sacroiliac joints were probably unable to support the animal on land for very long, suggesting that it was primarily aquatic. *Eotheroides* (four species) from France and *Sirenavus hungaricus* from Hungary were primitive dugongs that lived in the neighborhood of 45 million years ago. *Eosiren* (four species) was an early dugong that mostly lived in what is now the Fayum in Egypt. *Halitherium* (six species) was one of the most successful dugongs to appear in the Eocene. It lived in the warm waters of the island group that was Eocene Europe from around 40 million years ago until 12 million years ago. *Prototherium intermedium* was a dugong species that lived in the area that's now Spain and Italy from around 37 to 34 million years ago.

Recent DNA studies have verified that hyraxes and Sirenia (manatees and dugongs) are related to elephants, and they all belong to a group called Paenungulata ("almost ungulates"). The oldest and smallest known proboscidean is Morocco's *Phosphatherium escuillei*, which lived during the late paleocene-early Eocene time period. It was about 60 centimeters (2 feet) long and weighed around 15 kilograms (33 pounds). *Daouitherium rebouli*, a 300 kilogram (660 pound) tapir-like animal from around 55 million years ago, was also from Morocco and, like *Phosphatherium*, probably fed on aquatic plants. Another tapir-like Eocene proboscidean that fed on water plants was *Moeritherium*, which came as four species. The earliest *Moeritherium* was found in Senegal in deposits dated at least 40 million years ago. By 37 million years ago or so, it had also moved into Algeria, and it could also be found in Libya and Egypt by the end of the Eocene. It stood about 70 centimeters (2.3 feet) at the shoulder, was around 3 meters (9.8 feet) long, and probably lived like the modern hippopotamus. Generally, African specimens are more complete than the Asian specimens such as *Hsanootherium parvum* from Myanmar, *Jozaria palustris* from Pakistan, and *Lammidhania wardi* from Punjab. Neither *Phosphatherium*, *Daouitherium*, nor *Moeritherium* had long trunks or tusks although *Moeritherium*'s incisors were like hippopotamus teeth and could have been considered small tusks. Perhaps the oldest proboscideans with a trunk and tusks—though both were rather short—were the two known species of *Phiomia*, which lived in Libya around 35 million years ago. It had two, short tusks in the upper jaw and two,



### *Arsinoitherium zitteli*

*Arsinoitherium* (three species) is another Eocene paenungulate mammal (related to elephants and hyraxes) that lived in tropical rainforests and at the edge of swamps around 39 to 34 million years ago. These herbivores stood about 1.8 meters (5.9 ft) tall at the shoulders and were 3 meters (9.8 ft) long. *Arsinoitherium* had a pair of very large horns with solid bone cores that projected from above the nose and a second pair of tiny, knob-like horns on top of the head immediately behind the larger horns.

short, shovel-like tusks in the lower jaw, which it probably used to scoop water plants into its mouth.

Our Paleocene friend with the tiny brain, *Coryphodon*, continued on into the Eocene for several million years, its range extending all over the central United States as well as parts of England and China before it passed into history. A big brain is apparently not necessary to survive for several million years. Its descendent, *Hypercoryphodon*, carried on in China until the end of the Eocene, and the death of the last *Hypercoryphodon* marked the end of the pantodonts, the great herbivores of the Paleocene.

*Uintatherium* lived near Fort Bridger, Wyoming, during the early to middle portions of the Eocene period (45 to 40 million years ago). It was an herbivore, eating leaves, grasses, and shrubs. It lived near water and used its sabre-like canines to pluck the aquatic and marsh plants which comprised its diet.

Paleontology has always been a little disorganized because, unlike physics, it has no indisputable objective measures. Physics is like Olympic track and field, which are measured by objective quantities time or distance, but paleontology is like gymnastics, which are measured by subjective opinion of how the performer fits a set of agreed-upon principles. Nowhere is paleontology more disorganized than with the group of animals called Perissodactyla. Perissodactyla (hoofed mammals with an odd number of toes, such as horses) are herbivorous mammals with either one or three toes on each foot.

For those who like to know how things fit together, nearly all experts agree that living Perissodactyla are organized into three families like the University of Michigan does: Tapiridae (tapirs), Rhinocerotidae (rhinoceroses), and Equidae (horses, asses, and zebras). But paleontologists tend to disagree more on the organization when extinct animals are included. Some divide Perissodactyla into Hippomorpha (horse-like animals and their extinct relatives), Ceratomorpha (rhinoceroses, tapirs, and their extinct relatives), and Ancylopoda (some odd, now-extinct animals). Others divide Perissodactyla into just Hippomorpha and Ceratomorpha, placing the extinct Ancylopoda animals in those two divisions. On the other hand, The Paleobiology Database hosted by the University of California, Santa Barbara, says that the term Hippomorpha is "disused." Although there are numerous published descriptions of how Eocene odd-toed hoofed mammals relate to one another, none are the last word. They all have the same cast of characters, but the plots that tie the cast together are all a little different.

All plots share the same theme, though: The Eocene was the heyday of the Perissodactyla. They would never again be as numerous and diverse as they were during the Eocene, which had over 320 species distributed among more than 100 genera. Modern Perissodactyla comprise around 17 species distributed among six genera and three families. An enduring theme of evolution is the rise, glory, and fall of life, rather like the Hindu trinity of gods: Brahma (the creator), Vishnu (the preserver), and Shiva (the destroyer).

Like all animal types that had evolved during the previous hundreds of millions of years, Perissodactyla began small, then grew larger. A typical example is the *Heptodon* to *Colodon* lineage of critters that sort of resembled a modern tapir although the group probably lacked the short tapir trunk. The four or so species (depending on which expert you believe) of *Heptodon* from early Eocene western North America weighed around 15.5 kilograms (34 pounds). Late Eocene *Colodon*, on the other hand, is estimated to have weighed as much as 44.7 kilograms (98 pounds). *Heptodon* had several cousins, each with two or more species: *Helaletes* from early Eocene western North America, *Desmatotherium* from middle Eocene western North America, and *Colodon*, which left many remains in late Eocene rocks of western North America.

Other Eocene odd-toed ungulates were somewhat like rhinoceroses but without the horn. One group of these rhino-like animals are called the running rhinoceroses because early genera were small and had rather long legs that enabled them to move relatively fast. These early genera might have looked almost like small horses, but later genera in the usual start-small-grow-larger scenario were more massive, like true rhinos. There were about six genera of Eocene running rhinos beginning 55 million years ago with eight species of *Hyrachyus*, which is estimated to have been about 1.5 meters (5 feet) long and have weighed between 22.6 and 71.7 kilograms (50 to 158 pounds). *Hyrachyus* bones have been found in Asia, Europe, and North America, suggesting that some land bridges existed during the early Eocene between Eurasia and North America either through Greenland, Alaska,

or both, enabling some migration between the continents. The last genus of the lightweight running type, *Hyracodon*, had long, slender legs with three toes on each foot and typically rhinocerotid cheek teeth. The ten species of *Hyracodon* weighed between 18 and 135 kilograms (40 to 300 pounds) and lived in western North America from around 40 million years ago until around 21 million years ago, the early Miocene.

