Most of the fossil evidence of primate evolution from North America comes from a series of geological basins in the Rocky Mountain region that contain fossil-bearing sedimentary deposits dating to the Early Cenozoic era (post-65 million years ago (Ma)). While these deposits range from Mexico to Canada, most North American fossil primates have been recovered in Montana, Utah, Colorado, New Mexico, Texas, and especially Wyoming. The American West is where the nineteenth-century origins of vertebrate paleontology can be found, as a result of the pioneering work of men like Joseph Leidy, Edward Drinker Cope, Othniel C. Marsh, and Henry Fairfield Osborn. Among the plethora of new fossil mammals named and described by these early American paleontologists are the first primates discovered in North America, including well-known Eocene taxa like *Omomys* (1869), *Notharctus* (1870), and *Hemiacodon* (1872).

Today, the American West remains a rich source of fossil primates and other mammals from the Early Cenozoic and an area of intense fieldwork by multiple research teams interested in the early stages of primate and mammalian evolution.

Any discussion of fossil primates in North America must start with a determination of which fossil taxa should be included within the Order, and this problem is particularly contentious when dealing with the earliest potential primates, the extinct Plesiadapiformes. A highly diverse group of mostly Paleocene, Laurasian (i.e., found in Laurasia, an ancient, northerly landmass that eventually divided into the European, Asian, and North American landmasses) arboreal mammals, Plesiadapiformes has long been considered to be the sister taxon of Euprimates, and have been included either as a Suborder within Primates or as a separate Order of archaic, primate-like mammals. While several plesiadapiform genera are known from partial skeletons (*Plesiadapis* and *Carpolestes* from the Bighorn Basin of Wyoming) or skulls (*Ignacius* from the Bighorn Basin of Wyoming, and *Palaechthon* from the San Juan Basin of New Mexico), most of the fossil evidence of the group is restricted to jaws and teeth. The molar teeth of plesiadapiforms resemble those of early euprimates in a series of features, including the presence of low and rounded cusps, low trigonids (the three major cusps of the lower molars) and broad talonids (the low basin or “shelf” at the posterior end of lower molars), long lower third molars with hypoconulids (the distal-most cusps on the talonids of the lower molars), and quadrate (four-cusped) upper molars with hypocones (one of the main cusps, on the distal-lingual part of the tooth). Conversely, the anterior dentition among plesiadapiforms is extremely derived and typically includes large and procumbent central incisors, and the loss of lateral incisors and sometimes canines, with resultant large diastemas (a gap in the middle of the tooth row) and reduced dental formulas.

While certain features of the auditory bulla (a hollow bony protuberance enclosing the middle and inner ear) and internal carotid circulation may link some plesiadapiforms with euprimates, the overall form of the plesiadapiform skull and skeleton is distinctly more primitive than that of living primates. Plesiadapiforms have long snouts with small braincases and laterally facing orbits, they lack postorbital bars and petrosal bullas (part of the petrosal bone that protects the ear and which is a distinguishing feature of euprimates), and they retain claws on all digits of their nonopposable hand and foot—with the exception of *Carpolestes* which, uniquely among plesiadapiforms, had an opposable, nail-bearing hallux or big toe (Bloch and Boyer 2002).

This curious combination of dental features suggests that plesiadapiforms had undergone a shift from insectivory to herbivory, although
certainly the 11 identified families with more than 40 included genera (Rose 2006) would have presented much adaptive and dietary variability. Furthermore, it is generally well accepted that most plesiadapiforms were too derived to have been directly ancestral to any Eocene euprimates. One plesiadapiform that lacked major anterior dental specializations and reduced dental formula was *Purgatorius*, from the earliest Paleocene of McCone County in eastern Montana. While a phylogenetic relationship between *Purgatorius* and Euprimates was first suggested over 40 years ago, based entirely on dental similarities, a recent study of its ankle bones (Chester et al. 2015) strongly suggests that *Purgatorius* was a nimble arboreal climber that may have been seeking out the flowers and fruits available in the forest canopy with the spread of angiosperms (flowering plants) in the immediate aftermath of the mass extinction at the Cretaceous–Paleogene boundary at 65 Ma. This transition may very well mark the adaptive shift that led to the evolution of all later primates.

