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Michael O. Woodburne,
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Michael O. Woodburne¹,
Gregg F. Gunnell², and
Richard K. Stucky³

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ABSTRACT—Climatic warming at the beginning of the Early Eocene Climatic Optimum (EECO) resulted in major increases in plant diversity and habitat complexity reflective of temporally unique, moist, paratropical conditions from about 53–50 Ma in the Western Interior of North America. In the early part of the EECO, mammalian faunal diversity increased at both local and continental scales in conjunction with a major increase in tropicity resulting from mean annual temperatures reaching 23°C and mean annual precipitation approaching 150cm/yr. A strong episode of taxonomic origination (high number of first appearances) in the latest Wasatchian and earliest Bridgerian Land Mammal Ages apparently was in response to these greatly diversified floral and habitat associations along with increasing temperature and precipitation. This is in contrast to a similar increase in first appearances at the beginning of the Wasatchian (Paleocene-Eocene Thermal Maximum, or PETM) that can be traced instead to climate-induced transcontinental immigration. In the later part of the EECO, from Br-1b–Br-3, climatic deterioration resulted in a major loss of faunal diversity at both continental and local levels, apparently mirroring climatic deterioration. Relative abundance shifted from diverse, evenly distributed communities to much less diverse, skewed distributions dominated by the condylarth *Hyopsodus*. Evolutionary innovation through the 53–50 Ma interval included a modest overall increase in body size and increased efficiency in carnivory and folivory as reflected by within-lineage patterns of evolution. Rather than being “optimum,” the EECO engendered the greatest episode of mammalian faunal turnover of the first 15 million years of the Cenozoic era, with both first and last appearances at their highest levels. Both the PETM and EECO faunas were climatically shaped.

¹Department of Geology, Museum of Northern Arizona, Flagstaff, Arizona 86001, U.S.A.
mikew@npgcable.com

²Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.
ggunnell@umich.edu

³Denver Museum of Nature & Science, Denver, Colorado 80205, U.S.A. rstucky@dmns.org

This report highlights the role of climate in shaping faunal dynamics of the early Paleogene. The Early Eocene Climatic Optimum (EECO) recorded the highest mean ocean temperature of the Tertiary period (Wolfe 1978; Wolfe & Poore 1982; Miller et al. 1987; Prentice & Matthews 1988; Zachos et al. 2001, 2008). This phenomenon began about 53 Ma and persisted to about 50 Ma (e.g., Clyde et al. 2001; Zachos et al. 2001, 2008), and occurred in the context of the overall relatively warm conditions that characterized the early Cenozoic from the Paleocene to about medial Eocene. Koch et al. (2003) indicate that the Eocene warm temperature interval (EWI = EECO), began at about chron C23n.2n, coeval with the beginning of the Bridgerian NALMA at 51 Ma. Smith et al. (2008) proposed a revision of the basal age of C23n.2n at about 50.5 Ma but still utilize 53 Ma as the beginning of the EECO.

Zachos et al. (2001) documented early Cenozoic (ca. 66.5–46 Ma) global oceanic temperatures that ranged from 8–10°C (Fig. 1). In addition to the very short-lived PETM (Paleocene-Eocene Thermal Maximum; duration of about 170 ky; Bains et al. 2003; Koch et al. 2003; Wing et al. 2005; Zachos et al. 2008), the ocean temperatures during the EECO surpassed the general range by about 2°C from about 53–50 Ma (increased to about 12°C).

Fossil land plants provide us with estimates of mean annual temperature (MAT) and mean annual precipitation (MAP) for the Western Interior of North America. Fig. 1 indicates that in the late Paleocene, MAT rose from about 10°C to 18°C, based on paleofloras from the Green River Basin and vicinity. During the PETM, MAT increased dramatically to about 20°C and then fell back to about 18°C en route to a low of 15°C in Wasatchian biochron Wa-5, just prior to the beginning of the EECO (about 53 Ma). Subsequently MAT rose rapidly through 17°C (Latham flora, Wa-6, 53 Ma) to about 22°C (Wa-7, Sourdough flora, somewhat younger than 53 Ma), rose further to about 23°C at 52 Ma (Wa-7, Niland Tongue flora), declined to about 20°C in the early Bridgerian (50 Ma, Little Mountain flora, late biochron Br-1a), and then declined further to about 15°C at the time of the Green River flora (about 47 Ma, Uintan biochron Ui-1). Oxygen isotope composition of biogenic apatite from mammal

teeth at the time of the PETM suggests that MAT actually reached 26°C (Fricke & Wing 2004), but for the purposes of this report the plant-based climatic interpretations are followed.

Clyde & Gingerich (1998) report on substantial modification of the land mammal community during the PETM, the effects of which persisted at least into the later part of the Wasatchian North American Land Mammal Age (NALMA). Wing et al. (2005), Wing & Lovelock (2007), and Smith et al. (2007) record strong floral change in the Bighorn Basin during the PETM with a brief virtual disappearance of conifers, but just how this played into the modification of the mammalian community remains to be determined. Wing & Harrington (2001) suggested that changes in the mammalian fauna in the early Wasatchian likely stemmed from competition between endemic taxa and new immigrants (the “individualistic” pattern of Wing et al. 2005), and this seems plausible for post-PETM intervals of the early Wasatchian.

This report focuses on the EECO and the plant and land mammal record from the latest Wasatchian and Bridgerian NALMAs. The earliest Eocene hyperthermal event (PETM) is considered to have abetted intra- and intercontinental dispersal of plants and land mammals (Tiffney 1994, 2000; Gingerich 2003). The land mammal population of the EECO apparently was influenced by a different set of parameters (climate and floral change absent immigration) as developed below and as initially suggested by Stucky (1992, 2007). In developing data for a report such as this we recognize that sampling is likely uneven across the temporal intervals utilized, but at the present scale this cannot be avoided.

The report begins with a brief summary of plant and mammalian evolution during the Late Cretaceous to the early Wasatchian in the Western Interior of North America and then follows that background with an appraisal of the EECO.

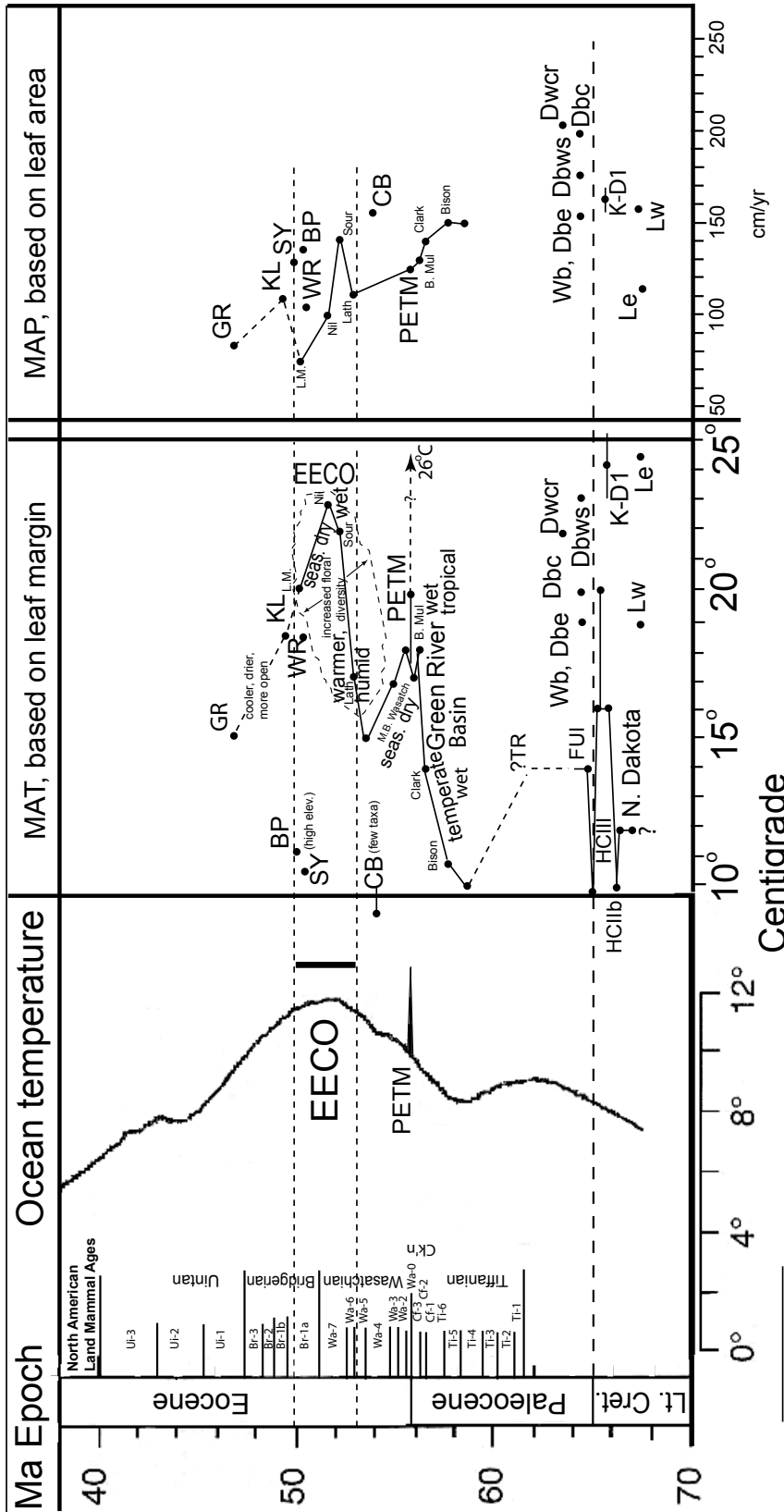


Figure 1. Summary of temperature and rainfall for the Western Interior of North America. Ocean temperatures rose gradually from the late Cretaceous into the early Eocene and then declined toward the late Eocene. The megafossil record responds in a generally similar way at least from the late Paleocene to the late Eocene, with a strong transient excursion at the PETM and a similarly warm interval during the EECO from about 53–50 Ma. During the EECO, mean annual rainfall gradually decreased from about 150cm/yr to 100cm/yr. From about 50 Ma, both MAT and MAP, as well as tropicality, decrease sharply. Sources cited in figure.

Ocean temperature after Zachos et al. (2001)

Green River Basin floras after Wilf (2000): Bison = Bison Basin; Clark = Clarkforkian; B. Mul = Big Multi; M.B = main body, Wasatch Fm; Lath = Latham; Sour = Sourdough; Nil = Niland Tongue; L.M. = Little Mountain. seas. dry = seasonally dry.

Denver Basin floras (Wb; Dbe; Dbw, Dbws) after Johnson et al. (2003). Wb = West Bijou; Dbe = eastern Denver Basin; Dbw = central Denver Basin; Dbws = Scotty's Palm; Dwcr = Castle Rock. Lw = western Laramie Fm. (CO); Le = eastern Laramie Fm.

Other floras after Wing and Greenwood (1993) and Wilf et al. (1998). BP = Bear Paw (MT); SY = Sepulcher (Yellowstone); CB = Camels Butte, GR = Green River, KL = Kisinger Lakes, WR = Wind River (WY). The low MAT for BP and SY apparently reflects higher elevation; that for CB is due to there being too few taxa (Fricke & Wing 2004).

North Dakota record after Wilf et al. (2003). HCIIIb and HCIII are from the Hell Creek Fm.; FUJ is from the Fort Union Fm.; ?TR is Tongue River flora possibly similar to FUJ.

Line showing PETM MAT at 19.8 °C based on Wing et al. (2005); dashed line and arrow increase to 26 °C based on bone isotopic data (Fricke & Wing 2004) is not used in the text.

Methods

Definitions and Abbreviations

CIE: Carbon Isotope Excursion, sharp decrease in $\delta^{13}\text{C}$ recorded at the beginning of the Sparnacian stage/age and the Wasatchian NALMA (Thiry et al. 2006); CIE lasted about 86,000 years (Bains et al. 2003; Koch et al. 2003).

EECO: Early Eocene Climatic Optimum (see text).

Elmo: Hyperthermal event that transpired about 53 Ma, duration about 46,000 years; estimated to reflect an ocean temperature increase of 3–4°C, or about one-half the magnitude associated with the PETM (Lourens et al. 2005).

FAD: First Appearance Datum, first stratigraphic occurrence of a taxon, considered to have been synchronous over a specified geographic region (Woodburne 1996).

Hyperthermal: Brief interval of extreme global warmth and massive carbon addition (Zachos et al. 2008).

ky: Kiloyear, a segment of geologic time 1,000 years in duration or the age of an event (e.g., 200,000 years ago) without reference to a point or a set of points on the radioisotopic timescale.

LAD: Last Appearance Datum, last stratigraphic occurrence of a taxon, considered to have been synchronous over a specified geographic region (Woodburne 1996).

Ma: Megannum. One million years in the radioisotopic timescale (e.g., 10 Ma refers to the 10 million year point on the timescale).

m.y.: Segment of geologic time 1 million years in duration or the age of an event (e.g., 10 million years ago) without reference to a point or a set of points on the radioisotopic timescale.

NALMA: North American Land Mammal Age (Woodburne 2004), an interval of time based on mammalian biochronology. Tiffanian, Clarkforkian, Wasatchian, Bridgerian, and Uintan NALMAS are discussed in this report (see Fig. 1).

PETM: Paleocene-Eocene Thermal Maximum, short-term dramatic pulse of global warming at the Paleocene-Eocene boundary.

Suprageneric group: Collective term for any taxonomic group above the genus, generally following the classification of McKenna & Bell (2002).

Floral Terms

(Vegetation Classification of Graham 1999)

Tropical forest (paratropical to tropical): MAT ca. 25°C; subhumid, MAP ca. 165cm/yr; little seasonality; growth rings absent to weak; broad-leaved, evergreen, single-tiered, open canopy vegetation; leaves mostly entire-margined, thick textured, few drip tips.

Tropical rain forest: mean temperature of coldest month not below ca. 18°C; MAT ca. above 25°C; MAP above 165cm/yr; no pronounced dry season; broad leaved, evergreen, multistratal; drip tips, lianas (high-climbing woody vines), and buttressing common (supporting of trees or vines by each other); leaves sclerophyllous, mostly mesophyllous (megaphyllous in substratum); entire-margined leaves majority (above 75%).

Paratropical rain forest (=subtropical of authors): may experience some frost; MAT 20–25°C; no extended dry season; precipitation may be seasonal; floristically like tropical rain forest, mostly broad-leaved evergreens with some deciduous plants; woody lianas diverse; buttressing present; mostly entire-margined leaves (57–75%).

Subtropical forest: frost present but not severe; MAT between 13°C and 18°C; mean of coldest month between 0°C and 18°C; more seasonal rainfall; sclerophylls abundant; few lianas; no buttressing; mostly broad-leaved evergreen forest with some conifers; entire-margined leaves 39–55%.

Notophyllous broad-leaved evergreen forest (ecotonal; oak-laural forest of eastern Asia): mean of coldest month about 1°C; MAT about 13°C; some broad-leaved deciduous trees present; conifers not common; woody climbers abundant; buttressing absent; sclerophyllous; no drip tips; entire-margined leaves 40–60%.

Warm-temperate forest: temperatures fall below 0°C for several months (mean coldest month between

-3°C and 2°C); pronounced seasonality in climate; MAT between 11°C and 13°C; broad-leaved deciduous forest, with conifers; broad-leaved evergreens present but not dominant; entire-margined leaves about 30–38%.

Polar-broad-leaved deciduous forest: MAT about 7°C to 15°C; distinct growth rings; leaves large, thin textured.

Megathermal: MAT above 20°C.

Mesothermal: MAT between 20°C and 13°C.

Microthermal: MAT less than 13°C.

Modern counterparts of plant families and other suprageneric groups referred to in the text are from Stevens (2007) and Heywood (1993).

Mammalian Ecological Categories

Herbivore: utilizing plant resources including both high-energy and low-energy herbaceous foliage.

Insectivore: utilizing high-energy insect or arthropod resources.

Hypercarnivory: utilizing exclusively high-energy vertebrate resources.

Carnivore: utilization dominated by high-energy vertebrate resources but may include other high-energy resources (insects, invertebrates).

Omnivore: food dominated by high-energy fruits, seeds, and insects but may also utilize high-energy vertebrate resources.

Small size: less than 1 kilogram.

Medium size: 1 to 10 kilograms.

Large size: greater than 10 kilograms.

Mammalian Biochrons

The mammalian biochron timescale (Fig. 1) follows Secord et al. (2006) for the interval from Tiffanian biochron Ti-3–Wasatchian biochron Wa-1, and Woodburne (2004; Fig. 8.5) from Wa-1–Wa-4. Biochron Wa-M (Gingerich & Smith 2006) is included in Wa-0. The intervals Wa-4 through the early Uintan NALMA follow Smith et al. (2008). The PETM correlates to the beginning of Wa-0 (Koch et al. 2003) at 55.8 Ma (Secord et al. 2006; but see Lourens et al. 2005). The Bridgerian revision (Smith et al. 2008) has the effect of lowering

the Wa-7–Br-1a boundary to about 51 Ma relative to that shown in Woodburne (2004). In addition, Br-0 is not used as the basal biochron of the Bridgerian, based on the observation that the Gardnerbuttean subage is indistinguishable from those typically designated as Br-1a (Gunnell & Stucky, pers. observation). In this report, the faunas of Br-0 and Br-1a in the literature are combined into a single unit, Br-1a.

Floral Background

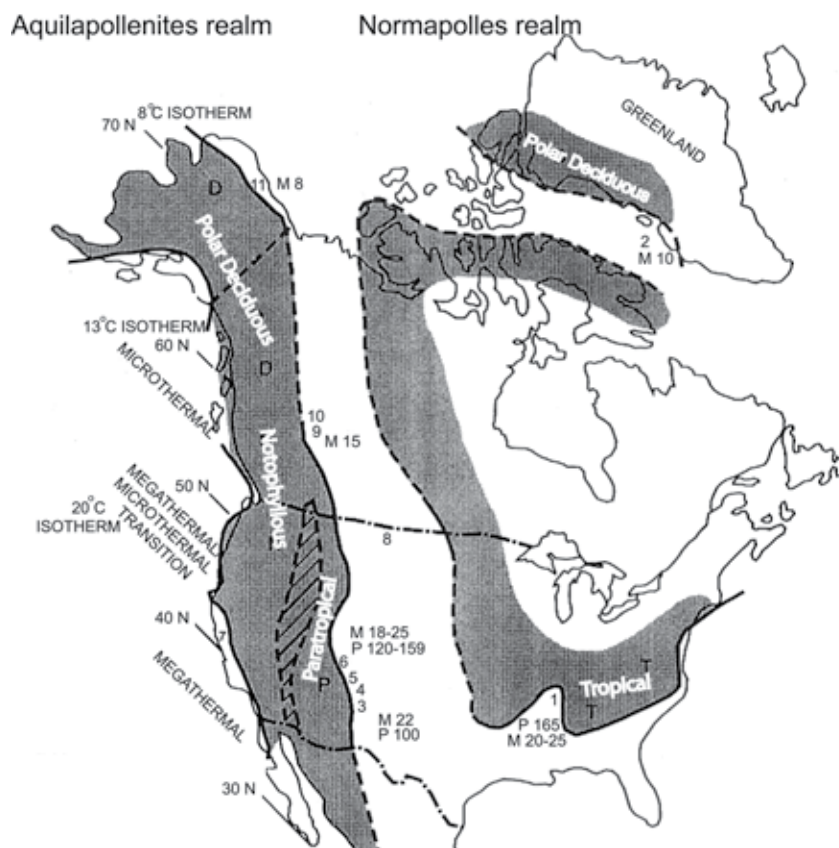
This section provides a summary of the past floral and climatic setting for the late Paleocene–early Eocene interval in western North America prior to a consideration of the mammalian faunas that lived during those times. Floras of the Late Cretaceous and early Paleocene are briefly summarized to provide basal perspective.

Late Cretaceous Floras and Climate

Graham (1999: 150) suggested that Late Cretaceous floras in North America indicate warm climates that overall are drier in the southeast and progressively wetter and more seasonal westward and northward. Late Cretaceous floras commonly appear to have been drier than those of the Paleocene.

Overall climatic conditions in the Late Cretaceous were warmer and at least seasonally drier in the eastern part of the United States than to the west and north (Graham 1999). The boundary between megathermal and mesothermal conditions at present is about 30° N (versus 45° N in the Maastrichtian; Fig. 2); that between mesothermal and microthermal conditions at present is 45° N (versus 65° N in the Maastrichtian). This indicates a much shallower temperature gradient in the Maastrichtian than at present.

In general terms, it appears that angiosperms diversified in the Maastrichtian with all major dicot groups represented. Gymnosperms also were diverse, as represented by the Cupressaceae (evergreens similar to *Sequoia* as well as cypress) in an emergent open canopy woodland, especially in the Western Interior (localities 3–6, Fig. 2 and Graham 1999: 157). At the continental scale, monocots were represented by palms and Zingiberales (herbs). Dicots included magnolias, Hamamelidae



After Graham (1999; fig. 7.8)

Figure 2. Aquilapollenites realm and Normapolles realm reflect the distribution of pollen of those types. M = MAT (mean annual temperature). P = MAP (mean annual precipitation). Localities: 1, McNairy Sand Formation, Tennessee; 2, Lower Atanekerdluk Flora, Greenland; 3, Vermejo Flora, Texas; 4, Raton Basin, New Mexico; 5, Denver Formation, Colorado; 6, Laramie Formation, Colorado; 7, Patterson Flora, California; 8, Hell Creek-Lance basins, Montana; 9, Scollard, Alberta; 10, Coalspur, Alberta; 11, Prince Creek, Alaska. 70 N, etc., are paleolatitudes.

(witch hazel), Aceraceae (relatives of the living maples), Ranunculidae, Dilleniidae, and Saxifragaceae (saxifragas: currant, gooseberry, hydrangea), which formed a low understory beneath the conifers.

Western North American megafloreal sites are mostly found along the western margin of the midcontinental seaway from which the *Aquilapollenites* group extends to Asia (Fig. 2). Paleofloras in western New Mexico, Colorado, and the Powder River Basin of Wyoming and Montana reflect paleolatitudes of about 40–46° N. These sites record paratropical forests composed mostly

of broad-leaved evergreens with about 71% entire-margined leaves. MAT is 21–22°C (low megathermal) in the south and 18°C (mesothermal) in the north (Powder River Basin). MAP ranged from about 100cm/yr in the south to 120cm/yr in the north.

Denver Basin. Johnson et al. (2003) indicated that all Denver Basin floras were dominated by dicotyledonous angiosperms, with conifers playing a lesser role as compared to contemporaneous floras in Wyoming. In the Late Cretaceous there appears to be a pre-orogenic Laramie Formation flora (Lw, Le: Fig. 1) and a synorogenic D1

flora. Both appear generally similar, relatively diverse, and spatially heterogeneous, similar to those of the Hell Creek Formation in the Dakotas.

Floras from the Laramie Formation, 68–69 Ma, are dominated by dicotyledonous angiosperms, and lesser amounts of ferns, palms, and herbaceous lycopods. Sites in the western part of the area adjacent to the present Front Ranges (Lw: Fig. 1) give a MAT of about 19°C and a MAP of about 159cm/yr, whereas those in the far eastern part of the area (about 100 km distant; Le: Fig. 1) give a MAT of about 25°C and MAP of about 118cm/yr (see Johnson et al. 2003: fig. 4).

One of the youngest Cretaceous floras, from the K-D1 sequence (about 66 Ma), is dominated by dicotyledonous angiosperms, with abundant palms, other monocots, ferns, and herbaceous lycopods. Conifers and cycads are rare. MAT is about 23–26°C, MAP 155–169cm/yr. In general, the Denver Basin floras lived under warmer conditions than those of the Williston Basin and other sites to the north.

Williston Basin. Johnson (2002) showed that Late Cretaceous forests from the Hell Creek Formation of southwestern North Dakota and adjacent areas in the Williston Basin (Fig. 3) were composed of angiosperm-dominant floras with a minor (10%) component of other plants. Three floral zones were recognized, as well as two multifacial megafloras. The uppermost, HCIII flora (Fig. 1), which lived just prior to the K-T boundary, is significantly more diverse than previous Hell Creek floras and suggests strong climatic warming 300–500 ky before the end of the Cretaceous. Wilf et al. (2003) estimated a MAT of 16–18°C, with a short-lived peak of about 20°C for the HCIII flora. A lithofacies-limited HCIIb flora (Fig. 1) is composed of mostly herbaceous plants and may indicate a locally cooler interval (10°C or less).

The Hell Creek Flora angiosperms include a diverse association of Lauraceae, Platanaceae, Magnoliaceae, Cericidiphyllaceae, Araceae, and Arecaceae (Palmae), as well as Berberidaceae, Ranunculaceae, Cannabaceae, Urticaceae, Ulmaceae, Malvaceae, Rosaceae, Rhamnaceae, and Cornaceae. Trees are typically small- to medium-sized and commonly have lobate leaves. Non-angiosperm elements of the Hell Creek Flora are rare ferns, a cycad, a ginkgo, and cupressacean conifers (similar to *Sequoia*).

Early Paleocene Floras and Climate

Graham (1999: fig. 5.12) showed that in the early Paleocene the midcontinental seaway was largely gone and a tropical rain forest on the east coast gave way on the eastern margin of the Rocky Mountains district to paratropical rain forests in the Wyoming-Montana region, and to polar deciduous broad-leaved deciduous forests to the north (South Dakota; Alberta). As indicated in Fig. 1, the oceanic temperature shows a gradual rise from about 8°C at the K-T boundary to a peak of about 9°C near the medial Paleocene at ca. 61 Ma (Zachos et al. 2001).

The Paleocene plant record summarized in this report behaved nearly in concert with the oceanic temperatures except that the actual temperatures and their ranges were greater on land than in the ocean (Fig. 1). The Rocky Mountains began to be uplifted in the Late Cretaceous and early Paleocene (Raynolds 2002), adding to the potential climatic and habitat diversity of the region.

Denver Basin. Johnson et al. (2003) arranged the early Paleocene floras of the Denver Basin into three subgroups. In the east (Fig. 1: Dbe), at about 65–64 Ma, MAT is about 19°C and MAP 155cm/yr. Floras represent angiosperm-dominated fluvial and lacustrine settings, with swampy sites supporting palms, sycamores, and Cupressaceae.