Another rhino family of at least six genera, sometimes called aquatic rhinos, lived in rivers and lakes throughout North America and Eurasia (reinforcing the existence of land bridges between North America and Eurasia) in a lifestyle more like modern hippos than rhinos. Hippos are artiodactyls, or even-toed ungulates, however, whereas the aquatic rhinos like *Amyrnodon* were odd-toed perissodactyls. The four species of *Amyrnodon*, which weighed between 58 and 244 kilograms (130 and 537 pounds), thrived in China and North America throughout the Eocene and Oligocene. About half of the aquatic rhino genera, such as 283 to 600 kilogram (625 to 1320 pound) *Metamynodon* from North America (40.4 to 33.3 million years ago), didn't survive the Eocene, though their time on Earth was longer than that of us humans.

Brontotherioidea is another family of extinct rhino-like mammals and are probably more closely related to horses than their second or third cousins, the running and water rhinos. Brontotherioidea lived throughout the entirety of the Eocene and into the Oligocene. Early forms were about the size of modern tapirs, between 0.74 and 1.04 meters (2.4 and 3.5 feet) tall at the shoulder and weighed between 227 and 363 kilograms (500 and 800 pounds). They had 4 toes on the forefoot and 3 on the hind foot.

Of the 104 Eocene Perissodactyla genera, only 16 made up the beginning of the horse lineage. Horses comprised only about 85 of the over 320 Eocene Perissodactyla species. Ten genera (48 species) made up the Palaeotheriidae from Europe, which was a parallel group to the modern horse lineage and destined to become a dead end. *Palaeotherium* was typical of the group, standing about 75 centimeters (2.5 feet) tall at the shoulder and weighing around 30 kilograms (66 pounds), which is about the size of a Doberman Pinscher. *Propalaeotherium*, from the earliest Eocene and sometimes considered the ancestor of *Palaeotherium*, were smaller animals, ranging from 30 to 60 centimeters (1 to 2 feet) at the shoulder and weighing around 10 kilograms (22 pounds). Amazingly well-preserved fossils from Germany's Messel pit show that they ate berries and leaves. Like nearly all other Eocene Perissodactyla, all species of horse had three-toed feet.

Palaeotheriidae were first cousins to the Equidae, the line that's given us the modern horse. The most famous of the five genera of Eocene Equidae is *Hyracotherium* (a dozen or so species) which first appeared about 52 million years ago in Europe and North America. It's called Eohippus in the United States. In 1841, English palaeontologist Richard Owen discovered a partial skeleton of *Hyracotherium*; in 1876, American palaeontologist Othniel Marsh found a full skeleton of Eohippus. Eventually, the two specimens





### *Mesohippus*

*Mesohippus* was a three-toed early horse from the middle to late Eocene that stood about 2 feet tall. It ran primarily on its middle toe as successive species continued the transition to a single hoof.

were determined to be the same animal genus, so the name *Hyracotherium* takes precedence because it was published first. Owen called his find *Hyracotherium* because he mistakenly thought it was a hyrax. *Hyracotherium* averaged 60 centimeters (2 feet) in length, stood 30 centimeters (1 foot) high at the shoulder, and weighed around 8 kilograms (17.5 pounds), which is a little smaller than a Fox Terrier. It had four toes on each forefoot and three toes on each hind foot, each toe on each foot ending in a small hoof.

Early horse ancestors also had a non-working toe like a dog's dewlap, which gradually disappeared in later genera. *Orohippus* was similar to *Hyracotherium* and first showed up in the fossil record around 2 million years after *Hyracotherium* first appeared. The two coexisted for a while, but *Orohippus* left fewer fossils than *Hyracotherium*. Around 47 million years ago, a genus called *Epihippus* appeared. *Epihippus* continued the improvement in grinding teeth that *Orohippus*, its probable ancestor, had begun. *Mesohippus*, from the middle to late Eocene, had longer legs than *Hyracotherium* and stood about 60 centimeters (2 feet) tall, primarily on its middle toe. Unlike earlier horses, its teeth had a gap behind the front teeth, where the bit rests in the modern horse. All Eocene herbivores browsed primarily on berries and shrub leaves because grass was not yet widespread.

The first even-toed ungulates (Artiodactyla, or modern cattle, sheep, deer, pigs, camels, etc.) appeared during the Eocene. Their ancestry is not entirely clear, but they seem to have appeared all over the northern hemisphere almost simultaneously. The basic characteristic that identifies them is how the astragalus (or talus) bone in their ankle is shaped. Artiodactyls have a unique astragalus that has a little groove, often described as pulley-shaped, called a trochlea, on both ends. This double-pulley astragalus gives the foot a little more flexibility than does a single-pulley astragalus (like Perissodactyla and all other mammals have). Artiodactyls have developed

two basic body plans: a plan with a large head, long heavy body, and short legs like pigs and hippos; and a more gracile, long-legged plan like deer and cattle.

There were around 410 species of Eocene Artiodactyla distributed among nearly 140 genera that came and went during the period's 22 million years. Unlike their odd-toed cousins, Artiodactyla have remained numerous, comprising 80 to 90 modern genera and 220 to 240 living species depending on which expert you consider most knowledgeable. In 2010, the University of Michigan's Animal Diversity Web listed 89 genera and 243 species whereas the Integrated Taxonomic Information System, which is a collaboration between the governments of Canada, the United States, and Mexico, listed 81 genera and 220 species. Someday there will be an agreement on the extent of variations in the genome that can be included in a species, and the definition of species will be more objective. Until then, what constitutes a species will remain subjective and, hence, variable.

Obviously, the number of toes or the shape of their astragalus doesn't contribute to the success of Artiodactyla compared to Perissodactyla. The trait that's the true determiner of the relative success between the two is how well the two groups gain sustenance from their food. With the exception of pigs, both groups are herbivores. Animals don't have a system of their own for breaking plant cellulose down into a form they can use, so they get help from bacteria that ferment the cellulose in their gut. Perissodactyls are hindgut fermenters. They have simple stomachs that don't contribute much toward breaking down cellulose, so nutrients in their stomach contents are insufficiently prepared to be absorbed when they flow into the small intestine, which is generally responsible for absorbing most of the nutrients in food. Perissodactyls' small intestine empties into a special sack-like extension of the large intestine where bacteria further digest cellulose. This fermentation late in the digestive process means that quite a bit of the protein and other nutrients produced by the fermenting bacteria are lost through the feces, putting hindgut fermenters at a slight disadvantage compared with foregut fermenters like herbivorous artiodactyls.

Herbivorous artiodactyls have more complex stomachs than perissodactyls. Some artiodactyls such as camels, llamas, alpacas, and chevrotains have three-chambered stomachs, and ruminants have four-chambered stomachs. These extra stomach chambers enable fermentation to occur before the stomach contents empty into the small intestine, improving the artiodactyls' efficiency of nutrient uptake over perissodactyls. The ruminants' ability to chew the cud is a further improvement. The improved nutrient uptake efficiency of artiodactyls compared with perissodactyls is evident when comparing horse feces, which always has undigested matter in it, with cow dung, which seldom has undigested matter in it. This difference in the efficiency with which an animal gains sustenance from its food is typical of the myriad of conditions that drives evolution.