As the Paleocene came to an end at ca. 56 Ma, plesiadapiform diversity was in serious decline, and by the Middle Eocene, their extinction was complete. In fact, the Paleocene–Eocene boundary has long been recognized as a locus of major faunal turnover from an archaic to a more modern mammalian fauna, marked by the first appearance and dispersion across the northern continents of a number of modern mammalian Orders including Primates, Artiodactyla (even-toed ungulates), Perissodactyla (odd-toed ungulates), Rodentia, and Carnivora. Eocene (eu)primates are characterized by the suite of morphological features that has long defined the Order, including reduced snouts and olfaction, postorbital bars and forward-facing orbits, color vision, petrosal bullae, grasping limbs with nails, and an opposable hallux. Faunal turnover and dispersal at the Paleocene–Eocene boundary are coincident with perhaps the most significant global warming event in the entire 65 million years of the Cenozoic era, the so-called Paleocene–Eocene Thermal Maximum (PETM). Marked by an extraordinary negative excursion in the carbon isotopic signature of both marine and terrestrial sediments from around the globe, the PETM was likely caused by an enormous injection of methane (CH₄) into the atmosphere from marine clathrate deposits (methane trapped within water in ice-like structures) and resulted in extreme ocean acidification and an increase of average global temperatures of about 5°C, occurring over a period of perhaps 20,000 years (Zachos, Dickens, and Zeebe 2008). Study of the PETM supports the notion that climate change has been a major driver of evolutionary change in the past, as evidenced by apparent dwarfing of earliest Eocene horses in the Bighorn Basin (Secord et al. 2008), rapid dispersal of primates (and other mammalian groups) across high-latitude forests between Asia, North America, and Europe (Beard 2008), and the overall very high levels of extinctions and origins that occurred among mammals (including primates) at this time.

Another approach to determining the antiquity of Primates involves molecular estimates of the age of origin of crown clades, and for much of the 1990s, there were large discrepancies between these estimates and the ages of the first known fossils of these clades. While molecular studies put the origin of most placental mammal clades (including Primates) well back into the Cretaceous, often as early as 80 or more million years ago, the earliest fossils of these clades were always post-Cretaceous, sometimes 30 million years younger than the molecular estimates suggested. More recent studies have significantly lessened the discrepancies between molecular, morphological, and paleontological estimates of the origins of crown group placental mammals and of crown Primates, and have served to bring the molecular estimates of clade origins much closer to the age of first appearances of these clades in the fossil record. Steiper and Seiffert (2012) convincingly demonstrated the existence of a slowdown in molecular substitution rates in multiple primate lineages which suggests an origination of crown primates close to the Cretaceous–Paleogene boundary. Yoder and Yang (2004) used multiple gene loci and Bayesian methods to date the origin of crown Lemuriformes to the Paleocene, ca. 62 Ma. Finally, the phylogenetic analysis of an extraordinarily large and complete morphological dataset from 86 fossil and living mammalian species supports an “explosive” radiation of most placents (including Primates) in the Early Paleocene (O’Leary et al. 2013), and this new and emerging consensus
is in good agreement with the fossil record of primate evolution in North America.

The fossil record of North American primates is, to a large extent, the record of two major groups of Eocene forms recovered mostly from the Rocky Mountain region of the United States. These groups are often represented by two superfAMILY-level taxa, Adapidoidea and Omomyoidea, both of which appear rather abruptly at or near the base of the Eocene in North America, most likely as immigrants from Asia in the context of PETM global warming (Beard 1998). Both families are also found in Europe. A common but simplistic interpretation of these earliest Euprimates is that they represent the divergence between Strepsirhini (Adapidae) and Haplorhini (Omomyidae), but this notion is far from established. Certainly, adapoids bear an overall resemblance to the modern tooth-combed strepsirhines of Africa, Asia, and Madagascar—in spite of the fact that no North American adapoids are known to have a tooth comb. Resemblances between adapoids and crown strepsirhines can be identified in details of dental, cranial, and postcranial morphology, but determinations of whether many of these similarities are shared derived features or primitive retentions are often contentious. Similarly, some omomyoids bear striking resemblances to crown haplorhines (especially Tarsius) in some details of cranial (e.g., tubular ectotympanic (the bony ring that holds the eardrum)) and postcranial anatomy (e.g., partial fusion of distal tibia and fibula, elongated calcaneus), but there is again no certainty that any of these resemblances are derived similarities that reflect close phylogenetic relationship.

The morphological and presumed behavioral distinctions between adapoids and omomyoids are often drawn in very broad strokes: adapoids had long snouts and small eyes (reflecting diurnal habits), while omomyoids had large eyes (indicating nocturnality) and reduced snouts; adapoids had large canines and small incisors, while omomyoids had large incisors and small canines; adapoids were larger in body size, ate fruits and leaves, and were arboreal quadrupeds, while omomyoids were small in size, ate fruits and insects, and relied to a great extent on leaping. However, this kind of very generalized comparison almost certainly obscures more than it reveals about the differences between these diverse and speciose groups that together comprise about 75 genera and 180 species (Rose 2006).

Early Eocene Cantius and Middle Eocene Notharctus are the best-known North American members of the adapoid family Notharctidae, being represented by several skulls and skeletons, and thousands of jaws and teeth from, among other places, the Greater Green River and Bighorn basins in Wyoming. Cantius is the oldest and most primitive North American notharctid and is close to the ancestry of all later adapoids (including the entirely European family Adapidae). Detailed studies of Cantius, Notharctus, and other related forms suggest that the notharctid dentition evolved gradually throughout the Eocene to develop hypocones, mesostyles, reduced paraconids, and broad trigonid basins. While both taxa (and indeed most other adapoids) retained a primitive dental formula of 2-1-4-3, the molar teeth of Cantius have bunodont (low and rounded) cusps that reflect a mostly frugivorous diet, while Notharctus has more sharply crested molar teeth that appear better adapted for a folivorous diet. Notharctus also shared a fused mandibular symphysis with nearly all other known adapoids except Cantius. Postcranially, both are quite similar to modern lemuriforms like Lemur and Varecia, with long and powerful hindlimbs and an opposable hallux and pollex. While both Cantius and Notharctus were clearly well adapted for powerful grasp-leaping in an arboreal environment, they were not specialized vertical climbers and leapers.