Barclay et al. (2003) described the early Paleocene West Bijou Site flora from the eastern Denver Basin, recovered a few meters above the K-T boundary (Fig. 1: Wb). This early Paleocene flora has 49 leaf types distributed among dicotyledonous angiosperms (74%), monocotyledonous angiosperms (10%), ferns (11%), and conifers (5%). Dicots show 36 morphotypes and dominate the flora. The palm, *Sabalites* sp., is a common monocot. Deposits reflect mainly floodplain environments, with local ponds and swamps. MAT is 19°C and MAP ranges from 152–305cm/yr, probably closer to 155cm/yr. The West Bijou angiosperm-dominated flora is typical of the Fort Union I (FUI) floras of the Great Plains. Johnson & Hickey (1990) considered the floras impoverished relative to those of the Late Cretaceous.

The West Bijou flora represents a broad-leaved forest that lived on a low-relief floodplain with local



Figure 3. Map of localities for the main late Paleocene and early Eocene floral samples in North America, from various sources.

conifer-dominated swamps (Barclay et al. 2003). The climate was warm and equable: palms show lack of freezing; crocodiles and champsosaurs indicate wet, warm conditions. Paleocene deposits also include gar scales and large turtles. Drab-colored soils suggest a lack of summer oxidizing conditions.

In the central part of the Denver Basin (Fig. 1: Dbc), early Paleocene floras indicate a MAT of 19–21°C and a MAP of 196cm/yr. Floras are not as diverse as those to the west and have different species composition than those to the east. Dicotyledonous angiosperms dominate, and palms and ferns are locally common. Conifers are very rare.

In the west, an early Paleocene site (Scotty's Palm, Fig. 1: Dbws) has a MAT of 23°C and a MAP of 179cm/yr, and angiosperms dominate. Stratigraphically higher, the Castle Rock flora (ca. 64 Ma, Fig. 1: Dwcr) indicates a MAT of 22°C and a MAP of 204cm/yr. The Castle Rock flora is very diverse and considered to reflect a paratropical rain forest setting. Another site, Sick of Sycamores, stratigraphically and geographically similar to Castle Rock, is dominated by a large-leaved sycamore, with a MAT of 18°C and a MAP of 233cm/yr, about 3°C cooler and substantially wetter than the very nearby Castle Rock site.

Williston Basin. Johnson (2002) described the FUI flora from the Ludlow Member of the Fort Union Formation (Fig. 1). The FUI flora was considered depauperate relative to the Hell Creek floras and was dominated by taxa previously characteristic of plants that lived in coal swamp to brackish wetland conditions in the Late Cretaceous. This floral facies coincided with the development of the Cannonball seaway in southwestern North Dakota, which began locally in the Late Cretaceous but expanded in the early Paleocene. The impoverished Ludlow Flora is composed of a few ferns, no cycads, no ginkgoes, and a few conifers (Cupressaceae). The angiosperms continued to dominate, but are much less diverse than those of the Hell Creek and are composed of many fewer families. Platanaceae, Cercidiphyllaceae, and Cornaceae persevere, along with less common Betulaceae and Flacourtiaceae. Palms are present in the basal 20m of the Fort Union Formation, as well as in the uppermost 20m of the Hell Creek Formation, possibly reflective of moist lowland conditions

associated with the Cannonball Sea. Numerous aquatic plants included the extinct *Quereuxia*, *Limnobiophyllum*, *Ceratophyllum*, *Paleonelumbov Nelumbium*, cf. *Harmsia*, *Paranymphaea*, and *Porosia*. Overall (and except for the palms), these plants seem to be survivors of the coal-lignite facies uncommonly found in the Late Cretaceous but recognized in the latest Cretaceous Ludlow Member of the Fort Union Formation (FU0 facies), where it locally occurs stratigraphically below the K-T boundary. Elements of the Ludlow Member flora persist and comprise the entire association in the early Paleocene, comparable to that of the West Bijou flora of the Denver Basin, although they apparently lived under somewhat cooler conditions (Fig. 1).

Medial Paleocene Floras and Climate

Fig. 1 shows a lack of floras of about medial Paleocene age (61–64 Ma). Apparently (Graham 1999) Greenland coastal communities were represented by a mesothermal climate (163R), whereas those to the south (Big Bend, Texas) contained trees without growth rings in a megathermal climate. In between those extremes, a paratropical rain forest occupied the Western Interior region (Graham 1999).

Johnson (2002: 373) notes that the early Paleocene conditions in the Williston Basin area likely continued into the medial Paleocene, as recognized by Williams (1988) in the Tongue River Member of the Fort Union Formation. Several species in this flora apparently persist from the Ludlow Member flora and suggest some medial Paleocene stasis in southeastern Montana, at least. Thereafter (from 61 Ma: Fig. 1) oceanic temperatures dropped back to 8°C at about 58 Ma and rose to about 10°C at the end of the Paleocene.

Late Paleocene and Early Eocene Floras and Climate

In the late Paleocene, microthermal vegetation was found in the high northern latitudes, and only in the far north was there an apparent response to lack of winter sunlight. The late Paleocene–early Eocene Thyra Ø flora from northeastern Greenland includes numerous angiosperms mixed with broad-leaved evergreens, indicating

a MAT of 15–20°C and a nearly frost-free microthermal climate in the extreme far northeast (Graham 1999).

Greater Green River Basin. Wilf (2000) studied floras of late Paleocene and early Eocene age from the greater Green River Basin of North America (Green River, Great Divide, Washakie, and Sand Wash basins: Fig. 3). In this region, three major episodes of floral change are recorded. The first was in the early Clarkforkian NALMA, where an increase in temperature from temperate to subtropical conditions (12–19°C; 130–150cm/yr precipitation) was accompanied by an influx of rare tropical taxa (Fig. 1). Mild climates with some seasonality occurred in the early Wasatchian, as MAT dropped to about 15°C (rainfall apparently about 100cm/yr).

The second major change involved floras of the middle and late Wasatchian (Lysitean [=Wa-6] through Lostcabinian [=Wa-7]) and early Bridgerian, at the beginning of the EECO. An increase in MAT to tropical conditions occurred along with a major increase in floral diversity (MAT increased to around 23°C and rainfall to 140cm/yr). Thereafter, MAT retreated to about 20°C and seasonally drier conditions developed in the early Bridgerian at about 50 Ma (L.M., Fig. 1), representing the third floral turnover.

The Latham flora (Fig. 1) at the beginning of the EECO (53 Ma) indicates that MAT was about 17°C, MAP about 120cm/yr. This flora records a major influx of tropically adapted plants indicating mild, humid conditions. New plants include palms, ginger, the tree fern (*Cnemidaria*), and aquatic fern (*Salvinia*) of tropical to subtropical affinity. Wet conditions are indicated by ferns as well as the contemporaneous Latham Coal, but surrounding areas (not at the depocenter) may have been drier (Wilf 2000). The subtropical climate indicated by this and the Sourdough and Niland floras separate the seasonally dry conditions of the (earlier) Wasatch Formation from those of the later Green River Formation.

The Sourdough flora (Fig. 1: MAT 21°C, MAP 140cm/yr) recorded a return to high temperatures and humid conditions at about 52 Ma (Lostcabinian). Dicot families of tropical affinity and persistence of thermophilic non-dicots (palms, ginger, tree ferns, ferns) indicate high temperatures. Thick leaves show that this

was a broad-leaved evergreen forest. Hydrophilic plants include water lily, horsetails, and ferns. Subtropical conditions are derived from the presence of deciduous alder, poplar, and the hickory-like *Platycarya*. The Sourdough flora shows an 87% species turnover relative to those of the Paleocene and shares many species with Lostcabinian floras of the Elk Creek section of the Bighorn Basin (Wilf 2000).

Subsequently, temperatures rose again, as indicated by the Niland Tongue flora at ca. 51.5 Ma, where MAT was about 23°C, MAP 100cm/yr (Fig. 1). Plants were like those of the Sourdough flora, with subtropical and tropical pollen as well; moist conditions are reflected by coal beds, horsetails, and species of ferns, but precipitation was less than at the time of the Sourdough flora (Wilf 2000). The Tipton Shale follows the Niland Tongue and shows more seasonally arid conditions (along with the overlying Wilkins Peak Member of the Green River Formation: Roehler 1993).

As indicated on Fig. 1, the Little Mountain flora (Wilkins Peak Member and Laney Shale of the Green River Formation in southwestern Wyoming; Smith et al. 2007) is of early Bridgerian age (late Br-1a, ca. 50 Ma) and records a MAT of about 19.6°C and a MAP of about 75.8cm/yr (Wilf 2000). The still warm subtropical climate was somewhat cooler than in the Niland Tongue, and rainfall more seasonal. Roehler (1993) and Smith et al. (2008) report the beginning of evaporitic deposition in the Green River Formation at about this time (also Carroll et al. 2008). Among other plants, this flora contains occasional ferns, horsetails, and hornwort, modern representatives of which live in shallow to ephemeral freshwater habitats of tropical to subtropical regions.

The Little Mountain flora is highly species-rich and diverse, with many new species. Eighty-six percent represent first appearances, and 88% of the species from the Sourdough and Niland Tongue floras are not found at Little Mountain, all of which indicates a strong floral turnover at this time. Floral affinities of Little Mountain are with the Green River, Wind River, and Florissant floras (Wilf 2000; see Fig. 3) and reflect increased deterioration from the wetter conditions in the earlier part of the EECO.

Bighorn Basin. Wing et al. (1995) integrate the Paleogene mammalian and megafossil plant record of the Bighorn Basin region, which contains abundant plant as well as mammalian fossils in conjunction with each other in a well-documented biochronological framework. Wing et al. (1995), employ Appearance Ordination Event methodology to derive not only estimates of taxonomic richness but also the calibration of the sample ages. In the following discussions and in Figures 4–9 emphasis is placed on NALMA temporal assignments rather than numerical ages. Similar to Maas et al. (1995) the mammalian biochronological succession ranges from Puercan through Wa-7 NALMAs (Fig. 4), and includes data from the Crazy Mountain Basin, Montana, as well as the Bighorn, Wind River, and Powder River basins of Wyoming (Fig. 3).

As indicated in Fig. 4, Wing et al. (1995) showed a base level of about 12 mammalian genera in the Puercan. In the Torrejonian this rose to about 50 genera, and dropped to about 45 genera in the early Clarkforkian. The number of genera rose to about 60 in the late Clarkforkian, and peaked at about 75 genera in the medial Wasatchian (ca. 53 Ma). The number at the end of the Wasatchian fell to about 68 genera (at about 50 Ma). Two times of steep rise in generic diversity are recorded from the Puercan to the Torrejonian and from the Clarkforkian to medial Wasatchian.

The correlated megafossil plant record shows an increase from only a few species in the Puercan to about 35 species for the late Paleocene, a climax of about 40 species in the early Clarkforkian, and a sharp decline at the Paleocene/Eocene boundary (to 26 species). This proportionality is preserved in Wing (1998), although actual taxon counts are somewhat greater. The pattern is concurrent with a rise in mammalian diversity and apparently increasing MAT.

The MAT reconstruction in Wing et al. (1995) is somewhat more positively linear than in Wing (1998). As indicated in Fig. 5, MAT rose in the Paleocene from about 13°C in Cf-1 to 14°C in Cf-2 to its peak in Cf-3 at 18°C. For the Eocene (using Wa-1 as the beginning of the Eocene), MAT is at about 18°C in Wing (1998). Plant species' richness falls to about 40 in Wa-2, rises briefly to

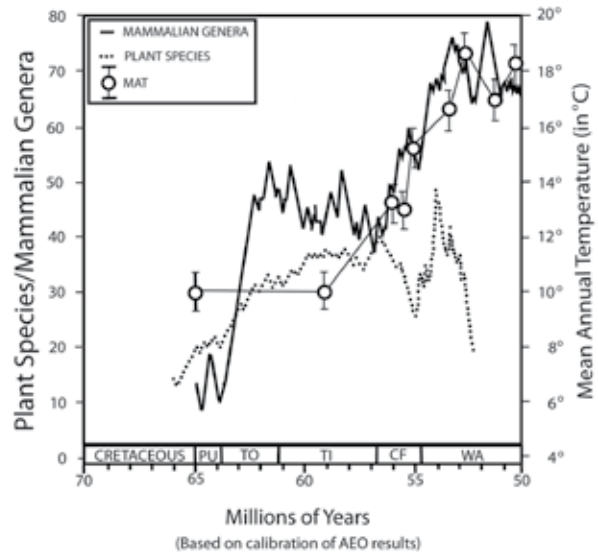


Figure 4. Census of plant and mammalian diversity for the Late Cretaceous to late Wasatchian (Wa-7) of the Bighorn Basin, Wyoming, after Wing et al. (1995: fig. 6). Mammalian generic diversity is calculated using Appearance Ordination Event methodology.

near 45, and then falls again to about 40 with a MAT of about 16°C (Wa-3). Richness falls unevenly to a low of 33 in Wa-4 (MAT of 11°C), recovers to a local plateau of 37 (MAT about 15°C) in Wa-6, and rises abruptly to a high of 54 (MAT of 22°C) in Wa-7. With the possible exception of a MAT of 11°C in Wa-4, these estimates of MAT are comparable to those of Fig. 1. In the Eocene part of the record, the trend in floral richness follows that of MAT.

Wing (1998) indicated that many of the floral novelties that occur in Wa-7 are interpreted as having living representatives of subtropical to tropical distribution. On the other hand, Wing (1998) noted that one of earliest occurrences of diverse tropical plant types is recorded in Wa-6 (see Latham Flora, Lath, Fig. 1), which has a MAT of 17°C, and that the subsequent diversity of Wa-7 plants is consistent with its higher temperature (Wa-7 MAT of 22°C). Wing (1998) also points out that many megafossil plants that appear in the beginning of the Clarkforkian are characteristic of extant subtropical to tropical climates (ginger and banana families and cycads) and others of that climatic affinity also are present in Wa-1 floras. Still, yet others present in Wa-1 assemblages are

Bighorn Basin estimated late Paleocene and early Eocene MAT and plant standing richness

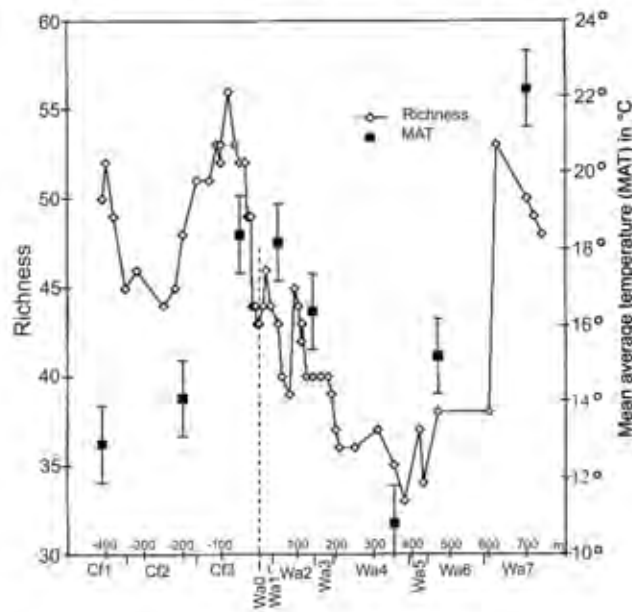


Figure 5. Based on samples from the Bighorn Basin and adjacent areas in the Western Interior of North America, after Wing (1998: fig. 17.11; Wasatchian biochrons supplied by A. Chew). Note that biochron Wa-0 was poorly documented in 1998.

of temperate to subtropical affinity. Overall, the record reported in Wing et al. (1995) and Wing (1998) is comparable to that of Wilf (2000) for the Green River Basin and is summarized in Fig. 1.

Other areas. The Kisinger Lakes and Wind River Basin floras to the west and southwest, respectively (Fig. 3), record MAT levels somewhat cooler and more moist than Little Mountain (Wing & Greenwood 1993; Wilf et al. 1998). According to Graham (1999), the Kisinger Lakes flora reflected a subtropical forest (wet summers, dry winters) and the Wind River flora apparently was comparable.

Summary. Based on the above information, floras associated with the EECO in western Wyoming reflect a sharp increase in MAT to 23°C, with wet, paratropical conditions at its beginning and then a retreat to more seasonally dry conditions, but with MAT still at megathermal levels (ca. 20°C). In the later part of the early

Bridgerian (ca. 50 Ma), Wilf (2000) interprets the MAT at near 20°C and a MAP of 80cm/yr, with conditions becoming drier and more seasonal (less tropical). The Wasatchian–Bridgerian turnover apparently reflected initial increased tropicality with subsequent development of seasonal aridity, and seems to have been the main influence for changes in primate dominance and diversity near the Wasatchian–Bridgerian boundary (Beard et al. 1992; Gunnell 1998; Wilf 2000), as well as the other changes in mammal faunas discussed below.

Late Paleocene and Early Eocene Mammal Faunal Composition

This section is summarized from the Appendix, Tables 1–5. Fig. 6 shows the expression of generic numbers through the late Paleocene and early Eocene. Fig. 7 is a compilation of the FADs and LADs for each biochron based on the number of taxa involved. Fig. 8 is comparable, except that the percentage relative to the entire fauna is displayed.

Tiffanian

As summarized here, the medial to late Tiffanian represents a background level of faunal dynamics associated with a very small number of immigrants that lived under a moist, temperate climate (MAT about 11°C; MAP about 150cm/yr; Fig. 1: Bison). This interval forms a baseline for comparison with later biochrons.

The medial Tiffanian (Ti-3) begins with a standing crop of mammals that consisted of:

Scansorial or terrestrial, insectivorous-omnivorous

Marsupialia: peradectine didelphids

Lipotyphla: leptictids

Erinaceomorpha: litochoerines, erinaceids, and diacodontines

Soricoidea: nyctitheriids

Ferae: palaeoryctids, cimolestids, pantolestids

Condylarthra: arctocyonids

Arboreal or primate-like, insectivorous-omnivorous

Dermoptera: plagiomenids

Primates: uintasoricine microsyopids, plesiadapids, micromomyids, picrodontids, and carpolestids

Ferae: apatemyids

Small herbivores

Multituberculata: ptilodontoids, taeniolabidids

Primates: paromomyids

Terrestrial diggers

Taeniodonta: stylinodontids

Small- to large-sized herbivores

Condylarthra: oxyclaenids, hypsodontids, and phenacodontids

Pantodonta: titanoideids

Carnivores

Carnivora: viverravids

Mesonychia: mesonychids

Figs. 6–8 and Appendix, Table 2 indicate that Ti-3 has a total of 73 genera and that 13 of these are FADs, with a plesiadapid primate (*Chiromyoides*) being an immigrant (Appendix, Table 3). The remaining 12 new endemic taxa include:

Scansorial or terrestrial, insectivorous-omnivorous

Pantolesta: pantolestids (*Palaeosinopa*)Lipotyphla: *Talpavoides*, *Litolestes*

Arboreal or primate-like, insectivorous-omnivorous

Primates: micromomyids (*Micromomys*) and plesiadapids (*Chiromyoides*; scansorial)

Fossorial

None

Medium- to large-sized herbivores (mostly), terrestrial

Condylarthra: arctocyonids (*Lambertocyon*), hypsodontids (*Aletodon*, *Dorralestes*)Pantodonta: barylambdids (*Barylambda*) and cyriacotheriids (*Cyriacotherium*)

Carnivores

Carnivora viverravids (*Didymictis*): scansorial, terrestrialCreodonta oxyaenids (*Tyttbaena*): terrestrial

This list indicates increases in all categories except fossorial taxa. As summarized by Hooker (2000), these taxa were adapted mostly (50%) to an insectivorous diet rather than one of browsing herbivory (10%), with the remainder being unspecified, but apparently largely omnivorous to carnivorous forms (Fig. 9). About 26% of the taxa were scansorial, 13% arboreal, and 12% terrestrial in locomotor capabilities, with somewhat less than 50% being of unspecified type.

Among Ti-3 taxa, MacLeod & Rose (1993) indicate that scansorial taxa include the plesiadapid primates *Nannodectes* (Ti-3–Ti-5) and *Plesiadapis* (Ti-3–Wa-1), and the arctocyonid condylarth *Thryptacodon* (Ti-3–Br-1b). Cursorial forms are represented by the phenacodontid condylarth *Phenacodus* (Ti-3–Br-3).

Based on Morlo & Gunnell (2003) it is possible that viverravids (*Didymictis*, Ti-3–Duchesnean) also were scansorial scavengers; oxyaenids were terrestrial hypercarnivores, and mesonychids were among the larger hypercarnivores. Gunnell (1998) evaluated numbers of specimens in various categories to propose that the main herbivores were members of the Plesiadapidae (Primates), although phenacodontid condylarths and ptilodontid multituberculates also occupied that niche. This is comparable to numbers of genera shown in Figs. 10 (ptilodontids) and 13 (plesiadapids), but hypsodontid condylarths (Fig. 14) also were abundant small herbivores. Barylambdid pantodonts (Fig. 15) were diverse as well, along with stylinodontid taeniodonts (Fig. 12), palaeoryctid cimolestans, and erinaceid erinaceoids (Fig. 11). Gunnell (1998) indicated that carnivorous mammals in Ti-3 were dominated by arctocyonid condylarths, followed closely by viverravid carnivores, with oxyaenid creodonts and mesonychians filling minor roles (Fig. 12).

The diversity of Pantodonta is perhaps the most singular new factor in the Ti-3 fauna (Appendix, Table 3), coincidental with the demise of the mioclaenine condylarths and other members of more archaic groups (*Paromomys*, *Elphidotarsius*), which last occur in Ti-3 (Appendix, Table 4).

The basic standing crop of mammals is relatively constant for the remainder of the Tiffanian (from Ti-3), with numbers falling to a low of 52 genera in Ti-6. Ptilodontid multituberculates dominate the rodent-like niche (Fig. 10). Notable additions to the fauna are barylambdid pantodonts (*Haplolambda*, *Ignatiolambda*) and hypsodontid condylarths (*Phenacodaptus* in Ti-4; see Figs. 14 and 15). The increased number and percentage of LADs in Ti-4 and Ti-5 (Figs. 7 and 8; Appendix, Tables 2 and 4) appear to reflect extinction of relatively archaic suprageneric groups, such as taeniolabidid and

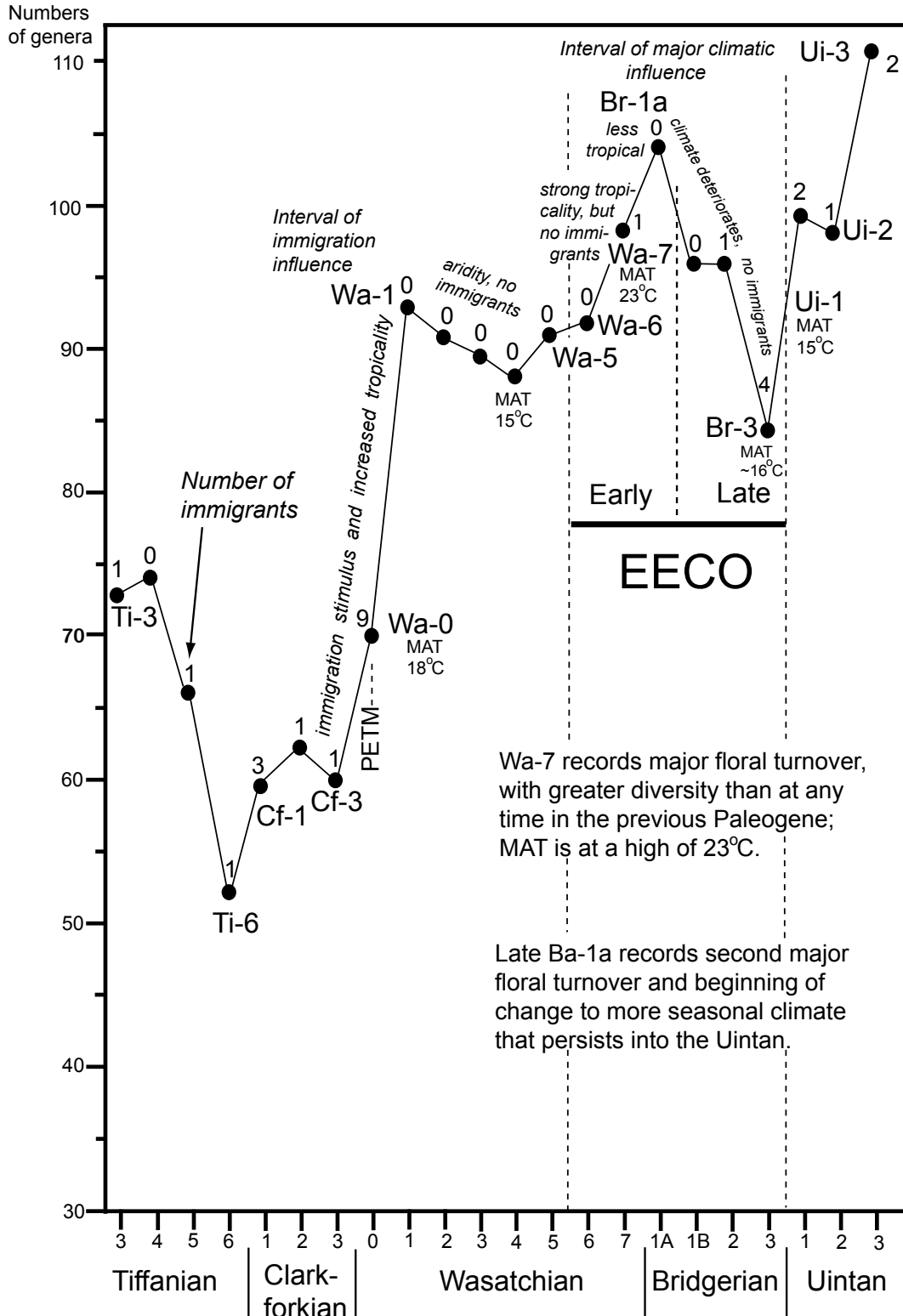


Figure 6. Census of mammal taxonomic richness in the late Paleocene and Eocene, (medial Tiffanian to Uintan mammal biochrones, with numbers of immigrants and climatic settings), after Table 1a. This reflects the actual numbers of genera, in contrast to Fig. 4.