The Eocene was when the even-toed ungulates are considered to have begun to separate into the three modern artiodactyl branches: Suiformes



(sometimes called Suina) such as pigs, ruminants like cattle and deer, and Tylopoda such as camels and llamas. Eocene forms were very primitive compared to their modern counterparts, so assigning them to one of these three branches is sometimes academic at best and fanciful at worst. Moreover, an animal is sometimes known by only the barest of remains; *Paraphenacodus* has been classified by one published source as being in the Suiforme Suborder, the Dichobunoidea Superfamily, and Dichobunidae Family even though it's known by only one tooth.

The earliest artiodactyls known are the 13 or so species of *Diacodexis*, which lived throughout the northern hemisphere. Fossils of this little animal, which weighed 1.13 to 4.08 kilograms (2.5 to 9.0 pounds), have been found in European rock strata dated from 55.5 to 47.9 million years ago and in North American rocks dated from 54.8 to 50.0 million years ago. Although it's sometimes classified as a Suiforme, it probably resembled the modern Asian mouse deer more than a pig because it was lightly built and its hind limbs were longer than its front limbs. It had five toes on each foot, but the third and fourth toes were elongated, presaging the animal's even-toed brethren to come. *Diacodexis* was soon joined by seven species of *Bunophorus*, which lived between 55.4 and 51.8 million years ago in Europe and between 53.5 and 50.0 million years ago in North America. At 6.75 to 19.5 kilograms (14.9 to 43.0 pounds), it was larger than *Diacodexis*. Both critters lived in a subtropical to tropical rainforest that included evergreens, vines, palms, fern trees, and ferns. They probably ate fruit, seeds, and leafy vegetation.

Most Eocene artiodactyl genera didn't enjoy the longevity and the variety of species and habitat that *Diacodexis* and *Bunophorus* did. For example, the single known species of *Eolantianius* lived only in China and for less than a million years. Of the twenty known Early Eocene artiodactyls (the Early Eocene lasted between 55.8 and 48.5 million years ago), eleven lived on into the Middle Eocene period (the Middle Eocene lasted between 48.5 and 37.1 million years ago). The most successful Early Eocene artiodactyls other than *Diacodexis* and *Bunophorus* were *Antiacodon*, whose four species were scattered across the western United States between 52.6 and 43.8 million years ago, and *Helohyus*, which had three species scattered across the western United States and China sometime between 50.3 and 37.2 million years ago.

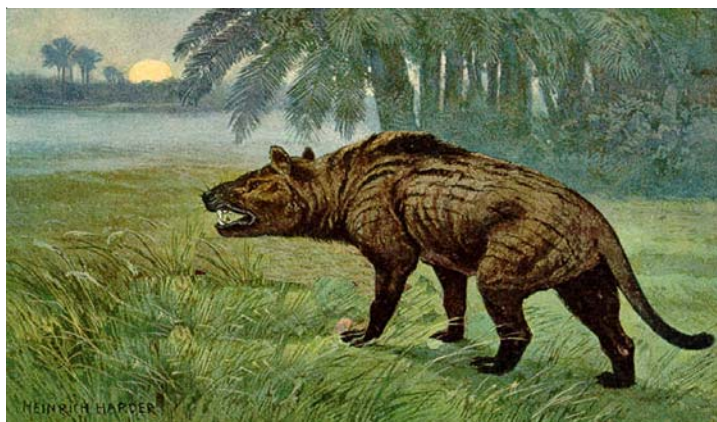
During the 11.4 million years of the Middle Eocene, over 93 artiodactyl genera are known to have appeared in the fossil record. Many of these were relatively unsuccessful; 44 didn't survive into the Late Eocene. Among the those that perished during the Middle Eocene were 27 genera that, like Germany's *Hallebune*, had only one known species, and among these 27 were eight genera like India's *Metakatius* that survived for a million years or less. On the other hand, there were some Middle Eocene genera like *Achaenodon* from the western United States and Europe's *Haplobunodon* that either were so well adapted or lived in such a benign environment that they evolved four or five species and survived for eight to ten million years.

But the most successful Eocene artiodactyls appeared in the Middle Eocene and survived to the end of the Period or on into the Oligocene. Genera like *Protoreodon* from western North America and eastern Asia's *Anthracothea* evolved five to ten known species and survived for twelve to fourteen million years to the very end of the Period. Most of the longest-surviving genera lived in western North America, but it's unclear at this time whether that's an indication of a more favorable North American environment or simply an artifact of more diligent collection. Nevertheless, North American genera like *Agriochœrus*, *Hypertragulus*, and *Archaeotherium* each evolved over ten species and survived through the Oligocene and well into the Miocene.

Throughout the Eocene, many artiodactyl genera remained in the small herbivore niche of under 20 kilograms (44 pounds), but many others grew much larger. By the middle of the Period, *Achaenodon robustus* appeared in the western United States and weighed 580 to 775 kilograms (1280 to 1700 pounds). But the true heavyweight was *Archaeotherium*. *Archaeotherium mortoni* appeared in North America around 38 million years ago at 368 kilograms (810 pounds), and its cousin, *Archaeotherium lemleyi*, from the early Oligocene, weighed in at 2160 kilograms (4760 pounds). The genus finally ended around 25 million years ago with its largest species: 5500 kilogram (12,100 pound) *Archaeotherium trippensis*, which was approximately the size of an elephant.

All these even- and odd-toed horse-like, rhino-like, pig-like, and deer-like hoofed mammals needed predators to control their populations, and the Paleocene holdover creodonts, which looked somewhat cat-like, were among the more successful. They first appeared at the very end of the Paleocene (*Tytthaena parrisi* and *Dipsalodon churchillorum* 60.2 million years ago in Wyoming) and finally met their end when the last species, *Dissopsalis carnifex*, became extinct 8 to 9 million years ago in what is now Pakistan. There are at least 60 known Eocene creodont genera comprising over 170 species, and another 25 or so genera appeared during the Oligocene and Miocene. The most successful genus by far was *Hyaenodon*, which boasted 27 Eocene species (although some might be duplications), and another 13 or so appeared during the Oligocene and Miocene. According to the Paleobiology Database, they first appeared around 40.4 million years ago and finally became extinct around 15.97 million years ago. Their fossils are found throughout Eurasia and North America. They occupied every predator niche from among the largest down to diminutive late Eocene *H. microdon* and *H. mustelinus* from North America, which probably weighed about 5 kilograms (11 pounds).

There were other successful genera such as equally ubiquitous *Prototomus* (11 species) and *Sinopa* (10 species) from western United States. On the other hand, there were many relatively unsuccessful genera such as Wyoming's *Gazinocyon*, Myanmar's *Orienspterodon*, France's *Francotherium*, Morocco's *Boualitomus*, India's *Indohyaenodon*, Egypt's *Masrasector*, and Mongolia's *Sarkastodon*, each of which have only one known species and



### *Hyaenodon*

This is a Heinrich Harder painting of *Hyaenodon*, the most successful predator of the Eocene and Miocene. According to the Paleobiology Database, this genus survived for over 24 million years and produced around forty species.

survived for just a few million years.