Compared to the adapoids, omomyoid primates are taxonomically more diverse in the Eocene of North America, with more than 30 genera being represented. These taxa comprise two subfamilies, the anaptomorphines and omomyines, although there has historically been a lack of stability in the placement of certain groups within one or the other subfamily (e.g., members of the tribe Washakiini). The earliest known omomyoid primate, Teilhardina, is known from Europe, Asia, and North America, and it is likely that a species of Teilhardina lies at the base of the entire omomyoid clade. As mentioned above, all omomyoids share certain traits, specifically cranial features (e.g., a short snout and large eyes), that have historically linked them anatomically with tarsiers. However, there does exist within this group diversity in body mass, diet, and, to a
In lesser extent, locomotor adaptations. Omomyoids varied in body mass from less than 500 g to more than 2 kg. Dietary preferences ranged from primarily frugivorous to mixed feeding to primarily faunivorous. Furthermore, while there are strong locomotor similarities found in all North American omomyoids for which we have postcranial material, differences in the degree to which leaping was incorporated have been demonstrated through analyses of the hindlimb.

Three important omomyoid taxa from North America that are well known from both cranial and postcranial remains are *Teilhardina*, *Shoshonius*, and *Omomys*. These taxa can help to illustrate some of the similarities and differences found within Omomyoidea. *Teilhardina* is the most primitive omomyoid and is atypical compared to other omomyoid taxa in that it preserves all four premolars, similar to the early adapoid *Cantius*. Almost all other omomyoids show a reduced anterior dentition, accompanied by the loss of one or two premolars. Strait (1991) has reconstructed the diet of multiple species of *Teilhardina* as largely frugivorous based on measurements of molar shearing. The postcranial skeleton of *Teilhardina* is similar to other omomyids, as well as extant cheirogaleids, in displaying adaptations for climbing and some leaping (Gebo 1988). The postcranial skeletons of the omomyines, *Shoshonius* and *Omomys*, share many similarities with *Teilhardina*, and also exhibit adaptations to an active quadrupedal locomotor style that included climbing and leaping, though with perhaps a greater degree of leaping in *Omomys* (Anemone and Covert 2000; Dagosto, Gebo, and Beard 1999). In addition, all three taxa similarly show no dedicated adaptations toward vertical clinging. However, based on evidence from dental remains, the dietary preferences of both *Shoshonius* and *Omomys* differ markedly from *Teilhardina* in being largely insectivorous (Strait 1991).

Climatic deterioration at the transition from the Middle to the Late Eocene resulted in major environmental changes to the North American ecosystems that had for so long nurtured the existence of tropical-adapted primates. As the climate became cooler and drier, closed-canopy tropical and semitropical forests were replaced by more open woodland–savannah habitats, and by the Late Eocene a single adapoid (*Rooneyia*) and a single omomyoid (*Chumashius*) were all that remained of the enormous diversity of North American primates that had flourished in the Early Eocene. By 35 Ma, primates had disappeared from North America. Essentially the same fate awaited European primates at the Eocene–Oligocene boundary (ca. 33 Ma), when a massive mammalian extinction and faunal turnover event known as the Grande Coupure occurred, also as a result of climatic cooling and aridification. However, a recent paper (Samuels, Albright, and Fremd 2015) about an enigmatic Oligocene fossil known from South Dakota, Nebraska, and Oregon—with the nearly unpronounceable name of *Ekgmowechashala*—indicates that the story of nonhuman primate evolution in North America was not over at the end of the Eocene.

Most authorities consider *Ekgmowechashala* to be a primate of some sort: it has been classified as an adapoid by some and an omomyoid by others, although it has also been argued to be a dermopteran or flying lemur. New and extremely well-dated material from Oregon reported by Samuels et al. (2015) suggests that *Ekgmowechashala* represents an adapoid that migrated from Asia to North America (across Beringea) in the Late Eocene or Early Oligocene, perhaps 6 million years after primates had disappeared from North America. By 26 Ma, during the Late Oligocene, *Ekgmowechashala* met the same fate as its Eocene adapoid and omomyoid precursors. From this point until *Homo sapiens* arrived in the New World (also via Beringia) more than 25 million years later, the North American continent was devoid of any members of the Order Primates.

SEE ALSO: Adapiform; Climate Change and Primate Evolution; Euprimate(s); Omomyid; Origins of Primates—Debates and Controversies; Paleocene and Eocene Primates; Plesiadapiform; *Purgatorius*, *Teilhardina*

REFERENCES


FURTHER READING