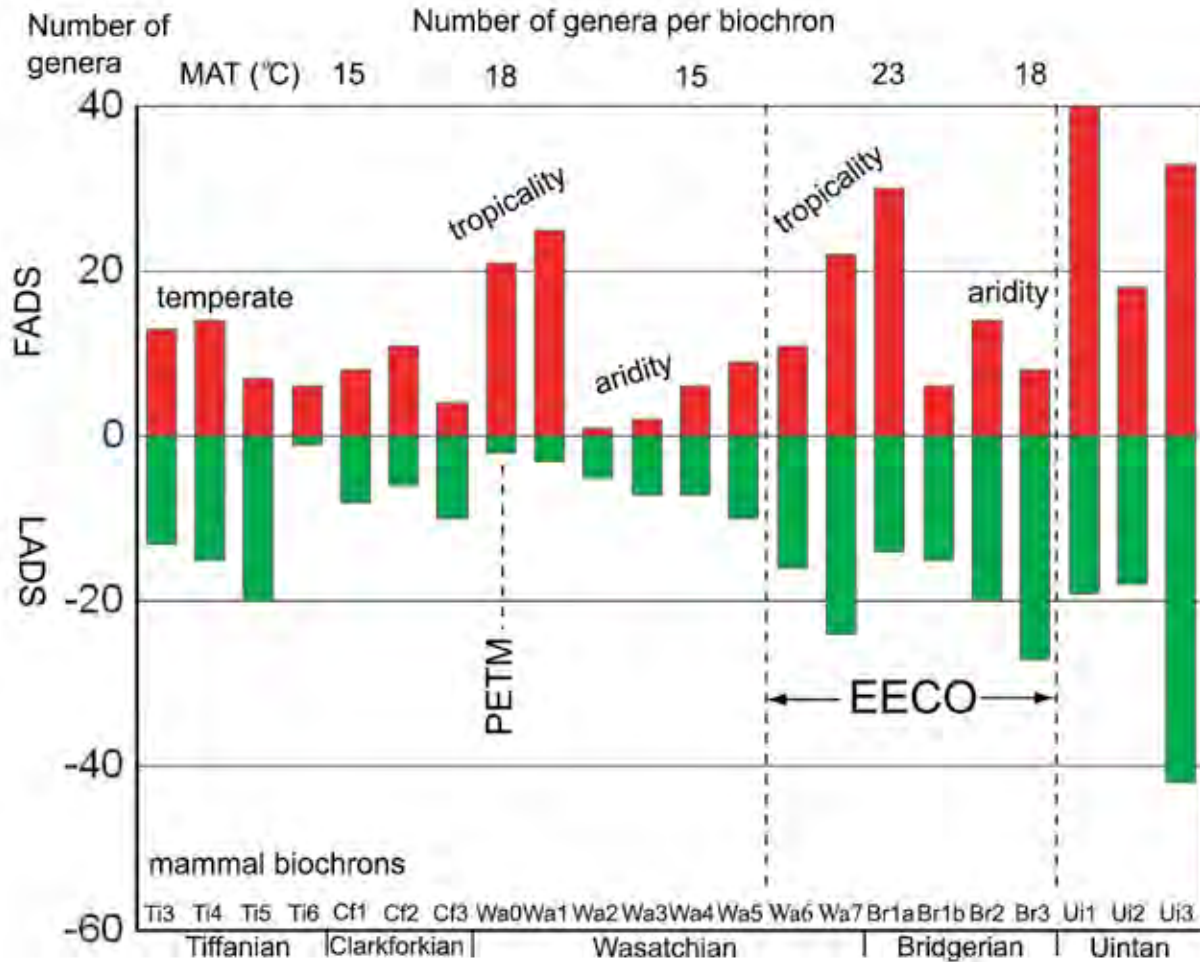


Figure 7. Portrayal of FADs and LADs for North American late Paleocene and early Eocene mammals, based on numbers of genera. Positions of PETM, EECO, and mammal biochrons, are indicated. Selected figures for MAT and general climatic conditions follow Fig. 1 and the text.

sloanbataarid multituberculates, microdontid primates (Fig. 10), peripitychid condylarths (Fig. 14), and a loss of tricuspidontine and some hyposodontid condylarths.

Immigrants in Ti-5 and Ti-6 (Appendix, Table 3) are arctostyloids (*Arctostylops*) and uintatheres (*Prodinoceras*), respectively. Fig. 9 suggests that Ti-5 faunas were less insectivorous and somewhat more herbivorous (browsing) than in Ti-3, and that a slight reduction in arboreality was accompanied by a rise in scansoriality and terrestriality.

Gunnell (1998) indicated that plesiadapids

continued their herbivore dominance from Ti-3, with phenacodontids next in frequency, followed by the nearly insignificant ptilodontids. Similarly, the arctocyonids, viverravines, and oxyaenines maintained their relative carnivore roles in Ti-3–Ti-6 (see also Figs. 12, 14).

In summary, the Tiffanian (beginning with Ti-3) can be characterized as having very few immigrations to help fuel phyletic diversification. Therefore the waxing and waning of suprageneric groups was generated internally, perhaps under a moderate MAT increase accompanied by moist, temperate conditions (Fig. 1).

Percent of total number of genera per biochron

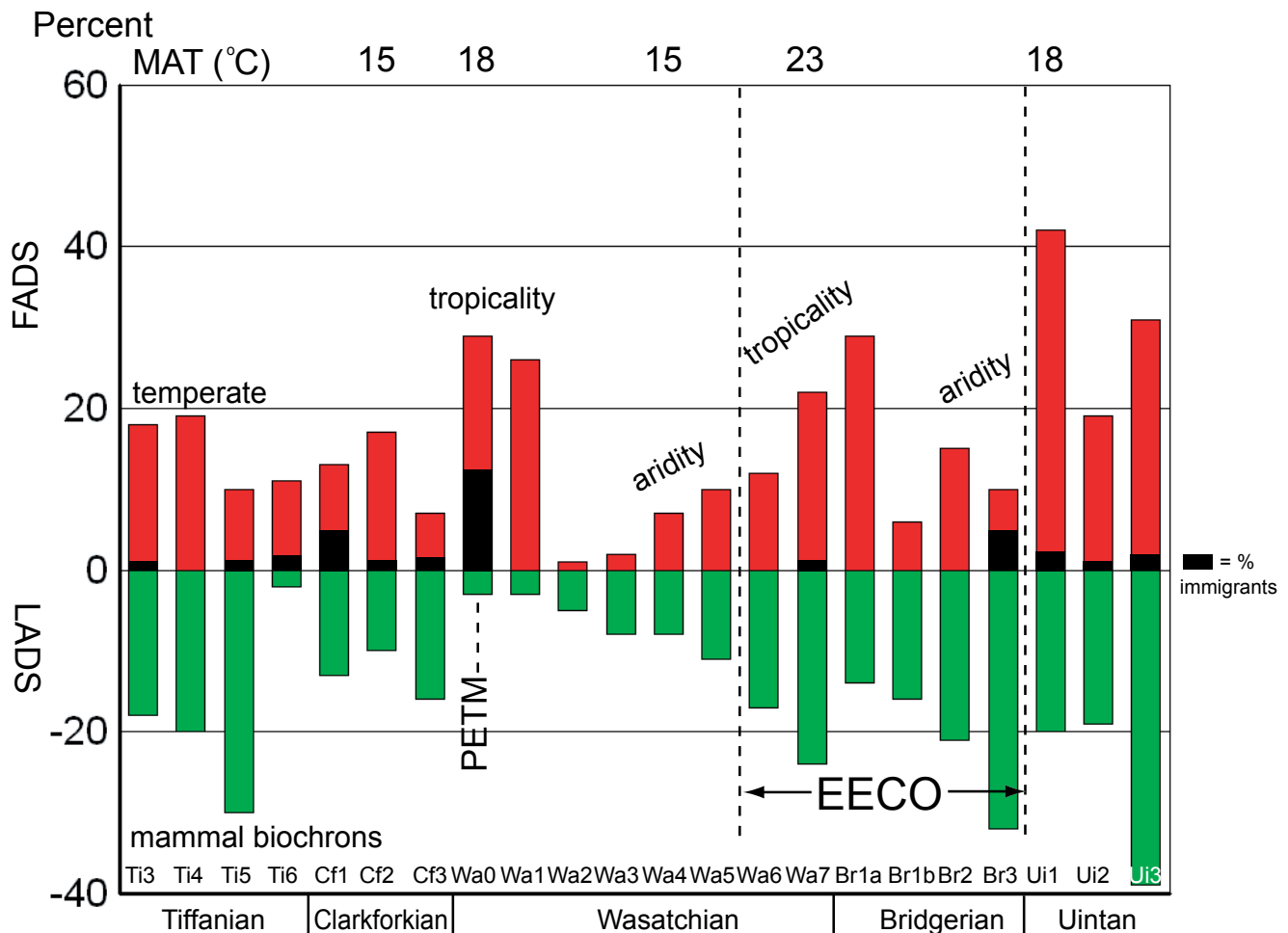


Figure 8. Portrayal of FADS and LADS for North American late Paleocene and early Eocene mammals, based on percentage relative to total number of taxa in each biochron. Positions of PETM, EECO, and mammal biochrons are indicated. Selected figures for MAT and general climatic conditions follow Fig. 1 and the text. Black portions of the bars show % immigrants.

Clarkforkian

The Clarkforkian witnessed a modest but distinct increase in immigration and generic diversity as compared with the Tiffanian. A new immigrant uintathere (*Prodinoceras*) in Ti-6 (Appendix, Table 3) apparently contributed to the herbivorous contingent of the Clarkforkian (Cf-1: Appendix, Table 3), as did the immigrant microparamyine rodent (*Acritoparamys*), the til-lodont (*Azygonyx*), and the pantodont (*Coryphodon*).

Additional herbivores are provided by the immigrant rodent (*Alagomys*), as well as the indigenous *Microparamys*, *Paramys*, and *Franimys*, along with an indigenous fossorial pholidotan (*Palaeonodon*) in Cf-2.

Gunnell (1998) recorded the growing prime herbivore status of the phenacodontids in this interval, with plesiadapids followed by hyopsodontids in diminished importance, generally comparable to diversity patterns in Figs. 13 and 14. Carnivores were dominated

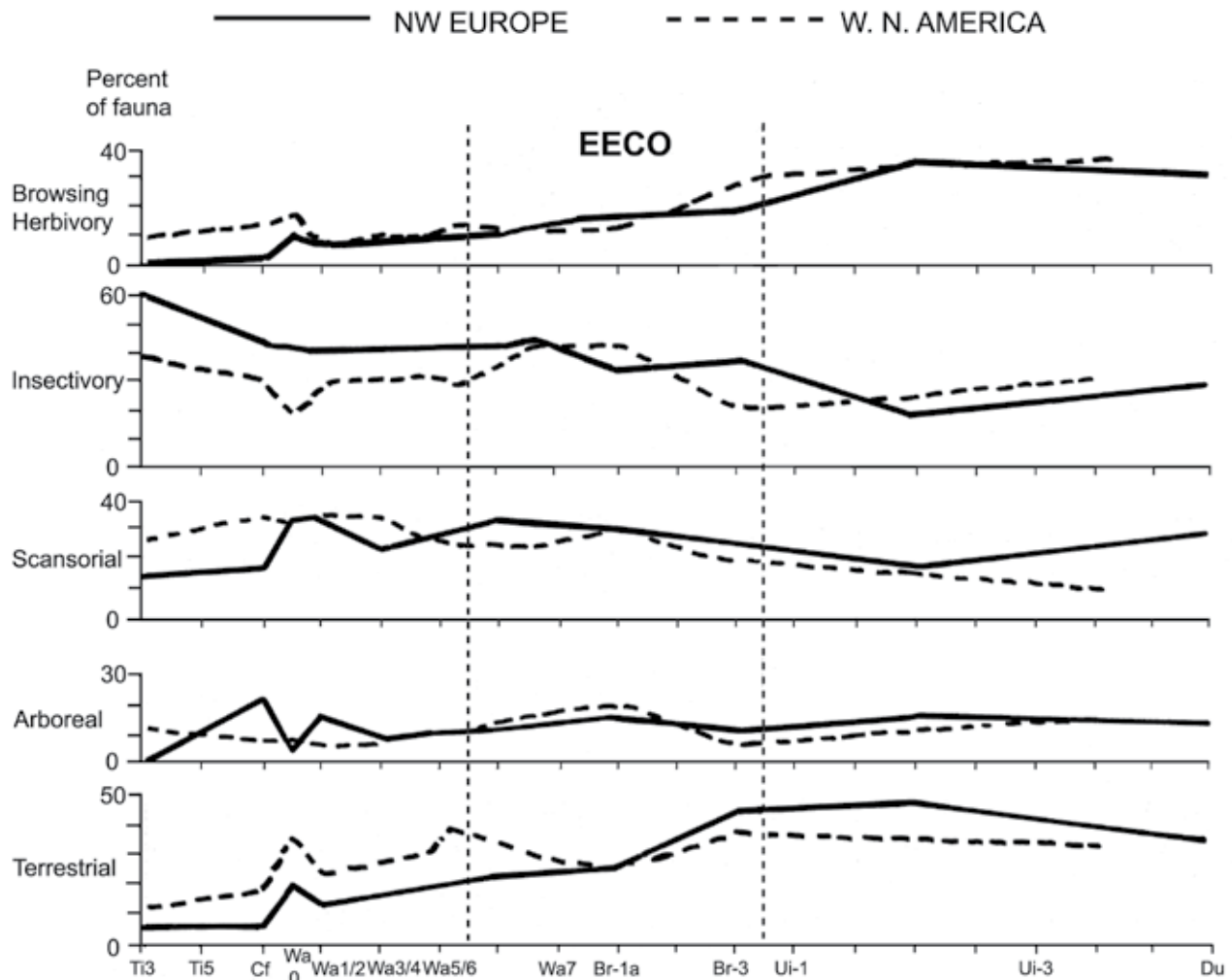


Figure 9. Adaptive zones for mammals of late Paleocene and early Eocene age, after Hooker (2000: fig. 1).

by viverravids, at least one of which (*Viverravus*, Ti-4–Br-3) was a scansorial scavenger (Morlo & Gunnell 2003). Oxyaenines (Fig. 12) and mesonychids were also noteworthy, but of lesser importance in both diversity and abundance (Fig. 12).

A reasonably steady increase to 60 genera by the end of the Clarkforkian (Fig. 6) was therefore aided and abetted by FADs that contributed up to 18% of the total taxa (in Cf-2), of which 9% were immigrants (Percent of FADS: Appendix, Table 2). In comparison with Ti-3–Ti-6, the percent immigrant contribution to FADs was substantially greater in Cf-1–Cf3 (9–38% of FADS: Appendix,

Table 2), and the immigrant percent contribution to the total number of genera also was greater in the Clarkforkian (2–5% of total: Appendix, Table 2) than in the Tiffanian. The standing crop was diminished during this interval by losses in ptilodontid multituberculates (now down to two genera as compared to as many as seven earlier in the Tiffanian; Fig. 10), a stylinodontine taeniodont (Fig. 12), and a few others. Other LADs (Appendix, Table 4) appear to be minor anagenetic losses within ongoing families.

Fig. 1 indicates that at least in the Green River Basin area, the climate tended to become somewhat

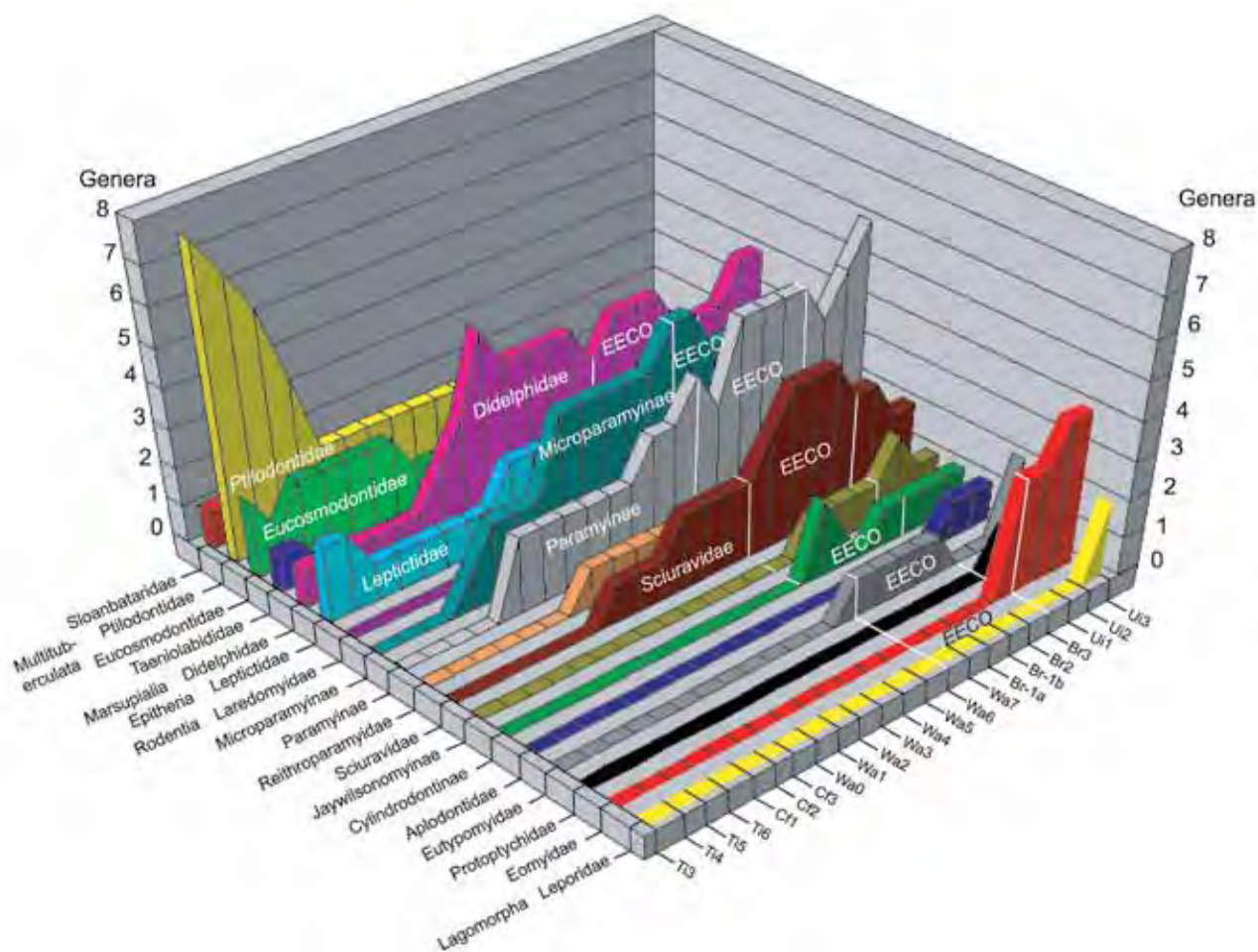


Figure 10. Chart of the temporal distribution and generic diversity of family and subfamily groups of multituberculates, marsupials, leptictids, and rodents from Ti-3–Ui-3. After Appendix, Table 1.

more tropical (higher MAT, about 14°C to 19°C; MAP of about 130cm/yr), but as indicated by Wing et al. (1995; Fig. 4) plant diversity tended to drop during this interval in the Bighorn Basin, contrary to the rise in mammalian taxa (congruent with Fig. 5).

In summary, it appears that the faunal patterns for the Paleocene are relatively unremarkable. FADs and LADs are about in balance and modest in scope, except for Ti-6 (Figs. 7 and 8). MAT became warmer during the Clarkforkian, and Wing (1998) invoked relatively high temperatures to facilitate the immigrations that are taxonomically important in the Clarkforkian (e.g., introduction of the Rodentia) and contributed about

5% of the new genera for this interval. If these taxa are removed from consideration, there would be no dramatic increase in the taxa of that time, however, and it seems that if climate played a role in this instance beyond facilitating immigration, its effect was relatively minor.

The PETM and Immigration Stimulus in the Early Wasatchian

The early Wasatchian mammalian fauna appears to have behaved differently from that of the Paleocene. The episodes centered on Wa-0 and Wa-1 involved faunal response to a sharp interval of mammalian immigration (McKenna 1975) during which climate changed strongly

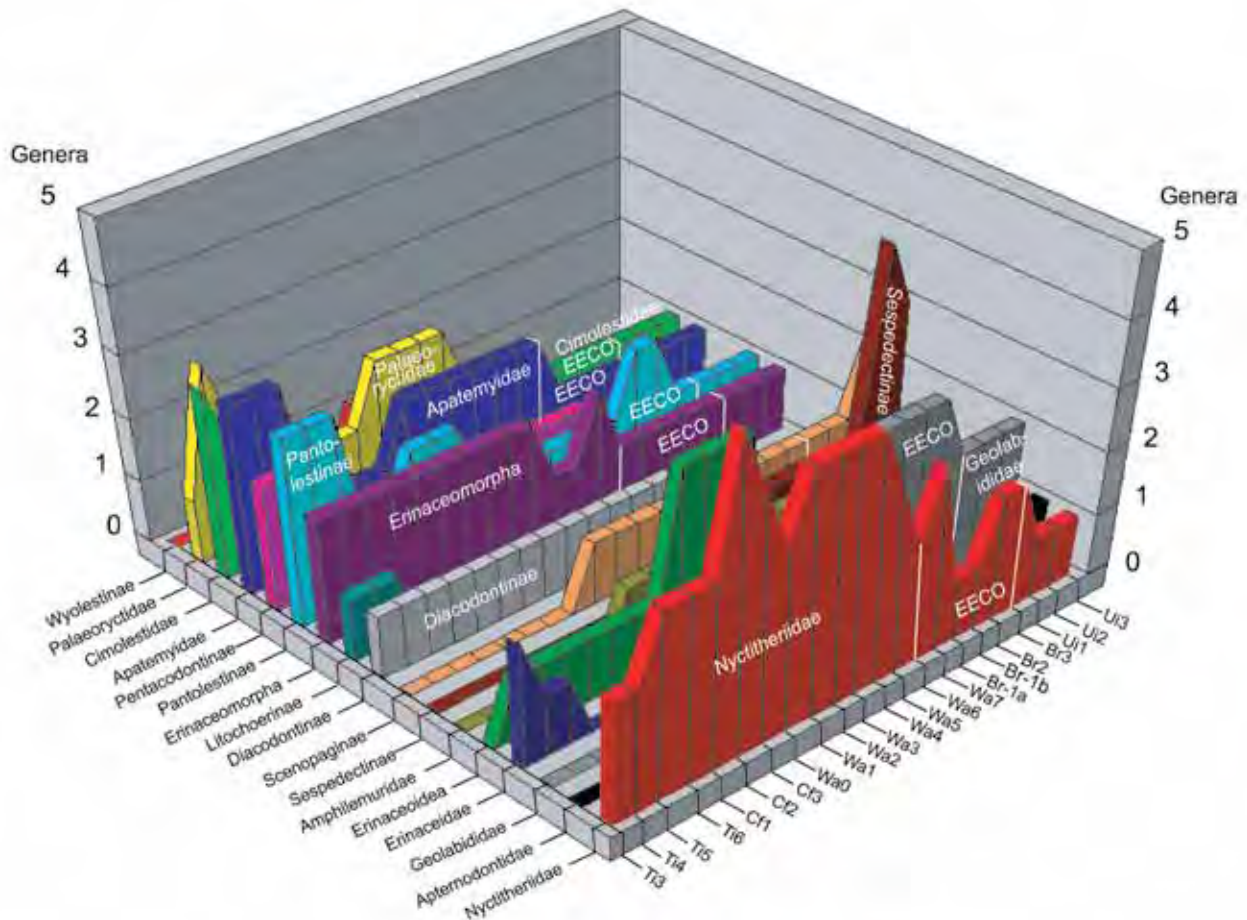


Figure 11. Chart of the temporal distribution and generic diversity of family and subfamily groups of insectivorous mammals from Ti-3–Ui-3. After Appendix, Table 1.

but plant diversity did not, except briefly during the PETM (Wing et al. 2005).

Immigrants at the beginning of the Wasatchian (Wa-0: Appendix, Table 3) are hyaenodontid creodonts (*Arfia*, *Prototomus*, *Prolimmocyon*, *Acarictis*), the notharctine (*Cantius*) and anaptomorphine (*Teilhardina*) primates, the dichobunid artiodactyl, *Diacodexis*, the equid, *Hyracotherium*, and the lipotyphlan, *Macrocranium* (Smith et al. 2002). The other taxa indicated as immigrant in Woodburne (2004: figs. 8-4, 8-5) are interpreted here as indigenous in Wa-0. Wa-0 also saw the beginning of new taxa in the following categories:

Insectivorous-omnivorous

Didelphid marsupials (*Copedelphys*), apatemyid (*Apatemys*), apternodontid soricomorphs (*Parapternodus*, *Koniaryctes*)

Terrestrial diggers

Tillodontia (*Esthonyx*)

Small-sized herbivores

Rodentia: reithroparamyid (*Reithroparamys*);
sciuravid myomorph (*Knighthomys*)

Carnivores

Creodonta: limnocyonines (*Prolimmocyon*),
hyaenodontines (*Prototomus*, *Acarictis*), oxyaenids (*Oxyaena*)

Carnivora: miacids (*Vulpavus* and *Miacis*)

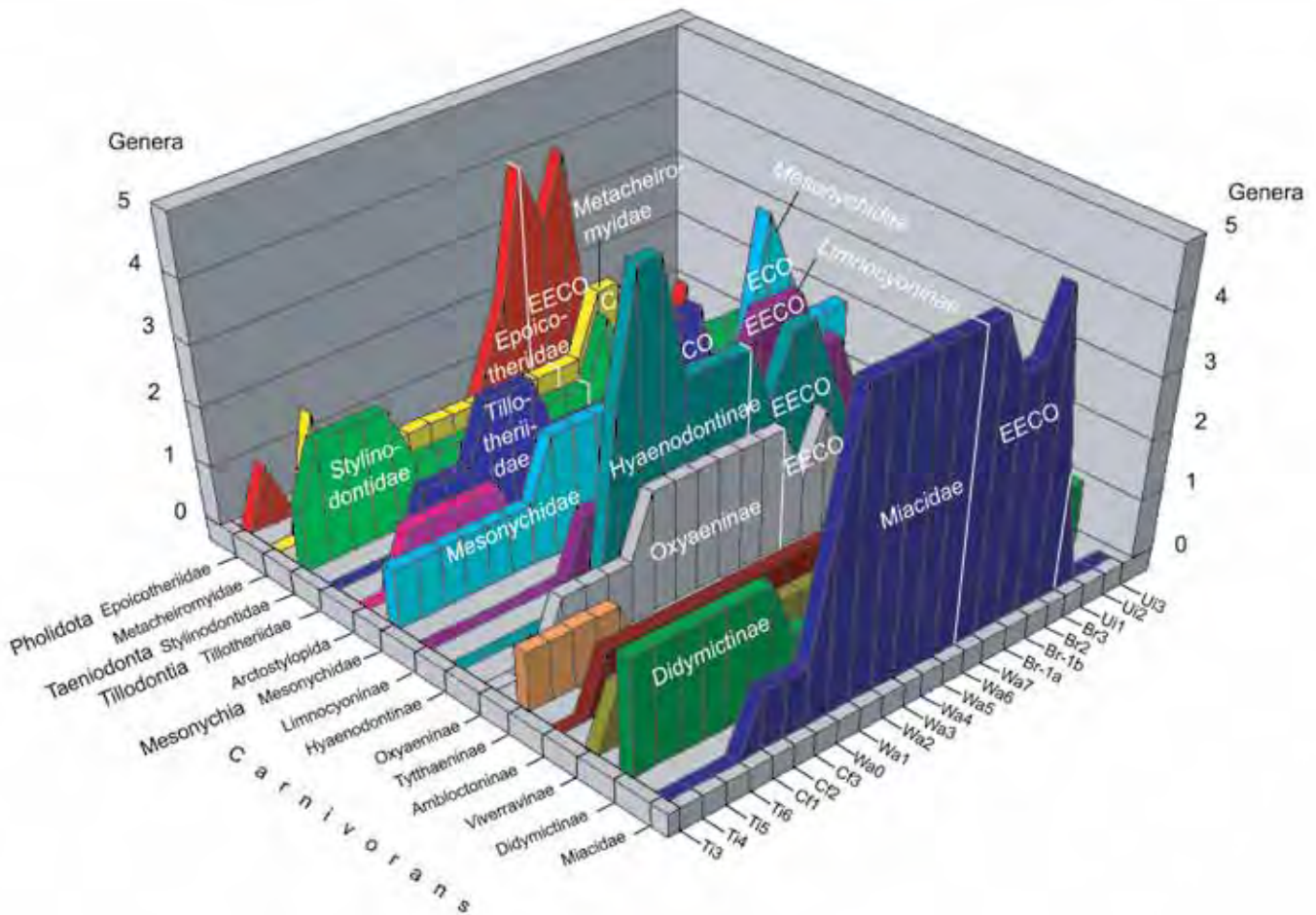


Figure 12. Chart of the temporal distribution and generic diversity of family and subfamily groups of carnivorans, pholidotans, and Tillodontia from Ti-3–Ui-3. After Appendix, Table 1.