These creodonts probably share a common Paleocene ancestor with primitive true carnivores, which also first appeared in the fossil record late in the Paleocene. These primitive carnivores are separated into two families: Viverravidae and Miacidae. The Viverravidae were probably the oldest because Alberta's *Pristinictis connata* appeared around 60.2 to 56.8 million years ago. Viverravidae were generally small critters such as *Simpsonictis*, which weighed approximately 0.14 kilograms (0.31 pounds), and *Didymictis*, which weighed around 3.6 kilograms (7.9 pounds). Eight of the eleven (per Paleobiology Database taxon 40992) Viverravidae genera first appeared during the late Paleocene in western North America. The late bloomers, *Viverriscus* and *Variviverra*, appeared 55.8 million years ago, at the beginning of the Eocene. They all died out before the Eocene was half over. The shape of their skulls and number of molars suggest that they were related to cats, but no direct link has been established. They probably ate insects, lizards, and small mammals.

The miacids were the other primitive carnivore group. Nearly all of the 19 or so miacid genera died out by the end of the Eocene, and only *Miacis* (58.7 to 33.9 million years ago) is considered a "true" carnivore and possibly the ancestor of all modern carnivores. Some as-yet unknown creature was the ancestor of the creodonts and miacids, most of which died out leaving no descendants, and only some member of the Miacids, probably *Miacis*, begat the carnivores. The miacids generally had a greater brain-to-body size ratio than the creodonts, which might indicate a superior intelligence.

*Miacis* was five-clawed, about 30 centimeters long (the size of a weasel), and lived in what is now North America and Europe. The miacids retained some of the primitive characteristics that creodonts had such as low skulls, long slender bodies, long tails, and short legs. *Miacis* retained the

creodont number of teeth, 44, although some of the teeth were smaller. The hind limbs were longer than the forelimbs, the pelvis was very dog-like, and the vertebrae had some specialized traits. It had retractable claws, agile joints for climbing, and binocular vision. Like many other early carnivores, it was well suited for a lifestyle in trees with needle sharp claws and limbs and joints that resemble those of modern carnivorans. *Miacis* was probably an agile forest dweller that ate eggs and fruits and preyed on smaller mammals, reptiles, and birds.

The genus *Miacis* had 17 to 22 species, depending on the expert, and lived throughout the 22 million years of the Eocene. Other Eocene predators that the University of California, Santa Barbara's Paleobiology Database officially places in the Order Carnivora lacked the genetic make-up to be as prolific and successful as *Miacis*, their genera either producing only one species (e.g., *Pugiodens*, *Adracon*, *Chalicyon*) or living for less than four million years (e.g., *Pristinictis*, *Cynodictis*, *Guangxicyon*).

On the other hand, some Eocene members of Carnivora lived long and prospered. For example two species of *Daphoenus*, *D. demilo* and *D. lambei*, lived in western North America around 42 to 38 million years ago, three other species (*D. hartshornianus*, *D. vetus*, and *D. ruber*) lived in the north central United States during the Oligocene, and *D. socialis* lived in Oregon sometime in the range of 20.6 to 16.3 million years ago. *Daphoenus* was one of a group of carnivores called bear dogs because they had characteristics of both bears and dogs. Other Eocene bear dogs were *Daphoenictis* and *Brachyrhynchocyon* from western North America, *Cynodictis* from Europe, and *Guangxicyon* from China. *Daphoenus* weighed about 7.84 kilograms (17.3 pounds), about the size of a present-day Desert Coyote. They had short legs more suited for quick sprints than long distance running, so they probably ambushed their prey and scavenged. Fossil footprints suggest they walked flat-footed like modern bears.

Another Eocene predator family, the Nimravidae, was also somewhat related to creodonts according to some experts. Called false saber-toothed cats, nimravidae bore a superficial resemblance to infamous saber-toothed *Smilodon* of our cave-man past but had too many differences to be called a feline-like *Smilodon*. The long canine teeth of both the Nimravidae and later saber-toothed cats is an example of what paleontologists call convergent evolution, which is the same trait appearing independently in two or more unrelated genera, often at different times. Convergent evolution is a result of a specific trait in a species that became extinct becoming once more a favorable response to conditions that exists in the environment at some time and place later than the extinct species, so it reappears. In other words, species "A" develops a trait but becomes extinct; later, species "B" unrelated to species "A" develops the trait also. Either a mass extinction unrelated to the trait, or the environment changes such that the trait is temporarily no longer favorable, or perhaps even becomes unfavorable, drives the first species to extinction. *Dinictis felina* and *Hoplophoneus mentalis*, both from western North America, were among the first false saber-

toothed cats to make an appearance between 38.0 and 33.9 million years ago. Some species of nimravidae lived as recently as seven million years ago.

The most successful Eocene Carnivora that can be assigned to the canine family, Canidae, was *Hesperocyon*, although it really didn't look like what we think of as a dog. *Hesperocyon* fossils have been found at locations in Montana and Saskatchewan that date to as far back as 42 million years ago, but the specific species of these early remains are unidentifiable. Fossils identifiable as *H. gregarius* and *H. paterculus* have been found at numerous locations throughout western North America that date to as old as 38 million years ago. *H. pavidus* remains as young as 20.6 million years ago have been found in the western United States. The typical Eocene *Hesperocyon* was 80 centimeters (2 feet 8 inches) long, weighed 1.67 to 1.73 kilograms (3.68 to 3.81 pounds), and looked more like a civet or a small raccoon than a canine. Its body and tail were long and flexible, and its limbs were weak and short. However, its teeth showed it was a canid. Xiaoming Wang, Curator, Natural History Museum of Los Angeles, has suggested that *Hesperocyon* was the ancestor of all Hesperocyoninae and, ultimately, all canines.

Ironically, the mesonychids, predators of the artiodactyls and perissodactyls, were themselves hoofed mammals. Each of their toes ended in a small hoof instead of a claw. They sort of resembled a modern wolf and are sometimes called wolves on hooves. Actually there's no firm agreement among paleontologists that mesonychids were predators; Zhou and co-workers wrote in the June 1995 issue of the *Journal of Vertebrate Paleontology* that "They are generally considered to be cursorial [adapted, or having legs adapted for running] *Hyaena*-like carron feeders..." Like hyaenas, mesonychids had teeth that were adapted for crushing bones, which supports the view that they were largely scavengers, but also like some hyaenas, they probably also hunted.

Eocene mesonychids were holdovers from Paleocene ancestors like *Yangtanglestes* from China, where the group probably originated. One of the earliest, *Dissacus*, first appeared around 63 million years ago and survived into the Eocene, to around 49 million years ago. It developed nine species, spread all over the northern hemisphere, and was small, about the size of a German Pinscher (not the Doberman Pinscher) or Basenji. If it hunted, its prey would have been ungulates like *Diacodexis*, which was about a third of *Dissacus*'s size. *Pachyaena* first appeared at the dawn of the Eocene, so it coexisted with *Dissacus* for the last seven million years of *Dissacus*'s existence. It also had the same range, but *Pachyaena* survived until around 37 million years ago. It was about the size of a coyote or small bear. *Mesonyx* was the first of the group to be discovered (around 1870 in Wyoming) and gave the group its name. It first appeared in the fossil record about 50 million years ago and survived for around 13 million years. Of the 20 or so mesonychid genera, only *Mongolestes* survived into the Early Oligocene epoch.



