
An anachronistic Clarkforkian mammal fauna from the Paleocene Fort Union Formation (Great Divide Basin, Wyoming, USA)

ROBERT L. ANEMONE^{|1|} and WENDY DIRKS^{|2|}

|1| **Department of Anthropology, Western Michigan University**
Kalamazoo, MI 49008-5306, USA. E-mail: robert.anemone@wmich.edu

|2| **Oral Biology, School of Dental Sciences, Newcastle University**
Framlington Place, Newcastle-upon-Tyne, NE2 4BW, United Kingdom. E-mail: wendy.dirks@ncl.ac.uk

| ABSTRACT |

The Clarkforkian (latest Paleocene) North American Land Mammal Age (NALMA) remains a relatively poorly sampled biostratigraphic interval at the close of the Paleocene epoch that is best known from the Bighorn Basin of northwestern Wyoming. A period of global warming between the cooler early and middle Paleocene and the extreme warming of the early Eocene, the Clarkforkian witnessed significant floral and faunal turnover with important ramifications for the development of Cenozoic biotas. The combination of warming global climates with mammalian turnover (including likely intercontinental dispersals) marks the Clarkforkian and the succeeding Wasatchian (Earliest Eocene) NALMAs as periods of intense interest to paleobiologists and other earth scientists concerned with aspects of biostratigraphy and with the biotic effects of climate change in the past. In this paper we describe a new Clarkforkian mammalian fauna from the Great Divide Basin of southwestern Wyoming with some surprising faunal elements that differ from the typical suite of taxic associations found in Clarkforkian assemblages of the Bighorn Basin. Several different scenarios are explored to explain this “anachronistic” assemblage of mammals from southern Wyoming in relation to the typical patterns found in northern Wyoming, including the concepts of basin-margin faunas, latitudinal and climatic gradients, and a chronologically transitional fauna. We suggest that the observed faunal and biostratigraphic differences between southern and northern Wyoming faunas most likely result from latitudinal and associated climatic differences, with floral and faunal changes being reflected somewhat earlier in the south during this period of marked climate change.

KEYWORDS | Clarkforkian. Paleocene-Eocene boundary. Paleoclimatology. Global warming.

INTRODUCTION

The Paleocene-Eocene (PE) boundary has become a period of intense interest among many earth scientists in

recent years as a result of the growing realization that it marks perhaps the most significant episode of global warming during the entire Cenozoic Era (Aubry et al., 1998; Huber et al., 2000; Wing et al., 2003). Vertebrate

paleontologists and paleoanthropologists have been particularly interested in exploring the possible evolutionary effects of global climate change on the fossil vertebrate faunas spanning the PE boundary (Beard, 1998; Beard and Dawson, 1998, 1999; Clyde and Gingerich, 1998; Gunnell, 1998; Hooker, 1998, 2000; Bowen et al., 2002; Gingerich, 2003) and a significant, if not uncontested body of theory has arisen concerning the importance of climate change as a driver of biotic evolution (Janis, 1993; Vrba, 1993, 1995, 1996; Vrba et al., 1995; see Alroy et al., 2000 for a different view; Raia et al., 2000; Cornette et al., 2002; Mercer and Roth, 2003). This work is of general interest because understanding the biological effects of major episodes of global warming in the past can provide new perspectives and perhaps even a predictive understanding of the effects of global warming on the modern biota (Dukes and Mooney, 1999; Hellberg et al., 2001; Stenseth et al., 2002; Walther et al., 2002; Root et al., 2003; Pounds et al., 2006; Thomas et al., 2006). For mammalian paleontologists, the central questions concerning climate change and evolutionary transitions at the PE boundary involve two major faunal turnovers bracketing the Clarkforkian NALMA. The beginning of the Clarkforkian age is defined by the first appearance in North America of Rodentia and it is generally considered to be latest Paleocene in age (Archibald et al., 1987; Lofgren et al., 2004). Other important first appearances at the beginning of the Clarkforkian include the pantodont *Coryphodon*, the condylarth *Haplomylus*, and the tillodont *Esthonyx* (Lofgren et al., 2004). The Clarkforkian ends (and the Wasatchian begins) with the simultaneous appearance of Perissodactyla (*Hyracotherium*), Artiodactyla (*Diacodexis*), omomyid (*Teilhardina*) and adapiform (*Cantius*) euprimates, and hyaenodontid creodonts (Robinson et al., 2004). Most of the defining first appearances at the onset of the Clarkforkian and of the Wasatchian are considered to be intercontinental dispersals reflecting an Asian origin in the Paleocene for each of these North American taxa (Beard, 1998; Beard and Dawson, 1999; Bowen et al., 2002; Lofgren et al., 2004; Smith et al., 2006; see Hooker and Dashzeveg, 2003 and Zack et al., 2005 for alternative hypotheses concerning the origins of equoids and *Haplomylus*, respectively). Since mammalian dispersals between Asia and North America (and between North America and Europe) were most likely across high latitude land bridges, warming climates are thought to have played a critical role in creating forested corridors that would have facilitated these population movements. In this way, the study of the mammalian fauna of the Clarkforkian and succeeding Wasatchian ages can provide insight into the effects of climatic warming on faunal dispersals that played a role in the origins of several important modern mammalian orders.