Mesonychia: *Pachyaena*

These FADs make up about 30% of the total population (Percent FADs, Appendix, Table 2), overwhelmingly surpass the LADs in this biochron (Figs. 7 and 8), and record a reduction of eucosmodontine multituberculates (now only represented by *Neoliotomus*), as well as the loss of a pantolestid cimolestean (*Thelysia*) and an oxyclaenid condylarthran (*Princetonia*; Appendix, Table 4). The standing crop population now has been increased by the insectivorous didelphid (herpetotherine) marsupials (Fig. 11), limnocyonine, hyaenodontine, and oxyaenine carnivorans (Fig. 12), arboreal adapid

(notharctine) and omomyid (anaptomorphine) euprimates (Fig. 13), as well as small herbivores—microparamyine, reithroparamyid, and sciuravid rodents (Fig. 10), dichobunid artiodactyls (Fig. 14) and larger herbivores (*Perissodactyla* [Equidae, Fig. 15]). The immigrant and other new taxa comprise a major increase relative to Cf-3 (Fig. 6).

As reviewed in Hooker (2000), Wa-0 reflected a distinct local peak in browsing herbivores and terrestrial taxa, along with an accompanying sharp drop in insectivores (Fig. 9). Whereas phenacodontid condylarths and plesiadapid primates were the major herbivores in the

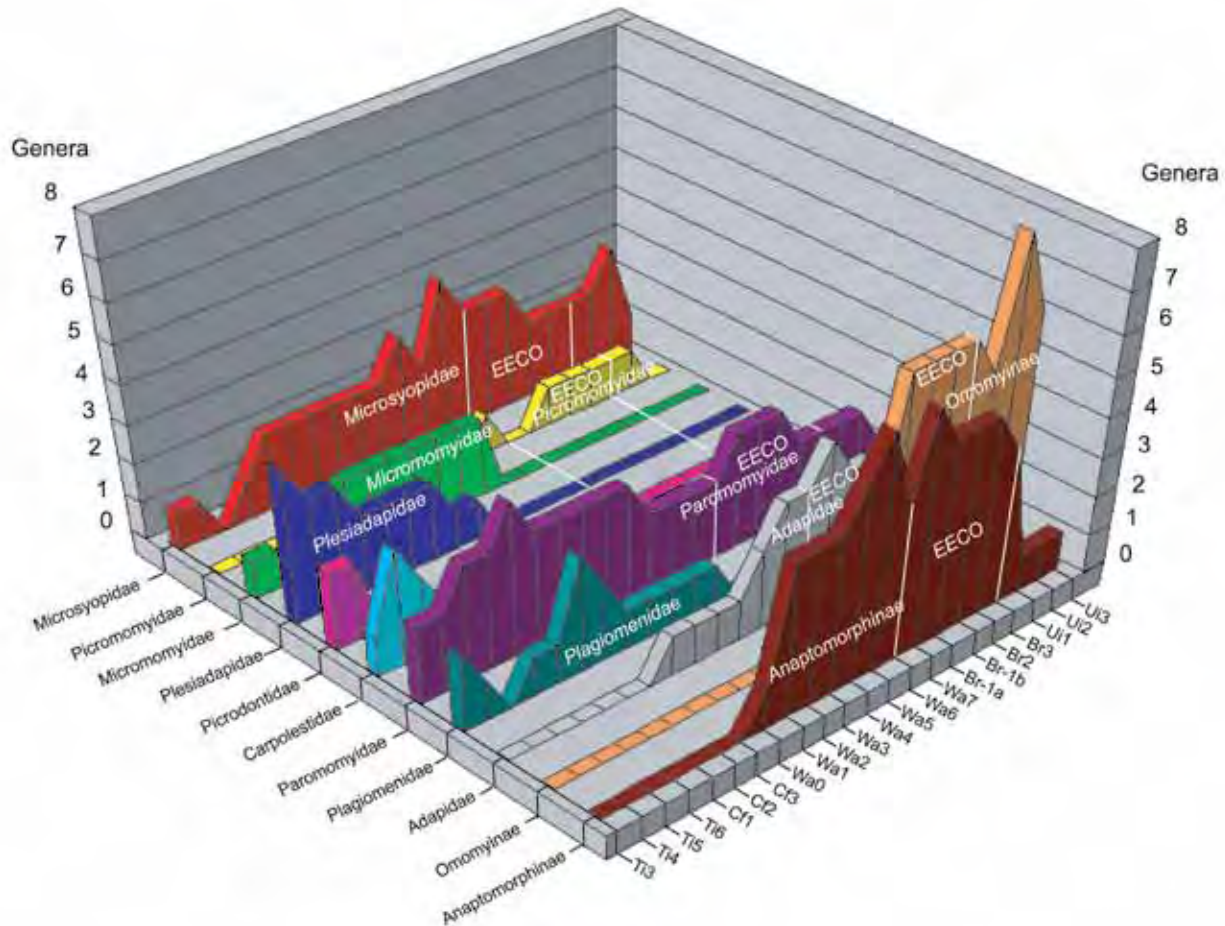


Figure 13. Chart of the temporal distribution and generic diversity of family and subfamily groups of primate and primate-like taxa from Ti-3–Ui-3. After Appendix, Table 1.

late Clarkforkian (Cf-3), in the Wasatchian this niche was occupied by hyopsodontid condylarths, followed by equid perissodactyls and dichobunid artiodactyls (Gunnell 1998). Similarly, viverravids, oxyaenids, hyaenodontids, and mesonychids were the major carnivores in the late Clarkforkian versus a rising importance of miacids, viverravids, and some hyaenodontids (Wa-3) in the Wasatchian.

Morlo & Gunnell (2003) indicate that Bridgerian limnocyonine hyaenodontids were weasel-like hypercarnivores, so it is possible that *Prolimnocyon* (Wa-0–Br-1a) was similarly adapted. Hyaenodontines (*Prototomus*,

Arfia, *Acarictis*) may have been scavengers, as also suggested for *Viverravus*. MacLeod & Rose (1993) suggest that *Cantius* (Wa-0–Br-1b) and *Vulpavus* (Wa-0–Br-2) were scansorial, that *Hyracotherium* (Wa-0–Ui-1) was a cursorial herbivore, and that *Pachyaena* (Wa-0–Br-2; Mesonychidae) was a cursorial carnivore.

Wa-0 is associated with a major increase in MAT to about 20°C that lasted only a few thousand years. The approximately concurrent immigration episode apparently included the dwarfing of certain lineages (*Ectocion*, *Copecion*, *Hyracotherium* [Gingerich 2003], *Prodiacodon*, *Macrocranion*, *Leptacodon*, *Wyonycteris*,

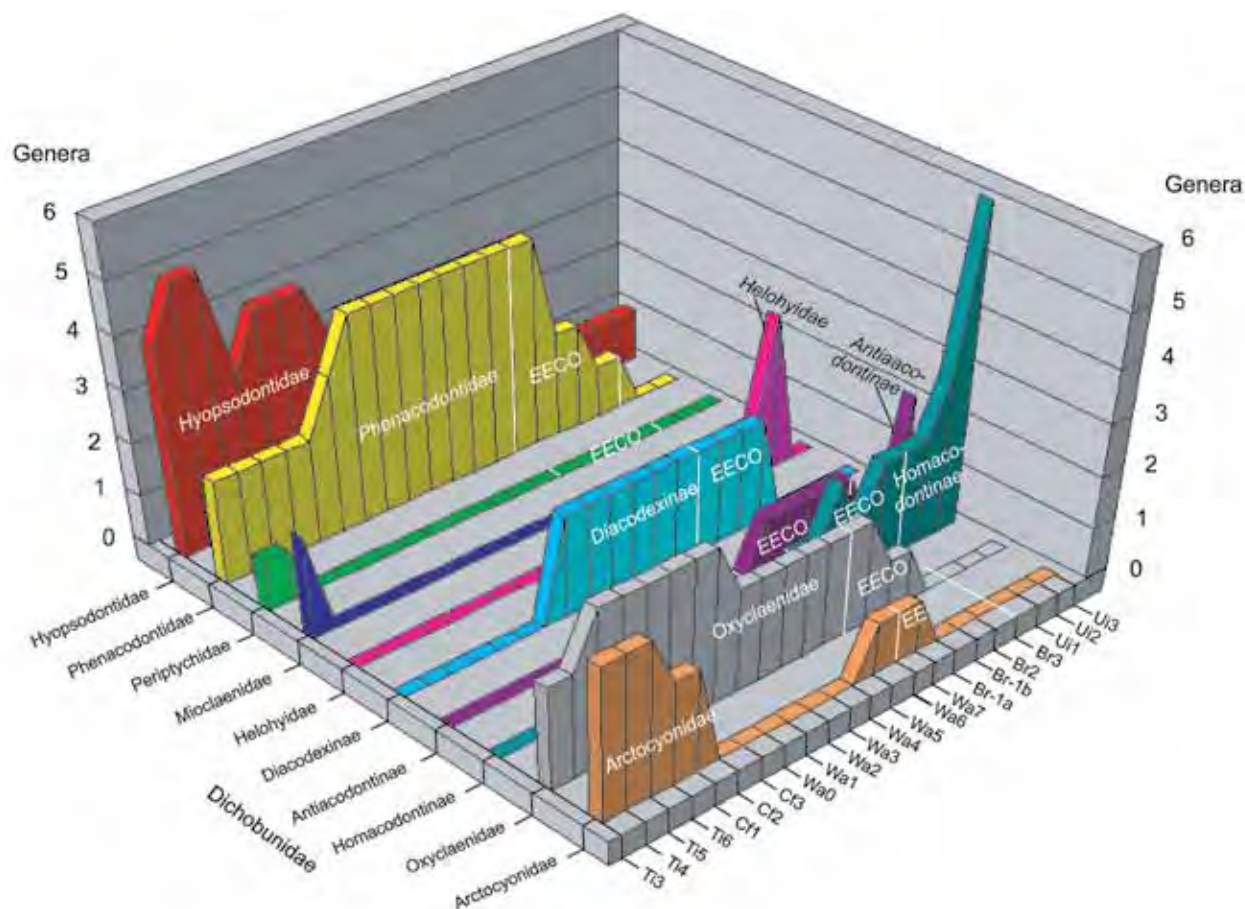


Figure 14. Chart of the temporal distribution and generic diversity of family and subfamily groups of small herbivorous mammals from Ti-3–Ui-3. After Appendix, Table 1.

Niptomomys [Strait 2004], and *Uintacyon* [Heinrich et al. 2008]). Clyde & Gingerich (1998) also suggest that major faunal renovations at this time resulted from immigrants with adaptations for herbivore, carnivore, omnivore, insectivore, and frugivore niches, whereas in the Clarkforkian omnivores and insectivores were dominant (Fig. 9). Dwarfing is attributed to climatic modification, but the ecologic niche specializations are associated with the effects of immigration. According to Clyde & Gingerich (1998), herbivores and frugivores became dominant within the Wasatchian after Wa-0 on an individual basis, but all categories are abundant in Wasatchian strata relative to those of the Clarkforkian.

The earliest Eocene warming (PETM) is considered

to have abetted intra- and intercontinental dispersal of plants and land mammals (Rose 1981; Tiffney 1994, 2000; Gingerich 2003). Tiffney (1994) characterized the high-latitude flora as consisting of warm temperate-to subtropical-adapted taxa that survived a mean coldest month temperature of about 10°C. As indicated above, the Thyra Ø flora of northwest Greenland indicates a MAT of about 15°C.

The discussion above illustrates the strong role played by immigration in affecting Wa-0 faunal dynamics, the impetus of which seems to have carried over into subsequent biochrons of the Wasatchian. Wa-1 shows a strong rise in numbers of taxa (95: Appendix, Table 2, Fig. 6) and a strong number of FADs (27% of the total

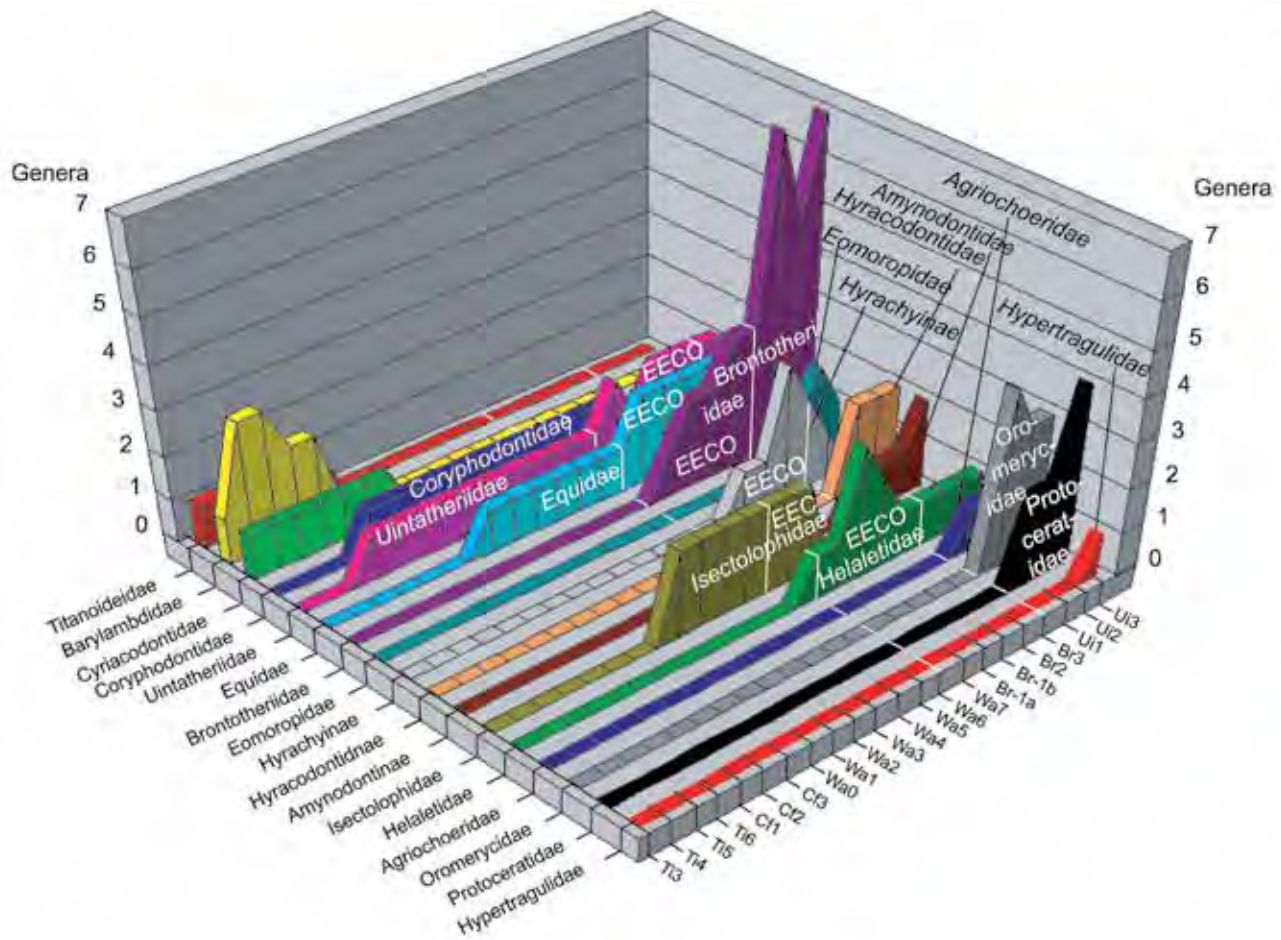


Figure 15. Chart of the temporal distribution and generic diversity of family and subfamily groups of large herbivorous mammals and selenodont artiodactyls from Ti-3–Ui-3. After Appendix, Table 1.

fauna) versus very few LADs (3%: Percent LADs, Appendix, Table 2), with no immigrants (Appendix, Table 3). Appendix, Tables 2 and 5 show that Wa-0 immigrations account for about 43% of the FADs in that biochron, in contrast to the situation in Wa-1 (no immigrants and a somewhat larger number of FADs). Apparently the immigration stimulus of Wa-0, coeval with an increase in temperature, resulted in vigorous speciation in Wa-1 that accounts for the greatest single numerical increase of any biochron considered herein (Fig. 6). It is additionally remarkable that this increase in taxa took place over a span of about 0.2 Ma (Appendix, Table 5). In contrast, comparable but smaller increases in taxa (Fig. 6) took place within intervals of about 5.1 m.y. (Wa-4–Br-1a) or

about 8 m.y. (Br-3–Ui-3).

Immigration stimulus thus contributed in Wa-1 (see Appendix, Table 3 for complete list) to an increase in the diversity of insectivorous-omnivorous taxa (Fig. 11), including didelphid (herpetotheriine) marsupials (*Herpetotherium*), leptictidans (*Palaeictops*), palaeoryctid (*Eoryctes*), wyolestid (*Wyolestes*) and didelphodontan (*Didelphodus*) cimolestans, pentacodontine pantolestans (*Amaramnis*), erinaceid (*Dartoni*, *Auroralestes*) and creotarsid (*Creotarsus*) erinaceomorphs, as well as geolabibid (*Centetodon*, *Batodonoides*) and nyctitheriid (*Plagiostenoides*) soricomorphs. New small herbivores are represented by microparamyine rodents (*Lophiparamys*, *Apatosciuravus*; Fig. 10). Arboreal groups include

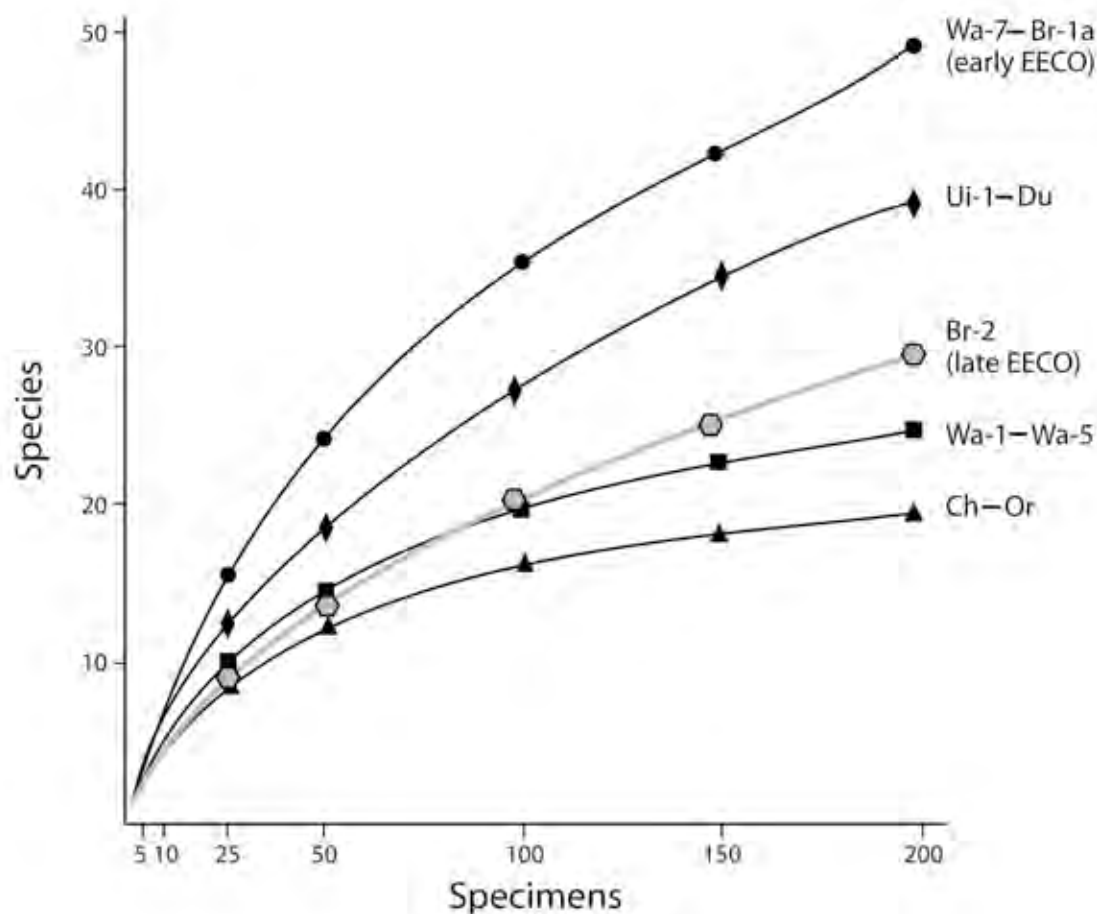


Figure 16. Rarefaction analysis of species diversity in Eocene and early Oligocene intervals in North America. The number of species (Y axis) is compared with the number of specimens from each interval (X axis). Early Wasatchian (Wa1-5, squares), latest Wasatchian and earliest Bridgerian (Wa-7-Br-1a, circles), medial Bridgerian (Br-2, gray polygons), Uintan and Duchesnean (Ui-2-Du, diamonds), and Chadronian and Orellan (Ch-Or, triangles). Specimen counts are based on individual fossiliferous horizons and are not generalized from stratigraphic intervals. Note the high levels of species diversity during the early part of the EECO that dramatically drop during the medial Bridgerian after the optimum. The figure suggests that the alpha species diversity for Wa-7-Br-1a is more than 1.5 times greater than during Br-2, indicating a drop in alpha diversity after the early EECO that is reflective of high levels of both point diversity and continental diversity during that time. Data derived from Denver Museum of Nature & Science collections for Br-2 and from Stucky (1992) for the other intervals.

anaptomorphine euprimates (Fig. 13). New large herbivores (Fig. 15) are isctolophid perissodactyls and new carnivores (Fig. 12) include hyaenodontine creodonts (*Galecyon*, *Tritemnodon*) and miacids (*Vassacyon*, *Oodectes*).

This new standing crop population (Appendix, Table 4) lost only didelphid marsupials (*Esteslestes*), creotarsine erinaceoids (*Creotarsus*), and the last plesiadapid primates (*Plesiadapis*), apparently from intrapopulational competition. Fig. 1 suggests that these taxa were living under still subtropical conditions (crocodilians are present: Wilf 2000) but some seasonal drying, with MAT at about 18°C and MAP of about 110cm/yr (black dot just above the PETM on Fig. 1).

In summary, immigration stimulus during Wa-0 resulted in the strongest increase in new taxa up until that time in the Paleogene record of fossil mammals in North America. The speciation derived from this innovation not only resulted in dwarfing on the one hand (apparently abetted in part by climate), but also as a response to the diversity of herbivore, carnivore, omnivore, insectivore, and frugivore niches exploited by the immigrants. It seems inescapable that this diversity fueled the 25% increase in Wa-1 genera relative to those of Wa-0.

Synchronous Dispersal at the PETM

The global scale of the PETM suggests that the Wa-0 immigration episode was virtually synchronous across North America, at least. Wing et al. (2005), Wing & Lovelock (2007), and Smith et al. (2007) record strong floral change in the Bighorn Basin during the PETM in terms of a brief virtual disappearance of conifers. Still, the earliest Wasatchian saw a decrease in floral diversity as compared with the Clarkforkian (Fig. 5). The Wa-0 immigrations transpired during a very short interval of time, regardless of floral facies in the Western Interior of the United States.

Effective Stasis in the Medial Wasatchian

Much of the remaining earlier Wasatchian (Wa-2–Wa-5) was relatively unremarkable. The number of taxa (Fig. 6) shows a gradual retreat to 91 genera (Appendix,

Table 2), possibly a reflection of more seasonally arid climates (Figs. 1, 6–8). There are no immigrants (Appendix, Table 3), and the basic mammalian population is stable, undergoing what appear to be internal adaptive adjustments. Chew (2005) reports an increase in species diversity during this interval contemporaneous with an apparent rise in temperature (also see Secord et al. 2008 for a discussion of early Wasatchian paleohabitats). The number of FADs and LADs gradually increase through the interval from a low of 1% and 5% in Wa-2 to a high of 10% and 11%, respectively, in Wa-5. Rodents, pholidotans, and various suprageneric groups of primates and euprimates make steady gains. Wa-3 records the last occurrence (Appendix, Table 4) of taeniolabidoid multituberculates (*Neoliotomus*), apternodontid soricomorphs (*Parapternodus*, *Koniaryctes*), and micromomyid primates (*Tinimomys*, *Chalicomomys*) (Fig. 13). Wa-4, which begins at Biohorizon A of Schankler (1980), records the first omomyine primate (*Steinius*), a new notharctine primate (*Copelemur*), and includes a number of species-level changes as well (Chew 2009). In addition, wyolestine (*Wyolestes*) and palaeoryctid (*Palaeoryctes*) cimolestans, erinaceoids (*Dartoni*, *Auroralestes*), a nyctitheriid soricoid (*Plagioctenoides*), a plagiomenid dermopteran (*Plagiomene*), and an anaptomorphine euprimate (*Pseudotetonius*) drop out in Wa-4 (Appendix, Table 4). Wa-5 records the first picromomyid (Fig. 13) primates (*Picromomys*), and Wa-5 LADS (Appendix, Table 4) include *Mimoperadectes*, *Ottoryctes*, *Talpaoides*, *Leipsanolestes*, *Wyonycteris*, *Niptomomys*, *Picromomys*, *Teilhardina*, *Arapabovius*, and *Tetonius*. Clyde et al. (2007) noted that the base of Wa-5 may correspond in time with the short-lived Elmo hyperthermal (Lourens et al. 2005) but that its signature was not recognized in the Bighorn Basin.