Until the beginning of the third millennium, mesonychids were thought to be the ancestors of whales primarily because both whales and mesonychids have unusual triangular molar teeth and share a few additional physical traits. But DNA research has revealed that whales have a close relationship with the artiodactyl hippopotamus. Moreover, whale flippers have a double-pulley astragalus like artiodactyls, so current consensus is now that hippos and whales share a common artiodactyl ancestor. Unfortunately, we have no mesonychid DNA to compare with whales to see how close they are. So therefore, although the issue of mesonychid ancestry of whales will probably never be completely laid to rest, we do know that hippos and whales share a common ancestor.

The identity of that ancestor is under debate as of 2010, but the two leading contenders are *Indohyus* and *Pakicetus*, both of which were found in Pakistan. Both were small, four-legged, furry land animals that were semiaquatic and had some physical features in common with whales, such as the shape of their ear region that is characteristic of whales and not found in any other genera. *Himalayacetus subathuensis*, found in India, seems to be older than either *Indohyus* and *Pakicetus* and might be closer to the true common ancestor than either. The timeline seems to favor *Pakicetus* and *Himalayacetus* over *Indohyus*, however, because they go back to almost 55 million years ago whereas *Indohyus* goes back no more than 48 million years ago as far as we know here in 2010. And the more advanced whale *Ambulocetus* ("walking whale") was swimming the seas around 50 million years ago. The true common ancestor of whales and hippos is probably a Paleocene critter that hasn't been found yet. Though *Ambulocetus* was clearly amphibious, its back legs were better adapted for swimming than for walking on land. Chemical analysis of its teeth shows that it was equally at home in both salt and fresh water.

Paleontologists have recovered remains of around 40 genera of primitive whales, such as *Remingtonocetus* and *Protocetus*, that date between 48 and 40 million years ago, and nearly all were found in Pakistan, which was on the shore of the remnants of the ancient Tethys Sea at that time. These primitive genera probably stayed and hunted in shallow water.

Between 40 and 34 million years ago, whales such as *Basilosaurus* and *Dorudon* were leaving the shallows of the Tethys sea and roaming the world. Their fossils have been found from North America to Pakistan. They had all but lost their hind limbs, and their nostrils were about midway between their nose and the top of their head. *Basilosaurus* was the larger of the two, measuring between 15 and 25 meters (49 and 82 feet) long.

Several other animals appeared during the Eocene that are generally considered to be some sort of ancestor to modern forms. A primitive bear, *Parictis*, first appeared around 38 million years ago in western North America. There were at least six species in the time frame 38 to 33.9 million years ago. It was very small, between 1 and 3.34 kilograms (2.2 and 7.36 pounds). *Parictis* is known only by teeth and skulls, so little is known of it. *Plesiocyon*, which is loosely associated with modern seals and walrus appeared around



Adapted from Pavel Riha (WIKI)

### *Basilosaurus*

*Basilosaurus* vertebrae were so common in the early nineteenth century Louisiana and Alabama and so large that they were used to make furniture and as blocks to support cabins.

38 million years ago. *Mustelavus priscus*, which is loosely associated with the badger/otter/weasel family appeared around 38 million years ago. Not enough is known about *Plesiocyon* and *Mustelavus* to firmly determine whether or not they're closely related to modern forms.

At various times and places during the Eocene, there lived around 150 genera of primates comprising at least 285 species, 28 of which were hold-overs from the Paleocene. Ancestors of all the modern primates were among them. Modern primates are generally divided into two major groups: Strepsirrhini, which includes lemurs and lorises, and Haplorrhini, which includes tarsiers, monkeys, apes, and humans. Both groups can trace their ancestry to the Eocene.

As the Paleocene gave way to the Eocene during the great temperature surge of the Paleocene-Eocene Thermal Maximum (PETM), more than ten genera of Paleocene primates inhabited North America, with a couple of them (*Plesiadapis* and *Phenacolemur*) having spread to Europe. Most either were so rudimentary or left so few remains that they can not be identified with either of the two modern groups. The lone exception of these early forms is *Trogolemur*, which first appeared in Montana during the late Paleocene, around 60 million years ago. *Trogolemur* has been identified as one of the early ancestors of modern tarsiers (genus *Tarsius*), which are part of Haplorrhini. Even more interesting is the fossil of *Tarsius eoceanus*, a species of modern tarsiers, that has been found in China and dated to around 48 million years ago, making *Tarsius* the contemporary animal genus with the longest continuous record of existence. The nine species of modern *Tarsius* are small, nocturnal animals that live on the islands of Southeast Asia. They have enormous eyes; their eye sockets are larger than their brain. They're the only entirely carnivorous primate on Earth, preying mainly

on insects but occasionally on small birds, snakes, lizards, and bats.

All of these Paleocene holdovers except *Phenacolemur* and *Troglemur* died out by 48 million years ago, leaving room for 25 more rudimentary genera (42 species) that appeared between 55.8 and 40 million years ago. Most of these early forms had only one or two known species, but *Microsyops* was the exception. It had at least ten known species that roamed throughout the western United States between 55.8 and 42 million years ago.

Almost 110 primate genera that first appeared during the Eocene have been recognized as ancestor to the two modern groups, Strepsirrhini and Haplorrhini. Almost half are Tarsiiformes, a subgroup of the Haplorrhini related to *Tarsius*. They're found throughout the northern hemisphere, from *Tetonius* of Colorado and Wyoming to *Necrolemur* of France and Switzerland and on to Mongolia's *Altanius*. Most, such as Pakistan's *Indusius* and *Diablomomys* from Texas, had only one known species. But a few others, such as *Teilhardina* from Eurasia and western North America and Europe's *Pseudoloris*, had several species that we know of so far.

At least 16 Eocene Haplorrhini genera are ancestors of Anthropoidea, the subgroup that includes monkeys, apes, and humans. Eight of them are from northern Africa, and these include *Algeripithecus* from Algeria and *Catopithecus* from Egypt's Fayum. Most of the rest are from the Far East, such as *Eosimias* from China and Myanmar and Thailand's *Siamopithecus*. Of the Eocene Anthropoidea, only *Rooneyia* (Texas) is from the United States. None have been identified from Europe. Eocene Anthropoidea were not as prolific as other groups; 12 of the 16 genera had only a single species, and *Eosimias*, with four species, was the most successful. Of course, Anthropoidea later produced the currently most successful primate of them all as measured by world domination: *Homo sapiens*.

At least 40 genera of primitive Strepsirrhini, which is the lemur and loris group appeared during the Eocene. The large majority of them have been found in Europe, Asia, and northern Africa. Only 6 of the 40 have been found in the United States. Over half of the 40 genera produced only one species, such as India's *Asiadapis* or Egypt's *Afradapis*. On the other hand, the Strepsirrhini produced the most prolific primate genus of the Eocene: *Cantius*, whose ten or more species spread throughout the western United States and France from 55.8 to 42.0 million years ago. The most famous fossil of the Period is probably the single species of *Darwinius*, which was found in the Messel Pit in Germany. The exquisite detail of the *Darwinius* fossil is almost without equal in any other find of any sort.

Around 50 million years ago, a supervolcano erupted with a Volcanic Explosivity Index (VEI) of 7 in what is now Canada on the border between British Columbia and the Yukon, forming the Bennett Lake Volcanic Complex. The Volcanic Explosivity Index is a measure of the violence of an eruption; it combines the amount of ejecta and the duration over which the material is ejected, the more the material and the shorter the time period, the higher the VEI. Shield volcanos such as Mauna Loa eject enormous amounts of material but do so over such a long period of time that their VEI is only on

the order of 1 or so. Mauna Loa has ejected around 75,000 cubic kilometers ( $\text{km}^3$ ) of material, over ten times that of the largest known explosive volcano, but has done so over approximately 700,000 years. The VEI is similar to the Richter scale used to measure earthquakes. It's a simple numerical index of increasing magnitude of explosivity, each interval (e.g., 7 to 8) representing an increase of about a factor of 10 in the volume of erupted material. The largest eruption known had a VEI of 8. The 1980 eruption of Mount St. Helens had a VEI of 5, ejecting around  $1 \text{ km}^3$  of material. The 1883 eruption of Krakatoa had a VEI of 6 and ejected about  $21 \text{ km}^3$  of material. The Bennett Lake eruption ejected around  $850 \text{ km}^3$  of material. It's reasonable to speculate whether or not some genera that were present during that general time frame and produced only one species (such as *Aycrossia* and *Sphacorhysis*) might have met their end in the cataclysm.

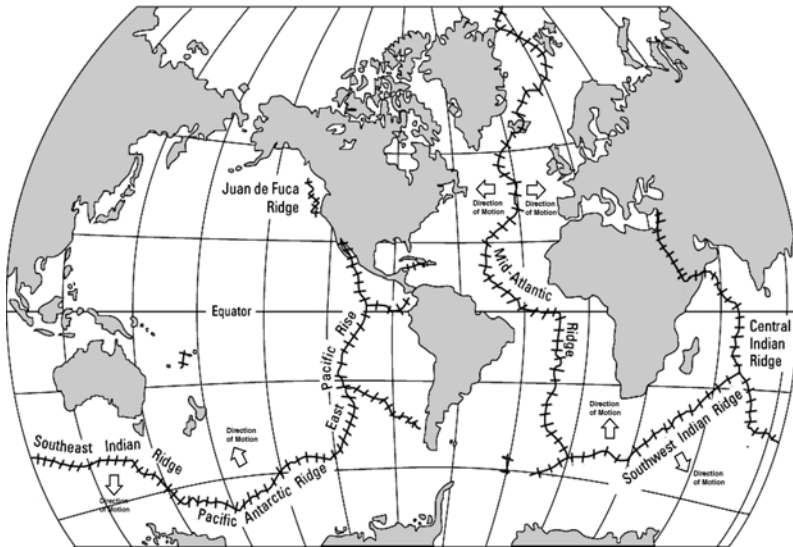
The Eocene began with the greatest temperature surge of the Cenozoic; then global temperatures declined during the middle part of the period. The late Eocene began with another temperature surge that was much more modest and short lived than the PETM.

### Oligocene (33.9 to 23.03 million years ago)

The Eocene ended with relatively close ancestors of all modern mammal groups present: armadillos, bats, bovids, camels and llamas, deer, elephants, horses, pigs, primates, rodents (including rabbits and hares), sea cows, sloths, tapirs, viverravines (which would give us cats, hyaenas, and mongooses during the Oligocene), vulpavines (which would give us bears, dogs, racoons, seals and walruses, and weasels during the Oligocene), and whales. From the beginning of the Oligocene, they would slowly evolve to their current forms.

Like many geologic time periods, the bounds of the Oligocene are specifically defined by the disappearance and/or appearance of an animal genus, usually an aquatic genus. The Oligocene is defined to have begun with the disappearance of a group of spiny plankton called the hantkeninids, which has been correlated with time to have occurred around  $33.9 \pm 0.1$  million years ago. The period is defined to have ended with the disappearance of plankton species *Reticulofenestra bisecta*, the appearance of *Paragloborotalia kugleri*, and the base of magnetic chronozone C6Cn.2n (the time period during which Earth's magnetic field had a specific polarity), which has been correlated with time to have occurred around  $23.03 \pm 0.05$  million years ago. Magnetic chronozones are important benchmarks for correlating time periods when no fossils are available.

The word "Oligocene" was coined in Germany around 1854 based on the German word "dürftig" (scanty), which was translated into Greek, a favorite language of paleontologists, as ολιγος and Anglicized as "oligos". This is a reference to the scantiness of new species that appeared during the period. The apparent "scantiness" was probably simply a reflection of the state of collections in 1854 rather than a true measure of the number of new species that appeared.



### Mid-Ocean Rift System

The motion of the continents can best be visualized from this U.S. Geologic Survey map of the mid-ocean rift system. The line traced out like a scar along the ocean depths is a line of relative weakness in the Earth's crust, "relative" being the key word. Hot magma welling up from deep in the earth's mantle strikes the underside of the crust along this line and splits into two streams flowing in opposite directions perpendicular to the rift. Friction with the crust's underside from the opposite-flowing magma streams causes tension, pushing the crust apart. Up-welling magma flows rather gently out through the gash, eventually creating a ridge on both sides of it, giving the system its more common name: the Mid-Ocean Ridge. The crust on both sides of the rift are moving directly away from one another. This rift system only partly defines the crustal plates, which are not shown.

During the Oligocene, plate tectonics continued to bring climate change that impacted evolution as life adjusted to new conditions. The Tethys Sea (a small remnant of the ancient Tethys Ocean that had existed when Pangea was formed) between Africa and Eurasia was still open somewhat (although now reduced to merely the Tethys Seaway), allowing a little free flow of ocean currents around the globe at low latitudes because North and South America had not yet joined. The Tethys Seaway completely closed around 20 million years ago as Africa joined Eurasia through the Sinai Peninsula. Readily available moisture from the Tethys Seaway and the low-latitude circumglobal current was probably the proximate reason why the tropics were forested all the way around the globe from northern Africa to the southern Far East, allowing animals adapted for forest living to evolve.

The Drake Passage had begun to open up 41 million years ago as the West Scotia Ridge pushed South America away from Antarctica. This allowed the Antarctic Circumpolar Current (ACC) to be established because South Africa had already separated from Antarctica during the Jurassic. The ACC isolated Antarctica, plunging it into a deep freeze, and its forests



were slowly replaced by glaciers that stored vast quantities of water, lowering global sea levels by as much as 100 meters (328 feet). The depth of the Antarctic ice pack and concomitant sea level drop varied throughout the Oligocene, and this variation has been correlated with the Milankovitch cycles mentioned on page 62. The Milankovitch cycles are the periodic variations in the tilt of the Earth's axis (obliquity) and in the Earth's orbital parameters, such as eccentricity (the degree to which the orbit is elliptical), that are caused by the cyclical variation in the gravitational tug Jupiter has on the Earth, which in turn arises from the varying geometry between them.

Thus, the warm, humid Eocene became a drier, cooler Oligocene. Global temperatures had not been as low since the end of the Carboniferous Period when great forests had removed much of the atmospheric carbon dioxide. In only 20 million years, between 53 and 33 million years ago, global temperatures changed from a high that was exceeded only by the 550 million year Phanerozoic Era maximum in the early Cambrian to a low that was only a little above the Phanerozoic minimum in the late Carboniferous. In spite of such an unprecedented variation in global temperature over such a short time, mammals not only survived but proliferated.