Hooker (2000) documented a slow rise in herbivory and arboreality during the interval, a plateau in insectivory, a drop in scansoriality, and a sharper rise in terrestriality during the interval (Fig. 9). Gunnell (1998) indicated that the main herbivores still were the hyopsodontid condylarths, followed by equid perissodactyls and dichobunid artiodactyls. Figs. 14 and 15 show a steady diversity in phenacodontid condylarths and in

isectolophid and helaetid perissodactyls as well. In Wa-3, the hyaenodontids comprised the main carnivores, supplanted in Wa 4–6 by miacids and viverravids, according to Gunnell (1998). Hyaenodontids were, however, larger in body size and likely preyed on the larger herbivorous mammalian taxa. Fig. 12 shows that miacids were the most diverse carnivores in this interval. In addition to the other groups analyzed (above), MacLeod & Rose (1993) add *Alocodontulum* (Wa-5–6; Pholidota, Epoicotheriidae) as having a fossorial adaptation.

Fig. 1 suggests that the climate during this interval remained seasonally arid, with MAT retreating to about 15°C and MAP at about 100 cm/yr in the Green River Basin area. This may be consistent with the overall decrease in taxa in the medial Wasatchian and relatively balanced numbers of FADs and LADs, but it is difficult to attribute an obvious role to climate, the 11°C MAT for Wa-4 in the Bighorn Basin notwithstanding (Wing 1998).

Fossil Mammals and the Early Eocene Climatic Optimum (EECO)

Late Wasatchian Beginning

The EECO began about 53 Ma with a substantial increase in oceanic temperature and continued to about 50 Ma. The equivalent of the mammalian record began with Wa-6 (Figs. 6–9) and continued to the end of the Bridgerian NALMA. Wilf (2000) indicates that the Latham flora (Fig. 1) records a MAT of 17°C and a MAP about 113cm/yr: mild, humid conditions in the Green River Basin. This is followed by the Sourdough Flora (Fig. 1), with a MAT of 21°C and a MAP 140cm/yr. As reviewed above, Wing (1998) documents the greatly increased floral diversity in Wa-7 as compared with earlier intervals (Fig. 5) in the Bighorn Basin.

Wa-6 shows the beginning of the numerical increases in the fauna (92 taxa). Although there are no immigrants (with the possible exception of *Heptodon*, not highlighted in Appendix, Table 3), the interval records (Fig. 10) the first eutypomyid (*Mattimys*) and other rodents (*Uriscus*, *Uintaparamys*, *Pauromys*), new omomyine (*Loveina*, *Jemezius*) and anaptomorphine (*Tatmanius*) euprimates (Fig. 13), as well as new

pholidotans (Fig. 12: *Pentapassalus*, *Dipassalus*). Wa-6 faunas from the Wind River Basin are dominated by the equid *Hyracotherium* (including various genera discussed by Froelich 2002).

The higher number of FADs in Wa-6 than in Wa-5 apparently reflects an increased speciation rate that is manifested, at least, in the total increase of taxa over those of Wa-5 (Fig. 6: Appendix, Tables 2 and 5), in spite of a proportionately greater percentage of LADs than FADs in Wa-6. In that context, Wa-6 records the extinction of ambloctonine oxyaenids (*Palaeonictis*), diacodontine erinaceomorphs (*Diacodon*), and apheliscine (*Apheliscus*) and hyopsodontine (*Haplomylus*) condylarths, as well as the reduction of hyaenodontine (*Arfia*) and oxyaenid (*Dipsalidictis*, *Palaeonictis*) creodonts and mesonychids (*Dissacus*: Fig. 12: Appendix, Table 4).

The contemporaneous Latham flora records a major influx of tropically adapted plants, indicating mild, humid conditions (Wilf 2000) as compared to earlier, seasonal, and more arid climates in the Green River Basin. As compared to Wa-2–Wa-5, the increase in total numbers of mammalian genera in Wa-6 relative to Wa-5 most likely reflects this climatic change regionally within the Western Interior. In the prior interval, not only did LADs exceed FADs but total numbers decreased (Fig. 6) in concert with the presence of seasonally more arid climates (Figs. 1, 7 and 8).

Wa-7 continues the increase in mammalian taxa (to 98) begun in Wa-6 and shows a high percentage of both FADs and LADs (22% and 24%: Appendix, Table 2), a strong advance over the levels in Wa-6 (Fig. 7). *Lambdotherium* is the only immigrant (Appendix, Table 3). Continuing members of the core fauna include insectivorous-omnivorous didelphid marsupials and geolabidid insectivorans (Figs. 10 and 11), the arboreal microsyopid and picromomyid, and paromomyid primates, as well as the notharctid, omomyid, and anaptomorphine euprimates (Fig. 13), the arboreal microsyopids (Fig. 13), and the small herbivore paramyine, sciuravine, and eutypomyid rodents (Fig. 10). *Elwynella* is a new paromomyid primate. *Anacodon* is present in Wa-7 (first appearing in Wa-5) and, along with homacodontine artiodactyls (Br-1a), can be common locally (Fig. 14). Among

homacodontines, *Hexacodus* is relatively abundant in southern Wyoming, but rare in central Wyoming (Gazin 1962; Stucky, pers. observation). *Meniscotherium* also shows a similar pattern of distribution, being much more common in southern Wyoming (Gazin 1962) and New Mexico. Large herbivores include uintatheriids, equid, helaletid, and brontotheriid perissodactyls (Fig. 15), whereas carnivorans include hyaenodontines, miacids, and mesonychids (Fig. 12).

New additions in Wa-7 are (Appendix, Table 3):

Insectivorous-omnivorous

Paradectid marsupials (*Armintodelphys*), erinaceids (*Entomolestes*), geolabidid soricomorphs (*Marsholestes*), nyctitheriid soricomorphs (*Nyctitherium*)

Arboreal (euprimates)

Notharctids (*Notharctus*), and omomyine (*Shoshonius*, *Hemiacodon*), and anaptomorphine (*Strigorbhysis*, *Trogolemur*, *Artimonius*) omomyids

Small herbivores

Sciuravid (*Tillomys*) and cylindrodontid (*Dawsonomys*, *Anomoemys*), myomorph, and ischyromyid sciuriform (*Strathcona*) rodents, and homacodontine artiodactyls (*Antiacodon*)

Terrestrial diggers

Tillotheriid tillodonts (*Megalesthonyx*) and stylinodontid taeniodonts (*Stylinodon*)

Large herbivores

Uintatheriid dinoceratans (*Bathyopsis*), equid (*Orohippus*), and other perissodactyls (*Lambdaotherium*)

Carnivores

Limnocyonine hyaenodontids (*Machaeroides*)

Within the above, new suprageneric groups include the cylindrodontid rodents, tupaiodontinae erinaceids, homacodontine artiodactyls, and lambdaotheriines. *Hyopsodus* again becomes the dominant mammal in terms of abundance, representing more than 20% of all specimens at most localities of Wa-7 age.

LADs in Wa-7 (Appendix, Table 4) are leptictid epithेरians (*Prodiacodon*), microparamyine sciuriforms (*Uriscus*), cylindrodontid myomorphs

(*Dawsonomys*), pentacodontine pantolestans (*Amararnnis*), epicotheriid pholidotans (*Palaeonodon*), stylinodontid taeniodonts (*Ectoganus*), esthonychid tillodonts (*Megalesthonyx*), oxyaenid creodonts (*Oxyaena*), miacid carnivores (*Vassacyon*), nyctitheriid soricoids (*Plagioctenodon*, *Leptacodon*), notharctid (*Pelycodus*), and omomyine (*Loveina*) and anaptomorphine (*Chlororbhysis*, *Absarokius*) euprimates, uintatheriid dinoceratans (*Prodinoceras*), oxyclaenine (*Chriacus*), and arctocyonid (*Anacodon*) procreodonts, phenacodontid condylarths (*Copecion*, *Meniscotherium*), perissodactyls (*Lambdaotherium*), and isectolophid tapiroids (*Homogalax*, *Cardiolophus*).

Wa-7 (equivalent to the Lostcabinian NALMA subage) is typified by faunal reorganization. Chief innovations appear to be an increased diversity of rodents, with the Cylindrodontidae being new (Fig. 10, but see Dawson & Beard 2007), the new Tupaiodontinae (*Entomolestes*), and increased diversity in the artiodactyls and perissodactyls. Fig. 1 (Sourdough) indicates that Lostcabinian Wa-7 faunas lived under wet and subtropical conditions (MAT 22°C and MAP 150cm/yr). According to Wilf (2000), the Wa-7 Sourdough flora demonstrates an 87% species turnover relative to those of the Paleocene and that the forests were more diverse than at any time earlier in the Eocene and late Paleocene in the Green River Basin. Wing (1998) demonstrates a comparable pattern for the Bighorn Basin. This increased niche diversity, reflected by an 87% turnover in plant species relative to those of the Paleocene, apparently influenced competition among mammals. This is shown by the numerical increase in generic diversity from Wa-6 (Fig. 6) as well as the losses summarized above and portrayed in Figs. 7 and 8. Similar to Wa-6, the fauna of Wa-7 increased in total numbers of taxa in spite of a significant percentage of LADs. Both faunas were living under floral settings reflective of warm, tropical conditions.

The Bridgerian Expansion

The Little Mountain Flora of the Green River Formation (Fig. 1) is of early Bridgerian age (late Br-1a, ca. 50 Ma; Wilf 2000). The MAT is about 19.6°C and MAP about 75.8cm/yr in a still subtropical warm climate that

is somewhat cooler and with more seasonal rainfall than previously. Occasional ferns, horsetails, and hornwort indicate shallow to ephemeral freshwater habitats in tropical to subtropical settings. The Little Mountain Flora reflects an early phase of the strong decrease in climate (MAT to 15°C, and MAP to 70–80cm/yr) and increase in seasonality that developed in the later part of the EECO.

Regardless of the somewhat less tropical conditions, the Bridgerian NALMA began with a major episode of new evolutionary diversification and a small number of deletions (13% LADs: Appendix, Table 2). The result is a very high number of genera in Br-1a (104: Fig. 6), and FADs (29%) far outnumber LADs (13%) in a major expansion of the fauna. There were no major suprageneric group extinctions. The number of FADs (30) is the largest of any biochron from Ti-3–Br-3 (Appendix, Table 2). Although some losses are entertained within Br-1a (see below), the main pattern for this biochron is origination and diversity development under a wet paratropical climate. FADs are (Appendix, Table 3):

Insectivorous-omnivorous

Pantolestine pantolestans (*Pantolestes*) and sespedectine erinaceoids (*Crypholestes*)

Arboreal

Picromomyid primates (*Alveojunctus*) and notharctine euprimates (*Smilodectes*), omomyine (*Washakius*, *Utabia*, *Uintanius*, *Omomys*) and anaptomorphine (*Aycrossia*, and in Br-1b, *Anaptomorphus*, *Gazinius*) omomyid euprimates

Small herbivores

Paramyine ischyromyids (*Quadratomus*, *Pseudotomus*); sciuravid myomorphs (*Taximys*, *Mysops*), eutypomyine myomorphs (*Armintomys*)

Fossorial

Epoicotheriid (*Tetrapassalus*) and metacheiromyid (*Metacheiromys*, *Brachianodon*) pholidotans

Large herbivores

Brontotheriid (*Palaeosyops*), hyracodontid (*Hyrachyus*), and helaletid perissodactyls (*Helaletes*), tillodonts (*Trogosus*), and helohyid artiodactyls (*Helohyus*, Br-1b)

Small herbivores

Homacodontine dichobunid (*Microsus*) and helaletid perissodactyls (*Selenaletes*)

Carnivores

Limnocyonine (*Iridodon*, *Thinocyon* [Br-1b], *Limnocyon* [Br-1b]), hyaenodontine (*Sinopa*) and oxyaenine (*Patriofelis*, *Malfelis*) creodonts, and the mesonychian (*Mesonyx*)

None of the above are immigrants, contra Woodburne (2004: fig. 8.5), with the possible exception of *Hyrachyus* (known from Asia and Europe, but direction of dispersal is not clear). For the moment, it is not listed in Appendix, Table 3.

New suprageneric groups that apparently evolved endemically are the Jaywilsonomyinae (Fig. 10: *Mysops*), elements of the Metacheiromyidae (*Metacheiromys*, *Brachianodon*: Fig. 12), helohyid (*Helohyus*) and homacodontine dichobunid (*Microsus*) artiodactyls (Fig. 14).

Until the Bridgerian, anaptomorphine euprimates had been the dominant subfamily of the family Omomyidae (Fig. 13). They first appeared in Wa-0, diversified by Wa-1, continued strongly through the Bridgerian, and began to diminish in the Uintan. Omomyine euprimates first appeared in Wa-4, were as diverse as the anaptomorphines, but became more abundant by Br-1a (Fig. 13), when they began a major proliferation that continued into the Uintan (e.g., Beard et al. 1992; Gunnell 1997).

Morlo & Gunnell (2003) indicated that the Bridgerian witnessed a major radiation of hypercarnivores that includes the following adaptive groups, many of which first occur in Br-1a but which also are part of a persistent carnivore contingent with elements having originated in prior times:

Small, hypercarnivorous limnocyonine hyaenodontid (weasel-like) creodonts (*Iridodon*, Br-1a; *Thinocyon*, Br-1b–Br-3; and *Limnocyon*, Br-1b–Ui-1)

Medium-sized hypocarnivorous, semi-aquatic pantolestids (*Pantolestes*, Br-1a–Duchesnean)

Hypercarnivorous, cursorial oxyaenids (*Patriofelis*, Br-1a–Br-3)

Cursorial, carnivorous hyaenodontids (*Sinopa*, Br-1a–Br-3; possible immigrant?)

Scansorial forms that include hyaenodontids

(*Tritemnodon*, Wa-1–Br-2; *Machaeroides*, Wa-7–Br-2), and viverravids (*Viverravus*, Ti-5–Br-3)
 Small-sized to larger-sized arboreal and carnivorous
 miacids (*Miacis*, Cf-1–Ui-3); *Vulpavus*, Wa-0–
 Br-2; *Palaearctonyx*, Br-2; *Öodectes*, Wa-1–Br-2)
 Small terrestrial carnivores (*Uintacyon*, Cf-1–Ui-3)
 Large hypercarnivorous oxyaenids (*Malfelis*, Br-1a)
 Larger bone-crushing forms (the mesonychids,
Mesonyx, Br-1a–Ui-3 and *Harpagolestes*,
 Br-2–Duchesnean)

Heinrich et al. (2008) proposed that *Uintacyon* emphasized shearing (herein suggested as hypercarnivorous) and that *Vassacyon* emphasized crushing and grinding.

Concurrently with this carnivore radiation, the EECO witnessed a major expansion of Rodentia (eight to ten new genera beginning in Wa-7), distributed among the Microparamyinae, Paramyinae, and Sciuravidae.

In addition to these, the well-known diversification and eventual dominance of omomyine over anaptomorphine euprimates took place in the Bridgerian, accompanied by the addition of homacodontine artiodactyls and the origin (Wa-7 and Bridgerian) of four subfamilies of brontotheriid perissodactyls.

The greatly increased diversity also is seen in rarefaction analysis (Foote 1992) as applied (Stucky 1992) to various Eocene to Oligocene faunas from western North America. Fig. 16 is based on Stucky (1992), with the addition of 18 new localities of Br-2. The result indicates that faunas from the Wa-7–Br-1a interval approximately doubled in diversity as compared with those of Wa-1–Wa-5 (Wa-6 samples not included, as insufficient for analysis). Diversity subsequently was dramatically reduced during Br-2 by approximately 40% for sample sizes of greater than 50 specimens (the basic unit of comparison throughout). The early EECO diversity increase and its later 40% decline was coincident with climatic and floral patterns discussed herein. One aspect of faunal instability apparently influenced by climatic decline is the fact that *Hyopsodus* is the most abundant mammal in Br-2 faunas.

Hooker (2000) suggested (Fig. 9) that the early part of the EECO (Wa-6–Br-1a) was marked by a high

level of insectivory, scansoriality, and arboreality. Minor decreases are recognized in microsomyid primates, phenacodontid condylarths, and isectolophine tapiroids. Pholidotans lose four of six genera, and anaptomorphine euprimates lose four of eight. These losses were associated with the extinction (in Wa-7) of arctocyonid condylarths.

Interestingly, the early part of the EECO was marked by a drop in terrestriality before its emergence later. The likely correspondence between this pattern and that of early tropicality versus later seasonal aridity, and potentially more open habitats, needs to be evaluated through analysis of floras and the environments inferred from paleosols.

In summary, the early part of the EECO, of which the taxa in Br-1a played a major part, was a period of substantial innovation, with more FADs from Wa-6–Br-1a (63: Appendix, Table 5) than in any time where three successive biochrons are considered together, except for Ui-1–Ui-3. As shown in Appendix, Table 5, the interval Cf-3–Wa-1 records a total of 50 FADs. Whereas both intervals were associated with an increase in relative tropicality (greatest for the early part of the EECO), the Cf-3–Wa-1 interval was not associated with a marked increase in floral diversity, in strong contrast to the EECO. This habitat difference likely was reflected in the greater FAD expansion in Br-1a than was the case for Wa-0, and a significant aspect of this may have been the pattern of taxon origination in areas marginal to the depositional basin (Gunnell & Bartels 2004) or in areas marginal to the Green River lake systems.

Whereas Wa-0 recorded dwarfing of some taxa as a result of climatic change and subsequent emphasis on somewhat greater body size to Wa-5 (Gingerich 2003) as well as niche expansion into increased diversity (Clyde & Gingerich 1998), the strong diversity development in Br-1a still is apparent. Some Br-1a localities show a body size profile reminiscent of patterns seen in Wa-0 but have not been thoroughly documented as yet (Stucky, unpublished data). Importantly, body size increases among almost all medium- to large body-sized taxa in most mammalian lineages that range from Br-1a–Br-1b and Br-2.

In addition, the number of LADs associated with

the FADs in Wa-6–Br-1a (Appendix, Table 5) provides a very sharp distinction relative to the Cf-3–Wa-1 interval, and it is tempting to suggest a role played here again by the much greater tropicality of climate and floral diversity associated with the early part of the EECO. The high species diversity and even (non-skewed) relative abundance curves, especially during Br-1a (Stucky 1992; Fig. 16), are quite similar to those from tropical mammalian communities today (Bourliere 1973; Eisenberg et al. 1979; Andrews et al. 1979; Flemming 1973). While each interval experienced an increase in relative tropicality, the record for the early part of the EECO suggests a much higher impact on the mammal biota, apparently reflected by both opportunities and stress supplied by the prevailing climatic, ecologic, and local tectonic influences.

The Bridgerian Crash

The later part of the EECO demonstrates a different pattern than the early part of this interval, apparently reflecting the continuing deterioration of the climate. Appendix, Table 5 shows that whereas the number of FADs in Br-1b–Br-3 is small (28), the number of LADs remains substantial (62), and total numbers of genera drop significantly (96 to 84; about 12%) from Br-1a–Br-3.

The interval from Br-1b–Br-3 reflects a major reorganization of the mammalian fauna. FADs in Br-1b are only 6%, and LADs comprise 16% of the fauna, which now reaches 96 taxa (Appendix, Table 2). There are no immigrants or new suprageneric groups in Br-1b and only *Telmathoberium* in Br-2. *Hyopsodus* increased to 61% of the fauna in Br-2 as a measure of the imbalance in the stressed biota (Stucky et al. 2006), which shows a concomitantly large number of rare taxa. New suprageneric groups in Br-3 consist of eomyine rodents (*Adjidaumo*, *Protadjidaumo*, *Paradjidaumo*) and amynodontine rhinos (*Amyndodon*), which apparently take advantage of the more open habitats, as does the uinatherid *Tetheopsis*. Of these, the rhinocerotoid *Amyndodon* is an immigrant (Appendix, Table 3). These new additions augment the herbivore components. Other FADs are omomyine (*Macrotarsius*, *Ageitodendron*) and anaptomorphine (*Sphacorhysis*) euprimates. Whereas singular

hyperthermal episodes (PETM) may have facilitated immigrations in the past, mesothermal conditions in the Western Interior of North America imply suitably warm, high latitude dispersal routes, even during the later part of the EECO.

In contrast to the relatively small number of FADs, taxonomic loss during the interval Br-1b–Br-3 is substantial (Figs. 7 and 8; Appendix, Table 4). The conclusion seems inescapable: that extinctions were promoted by the development of seasonally arid and cooler conditions. The coryphodontid (and thus all) pantodonts and long-lived oxyclaenid condylarths became extinct in Br-1b (Appendix, Table 4). Table 4 indicates that the Br-1b reductions and extinctions affected small insectivores, scansorial carnivores, and small and large herbivores.

The herbivorous *Tillodontia* last occur in Br-2 (Appendix, Table 4). In Br-3, adaptive groups that became extinct or diminished include fossorial metacheiromyid pholidotans, cursorial to scansorial carnivores (oxyaenids, some miacids, some viverravids), and herbivores (phenacodontid and homacodontine condylarths), as well as scansorial to arboreal rodents and primates. During this time of both faunal and climate deterioration, *Hyopsodus* increased to a total of 61% of the fauna in Br-2. Apparently *Hyopsodus* was able to exploit an element of the ecological resource during Br-2 that was either unavailable to, or vacated by, other taxa. It also is possible that the abundance of *Hyopsodus* in Br-2 faunas may be a localized phenomenon due to the strong representation of these faunas in the regionally predominant Bridger Formation localities. These localities may represent a biofacies related to the lacustrine nearshore depositional setting of the Bridger Formation as it intertongues with the lacustrine Green River Formation in the Green River Basin.

Adaptive groups that became diminished beginning with Br-1b (Appendix, Table 1) comprise the smaller omnivores to herbivores, including dichobunid artiodactyls and helaetid perissodactyls. Losses in larger herbivore groups pertain to brontotheriid, equid, hyracodontid, isctolophid, and helaetid perissodactyls. Carnivores showed declines inhyaenodontine, limnocyonine, and oxyaenid creodonts, miacids, viverrids,

mesonychids, and oxyclaenids.

In Br-3, additional adaptive groups undergoing reduction include the small herbivore microparamyine rodents (while eomyids originate). The once dominant anaptomorphine and omomyine primates begin their substantial reduction in Br-3, and miacid carnivores drop two genera (40%) in this biochron. Small herbivore condylarths (phenacodontids) become extinct in Br-3. Mesonychids expand in Br-2 but drop in Br-3, and limnocyonine carnivorans are reduced as well.

Of the approximately 25 non-carnivore and 11 carnivore taxonomic groups concerned, the greatest number of non-carnivores (12) is lost during Br-3, mirrored by a similar situation (5) of carnivores. Proportionately more non-carnivores are lost in Br-2 (5) than carnivores (4), a situation even more pronounced (8 non-carnivores versus 2 carnivores) in Br-1b.

In summary (Appendix, Tables 1, 2, 4, 5), the large number and diversity of gains and then losses and reductions in the EECO (from Wa-6–Br-3) is in striking contrast to virtually all other mammalian biochrons from Ti-3, except for the Uintan. There are very few immigrants, so this factor has no effect on the FADs or the higher number of LADs found in Br-1b, Br-2, and Br-3. Speciation in these biochrons apparently was driven by factors other than the stimulus of immigration, in seeming distinct contrast to the situation in Wa-0, with effects persisting to Wa-5. The strong increase in tropicality from Wa-6–Wa-7 and then its retreat from late Br-1a into the Uintan apparently was a stronger signal than the one associated with the PETM (as seen from the 19% decrease in the number of genera from Br-1a–Br-3 [from Fig. 6], and the greater proportion of LADs [Fig. 8], versus a 2% generic decrease from Wa-1–Wa-5, and fewer LADs). In the later part of the EECO, the large number of extinctions and reductions is all the more impressive from the viewpoint that most or all of the groups affected were apparently well-adapted only just previously. The climatic cooling from about 50 Ma onward (Fig. 1), with its progressively greater seasonal aridity, apparently drove many of the extinctions and reductions on the one hand, and must also have been at least in part responsible for the innovations (although small in number) recorded during this

interval. Eomyid rodents and various large herbivores likely adapted to the presence of more open conditions than had existed previously.

Hooker (2000) suggested that a singular aspect of EECO faunas was the presence of a large-sized herbivore guild (typified by large perissodactyls and uinatheres) with low-crowned cheek teeth and transversely organized shearing dentitions that were adapted to lush, tropical vegetation. Of these groups, the uinatheres persist through the Bridgerian and into the Uintan. Hooker (2000) also indicated that artiodactyls and perissodactyls contributed to the increase in browsing herbivores that mark the later part of the EECO (Br-1b–Br-3), as well as to the increase in terrestriality during that time.

But the much greater floral diversity associated with the early part of the EECO also must have provided a major stimulus not present in the earlier Wasatchian. The post-immigration faunal dynamics of the EECO were much more diverse and complex than the substantially more regular pattern (smaller generic loss, relatively fewer LADs) seen from Wa-1–Wa-5. Modification of habitats during this climatically drier interval also may be reflected by the progressive drop in total numbers of genera from Br-1a–Br-3 (Fig. 6). Part of this drop may be due to the sampling of different depositional environments from Wa-1–Wa-5 and from Br-1a–Br-3, but this is not yet clear.

Janis (2007) noted that morphological changes in various nominally herbivorous groups, as well as a major drop in $P\text{ CO}_2$ (Pearson & Palmer 2000), imply floral change during the EECO. Pearson & Palmer (2000) showed a strong drop in $P\text{ CO}_2$ at the beginning of the EECO, compatible with, but not predictive of, the warm temperatures of that time. This drop in $P\text{ CO}_2$ continued into the Uintan, with a short reversal at about 47 Ma. This pulse follows the beginning of the major cooling episode (at about 50 Ma) contemporaneous with the change from more tropical habitats to seasonally more arid conditions (Fig. 1) just after the EECO.