This was the time when whales began their great radiation (as paleontologists would say). Eleven new Oligocene species have been discovered in Australia, twenty-three in Eurasia, fifteen in North America, and one so far in South America. *Squalodon* was probably the most wide-spread genus with six Oligocene species being discovered from Japan to France and North America. Four new species appeared in North America and thirteen in Europe during the Neogene. The primitive sperm whale *Ferecetotherium kelloggi* appeared in Azerbaijan. Fossils of many different whale species have been found scattered around the globe, each found in sedimentary rocks that encompass only a very narrow time period as if each of the species lived only briefly in their own place and time and no other. Further analyses might find some of these that are currently considered to be different are, in fact, the same animal.

On land, the continents were pushed apart by rifts that are part of the globe-circling mid-ocean rift (ridge). As mentioned earlier, the South Atlantic rift has been pushing South America westward since it was sundered from Pangaea during the Jurassic Period. This westward push is causing the continent to collide with the Pacific Ocean Nazca Plate and a small section of the Antarctic Plate, both of which are being subducted under it. South America is unique in that the western edge of the continent lies on the edge of the plate, so this collision is causing South America to crumple along its western edge, forming the Andes mountain chain. The subducted Nazca and Antarctic Plates have been making the mountain chain an extremely active volcanic system: "The Andean volcanic arc includes over 200 potentially active Quaternary volcanoes, and at least 12 giant caldera/ignimbrite systems, occurring in four separate segments referred to as the Northern, Central, Southern and Austral Volcanic Zones." [Stern, C.R. (2004) *Revista Geológica de Chile*, 31(2):161 to 206.]

As the continents were pushed apart, their individual relationships between land and sea helped to create individual climates and foster individual

biospheres. South America became home to its own collection of mammals that included among its hundreds of species marsupials such as *Notogale mitis*, primitive sloths such as *Pseudoglyptodon*, armadillos such as *Prozaedus impressus*, and the horse-like notoungulate *Rhynchippus*. The similarity between *Rhynchippus* and primitive horses such as *Meshippus* is another example of convergent evolution, which is the tendency of animals from different evolutionary lines to develop similar characteristics in response to similar environmental pressures. *Rhynchippus* and *Meshippus* both evolved to take advantage of the grasslands of expanding plains environments. Both had teeth with a thick coating of enamel that would have increased tooth life expectancy despite the constant grinding that comes from grazing on tough plants.

Australia separated from Antarctica around the end of the Cretaceous, 65 million years ago, and has been driven northeast. Isolated from all other land masses for 65 million years, Australia developed its own unique, exclusively metatherian fauna.

Sometime between 28.4 and 23.03 million years ago, the island continent was home to a primitive balbarine kangaroo called *Wururoo dayamayi* and to *Marlu karya*, a ringtailed possum. *Wakaleo oldfieldi*, a marsupial lion walked what is now South Australia's Wipajiri Formation sometime late in the Oligocene time period. The oldest known wombat, *Rhizophascolonus crowcrofti*, also left its mark in the Wipajiri Formation. Remains of *Litokoala kanunkaensis*, a marsupial genus closely related to the modern koala, have been found in the Etadunna Formation of Ngama Quarry, Lake Palankarina, South Australia. Toward the end of the Oligocene, *Obdurodon insignis*, a monotreme species sometimes called the Riversleigh Platypus was also a resident of the Etadunna Formation in the Tirari desert. *Bulungu campbelli*, a bandicoot, lived in South Australia sometime between 26.1 and 23.6 million years ago. These are but a few of the rich variety of monotremes and Metatheria that inhabited Australia during the Oligocene.

The length of Atlantic sea floor between the midocean rift and the west coasts of Europe and Africa tells us that Eurasia and Africa have been moving east since they and the Americas separated. Africa had also separated slightly from Europe, making it another isolated land mass, but its separation was small enough that what was to be the cradle of the human race shared some species with Eurasia. For example, an indefinite species of *Orycteropus*, the living aardvark, left its remains in Kenya sometime between 28.4 and 23.03 million years ago, then passed on to Turkey, Moldova, Pakistan, and the Ukraine during the Miocene. Mastodon species *Palaeomastodon beadnelli*, *Palaeomastodon minor*, *Palaeomastodon parvus*, and *Palaeomastodon wintoni* left their remains in the part of Egypt called the Fayum as well as in Saudi Arabia sometime between 33.9 and 28.4 million years ago. Another mastodon, *Zygodolophodon* also left its remains in Kenya sometime between 28.4 and 23.03 million years ago before spreading during the Miocene to France, Germany, Slovakia, Kazakstan, North America (e.g., California, Colorado, Saskatchewan), and China among the many places it's been found.

The ease with which animals could travel between Africa and the northern continents of North America and Eurasia (though not all did) is further exemplified by our old friend from the Eocene, *Hyaenodon*, which was the apex predator of its time. Six species are known to have lived in Europe and another ten species in North America during the middle and late Eocene (between 48.6 and 33.9 million years ago). The only African representative was an indeterminate species found in early Oligocene sites in the Fayum. *Hyaenodon* finally died out in Kenya sometime between 20.43 and 13.65 million years ago. *Ancodon gorringeri*, generally considered to be a form of early hippopotamus, has been found in early Oligocene deposits in the Fayum. Remains of two species of the primate *Parapithecus* have been found in early Oligocene (33.9 to 28.4 million years ago) deposits in Egypt. Fossil remains of *Aegyptopithecus zeuxis*, generally considered to be an early catarrhine, have also been found in early Oligocene deposits in the Fayum. Catarrhines and platyrrhines, or New World Monkeys, together make up the higher primates. Catarrhines are divided into the lesser apes, or gibbons, and the great apes, which consist of orangutans, gorillas, chimpanzees, bonobos, and humans. Remains of the primate *Kamoyapithecus hamiltoni*, who some consider to be related to our early human ancestors, were found in Kenyan deposits that have been dated to range between 27.5 and 24.2 million years ago.

The section of the midocean rift that is south of Africa and has slowly been driving Africa and Antarctica apart since the Triassic has essentially pinned the African plate to southern Europe. Africa has very slowly been pushing into Europe, raising what was once simply an archipelago of individual islands to a complete continent (the lowering of sea level caused by extensive glaciation in Antarctica was a contributor). Europe has crumpled along a weakness in its geology to form the Alps. Subduction of ancient Tethys sea floor under Europe has created a moderate amount of volcanic activity such as Etna, Stromboli, and Vesuvius among Italy's numerous active and dormant volcanoes.

This dramatic alteration in European topography was accompanied by an equally dramatic shift in fauna, called the Grande Coupure, during which many native European genera and families became extinct, their places in the ecosystem being taken by immigrants from Asia. For example, the entire family Palaeotheriidae, which is distantly related to horses, the entire artiodactyl families Choeropotamidae and Dichobunidae, and the primate families Adapidae and Omomyidae completely disappeared from Europe in the early Oligocene even though they had been living there since the beginning of the Eocene, 55.8 million years ago. Among the new families were artiodactyl families Anthracotheriidae, which had been living in China since the middle Eocene (48.6 million years ago), and Entelodontidae, which had been living in China since the late Eocene (37.2 million years ago). These were joined by two rhinoceros subfamilies, Aceratheriinae (hornless rhinos; e.g., *Aceratherium*) and Rhinocerotinae.

The great Eurasian landmass was home to an equally great number of mammals. Several species of chalicotheres (perissodactyls with claws in-

stead of hooves) such as *Phyllotillon betpakdalensis*, which has been found in Kazakstan deposits dated as early as 28.4 million years ago and as late as the middle Miocene, 15.97 million years ago. Six species of another chalicotheres, *Schizotherium*, trod the soil of France, Germany, China, Mongolia, and Kazakstan as early as the middle Eocene, 37.2 million years ago, before disappearing by the end of the Oligocene. Chalicotheres finally died out in China during the Pleistocene, sometime between 2.588 and 0.012 million years ago. The last known fossil was found in the 122 meter thick fourth member of the Yuanmou Formation near Yunnan, China. Three species of *Paraceratherium*, a member of the rhino superfamily rhinocerotidae, lived in Pakistan, China, Mongolia, and Kazakstan at various times during the Oligocene. According to an interview with Hollywood special effects creator Phil Tippett that was published in the 24 May 2012 issue of *Wired*, *Paraceratherium* was the inspiration for the Empire's "walkers" in the 1980 science-fiction film *Star Wars: The Empire Strikes Back*.

Eurasia had their share of predators. Three species of previously mentioned *Hyaenodon* have been found in early Oligocene deposits (between 33.9 and 28.4 million years ago) in France and another species, *H. pervagus*, in early Oligocene deposits in China. Six species of the bear dog *Pseudamphicyon* have been found in French deposits dated between 33.8 and 29.2 million years ago. Several species close to true bears also lived in Eurasia during the Oligocene, such as *Amphicyonodon teilhardi* in Mongolia and four *Amphicyonodon* species in France during the early part of the period. Remains of the false sabre-tooth cat *Quercylurus major* have been found in numerous early Oligocene deposits throughout Europe. As mentioned previously, false saber-toothed cats are outwardly similar to true saber-toothed cats but have a few subtle physiological differences.

Although primates disappeared from Europe during the Grande Coupure, they remained in Asia. *Bugtipithecus inexpectans*, *Phileosimias brahuiorum*, *Phileosimias kamali* have been found in early Oligocene Pakistan. A fossil catarrhine, *Saadanius hijazensis*, has been found in Saudi Arabian deposits dated in the range of 29 to 28 million years ago.

Like South America, the western edge of the North American continent lies at the western edge of the North American plate, and like South America, the North American continent has crumpled along its western edge under the compression stress of the collision between the North American plate and the Juan de Fuca and Pacific plates. Thus, the Cascade Mountain Range rose. However, in North America, much of this compression stress was transmitted eastward in the North American plate to a weakness in the plate that exists along the western edge of the North American craton. A craton is the geologic foundation, or basement, of a land mass. It's the most stable and oldest (as much as 3 billion years old) layer of rock. The rock along the western part of the North American craton is around 2.5 billion years old. The compression stress caused the weakness along the western edge of the craton to buckle in the Laramide orogeny (mountain building), forming the Rocky Mountains.

As the Juan de Fuca and Pacific plates are being subducted under the North American plate, a series of over 20 volcanos, such as Mount St. Helens and Mount Ranier, and a few thousand separate volcanic vents appeared, forming what is called the Cascade Volcanic Arc. The U.S. Geological Survey says that the Cascade Volcanic Arc began erupting around 35 million years ago. Some of the eruptions were quite violent; eruptions of both the Long Valley Caldera around 760,000 years ago and Mount Mazama (now known as Crater Lake) around 7,700 years ago had VEIs of around 7.

North America was the home of a rich assortment of mammals and is the ancestral home of the modern species camel and llama although those species left the continent millions of years ago. Several genera of early horse lived in Oligocene North America. As many as thirteen species of *Meshippus*, and sixteen species of *Miohippus* roamed the great plains. They coexisted for perhaps 3 million years during the beginning of the Oligocene before *Meshippus* disappeared. Both genera walked on three toes with the middle toe dominant. The fourth and fifth toes of both genera were only vestigial. Horses became extinct in North America around 12,000 years ago, about the same time North American camels became extinct.

It's not unreasonable to speculate that these extinctions were due, in part, to weakening the genera by the survival pressures from repeated supervolcano eruptions that occurred in North America beginning with the La Garita eruption (VEI 8) in southwestern Colorado around 27.8 million years ago (Mya). La Garita is the largest known explosive eruption in Earth's history, ejecting around 5,000 km<sup>3</sup> of material. La Garita was followed by four VEI 8 eruptions of the Yellowstone Hotspot (Blacktail Tuff, 1,500 km<sup>3</sup>, 6 Mya; Kilgore Tuff, 1,800 km<sup>3</sup>, 4.5 Mya; Huckleberry Ridge Tuff, 2,500 km<sup>3</sup>, 2.1 Mya; and Lava Creek Tuff, 1,000 km<sup>3</sup>, 640,000 years ago). Tuff is a type of rock consisting of consolidated volcanic ash. The survival stress from these ecological disasters possibly weakened horse and camel genera to the point that they could not resist the extinction pressures from the invasion of human populations around 11,000 years ago.

This speculation is consistent with the somewhat controversial Toba catastrophe theory, which suggests that the Toba VEI 8 eruption between 69,000 and 77,000 years ago on Sumatra, Indonesia, caused a global volcanic winter lasting between 6 and 10 years and possibly a 1,000-year-long cooling episode which nearly wiped out the human race. The Toba eruption ejected around 2,800 km<sup>3</sup> of material, a little more than half of that ejected by La Garita. The Toba catastrophe theory is a proposed explanation for the bottleneck in human evolution that occurred around that time, which has been verified by DNA analyses.

Other Oligocene genera that have disappeared from North America include the horse-like *Hyracodon* (four species), the rhinoceroses *Subhyracodon* (three species), *Diceratherium* (five species), and *Menoceras* (three species).

Several genera of carnivorous bear dogs, such as *Daphoenodon* (five species), *Daphoenus* (three species), and *Temnocyon* (three species), were among the predators that kept the populations of North American herbivores in check. Fifteen or sixteen genera of true dogs, such as *Leptocyon* (two species) and



*Archaeocyon* ("beginning dog", three species), also helped fill the predator niche. Also working the predator niche were six genera of false saber-toothed cats, such as *Dinictis* (five species) and *Hoplophoneus* (seven species).

This is only a minuscule sample of fossil fauna from the North American Oligocene. Whether the richness of the North American fossil record reflects a true population or is simply an artifact of superior collection opportunities is unclear.

As the Cenozoic Period became modern times, the most significant, though not necessarily the most favorable, event in the history of life occurred: a unique primate evolved. This primate is the only species to understand how big the Universe is and how it works. It's the only species to move beyond being merely self-aware, but to speculate on the existence of something beyond all life as we know it. It's the only species to leave Earth and visit another place in the Universe. It's the only "higher species" (one more complex than microbes or insects) to have made a home everywhere on Earth. It's the only species capable of wholesale destruction of all higher forms of life and has teetered on that brink a couple of times before sanity returned. It's the only species capable of globally altering the Earth. It's a species that single handedly has driven numerous other species to extinction and that threatens countless more either directly or through loss of habitat. But, unfortunately, for all its brilliance and power, this species still does not fully understand itself.