As summarized by Janis (2007), this change in climate played a role in influencing the later Eocene decline of perissodactyls and the correlated rise of artiodactyls. Eocene perissodactyls ranged from small equids

(from Wa-0: Appendix, Table 1) with a body mass of about 5–10kg to very large brontotheriids (from Wa-7: Appendix, Table 1) with a body mass up to several thousand kilograms. Perissodactyls typically had lophodont and bunolophodont cheek teeth adapted to a folivorous diet.

Contemporary artiodactyls were smaller generally, with bunodont to bunoselenodont cheek teeth adapted to omnivory or possible folivory/frugivory. Representative artiodactyls included leptochocerids (Wa-6–Ui-3, at least) and helohyids (Br-1b–Ui-1). Based on their basically bunodont cheek teeth, these taxa were primarily unspecialized folivores/frugivores without the foregut fermentation capabilities that were developed by more derived artiodactyl groups beginning in the Uintan.

In the late medial Eocene (basically from Ui-1), a major change is reflected in the appearance (Janis 2007) of bunoselenodont to selenodont artiodactyls: Suiformes, Tylopoda, Ruminantia (Appendix, Table 1). In the later Eocene, many perissodactyls declined, including (Janis 2007) equids and a variety of tapiroids (isectolophids and helaletids, mostly gone by Br-3: Appendix, Table 1). More modern perissodactyls also appeared at this time, including amynodontid rhinocerotoids (from Br-3). At least for the artiodactyls, the acquisition of a more selenodont (bunoselenodont) dentition likely corresponded with the development of foregut fermentation capabilities. This suggested to Janis (2007) that the diet of these artiodactyls had shifted from more omnivorous to more folivorous. The acquisition of folivory may be reflected in the morphology of other groups as well, in that some perissodactyls, notharctine primates, rodents, and *Hyopsodus* developed progressively higher crowned and more lophodont to selenodont dentitions from Wa-6–Br-1a (Stucky, pers. observation).

While the earlier Eocene paratropical forests had provided a variety of plant food for small herbivores and omnivores (Wing 1998; Harrington 2001), the demise of small bunodont artiodactyls and bunodont archaic ungulates (“Condylarthra”: Appendix, Table 1) likely was related to the reduction of fruit as an available food source in the more seasonally arid climates that developed (Janis 2007).

More seasonal climates are considered (Janis 2007) to favor plants that differentially emphasized leaves having less fiber than stems (i.e., deciduous habits). This would favor the development of mammals capable of selecting (and consuming) higher-quality (lower fiber content) food and having more advanced methods of fermentation in the foregut (as developed by artiodactyls but not perissodactyls, which typically are hindgut fermenters).

Contemporaneous with this change in floras and mammals was a strong drop in the CO₂ content of the atmosphere (Pearson & Palmer 2000) and presumably in plants as well. Presumably, a high CO₂ content reflected less seasonality and resulted in higher floral productivity, which eventually led to higher plant as well as mammalian diversity. Prior to this time, with elevated amounts of atmospheric CO₂ plants would have produced an abundant but relatively low-quality food source, which would favor hindgut fermenters (perissodactyls) over foregut fermenters (Janis 2007).

Uintan NALMA

It is not the purpose of this report to examine the fossil mammals of the Uintan NALMA in any detail. Appendix, Table 5 indicates that, like the Bridgerian, the Uintan experienced only minor immigrations, and Appendix, Tables 1 and 2 indicate that some large herbivores were new in Ui-1 and Ui-2, and lagomorphs appeared in Ui-3. The strong and nearly equal number of both FADs and LADs throughout the interval could be taken as reflecting habitat changes as climate deteriorated subsequent to the EECO. Certainly, the progressive development of more modern groups beginning in Ui-1, such as aplodontid rodents, leptochocerid, agriochoerid, oromerycid, and protoceratid artiodactyls, has been well known and likely reflected the development of more open habitats. A similar interpretation could apply to the development of micropternodontid sorcids, hypertragulid artiodactyls, and some brontotheriid perissodactyls in Ui-3.

Summary

The Early Eocene Climatic Optimum spanned the interval from about 53–50 Ma. While the marine record manifested a relatively even temperature regime throughout the interval, the land plant record of the Western Interior of the United States reflected a sharp increase in tropicality during the first part of the interval, followed by a sharper retreat to more temperate and seasonally arid conditions. The early part of the EECO (Wa-6–Br-1a) revealed a pattern superficially similar to that seen from the Clarkforkian to early Wasatchian. But the two intervals reflected different stimuli and climatic conditions. The increase in mammalian taxonomic origination during the EECO apparently was a response to newly and greatly diversified floral associations, increased habitat complexity, and the spread of more tropical climates into the mid- and higher latitudes. In contrast, the immigration-driven stimulus of the earlier Wasatchian (PETM–Wa-0 followed by Wa-1) was accomplished under warm but not as strongly tropical conditions (and of shorter duration) in which floras and habitats were substantially less diverse and complex. The later part of the EECO (Br-1b–Br-3) apparently reflected a much greater degree of habitat and climatic stress than seen in any portion of the Wa-1–Wa-5 interval, especially signaled by the proportionately greater number of LADs and other measures of phyletic loss. In spite of localized population expansions, such as seen in *Hyopsodus*, the collective loss of taxa from Br-1b–Br-3 represents the greatest such episode documented from the late Paleocene to the medial Eocene.

Alroy et al. (2000) cautioned against assigning climate a direct role in fossil land mammal faunal changes during the Cenozoic era. The data assessed in this report seem to show instances (Tiffanian, medial Wasatchian) where climate was relatively benign and apparently served as the basic background upon which a relatively modest degree of faunal dynamism was developed. In those cases, both innovation (FADs) and extinctions/declines (LADs) were about in balance (save Ti-6), and both were of modest levels. In both intervals immigration played only a minor role or none at all. To the extent that climate was behaving in an opposite sense

collectively (rising temperature and moisture in the Tiffanian versus the opposite in the medial Eocene), the basically similar patterns of mammalian faunal dynamics indicate that the role of climate in those examples was inconsistent at best, and likely of no major influence.

The Clarkforkian and early Wasatchian (to Wa-1) interval witnessed an increasingly warm climatic setting, attaining moist, subtropical conditions by Wa-0. The plants were relatively diverse in the Clarkforkian, but this dropped strongly in the early Wasatchian. Mammalian generic numbers rose throughout this interval, with FADs and LADs being modest in scope and about in balance for the Clarkforkian. Immigrants are important taxonomically in the Clarkforkian (e.g., introduction of the Rodentia), and contributed about 5% of the new genera of the interval. If these taxa are removed from consideration, that would result in there being no dramatic increase in taxa of those times. While climate perhaps facilitated immigrations, Clarkforkian faunal increase was only modest.

The early Wasatchian (Wa-0–Wa-1) was strongly different in this regard. FADs grossly outnumbered LADs in the early Wasatchian, and generic numbers greatly increased as well. Early Wasatchian floras were substantially less diverse than in the Clarkforkian, however. Unless there is an inverse relationship between them, it appears that the plant record cannot account for the dramatic increase in mammal taxa and FADs of the time. Still, it is clear that immigration was of supreme importance in driving faunal innovation in the early Wasatchian and that the PETM favored the immigration episode recorded in Wa-0 and constrained the age of that episode accordingly. The faunal dynamics of the Wa-0 can be strongly associated with a brief but very positive pulse in climate.

For the EECO it appears that there were no immigrations on the one hand, but that climatic change played a major role in faunal dynamics of the time on the other. The growth and decline of mammal faunas of the EECO appears to directly reflect those aspects of the coeval floras and the waxing and waning of climate they represent.

Diverse floras of tropical to subtropical aspect

are recorded at the beginning of the EECO, and these continue, along with increasing MAT, to about 23°C, by Wa-7. The just antecedent Sourdough flora shows a major turnover wherein 87% of the taxa are new. Faunas in Wa-6 and Wa-7 show a strong increase in genera as compared to Wa-5 with a comparable increase in both FADs and LADs, and this pattern continues into Br-1a, all in the early part of the EECO.

The nearly equal proportions of FADs and LADs in the Wa-6–Br-1a interval are in sharp contrast to the situation in the later part of the EECO (Br-1b–Br-3), where LADs greatly outnumber FADs and the generic diversity shows its greatest decline in any part of the timescale considered herein.

Even though the climate was still warm and subtropical at the end of Br-1a, the MAT was distinctly cooler (20°C) and rainfall more seasonal. The Little Mountain flora is highly species-rich and diverse; 86% of taxa represent new species, and this strong floral turnover is indicated as well by the absence of 88% of the species that lived previously. The taxonomic character of the Little Mountain flora is very similar to that of the Green River, Florissant, and Wind River floras, which indicate comparably seasonal and even cooler conditions.

The floral turnover and climatic change that persisted in Br-1b–Br-3 is contemporaneous with the dramatic faunal change of the same interval. It therefore appears that faunal changes in both parts of the EECO were driven by climatic (and hence floral) change. Although Alroy et al. (2000) allude to the interval here discussed as the EECO as a potential candidate for climatic influence, the dramatic faunal and floral dynamics presented in this report make a very strong case in favor of climatic causes. Rather than being climatically “optimum,” the EECO fomented the greatest episode of faunal turmoil of the first 15 m.y. of the Cenozoic era.

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Appendix

Table 1. Land mammals of the medial Tiffanian, Clarkforkian, Wasatchian, Bridgerian, and Uintan NALMAs showing first occurrences (F) and last occurrences (L).

Taxon	Uj3	Uj2	Uj1	Br3	Br2	Br1b	Br1a	Wa7	Wa6	Wa5	Wa4	Wa3	Wa2	Wa1	Wa0	Cf3	Cf1	Tf6	Tf5	Tf4	Tf3	Classification generally follows McKenna & Bell (2002)
Theria																						Gunnell et al. 2008c
MULTITUBERCULATA																						Lofgren et al. 2004; Gingerich & Clyde 2001; Weil & Krause 2008
Cimolodonta																						Gunnell 1998; Weil & Krause 2008
Sloaneaartidae																						and earlier; Weil & Krause 2008
Philodontoidea																						
Philodontidae																						
Mesodma																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Neoplagiaulax																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Ectypodus																						and earlier; Lofgren et al. 2004; Weil & Krause 2008 to Ch3
Parecypodus																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Mimeodon																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Phlodus																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Baioimeus																						and earlier; Lofgren et al. 2004; Weil & Krause 2008
Prochetodon																						and earlier; Lofgren et al. 2004; Gingerich & Clyde 2001; Weil & Krause 2008
Taeniolethoidea																						
Eucosmodontidae																						and earlier; Lofgren et al. 2004.; Weil & Krause 2008 to Cf3
																						and earlier; Weil & Krause 2008
																						Gingerich & Clyde 2001; Weil & Krause 2008 to Wa3
																						and earlier; Lofgren et al. 2004; Weil & Krause 2008 to Ch3
																						Case et al. 2005
MARSUPIALIA																						
Didelphimorphia																						
Didelphidae																						
Peradectinae																						and earlier; Lofgren et al. 2004; Korth 2008 to Ch3
																						and earlier; Lofgren et al. 2004; Korth 2008
																						Korth 2008
																						Korth 2008 to Ar2
																						Korth 2008 to He1
																						Korth 2008
																						Korth 2008 to Or4
EPITHERIA																						
Leptictida																						
Leptictidae																						and earlier; Lofgren et al. 2004; Gunnell et al. 2008b
																						Gunnell et al. 2008b to Du
																						and earlier; Lofgren et al. 2004; Gunnell et al. 2008b to Tf3
																						Gunnell et al. 2008b

Taxon	Ti3	Ti4	Ti5	Ti6	Cf1	Cf2	Cf3	Wa0	Wa1	Wa2	Wa3	Wa4	Wa5	Wa6	Wa7	Br1a	Br1b	Br2	Br3	Ui1	Ui2	Ui3	Classification generally follows McKenna & Bell (2002)		
LAGOMORPHA																							Gunnell et al. 2008b to Du		
Leporidae																									
Palaeolaginae																									
																								Dawson 2008 to Or4	
																									Dawson 2008 to Ch2
RODENTIA																									
Alagomyidae																									Flynn 2008c
Laredomyidae																									Flynn 2008c
Sciuromorpha																									
Ischyromyidae																									Anderson 2008 to Wh2; Korth 1994; Stucky pers. comm. 2008
Microparamyinae																									Anderson 2008
																									Anderson 2008
																									Anderson 2008 to Ch2
																									Anderson 2008
																									Anderson 2008 to Du
																									Anderson 2008
																									Anderson 2008
Paramyinae																									Br2-3 after Gunnell & Bartels 1999; Anderson 2008 to Ch1
																									Anderson 2008 to Du
																									Korth 1994 to Ui3; Anderson 2008 to Ui3
																									Anderson 2008
																									Anderson 2008 to Du
																									Anderson 2008 to Ui3
																									Anderson 2008 to Ui3
																									Anderson 2008
																									Anderson 2008 to Ch4
Alluravinae																									Anderson 2008 to Ch1
																									Anderson 2008 to Du
Sciurida																									
Reithroparamyidae																									Anderson 2008 to Ui3
Myomorpha																									Walton & Porter 2008
																									Walton & Porter 2008 to Ui3
Sciuravida																									
Sciuravidae																									Walton & Porter 2008
																									Walton & Porter 2008
																									Walton & Porter 2008
																									Walton & Porter 2008 to Du
Jaywilsonomyinae																									Walsh & Storer 2008
																									Walsh & Storer 2008 to Du
Cylindrodontinae																									Walsh & Storer 2008

Taxon	Wc7	Wc6	Wc5	Wc4	Wc3	Wc2	Wc1	Wc0	Wc1	Wc2	Wc3	Wc4	Wc5	Wc6	Wc7	Br1a	Br1b	Br2	Br3	U11	U12	U13	Classification generally follows McKenna & Bell (2002)
<i>Anomoemys</i>															X								Walsh & Storer 2008
<i>Pseudocylindrodon</i>																		X	X	X	X		Walsh & Storer 2008 to Ch4
Aplodontidae																		X	X	X	X		Flynn & Jacobs 2008a to Ch3
Eutypomyidae														X				X					Flynn & Jacobs 2008b
																							Flynn & Jacobs 2008b to Du
Dipodidae																							Flynn & Jacobs 2008b to Du
Protophychidae																			X				Flynn 2008c
Incertae sedis																		X					Flynn 2008c
																							Flynn 2008c
Eomyidae																							Flynn 2008c to Ch4
																							Flynn 2008b to Du
																		X	X	X	X		Flynn 2008b to Wh1
																		X	X	X	X		Flynn 2008b to Ch2
																		X	X	X	X		Flynn 2008b to He2
Geomorpha, incertae sedis																							Flynn et al. 2008 to Ch3
																			X	X			Flynn et al. 2008
FERAE																							
Cimolestia									X														and earlier; Lofgren et al. 2004; Gunnell et al. 2008b
Wyolestinae									X	X													Gingerich & Clyde 2001
Palaeoryctidae									X	X	X												and earlier; Lofgren et al. 2004; Gunnell et al. 2008a to Wc4 Bloch et al. 2004
																							Gunnell et al. 2008b
									X														Gunnell et al. 2008b
																							Gunnell et al. 2008b
Diadelphodonta																							
Cimolestidae																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008b
																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008b
																							and earlier; Lofgren et al. 2004; Gingerich & Clyde 2001
																							Gunnell et al. 2008b
									X	X	X	X	X	X	X	X	X	X	X	X	X		Storer 1996; Gunnell et al. 2008b to Du
Apatotheria																							
Apatemyiidae																							and earlier; Gunnell et al. 2008b
																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008b
																							Gunnell et al. 2008b to Du
																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008b to T15
																							Gunnell et al. 2008b to Du
Pantolestia																							
Pantolestiidae																							
Pentacodontinae																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008b

Taxon	Ti3	Ti4	Ti5	Ti6	Cf1	Cf2	Cf3	Wc0	Wc1	Wc2	Wc3	Wc4	Wc5	Wc6	Wc7	Br7	Br1a	Br1b	Br2	Br3	Ui1	Ui2	Ui3	Classification generally follows McKenna & Bell (2002)	
	x	x																						and earlier; Lofgren et al. 2004; Gunnell et al. 2008b	
								x	x	x	x	x	x	x	x									Gunnell et al. 2008b	
Pantolestinae																x	x	x	x	x	x	x	x	Gunnell & Bartels 1999; Gunnell et al. 2008b to Du; Boyer & Georgi 2007	
	x	x	x																					and earlier; Gunnell et al. 2008b.	
	x	x	x																					and earlier; Lofgren et al. 2004; Gunnell et al. 2008b	
	x	x	x																					Gunnell et al. 2008b	
Pholidota																								Gunnell et al. 2008b	
																								Rose 2008a	
Epicotheriidae																								Rose 2008a	
																								Rose 2008a	
																								Rose 2008a	
																								Rose 2008a	
																								Rose 2008a	
																								Gunnell & Bartels 1999; Rose 2008a to Ui-1	
																								Rose 2008a	
Metacheiromiidae																								Rose 2008a	
																								Rose 2008a	
																								Rose 2008a	
																								Gingerich & Clyde 2001; Rose 2008a	
																								Gunnell & Bartels 1999; Rose 2008a	
																								Gunnell & Bartels 1999; Rose 2008a	
Taeniodonta																									
	x	x	x																					and earlier; Lofgren et al. 2004; Lucas et al. 1998 to Cf1	
																								Lucas et al. 1998; Gingerich & Clyde 2001 to T4	
																								Gunnell & Bartels 1999; Lucas et al. 1998 to Ui3	
Tillodontia																									
																									Lucas & Schoch 1998b; Lofgren et al. 2004; Gingerich 1989; Gingerich & Clyde 2001
																								Krishalka et al. 1987; Robinson et al. 2004; Lucas & Schoch 1998a	
																								Gingerich 1989; Gingerich & Clyde 2001	
																								Gunnell & Bartels 1999; Lucas & Schoch 1998b	
																								Gunnell & Bartels 1999; Lucas & Schoch 1998b	
Pantodonta																									
																									Lucas 1998
																								and earlier; Lucas 1998	
																								Lucas 1998	
																								Lucas 1998; Gingerich & Clyde 2001	
																								Gingerich & Clyde 2001	

Taxon	Ti3	Ti4	Ti5	Ti6	Cf1	Cf2	Cf3	Wa0	Wa1	Wa2	Wa3	Wa4	Wa5	Wa6	Wa7	Br1a	Br1b	Br2	Br3	Ui1	Ui2	Ui3	Classification generally follows McKenna & Bell (2002)
Ermaceomorpha	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			and earlier; Lofgren et al. 2004; Gingerich & Clyde 2001 Gunnell et al. 2008c
	x	x	x	x	x	x	x	x	x														Gunnell et al. 2008c
	x	x	x	x																			Gunnell et al. 2008c to Du
Litoherinae	x	x	x																				and earlier; Lofgren et al. 2004; Gingerich & Clyde 2001; Gunnell et al. 2008c
Diacodontinae	x	x	x	x	x	x	x	x	x	x	x	x	x	x									and earlier; Lofgren et al. 2004; Gingerich & Clyde 2001; Gunnell et al. 2008c; incl. <i>Diacocherius</i>
Sespedectidae																							
Scenopaginae																							Gunnell & Bartels 1999; Gunnell et al. 2008c
																							Gunnell et al. 2008c to Or3
Sespedectinae																							Gunnell et al. 2008c to Du
																							Gunnell et al. 2008c to Du
																							Gunnell et al. 2008c to Ch2
																							Gunnell et al. 2008c
Amphilemuridae																							Smith et al. 2002; Gunnell et al. 2008c to Du
Creolaridae																							Gunnell et al. 2008c
Erinaceoidea																							Gunnell et al. 2008c
																							Gunnell et al. 2008c
																							Gunnell et al. 2008c
Erinaceidae																							Lofgren et al. 2004; Gunnell et al. 2008c
																							Gunnell et al. 2008a
Tupaodontinae																							Gunnell et al. 2008c to Du
Soricomorpha																							
Geolabridae																							
																							Gunnell & Bartels 1999; Gunnell et al. 2008c to Ar3
																							Gunnell et al. 2008c
																							Gunnell et al. 2008c to Ui3
Soricoidae																							
Micropternodontidae																							Gunnell et al. 2008c to Ar3
Apternodontidae																							Gunnell et al. 2008c
																							Gunnell et al. 2008c to Ui3
Nyctitheriidae																							
																							Gunnell et al. 2008c to Or4
																							Gingerich & Clyde 2001; Gunnell et al. 2008c
																							Gingerich & Clyde 2001; Gunnell et al. 2008c
																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008c to Wa4
																							Gingerich & Clyde 2001; Gunnell et al. 2008c to Wa5
																							and earlier; Lofgren et al. 2004; Gunnell et al. 2008c
																							Stucky pers. comm. 2008
																							Gunnell & Bartels 1999; Gunnell et al. 2008a to Du
Amphidozootheriinae																							Gunnell et al. 2008c
Soricidae																							
Heterosoricinae																							Gunnell et al. 2008c

Taxon	U13	U12	U11	B-3	B-2	Br1b	Br1a	Wa7	Wa6	Wa5	Wa4	Wa3	Wa2	Wa1	Wa0	Cf3	Cf2	Cf1	Tf6	Tf5	Tf4	Tf3	Classification generally follows McKenna & Bell (2002)
ARCHONTA																							
Primates																							
Microsyopidae																							
Uintasortinae																							
<i>Uintasorex</i>																							
<i>Niptomomys</i>																							
<i>Nanajonius</i>																							
Microsyopinae																							
<i>Archodontomys</i>																							
<i>Microsyops</i>																							
<i>Megadelphus</i>																							
<i>Grasops</i>																							
Picromomyidae																							
<i>Picromomys</i>																							
<i>Alveojunctus</i>																							
Micromomyidae																							
Micromomyinae																							
<i>Micromomys</i>																							
Tinimomyinae																							
<i>Tinimomys</i>																							
<i>Chadicomomys</i>																							
Plesiadapidae																							
<i>Plesiadaptes</i>																							
<i>Chiromyoides</i>																							
<i>Nannodectes</i>																							
<i>Pronalobodectes</i>																							
<i>Plesiadaptes</i>																							
<i>Picrodus</i>																							
<i>Zanyclerus</i>																							
<i>Elphidotarsius</i>																							
<i>Carpodaptes</i>																							
<i>Carpomogodon</i>																							
<i>Carpolestes</i>																							
<i>Saxonella</i>																							
Paromomyidae																							
<i>Paromomys</i>																							
<i>Elucynella</i>																							
<i>Acidomomys</i>																							
<i>Ignacius</i>																							
<i>Phenacolemur</i>																							
Dermoptera																							
<i>Elpidophorus</i>																							
<i>Eudaemonema</i>																							
<i>Worlandia</i>																							
<i>Planetoberium</i>																							

Taxon	TI3	TI4	TI5	TI6	CI1	CI2	CI3	Wc0	Wc1	Wc2	Wc3	Wc4	Wc5	Wc6	Wc7	Br1a	Br1b	Br2	Br3	UI1	UI2	UI3	Classification generally follows McKenna & Bell (2002)	
<i>Plagiomene</i>					X			X															Rose 2008b	
<i>Taraka</i>								X												X			Rose 2008b	
Euprimates																								
Strepsithini																								
Lemuroidea																								
Adapidae																								
Notharctinae																								
<i>Canitius</i>					X			X	X	X	X	X	X	X	X	X	X	X	X				Gingerich & Clyde 2001; Gunnell et al. 2008d	
<i>Copelemur</i>								X	X														Gingerich & Clyde 2001; Gunnell et al. 2008d; Stucky pers. comm. 2008	
<i>Smilodectes</i>																X	X	X	X				Gunnell & Bartels 1999; Gunnell et al. 2008d	
<i>Notharctus</i>																X	X	X	X				Gunnell & Bartels 1999; Gingerich & Clyde 2001; Gunnell et al. 2008d	
<i>Pelycodus</i>													X	X	X								Gunnell et al. 2008d	
<i>Hesperolemur</i>																					X		Gunnell et al. 2008d	
Haplorhini																								
Tarsiiformes																								
Omomyidae																								
Omomyinae																								
<i>Steinius</i>								X	X															Gunnell et al. 2008d
<i>Omomyus</i>																								Gunnell & Bartels 1999; Gunnell et al. 2008d to Du
<i>Loveina</i>														X										Gunnell et al. 2008d
<i>Washakius</i>																								Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Shoshonius</i>																								Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Dyseodemur</i>																								Gunnell et al. 2008d
<i>Macrolarsius</i>																								Gunnell et al. 2008d to Du
<i>Hemiacodon</i>																								Gunnell et al. 2008d to Du
<i>Yaquius</i>																								Gunnell et al. 2008d
<i>Wyomomyus</i>																								Gunnell et al. 2008d to Du
<i>Ourayia</i>																								Gunnell 1998; Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Agelodendron</i>																								Gunnell et al. 2008d
<i>Utahia</i>																								Gunnell et al. 2008d
<i>Stoekia</i>																								Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Chipeleia</i>																								Gunnell et al. 2008d
<i>Uinitanius</i>																								Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Jemezius</i>																								Gunnell et al. 2008d
Anaptomorphinae																								
<i>Teilhardina</i>					X			X	X	X	X	X	X	X	X									Gingerich & Clyde 2001; Gingerich 1993; Smith et al. 2006
<i>Chlororhysis</i>																								Gunnell et al. 2008d
<i>Arapahobius</i>																								Gunnell et al. 2008d
<i>Aycrossia</i>																								Gunnell et al. 2008d
<i>Strigorhysis</i>																								Gunnell et al. 2008d
<i>Tetonius</i>																								Gingerich & Clyde 2001; Gunnell et al. 2008d to Wa5
<i>Anemorhysis</i>																								Gunnell et al. 2008d

Taxon	Ti3	Ti4	Ti5	Ti6	Cf1	Cf2	Cf3	Wa0	Wa1	Wa2	Wa3	Wa4	Wa5	Wa6	Wa7	Br1a	Br1b	Br2	Br3	Ui1	Ui2	Ui3	Classification generally follows McKenna & Bell (2002)
<i>Pseudototipotius</i>												X											Gunnell et al. 2008; Chew pers. comm. 2008
<i>Absarokitus</i>												X	X	X	X	X							Gingrich & Clyde 2001; Gunnell et al. 2008d to Br1; Chew pers. comm. 2008
<i>Tatmanius</i>														X									Gunnell et al. 2008d
<i>Anaptilomorphus</i>																X	X	X	X				Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Gazinius</i>																X	X	X	X				Gunnell & Bartels 1999; Gunnell et al. 2008d
<i>Trogolemur</i>															X	X	X	X	X			X	Gingrich & Clyde 2001; Gunnell et al. 2008d to Du
<i>Sphacorhynchus</i>															X	X		X					Gunnell et al. 2008d
<i>Arbimontius</i>														X	X	X							Gunnell et al. 2008d
UNGULATA																							
Dinocerata																							
Uinatheriidae				X	X	X	X	X	X	X	X	X	X	X	X	X							Lofgren et al. 2004; Lucas & Schoch 1998a
<i>Prodiaceras</i>															X	X		X					Gunnell & Bartels 1999; Lucas & Schoch 1998a
<i>Bathyopsis</i>																X	X	X	X				Robinson et al. 2004; Krishalka et al. 1987; Walsh 1996
<i>Uinatherium</i>																	X	X	X				Robinson et al. 2004
<i>Telheopsis</i>																	X	X	X				Robinson et al. 2004
<i>Eobasiliscus</i>																			X				Robinson et al. 2004
Condylarthra																							
Oxyclaenidae		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							and earlier; Lofgren et al. 2004; Archibald 1998 to Wa7
<i>Chriacus</i>															X								Gingrich & Clyde 2001; Archibald 1998
<i>Princetonia</i>															X	X							and earlier; Lofgren et al. 2004; Archibald 1998 to Br1
<i>Thryplacodon</i>															X	X							
Arctocyonidae																							
Loxolophinae		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							and earlier; Lofgren et al. 2004; Archibald 1998 to Wa7; Archibald 1998
<i>Mimotricentes</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Lambertocyon</i>																							and earlier; Lofgren et al. 2004; Archibald 1998
<i>Clanodon</i>																							Gingrich & Clyde 2001
<i>Anacodon</i>															X	X							
Hyopsodontidae																							
Tricuspidontinae		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							and earlier; Lofgren et al. 2004; Archibald 1998
<i>Litolomylus</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Metodon</i>																							and earlier; Lofgren et al. 2004; Archibald 1998 to Ch1; Archibald 1998
Hyopsodontinae		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							Archibald 1998; Archibald 1998 to Ch1
<i>Haplalates</i>																							Gunnell & Bartels 1999; Archibald 1998 to Ch1
<i>Dorracles</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Hyopsodus</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Haplomyllus</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Phenacodaptus</i>		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							Gingrich & Clyde 2001; Archibald 1998
<i>Apfeliscus</i>																							Gingrich & Clyde 2001; Archibald 1998
Phenacodontidae																							
Phenacodontinae		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							and earlier; Lofgren et al. 2004; Archibald 1998 to Br3
<i>Phenacodus</i>																							Gingrich & Clyde 2001; Archibald 1998
<i>Copeston</i>																							and earlier; Lofgren et al. 2004; Archibald 1998 to Br1
<i>Ectocion</i>		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							

Taxon	<i>Eomoropus</i>	<i>Gramergia</i>	<i>Uuitaceras</i>	<i>Telalaceras</i>	<i>Hyrachyus</i>	<i>Fouchia</i>	<i>Dilophodon</i>	<i>Triplopus</i>	<i>Epiriplopus</i>	<i>Amynodon</i>	<i>Metamynodon</i>	<i>Homogalax</i>	<i>Cardiophobus</i>	<i>Isectolophus</i>	<i>Helaletes</i>	<i>Selenalates</i>	<i>Heptodon</i>	<i>Colodon</i>	
	Wc0	Wc1	Wc2	Wc3	Wc4	Wc5	Wc6	Wc7	Br1a	Br1b	Br2	Br3	U11	U12	U13	Classification generally follows McKenna & Bell (2002)			
Eomoropidae														X					Coombs 1998; Robinson et al. 2004
Tapitomorpha														X	X				Coombs 1998; Robinson et al. 2004
Rhinocerotidae														X	X				Janis et al. 2008
Hyracodontidae														X	X				Janis et al. 2008 to Du
Hyrachyinae								X	X										Gunnell & Bartels 1999; Colbert & Schoch 1998
										X	X								Gunnell unpublished data
											X	X							Gunnell & Bartels 1999; Colbert & Schoch 1998
Hyracodontinae														X	X				Prothero 1998; to Du; Robinson et al. 2004
														X	X				Prothero 1998; to Du; Robinson et al. 2004
Rhinocerotidae														X	X				Wall 1998; Robinson et al. 2004
Amynodontinae														X	X				Robinson et al. 2004
Tapiroidea																			
Isectolophidae		X	X	X	X	X	X	X											Gingerich & Clyde 2001; Colbert & Schoch 1998
		X	X	X	X	X	X	X											Gingerich & Clyde 2001; Colbert & Schoch 1998
										X	X								Gunnell & Bartels 1999 Gunnell unpublished data
Helaletidae									X	X									Gunnell & Bartels 1999; Colbert & Schoch 1998
									X										Colbert & Schoch 1998
									X	X									Gingerich & Clyde 2001; Colbert & Schoch 1998
									X	X									Colbert & Schoch 1998 to Whitmeyar; Robinson et al. 2004

Table 2. Late Paleocene and early Eocene North American immigrant mammalian genera, FADs and LADs.

Biochron	Ti-3	Ti-4	Ti-5	Ti-6	Cf-1	Cf-2	Cf-3	Wa-0	Wa-1	Wa-2	Wa-3	Wa-4	Wa-5	Wa-6	Wa-7	Br-1a	Br-1b	Br-2	Br-3	Ui-1	Ui-2	Ui-3
Total Genera	73	74	66	52	59	62	60	70	93	91	89	88	91	92	98	104	96	96	84	99	98	111
Immigrant Genera	1	0	1	1	3	1	1	9	0	0	0	0	0	0	1	0	0	1	4	2	1	2
Percent of FADs	8	0	12	17	38	9	25	43	0	0	0	0	0	0	5	0	0	7	50	5	6	6
Percent of Total	1	0	2	2	5	2	2	13	0	0	0	0	0	0	1	0	0	1	5	2	1	2
FADs																						
Number	13	14	7	6	8	11	4	21	25	1	2	6	9	11	22	30	6	14	8	40	18	33
Percent	18	16	11	12	14	18	7	30	27	1	2	7	10	12	22	29	6	15	10	40	18	33
LADs																						
Number	13	15	20	1	8	6	10	2	3	5	7	7	10	16	24	14	15	20	27	19	18	42
Percent	18	20	30	2	14	10	17	3	3	5	8	8	11	17	24	13	16	21	32	19	18	38

Table 3. Summary of North American Ti-3–Ui-3 mammalian FADs. Immigrants are indicated in **boldface**.

Biochron	% FAD	Higher Taxon	Family	Genus
Ti-3	18	Pantolestia	Pantolestidae	<i>Palaeosinopa</i>
		Pantodonta	Barylambdidae	<i>Barylambda</i>
		Pantodonta	Cyriacotheriidae	<i>Cyriacotherium</i>
		Creodonta	Oxyaenidae	<i>Tythaena</i>
		Carnivora	Viverridae	<i>Didymictis</i>
		Lipotyphla		<i>Talpavoides</i>
		Lipotyphla	Erinaceidae	<i>Litolestes</i>
		Lipotyphla	Erinaceidae	<i>Cedrochoerus</i>
		Primates	Micromomyidae	<i>Micromomys</i>
		Primates	Plesiadapidae	<i>Chiromyoides</i>
		Condylarthra	Arctocyonidae	<i>Lambertocyon</i>
		Condylarthra	Hyopsodontidae	<i>Aletodon</i>
		Condylarthra	Hyopsodontidae	<i>Dorraletes</i>
Ti-4	19	Leptictida	Leptictidae	<i>Xenacodon</i>
		Cimolesta	Palaeoryctidae	<i>Aptoryctes</i>
		Cimolesta	Palaeoryctidae	<i>Lainoryctes</i>
		Ferae	Cimolestidae	<i>Protentomodon</i>
		Pholidota	Epoicotheriidae	<i>Amelotabes</i>
		Taeniodonta	Stylinodontidae	<i>Ectoganus</i>
		Pantodonta	Barylambdidae	<i>Haplolambda</i>
		Pantodonta	Barylambdidae	<i>Ignatiolambda</i>
		Carnivora	Viverridae	<i>Viverravus</i>
		Lipotyphla	Erinaceidae	<i>Leipsanolestes</i>
		Primates	Paromomyidae	<i>Phenacolemur</i>
		Primates	Carpolestidae	<i>Carpolestes</i>
		Primates	Carpolestidae	<i>Carpomegodon</i>
Condylarthra	Hyopsodontidae	<i>Phenacodaptus</i>		
Ti-5	10	Multituberculata	Eucosmodontidae	<i>Neoliotomus</i>
		Creodonta	Oxyaenidae	<i>Dipsalodon</i>
		Soricomorpha	Nyctitheriidae	<i>Plagioctenodon</i>
		Pholidota	Metacheiromyidae	<i>Mylanodon</i>
		Pholidota	Metacheiromyidae	<i>Propalaeonodon</i>
		Condylarthra	Oxycloenidae	<i>Princetonia</i>
		Arctostylopida		<i>Arctostylops</i>
Ti-6	11	Creodonta	Oxyaenidae	<i>Dipsalidictis</i>
		Primates	Microsypidae	<i>Arctodontomys</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Primates	Micromomyidae	<i>Tinimomys</i>
		Dermoptera	Plagiomenidae	<i>Planetetherium</i>
		Dinocerata	Uintatheriidae	<i>Prodinoceras</i>
		Dinocerata	Hyopsodontidae	<i>Apheliscus</i>
Cf-1	13	Rodentia	Ischyromyidae	<i>Acritoparamys</i>
		Tillodontia	Tillotheriidae	<i>Azygonyx</i>
		Pantodonta	Coryphodontidae	<i>Coryphodon</i>
		Carnivora	Miacidae	<i>Uintacyon</i>
		Primates	Microsyopidae	<i>Niptomomys</i>
		Primates	Micromomyidae	<i>Chalicomomys</i>
		Primates	Paromomyidae	<i>Acidomomys</i>
		Condylarthra	Hyopsodontidae	<i>Haplomyllus</i>
Cf-2	17	Rodentia	Alagomyidae	<i>Alagomys</i>
		Rodentia	Ischyromyidae	<i>Microparamys</i>
		Rodentia	Ischyromyidae	<i>Paramys</i>
		Rodentia	Ischyromyidae	<i>Franimys</i>
		Pantolestia	Pantolestidae	<i>Thelysia</i>
		Pholidota	Epoicotheriidae	<i>Palaeanonodon</i>
		Soricomorpha	Nyctitheriidae	<i>Wyonycteris</i>
		Soricomorpha	Nyctitheriidae	<i>Ceutholestes</i>
		Dermoptera	Plagiomenidae	<i>Worlandia</i>
		Dermoptera	Plagiomenidae	<i>Plagiomene</i>
		Condylarthra	Phenacodontidae	<i>Copecion</i>
Cf-3	7	Marsupialia	Didelphidae	<i>Mimoperadectes</i>
		Creodonta	Oxyaenidae	<i>Palaeonictis</i>
		Condylarthra	Hyopsodontidae	<i>Hyopsodus</i>
		Condylarthra	Phenacodontidae	<i>Meniscotherium</i>
Wa-0	29	Marsupialia	Didelphidae	<i>Copedelphys</i>
		Rodentia	Reithroparamyidae	<i>Reithroparamys</i>
		Rodentia	Sciuavidae	<i>Knightomys</i>
		Tillodontia	Tillotheriidae	<i>Esthonyx</i>
		Apatotheria	Apatemyidae	<i>Apatemys</i>
		Creodonta	Hyaenodontidae	<i>Prolimmocyon</i>
		Creodonta	Hyaenodontidae	<i>Prototomus</i>
		Creodonta	Hyaenodontidae	<i>Arfia</i>
		Creodonta	Hyaenodontidae	<i>Acarictis</i>
		Creodonta	Oxyaenidae	<i>Oxyaena</i>
		Carnivora	Miacidae	<i>Vulpavus</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Carnivora	Miacidae	<i>Miacis</i>
		Lipotyphla	Amphilemuridae	<i>Macrocranion</i>
		Lipotyphla	Apternodontidae	<i>Parapternodus</i>
		Lipotyphla	Apternodontidae	<i>Koniaryctes</i>
		Euprimates	Notharctinae	<i>Cantius</i>
		Euprimates	Anaptomorphidae	<i>Teilhardina</i>
		Mesonychia	Mesonychidae	<i>Pachyaena</i>
		Artiodactyla	Diacodexinae	<i>Diacodexis</i>
		Perissodactyla	Equidae	<i>Hyracotherium</i>
Wa-1	26	Marsupialia	Didelphidae	<i>Herpetotherium</i>
		Marsupialia	Didelphidae	<i>Esteslestes</i>
		Epitheria	Leptictidae	<i>Palaeictops</i>
		Rodentia	Ischyromyidae	<i>Lophiparamys</i>
		Rodentia	Ischyromyidae	<i>Apatosciuravus</i>
		Cimolesta		<i>Wyolestes</i>
		Cimolesta	Palaeoryctidae	<i>Eoryctes</i>
		Cimolesta	Cimolestidae	<i>Didelphodus</i>
		Pantolestia	Pantolestidae	<i>Amararnnis</i>
		Creodonta	Hyaenodontidae	<i>Galecyon</i>
		Creodonta	Hyaenodontidae	<i>Tritemmodon</i>
		Carnivora	Miacidae	<i>Vassacyon</i>
		Carnivora	Miacidae	<i>Oodectes</i>
		Lipotyphla	Sespedectidae	<i>Scenopagus</i>
		Lipotyphla	Sespedectidae	<i>Creotarsus</i>
		Lipotyphla		<i>Dartoni</i>
		Lipotyphla		<i>Auroralestes</i>
		Soricomorpha	Geolabididae	<i>Centetodon</i>
		Soricomorpha	Geolabididae	<i>Batodonoides</i>
		Soricomorpha	Nyctitheriidae	<i>Plagiocetenoides</i>
		Euprimates	Omomyidae	<i>Tetoni</i>
		Euprimates	Omomyidae	<i>Anemorhysis</i>
		Euprimates	Omomyidae	<i>Arapahovius</i>
		Perissodactyla	Isectolophidae	<i>Cardiolophus</i>
		Perissodactyla	Isectolophidae	<i>Homogalax</i>
Wa-2	1	Rodentia	Ischyromyidae	<i>Thisbemys</i>
Wa-3	2	Rodentia	Sciuravidae	<i>Sciuravus</i>
		Primates	Microsyopidae	<i>Microsyops</i>
Wa-4	7	Rodentia	Ischyromyidae	<i>Notoparamys</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Cimolesta	Palaeoryctidae	<i>Ottoryctes</i>
		Pholidota		<i>Tubulodon</i>
		Euprimates	Omomyidae	<i>Steinius</i>
		Euprimates	Omomyidae	<i>Pseudotetonius</i>
		Euprimates	Adapidae	<i>Copelemur</i>
Wa-5	10	Pholidota	Epoicotheriidae	<i>Alcodontulum</i>
		Erinaceomorpha		<i>Talpavus</i>
		Primates	Microsyopidae	<i>Uintasorex</i>
		Primates	Microsyopidae	<i>Megadelphus</i>
		Primates	Picromomyidae	<i>Picromomys</i>
		Euprimates	Adapidae	<i>Pelycodus</i>
		Euprimates	Omomyidae	<i>Absarokius</i>
		Euprimates	Anaptomorphidae	<i>Chlororhysis</i>
		Condylarthra	Arctocyonidae	<i>Anacodon</i>
Wa-6	12	Rodentia	Ischyromyidae	<i>Uriscus</i>
		Rodentia	Ischyromyidae	<i>Uintaparamys</i>
		Rodentia		<i>Pauromys</i>
		Rodentia	Eutypomyidae	<i>Mattimys</i>
		Pholidota	Epoicotheriidae	<i>Pentapassalus</i>
		Pholidota	Epoicotheriidae	<i>Dipassalus</i>
		Euprimates	Omomyidae	<i>Loveina</i>
		Euprimates	Omomyidae	<i>Jemezius</i>
		Euprimates	Omomyidae	<i>Tatmanius</i>
		Artiodactyla	Leptochoeridae	<i>Hexacodus</i>
		Artiodactyla	Helaletidae	<i>Heptodon</i>
Wa-7	22	Marsupialia	Peradectidae	<i>Armintodelphys</i>
		Rodentia	Sciuravidae	<i>Tillomys</i>
		Rodentia	Cylindrodontidae	<i>Dawsonomys</i>
		Rodentia	Cylindrodontidae	<i>Anomoemys</i>
		Rodentia	Ischyromyidae	<i>Strathcona</i>
		Taeniodonta	Stylinodontidae	<i>Stylinodon</i>
		Tillodontia	Tillotheriidae	<i>Megalestbonyx</i>
		Creodonta	Hyaenodontidae	<i>Machaeroides</i>
		Lipotyphla	Erinaceidae	<i>Entomolestes</i>
		Soricomorpha	Geolabididae	<i>Marsholestes</i>
		Soricomorpha	Nyctitheriidae	<i>Nyctitherium</i>
		Primates	Paromomyidae	<i>Elwynella</i>
		Euprimates	Adapidae	<i>Notharctus</i>
		Euprimates	Omomyidae	<i>Sbosbonius</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Euprimates	Omomyidae	<i>Hemiacodon</i>
		Euprimates	Omomyidae	<i>Strigorbhysis</i>
		Euprimates	Omomyidae	<i>Trogolemur</i>
		Euprimates	Omomyidae	<i>Artimonius</i>
		Dinocerata	Uintatheriidae	<i>Bathyopsis</i>
		Artiodactyla	Dichobunidae	<i>Antiacodon</i>
		Perissodactyla	Equidae	<i>Orobippus</i>
		Perissodactyla	Incertae Sedis	<i>Lambdaotherium</i>
Br-1a	29	Theria		<i>Aethomylos</i>
		Rodentia	Ischyromyidae	<i>Quadratormus</i>
		Rodentia	Ischyromyidae	<i>Pseudotomus</i>
		Rodentia	Sciuravidae	<i>Taxymys</i>
		Rodentia	Sciuravidae	<i>Mysops</i>
		Rodentia	Eutyromyidae	<i>Armintomys</i>
		Pantolestia	Pantolestidae	<i>Pantolestes</i>
		Pholidota	Epoicotheriidae	<i>Tetrapassalus</i>
		Pholidota	Metacheiromyidae	<i>Metacheiromys</i>
		Pholidota	Metacheiromyidae	<i>Brachianodon</i>
		Tillodontia	Tillotheriidae	<i>Trogosus</i>
		Creodonta	Hyaenodontidae	<i>Iridodon</i>
		Creodonta	Hyaenodontidae	<i>Sinopa</i>
		Creodonta	Oxyaenidae	<i>Patriofelis</i>
		Creodonta	Oxyaenidae	<i>Malfelis</i>
		Erinaceoidea	Sespedectidae	<i>Crypholestes</i>
		Primates	Picromomyidae	<i>Alveojunctus</i>
		Euprimates	Adapidae	<i>Smilodectes</i>
		Euprimates	Omomyidae	<i>Washakius</i>
		Euprimates	Omomyidae	<i>Utabia</i>
		Euprimates	Omomyidae	<i>Uintanius</i>
		Euprimates	Omomyidae	<i>Aycrossia</i>
		Euprimates	Omomyidae	<i>Omomys</i>
		Mesonychia	Mesonychidae	<i>Mesonyx</i>
		Artiodactyla	Dichobunidae	<i>Microsus</i>
		Perissodactyla	Brontotheriidae	<i>Palaeosyops</i>
		Perissodactyla	Brontotheriidae	<i>Eotitanops</i>
		Perissodactyla	Hyracodontidae	<i>Hyrachyus</i>
		Perissodactyla	Helaletidae	<i>Helaletes</i>
		Perissodactyla	Helaletidae	<i>Selenaletes</i>
Br-1b	6	Creodonta	Hyaenodontidae	<i>Thinocyon</i>
		Creodonta	Hyaenodontidae	<i>Limnocyon</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Euprimates	Anaptomorphidae	<i>Anaptomorphus</i>
		Euprimates	Anaptomorphidae	<i>Gazinius</i>
		Dinocerata	Uintatheriidae	<i>Uintatherium</i>
		Artiodactyla	Helohyidae	<i>Helohyus</i>
Br-2	15	Rodentia		<i>Elymys</i>
		Rodentia	Cylindrodontidae	<i>Pseudocylindrodon</i>
		Tillodontia	Tillotheriidae	<i>Tillodon</i>
		Carnivora	Miacidae	<i>Palaearctonyx</i>
		Lipotyphla	Nyctitheriidae	<i>Pontifactor</i>
		Euprimates	Omomyidae	<i>Wyomomys</i>
		Mesonychia	Mesonychidae	<i>Harpagolestes</i>
		Mesonychia	Mesonychidae	<i>Synoplotherium</i>
		Artiodactyla	Dichobunidae	<i>Homacodon</i>
		Perissodactyla	Hyracodontidae	<i>Dilophodon</i>
		Perissodactyla	Hyracodontidae	<i>Fouchia</i>
		Perissodactyla	Isectolophidae	<i>Isectolophus</i>
		Perissodactyla	Telmatheriinae	<i>Telmatherium</i>
		Perissodactyla	Brontotheriidae	<i>Mesatirbinus</i>
Br-3	10	Rodentia	Eomyidae	<i>Adjidaumo</i>
		Rodentia	Eomyidae	<i>Protadjidaumo</i>
		Rodentia	Eomyidae	<i>Paradjidaumo</i>
		Euprimates	Omomyidae	<i>Macrotarsius</i>
		Euprimates	Omomyidae	<i>Ageitodendron</i>
		Euprimates	Omomyidae	<i>Sphacorhysis</i>
		Dinocerata	Uintatheriidae	<i>Tetheopsis</i>
		Perissodactyla	Rhinocerotidae	<i>Amynodon</i>
Ui-1	42	Rodentia		<i>Prolapsus</i>
		Rodentia	Sciuravidae	<i>Pareumys</i>
		Rodentia	Aplodontidae	<i>Spurimus</i>
		Rodentia	Protoptychidae	<i>Protoptychus</i>
		Rodentia		<i>Floresomys</i>
		Pantolesta		<i>Simidectes</i>
		Dermoptera	Plagiomenidae	<i>Tarka</i>
		Creodonta	Hyaenodontidae	<i>Oxyaenodon</i>
		Carnivora	Miacidae	<i>Procyonodictis</i>
		Carnivora	Miacidae	<i>Prodapboenus</i>
		Carnivora	Miacidae	<i>Tapocyon</i>
		Soricomorpha	Apternodontidae	<i>Oligoryctes</i>
		Euprimates	Omomyidae	<i>Ourayia</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Dinocerata	Uintatheriidae	<i>Eobasileus</i>
		Artiodactyla	Helohyidae	<i>Achaenodon</i>
		Artiodactyla	Helohyidae	<i>Parahyus</i>
		Artiodactyla	Entelodontidae	<i>Brachyhyops</i>
		Artiodactyla	Leptochoeridae	<i>Hylomeryx</i>
		Artiodactyla	Leptochoeridae	<i>Bunomeryx</i>
		Artiodactyla	Agriocheridae	<i>Protoreodon</i>
		Artiodactyla	Oromerycidae	<i>Merycobunodon</i>
		Artiodactyla	Oromerycidae	<i>Malaquiferus</i>
		Artiodactyla	Oromerycidae	<i>Protylopus</i>
		Artiodactyla	Oromerycidae	<i>Oromeryx</i>
		Artiodactyla	Protoceratidae	<i>Leptotragulus</i>
		Artiodactyla	Protoceratidae	<i>Leptoreodon</i>
		Perissodactyla	Equidae	<i>Epibippus</i>
		Perissodactyla	Brontotheriidae	<i>Metatelmattherium</i>
		Perissodactyla	Brontotheriidae	<i>Metarbinus</i>
		Perissodactyla	Brontotheriidae	<i>Sphenocoelus</i>
		Perissodactyla	Brontotheriidae	<i>Dolichorbinus</i>
		Perissodactyla	Brontotheriidae	<i>Protitanotherium</i>
		Perissodactyla	Brontotheriidae	<i>Eubrontotherium</i>
		Perissodactyla		<i>Sthenodectes</i>
		Perissodactyla	Eomoropidae	<i>Grangeria</i>
		Perissodactyla		<i>Uintaceras</i>
		Perissodactyla	Hyracodontidae	<i>Triplopus</i>
		Perissodactyla	Hyracodontidae	<i>Epitriplopus</i>
		Perissodactyla	Helaletidae	<i>Colodon</i>
Ui-2	19	Marsupialia	Peradectidae	<i>Nanodelphys</i>
		Rodentia	Ischyromyidae	<i>Rapamys</i>
		Rodentia	Ischyromyidae	<i>Mytonomys</i>
		Rodentia	Ischyromyidae	<i>Eobaplomys</i>
		Rodentia		<i>Simimys</i>
		Rodentia		<i>Metanoiamys</i>
		Rodentia		<i>Griphomys</i>
		Lipotyphla	Sespedectidae	<i>Proterixoides</i>
		Lipotyphla	Sespedectidae	<i>Sespedectes</i>
		Lipotyphla	Sespedectidae	<i>Patriolestes</i>
		Primates	Microsyopidae	<i>Craseops</i>
		Euprimates	Adapidae	<i>Hesperolemur</i>
		Euprimates	Omomyidae	<i>Dyseolemur</i>
		Euprimates	Omomyidae	<i>Stockia</i>
		Euprimates	Omomyidae	<i>Chipetaia</i>

Biochron	% FAD	Higher Taxon	Family	Genus
		Artiodactyla	Leptochoeridae	<i>Mesomeryx</i>
		Perissodactyla	Eomoropidae	<i>Eomoropus</i>
		Perissodactyla		<i>Teletaceras</i>
Ui-3	31	Leptictida	Leptictidae	<i>Leptictis</i>
		Lagomorpha	Leporidae	<i>Procaprolagus</i>
		Lagomorpha	Leporidae	<i>Mytonolagus</i>
		Rodentia	Ischyromyidae	<i>Ischyromys</i>
		Rodentia	Laredomyidae	<i>Laredomys</i>
		Rodentia	Isectolophidae	<i>Churcheria</i>
		Rodentia	Isectolophidae	<i>Tapomys</i>
		Rodentia	Eutyromyidae	<i>Janimus</i>
		Rodentia	Eutyromyidae	<i>Microeutyromys</i>
		Rodentia		<i>Aulolithomys</i>
		Pholidota	Epoicotheriidae	<i>Epoicotherium</i>
		Erinaceomorpha	Sespedectidae	<i>Ankyledon</i>
		Soricomorpha	Micropternodontidae	<i>Micropternodus</i>
		Lipotyphla	Sespedectidae	<i>Scenopagus</i>
		Lipotyphla	Soricidae	<i>Domnina</i>
		Euprimates	Omomyidae	<i>Yaquius</i>
		Artiodactyla	Dichobunidae	<i>Ibarus</i>
		Artiodactyla	Dichobunidae	<i>Laredochoerus</i>
		Artiodactyla	Dichobunidae	<i>Tapochoerus</i>
		Artiodactyla	Dichobunidae	<i>Auxontodon</i>
		Artiodactyla	Dichobunidae	<i>Texodon</i>
		Artiodactyla	Dichobunidae	<i>Mytonomeryx</i>
		Artiodactyla	Dichobunidae	<i>Pentacemylus</i>
		Artiodactyla	Dichobunidae	<i>Apriculus</i>
		Artiodactyla	Protoceratidae	<i>Poabromylus</i>
		Artiodactyla	Protoceratidae	<i>Toromeryx</i>
		Artiodactyla	Hypertragulidae	<i>Simimeryx</i>
		Perissodactyla	Brontotheriidae	<i>Protitanotherium</i>
		Perissodactyla	Brontotheriidae	<i>Eotitanotherium</i>
		Perissodactyla	Brontotheriidae	<i>Diplacodon</i>
		Perissodactyla	Brontotheriidae	<i>Protitanops</i>
		Perissodactyla	Brontotheriidae	<i>Notiotitanops</i>
		Perissodactyla	Rhinocerotidae	<i>Metamynodon</i>

Table 4. Summary of North American Ti-3–Ui-3 mammalian LADs. Suprageneric groups (and the relevant genera) that become extinct are indicated in **boldface**.

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
Ti-3	18	Multituberculata	Ptilodontidae	<i>Baiotomeus</i>
		Multituberculata	Eucosmodontidae	<i>Allocosmodon</i>
		Leptictida	Leptictidae	<i>Myrmecoboides</i>
		Cimolesta	Cimolestidae	<i>Gelastops</i>
		Cimolesta	Cimolestidae	<i>Acmeodon</i>
		Dermoptera	Plagiomenidae	<i>Eudaemonema</i>
		Lipotyphla	Erinaceidae	<i>Cedrocherus</i>
		Primates	Paromomyidae	<i>Paromomys</i>
		Primates	Plesiadapidae	<i>Pronothodectes</i>
		Primates	Carpolestidae	<i>Elphidotarsius</i>
		Primates	Saxonellidae	<i>Saxonella</i>
		Condylarthra	Mioclaenidae	<i>Protoselene</i>
		Condylarthra	Mioclaenidae	<i>Promioclaenus</i>
Ti-4	20	Multituberculata	Ptilodontidae	<i>Mesodma</i>
		Multituberculata	Taeniolabididae	<i>Catopsalis</i>
		Leptictida	Leptictidae	<i>Xenacodon</i>
		Cimolesta	Palaeoryctidae	<i>Pararyctes</i>
		Cimolesta	Palaeoryctidae	<i>Lainoryctes</i>
		Cimolesta	Pentacodontidae	<i>Aphronorus</i>
		Cimolesta	Pentacodontidae	<i>Bisonalveus</i>
		Pholidota	Epoicotheriidae	<i>Amelotabes</i>
		Primates	Microsypidae	<i>Navajovius</i>
		Primates	Micromomyinae	<i>Micromomys</i>
		Primates	Picrodontidae	<i>Picrodus</i>
		Primates	Picrodontidae	<i>Zanycteris</i>
		Primates	Carpolestidae	<i>Carpomegodon</i>
		Dermoptera	Plagiomenidae	<i>Elpidophorus</i>
		Condylarthra	Periptychidae	<i>Periptychus</i>
Ti-5	30	Multituberculata	Sloanbaataridae	<i>Pentacosmodon</i>
		Multituberculata	Ptilodontidae	<i>Neoplagiaulax</i>
		Multituberculata	Ptilodontidae	<i>Mimetodon</i>
		Cimolesta	Palaeoryctidae	<i>Aptoryctes</i>
		Cimolesta	Cimolestidae	<i>Paleotomus</i>
		Cimolesta	Apatemyidae	<i>Unuchinia</i>
		Cimolesta	Apatemyidae	<i>Jepsenella</i>
		Cimolesta	Pantolestidae	<i>Propalaeosinopa</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
		Cimolesta	Pantolestidae	<i>Bessoecetor</i>
		Pantodonta	Barylambdidae	<i>Ignatiolambda</i>
		Lipotyphla		<i>Litolestes</i>
		Lipotyphla	Erinaceidae	<i>Litocherus</i>
		Primates	Plesiadapidae	<i>Nannodectes</i>
		Primates	Carpolestidae	<i>Carpodaptes</i>
		Pholidota	Metacheiromyidae	<i>Propalaeonodon</i>
		Pholidota	Metacheiromyidae	<i>Mylanodon</i>
		Condylarthra	Arctocyoniidae	<i>Claenodon</i>
		Condylarthra	Hyopsodontidae	<i>Litomylus</i>
		Condylarthra	Hyopsodontidae	<i>Haplaletes</i>
		Condylarthra	Hyopsodontidae	<i>Dorraletes</i>
Ti-6	2	Multituberculata	Ptilodontidae	<i>Ptilodus</i>
Cf-1	13	Cimolesta	Cimolestidae	<i>Protentomodon</i>
		Primates	Paromomyidae	<i>Acidomomys</i>
		Taeniodonta	Stylinodontidae	<i>Psittacotherium</i>
		Pantodonta	Barylambdidae	<i>Barylambda</i>
		Pantodonta	Barylambdidae	<i>Haplolambda</i>
		Creodonta	Oxyaenidae	<i>Tytthaena</i>
		Condylarthra	Arctocyoniidae	<i>Mimotricentes</i>
		Condylarthra	Arctocyoniidae	<i>Lambertocyon</i>
Cf-2	10	Rodentia	Alagomyidae	<i>Alagomys</i>
		Pantodonta	Titanoideidae	<i>Titanoides</i>
		Creodonta	Oxyaenidae	<i>Dipsalodon</i>
		Lipotyphla	Nyctitheriidae	<i>Limaconyssus</i>
		Dermoptera	Plagiomenidae	<i>Planetetherium</i>
		Condylarthra	Hyopsodontidae	<i>Phenacodaptes</i>
Cf-3	16	Multituberculata	Ptilodontidae	<i>Prochetodon</i>
		Multituberculata	Eucosmodontidae	<i>Microcosmodon</i>
		Pantodonta	Cyriacotheriidae	<i>Cyriacotherium</i>
		Carnivora	Viverravidae	<i>Protictis</i>
		Lipotyphla	Nyctitheriidae	<i>Ceutholestes</i>
		Primates	Plesiadapidae	<i>Chiromyoides</i>
		Primates	Carpolestidae	<i>Carpolestes</i>
		Dermoptera	Plagiomenidae	<i>Worlandia</i>
		Condylarthra	Hyopsodontidae	<i>Aletodon</i>
		Arctostylopida	Arctostylopidae	<i>Arctostylops</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
Wa-0	3	Pantolestia	Pantolestidae	<i>Thelysia</i>
		Condylarthra	Oxyclaenidae	<i>Princetonia</i>
Wa-1	3	Marsupialia	Didelphidae	<i>Esteslestes</i>
		Lipotyphla	Creotarsidae	<i>Creotarsus</i>
		Primates	Plesiadapidae	<i>Plesiadapis</i>
Wa-2	5	Tillodontia	Tillotheriidae	<i>Azygonyx</i>
		Creodonta	Hyaenodontidae	<i>Galecyon</i>
		Creodonta	Hyaenodontidae	<i>Acarictis</i>
		Lipotyphla		<i>Adumator</i>
Wa-3	8	Multituberculata	Eucosmodontidae	<i>Neoliotomus</i>
		Cimolesta	Palaeoryctidae	<i>Eoryctes</i>
		Lipotyphla	Apternodontidae	<i>Parapternodus</i>
		Lipotyphla	Apternodontidae	<i>Koniaryctes</i>
		Primates	Microsyopidae	<i>Arctodotomys</i>
		Primates	Micromomyidae	<i>Tinimomys</i>
		Primates	Micromomyidae	<i>Chalicomomys</i>
Wa-4	8	Cimolesta		<i>Wyolestes</i>
		Cimolesta	Palaeoryctidae	<i>Palaeoryctes</i>
		Lipotyphla		<i>Dartoni</i>
		Lipotyphla		<i>Auroralestes</i>
		Lipotyphla	Nyctitheriidae	<i>Plagioctenoides</i>
		Dermoptera	Plagiomenidae	<i>Plagiomene</i>
		Euprimates	Omomyidae	<i>Pseudotetonius</i>
Wa-5	11	Marsupialia	Didelphidae	<i>Mimoperadectes</i>
		Cimolesta	Palaeoryctidae	<i>Otiorcytes</i>
		Lipotyphla		<i>Talpavoides</i>
		Lipotyphla		<i>Leipsanolestes</i>
		Lipotyphla	Nyctitheriidae	<i>Wyonycteris</i>
		Primates	Micromomyidae	<i>Niptomomys</i>
		Primates	Picromomyidae	<i>Picromomys</i>
		Euprimates	Omomyidae	<i>Teilbardina</i>
		Euprimates	Omomyidae	<i>Arapahovius</i>
Euprimates	Omomyidae	<i>Tetonius</i>		
Wa-6	17	Multituberculata	Ptilodontidae	<i>Parectypodus</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
		Rodentia	Ischyromyidae	<i>Apatosciuravus</i>
		Rodentia	Ischyromyidae	<i>Notoparamys</i>
		Rodentia	Ischyromyidae	<i>Franimys</i>
		Cimolesta	Apatemyidae	<i>Labidolemur</i>
		Pholidota	Epoicotheriidae	<i>Alcodontulum</i>
		Creodonta	Hyaenodontidae	<i>Arfia</i>
		Creodonta	Oxyaenidae	<i>Dipsalidictis</i>
		Creodonta	Oxyaenidae	<i>Palaeonictis</i>
		Lipotyphla		<i>Diacodon</i>
		Euprimates	Omomyidae	<i>Steinius</i>
		Euprimates	Omomyidae	<i>Jemezius</i>
		Euprimates	Omomyidae	<i>Tatmanius</i>
		Mesonychia	Mesonychidae	<i>Dissacus</i>
		Condylarthra	Hyopsodontidae	<i>Haplomylys</i>
		Condylarthra	Hyopsodontidae	<i>Apheliscus</i>
Wa-7	25	Leptictida	Leptictidae	<i>Prodiacodon</i>
		Rodentia	Ischyromyidae	<i>Uriscus</i>
		Rodentia	Sciuravidae	<i>Dawsonomys</i>
		Cimolesta	Pantodontidae	<i>Amaramnis</i>
		Pholidota	Epoicotheriidae	<i>Palaeanonodon</i>
		Taeniodonta	Stylinodontidae	<i>Ectoganus</i>
		Tillodontia	Tillotheriidae	<i>Megalestonyx</i>
		Creodonta	Oxyaenidae	<i>Oxyaena</i>
		Carnivora	Miacidae	<i>Vassacyon</i>
		Lipotyphla	Nyctitheriidae	<i>Plagioctenodon</i>
		Lipotyphla	Nyctitheriidae	<i>Leptacodon</i>
		Euprimates	Notharctidae	<i>Pelycodus</i>
		Euprimates	Notharctidae	<i>Copelemur</i>
		Euprimates	Omomyidae	<i>Loveina</i>
		Euprimates	Omomyidae	<i>Chlororbysis</i>
		Euprimates	Omomyidae	<i>Absarokius</i>
		Dinocerata	Uintatheriidae	<i>Prodinoceras</i>
		Condylarthra	Oxyclaenidae	<i>Chriacus</i>
		Condylarthra	Arctocyonidae	<i>Anacodon</i>
		Condylarthra	Phenacodontidae	<i>Copecion</i>
		Condylarthra	Meniscotheriidae	<i>Meniscotherium</i>
		Perissodactyla	Incertae Sedis	<i>Lambdotherium</i>
		Perissodactyla	Isectolophidae	<i>Homogalax</i>
		Perissodactyla	Isectolophidae	<i>Cardiolophus</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
Br-1a	13	Rodentia	Sciuravidae	<i>Anomoemys</i>
		Rodentia	Eutypomyidae	<i>Armintomys</i>
		Pholidota	Metacheiromyidae	<i>Tubulodon</i>
		Pholidota	Epoicotheriidae	<i>Pentapassalus</i>
		Pholidota	Epoicotheriidae	<i>Dipassalus</i>
		Pantodonta	Coryphodontidae	<i>Coryphodon</i>
		Creodonta	Hyaenodontidae	<i>Iridodon</i>
		Creodonta	Hyaenodontidae	<i>Prolimnocyon</i>
		Creodonta	Oxyaenidae	<i>Mafelis</i>
		Primates	Microsypidae	<i>Megadelphus</i>
		Euprimates	Omomyidae	<i>Anemorhysis</i>
		Euprimates	Omomyidae	<i>Artimonius</i>
		Artiodactyla	Leptochoeridae	<i>Hexacodus</i>
		Perissodactyla	Isectolophidae	<i>Selenaletes</i>
Br-1b	16	Marsupialia	Didelphidae	<i>Armintodelphys</i>
		Cimolesta	Pantolestidae	<i>Palaeosinopa</i>
		Pholidota	Metacheiromyidae	<i>Brachianodon</i>
		Tillodontia	Tillotheriidae	<i>Estbonyx</i>
		Creodonta	Hyaenodontidae	<i>Prototomus</i>
		Dermoptera	Paromomyidae	<i>Elwynella</i>
		Euprimates	Notharctidae	<i>Cantius</i>
		Euprimates	Omomyidae	<i>Utabia</i>
		Euprimates	Omomyidae	<i>Absarokius</i>
		Condylarthra	Oxyclaenidae	<i>Thryptacodon</i>
		Condylarthra	Phenacodontidae	<i>Ectocion</i>
		Artiodactyla	Diacodexinae	<i>Diacodexis</i>
		Artiodactyla	Diacodexinae	<i>Bunophorus</i>
		Perissodactyla	Brontotheriidae	<i>Eotitanops</i>
Perissodactyla	Heleletidae	<i>Heptodon</i>		
Br-2	21	Rodentia	Ischyromyidae	<i>Acritoparamys</i>
		Rodentia	Ischyromyidae	<i>Stratbcona</i>
		Rodentia	Sciuravidae	<i>Knightomys</i>
		Rodentia	Eutypomyidae	<i>Mattimys</i>
		Rodentia	Dipodidae	<i>Elymys</i>
		Tillodontia	Tillotheriidae	<i>Trogosus</i>
		Tillodontia	Tillotheriidae	<i>Tillodon</i>
		Creodonta	Hyaenodontidae	<i>Machaeroides</i>
		Creodonta	Hyaenodontidae	<i>Tritemnodon</i>
		Carnivora	Miacidae	<i>Vulpavus</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
		Carnivora	Miacidae	<i>Palaearctonyx</i>
		Carnivora	Miacidae	<i>Oodectes</i>
		Lipotyphla	Geolabididae	<i>Marsbolestes</i>
		Euprimates	Omomyidae	<i>Sbosbonius</i>
		Euprimates	Omomyidae	<i>Wyomomys</i>
		Euprimates	Omomyidae	<i>Acrossia</i>
		Euprimates	Omomyidae	<i>Strigorbhysis</i>
		Dinocerata	Uintatheriidae	<i>Bathyopsis</i>
		Mesonychia	Mesonychidae	<i>Pachyaena</i>
		Perissodactyla	Hyracodontidae	<i>Fouchia</i>
Br-3	32	Pholidota	Metacheiromyidae	<i>Metacheiromys</i>
		Creodonta	Hyaenodontidae	<i>Thinocyon</i>
		Creodonta	Hyaenodontidae	<i>Sinopa</i>
		Creodonta	Oxyaenidae	<i>Patriofelis</i>
		Carnivora	Viverravidae	<i>Viverravus</i>
		Lipotyphla	Nyctitheriidae	<i>Pontifactor</i>
		Euprimates	Notharctidae	<i>Smilodectes</i>
		Euprimates	Omomyidae	<i>Ageitodendron</i>
		Euprimates	Omomyidae	<i>Uintanius</i>
		Euprimates	Omomyidae	<i>Anaptomorphus</i>
		Euprimates	Omomyidae	<i>Gazinius</i>
		Euprimates	Omomyidae	<i>Sphacorhysis</i>
		Dinocerata	Uintatheriidae	<i>Tetbeopsis</i>
		Condylarthra	Phenacodontidae	<i>Phenacodus</i>
		Mesonychia	Mesonychidae	<i>Synoplotherium</i>
		Artiodactyla	Dichobunidae	<i>Antiacodon</i>
		Artiodactyla	Dichobunidae	<i>Homacodon</i>
		Artiodactyla	Dichobunidae	<i>Microsus</i>
		Perissodactyla	Equidae	<i>Orobippus</i>
		Perissodactyla	Brontotheriidae	<i>Palaeosyops</i>
		Perissodactyla	Brontotheriidae	<i>Telmatherium</i>
		Perissodactyla	Hyracodontidae	<i>Hyrachyus</i>
		Perissodactyla	Isectolophidae	<i>Isectolophus</i>
		Perissodactyla	Helaletidae	<i>Helaletes</i>
Ui-1	20	Rodentia	Sciuravidae	<i>Pauromys</i>
		Rodentia	Sciuravidae	<i>Tillomys</i>
		Rodentia	Sciuravidae	<i>Taxymys</i>
		Rodentia	Sciuravidae	<i>Mysops</i>
		Pholidota	Epoicotheriidae	<i>Tetrapassalus</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
		Creodonta	Hyaenodontidae	<i>Limnocyon</i>
		Dermoptera	Plagiomenidae	<i>Tarka</i>
		Primates	Picromomyidae	<i>Alveojunctus</i>
		Euprimates	Notharctidae	<i>Notharctus</i>
		Dinocerata	Uintatheriidae	<i>Eobasileus</i>
		Artiodactyla	Helohyidae	<i>Helohyus</i>
		Artiodactyla	Helohyidae	<i>Achaenodon</i>
		Artiodactyla	Helohyidae	<i>Parahyus</i>
		Artiodactyla	Agriochoeridae	<i>Merycobunodon</i>
		Perissodactyla	Equidae	<i>Hyracotherium</i>
		Perissodactyla	Brontotheriidae	<i>Mesatirhinus</i>
		Perissodactyla	Brontotheriidae	<i>Eubrontotherium</i>
		Perissodactyla	Hyracodontidae	<i>Dilophodon</i>
Ui-2	19	Rodentia	Ischyromyidae	<i>Lophiparamys</i>
		Rodentia	Protoptychidae	<i>Protoptychus</i>
		Rodentia	Simimyidae	<i>Simimys</i>
		Rodentia		<i>Floresomys</i>
		Lipotyphla	Amphilemuridae	<i>Macrocranion</i>
		Lipotyphla	Sespedectidae	<i>Patriolestes</i>
		Primates	Microsyopidae	<i>Microsyops</i>
		Primates	Microsyopidae	<i>Craseops</i>
		Dermoptera	Paromomyidae	<i>Phenacolemur</i>
		Euprimates	Notharctinae	<i>Hesperolemur</i>
		Euprimates	Omomyidae	<i>Stockia</i>
		Euprimates	Omomyidae	<i>Chipetaia</i>
		Euprimates	Omomyidae	<i>Washakius</i>
		Artiodactyla	Leptochoeridae	<i>Mesomeryx</i>
		Perissodactyla	Brontotheriidae	<i>Sphenocoelus</i>
		Perissodactyla	Brontotheriidae	<i>Dolichorhinus</i>
		Perissodactyla	Eomoropidae	<i>Eomoropus</i>
		Perissodactyla		<i>Uintaceras</i>
Ui-3	39	Mammalia		<i>Aethomylos</i>
		Rodentia	Laredomyidae	<i>Laredomys</i>
		Rodentia	Ischyromyidae	<i>Thisbemys</i>
		Rodentia	Ischyromyidae	<i>Pseudotomus</i>
		Rodentia	Ischyromyidae	<i>Rapamys</i>
		Rodentia	Ischyromyidae	<i>Tapomys</i>
		Rodentia	Reithroparamyidae	<i>Reithroparamys</i>
		Rodentia		<i>Prolapsus</i>

Biochron	% LAD	Higher Taxon	Family/Subfamily	Genus
		Taeniodonta	Stylinodontidae	<i>Stylinodon</i>
		Creodonta	Hyaenodontidae	<i>Oxyaenodon</i>
		Carnivora	Miacidae	<i>Miacis</i>
		Carnivora	Miacidae	<i>Uintacyon</i>
		Carnivora	Miacidae	<i>Procynodictis</i>
		Carnivora	Miacidae	<i>Prodapboenus</i>
		Carnivora	Miacidae	<i>Tapocyon</i>
		Lipotyphla	Sespedectidae	<i>Scenopagus</i>
		Lipotyphla	Geolabididae	<i>Batodonoides</i>
		Primates	Microsypidae	<i>Uintasorex</i>
		Euprimates	Omomyidae	<i>Hemiacodon</i>
		Euprimates	Omomyidae	<i>Yaquius</i>
		Euprimates	Omomyidae	<i>Ourayia</i>
		Dinocerata	Uintatheriidae	<i>Uintatherium</i>
		Mesonychia	Mesonychidae	<i>Mesonyx</i>
		Artiodactyla	Leptochoerinae	<i>Ibarus</i>
		Artiodactyla	Leptochoerinae	<i>Laredochoerus</i>
		Artiodactyla	Antiacodontinae	<i>Auxontodon</i>
		Artiodactyla	Antiacodontinae	<i>Tapochoerus</i>
		Artiodactyla	Homacodontinae	<i>Texodon</i>
		Artiodactyla	Homacodontinae	<i>Hylomeryx</i>
		Artiodactyla	Homacodontinae	<i>Bunomeryx</i>
		Artiodactyla	Homacodontinae	<i>Mynonomeryx</i>
		Artiodactyla	Homacodontinae	<i>Pentecemylus</i>
		Artiodactyla	Homacodontinae	<i>Apriculus</i>
		Artiodactyla	Oromerycidae	<i>Malaquiferus</i>
		Artiodactyla	Protoceratidae	<i>Toromeryx</i>
		Perissodactyla	Equidae	<i>Epibippus</i>
		Perissodactyla	Brontotheriidae	<i>Eotitanotherium</i>
		Perissodactyla	Brontotheriidae	<i>Protitanotherium</i>
		Perissodactyla	Brontotheriidae	<i>Sthenodectes</i>
		Perissodactyla	Brontotheriidae	<i>Metarbinus</i>
		Perissodactyla	Brontotheriidae	<i>Metatelmatherium</i>
		Perissodactyla	Brontotheriidae	<i>Diplacodon</i>
		Perissodactyla	Eomoropidae	<i>Grangeria</i>
		Perissodactyla	Rhinocerotidae	<i>Amynodon</i>
		Perissodactyla	Rhinocerotidae	<i>Metamynodon</i>

Table 5. Mammalian faunal change in North American late Paleocene and Eocene biochrons. Note the large number of FADs (61) from Wa-6–Br-1a as compared to any consecutive three biochrons except for Ui-1–Ui-3. Note the large number of LADs in Br-2–Br-3 in the later part of the EECO.

Mammal age		Boundary From	To	Duration in m.y.	Immigrant % of FADs	Number of FADs	Number of LADs	Remarks
Uintan	Ui-3	43	40	3	6	33	42	Few immigrants; moderate speciation; strong LADs.
	Ui-2	45.4	43	2.4	6	18	8	Few immigrants; strong speciation; moderate LADs.
	Ui-1	47.25	45.4	1.85	5	40	19	Few immigrants; moderate speciation; moderate LADs.
Bridgerian	Br-3	48.4	47.25	1.15	50	8	27	Moderate immigrants; strong speciation; large LADs.
	Br-2	48.9	48.4	0.5	7	14	20	No immigrants; strong speciation; large LADs.
	Br-1b	49.55	48.9	0.65	0	6	15	No immigrants; little speciation; strong LADs.
	Br-1a	51.1	49.55	1.55	0	30	14	No immigrants; strong speciation; moderate LADs.
Wasatchian	Wa-7	52.65	51.1	1.55	5	22	24	Few immigrants; strong speciation; strong LADs.
	Wa-6	52.95	52.65	0.3	0	11	16	No immigrants; no speciation; moderate LADs.
	Wa-5	53.5	52.95	0.55	0	9	10	No immigrants; no speciation; moderate LADs.
	Wa-4	54.7	53.5	1.2	0	6	7	No immigrants; no speciation; moderate LADs.
	Wa-3	55.2	54.7	0.5	0	2	7	No immigrants; no speciation; minor LADs.
	Wa-2	55.5	55.2	0.3	0	1	5	No immigrants; no speciation; minor LADs.
	Wa-1	55.73	55.5	0.23	0	25	3	No immigrants; strong speciation; minor LADs.
	Wa-0	55.8	55.73	0.07	43	21	2	Strong immigrants; moderate speciation; minor LADs.
Clarkforkian	Cf-3	56.2	55.8	0.4	25	4	10	Moderate immigrants; moderate speciation; moderate LADs.

Mammal age		Boundary From	To	Duration in m.y.	Immigrant % of FADs	Number of FADs	Number of LADs	Remarks
	Cf-2	56.5	56.2	0.3	9	11	6	Moderate immigrants; moderate speciation; moderate LADs.
	Cf-1	57	56.5	0.5	38	8	8	Moderate immigrants; moderate speciation; moderate LADs.
Tiffanian	Ti-6	57.3	57	0.3	17	6	1	Few immigrants; strong speciation; minor LADs.
	Ti-5	58.3	57.3	1	14	7	20	Few immigrants; strong speciation; moderate LADs.
	Ti-4	59.5	58.3	1.2	0	12	15	No immigrants; no speciation; moderate LADs.
	Ti-3	60.3	59.5	0.8	8	13	18	Few immigrants; strong speciation; moderate LADs.

No immigrants = 0; Few immigrants = 1–2.

Moderate immigrants = 3–4; Strong immigrants = 6–8.

Speciation refers to that likely attributable to immigration.

Little speciation = immigrants are more than 40% of FADs.

Moderate speciation = immigrants are between 40% and 20% of FADs.

Strong speciation = immigrants are 1%–20% of FADs.

Minor LADs = <4; moderate LADs = >4 and <12; strong LADs = >12.

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During the Early Eocene Climatic Optimum

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Richard K. Stucky



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Cover photo: Type Section for the Lost Cabin Member of the Wind River Formation and Wa-7 (Lostcabinian North American Land Mammal Subage) in central Wyoming.
Photo by Jane Peterson.