THE CLARKFORKIAN NORTH AMERICAN LAND MAMMAL AGE (NALMA): A REVIEW

First conceived of in the early 20th century, the Clarkforkian age has undergone an interesting history of changes in definition and geochronological placement, including an attempt to remove it altogether from the ranks of North American Land Mammal Ages. Sinclair and Granger (1912) provided the first discussion of what would become known as the Clark Fork fauna based on their 1911 fieldwork for the American Museum of Natural History (AMNH) in the Clarks Fork Basin of northern Wyoming, a sub-basin of the Bighorn Basin. Two small mammalian assemblages from the upper part of the Fort Union formation were considered to bear a fauna that was younger than the Cretaceous but older than the Eocene. One was in the McCulloch Peaks area on the south side of the Shoshone River and the other was from the same stratigraphic level, northwest of the town of Ralston, along Big and Little Sand Coulees. Sinclair and Granger (1912: 60) suggested naming these rocks the “Ralston beds or Ralston formation”. Walter Granger and AMNH field crews returned to this part of the Bighorn Basin in 1912 and 1913, and obtained a large enough sample to demonstrate “clearly that this horizon is a very distinct one, older than the Gray Bull and perhaps representing the top of the Paleocene Series” (Granger, 1914, p. 204). In this paper Granger formally renamed these deposits the Clarks Fork beds after determining that the name Ralston was previously occupied as the Ralston Group in the Pennsylvanian. The original Clarks Fork fauna was dominated by phenacodontid condylarths (e.g., *Phenacodus* and *Ectocion*) and was argued to be pre-Eocene because of the absence of euprimates, artiodactyls, perissodactyls, and rodents. Additional collections of mammals have been recovered from these beds in the type area of the Clarks Fork basin by many Princeton University crews under the direction of Jepsen (1930, 1940), who renamed the rock unit from which these fossils were collected the Polecat Bench formation (Jepsen, 1940).

The Clarkforkian provincial mammal age (later North American Land Mammal Age or NALMA) was formally named and characterized for the first time by the Wood Committee (Wood et al., 1941, p. 9) in the following manner:

“Index fossil: *Plesiadapis cookei*.

First appearance: cf. *Coryphodon*, *Ectocion*, *Esthonyx*, *Oxyaena*.

Last appearance: *Carpolestes*, *Plesiadapis*.

Characteristic fossils: *Didymictis*, *Ectypodus*, *Phenacodus*, *Probathyopsis*, *Thryptacodon*.”

Although a systematic and largely successful first approximation at developing a mammalian biostratigraphy

for the entire Cenozoic, the Wood Committee Report continued to confuse lithostratigraphic, biostratigraphic, and biochronological units and to often “characterize” biochronologic units rather than “define” them. An example of this conceptual confusion can be illustrated by the Wood Committee’s definition of the Clarkforkian age as “based on the Clark Fork member (and faunal zone) of the Polecat Bench formation” (Wood et al., 1941, p. 9). The problem in this approach is that “whereas the mammal ages were characterized by biological criteria, their duration in time often was set by the temporal span (geochron) of the rock unit on which the age was based” (Woodburne, 1987b, p. 1-2). The independence of rock units and the fossils found therein is an analytical and conceptual approach that is essential to good biostratigraphic and geochronological practice (Woodburne, 1987c). Woodburne (2004, p. 13) suggests that one of the shortcomings of the Wood Report’s mammal ages is that they are not consistently defined on the basis of the first appearance of a single taxon, preferably an immigrant taxon. In spite of these conceptual shortcomings, the Wood Committee Report (Wood et al., 1941) was of significant and lasting value to North American vertebrate paleontology by virtue of its comprehensive zonation of the Cenozoic mammal record from North America. Although it has been superseded by more detailed and recent biostratigraphic work on Cenozoic mammals (Woodburne 1987a, 2004), it continues to provide the starting point for all biostratigraphic work by vertebrate paleontologists working with North American Cenozoic mammals today (Fig. 1).

The existence of a valid Clarkforkian biochron between the late Paleocene Tiffanian and the early Eocene Wasatchian was questioned in earnest by Wood (1967) as a result of his restudy of the early (pre-1930) collections

from the type area in the American Museum of Natural History and Princeton University Museum collections. Wood (op. cit.) found much to be critical of in these fossil collections, including poor or no stratigraphic control, fewer fossils than claimed in several early papers, many fossils thought to be from Eocene rather than from Paleocene beds, and the near absence of definitive Clarkforkian assemblages from outside the type area. He concluded that the fossil evidence for the existence of a Clarkforkian NALMA was extremely tenuous, and “scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation” (Wood, 1967, p. 28). It is unfortunate that Wood (op. cit.) was unaware of the many new specimens collected by Jepsen’s Princeton University field crews after 1930, since their inclusion might have suggested a very different conclusion.

The position of the Clarkforkian as a valid biochronological concept was secured with the publication of Rose’s (1981) monographic treatment of the Clarkforkian fauna and land mammal age. Utilizing the Princeton assemblage collected by Jepsen over four decades of field research in the Clarks Fork Basin, as well as the results of Rose’s own four years of fieldwork (1975-1978) with University of Michigan crews (under the direction of PD Gingerich), Rose (1981) provided a systematic revision of the entire Clarkforkian fauna in the type area. In addition, he critically summarized the evidence for faunal assemblages of Clarkforkian age from outside the type area in North America, examined the question of intercontinental faunal correlations (with Asia and Europe), and suggested the placement of the Clarkforkian age astride the Paleocene-Eocene boundary. Rose’s (1981) definition of the Clarkforkian is essentially the same as the current conception. The Clarkforkian is a valid NALMA that begins with the first appear-

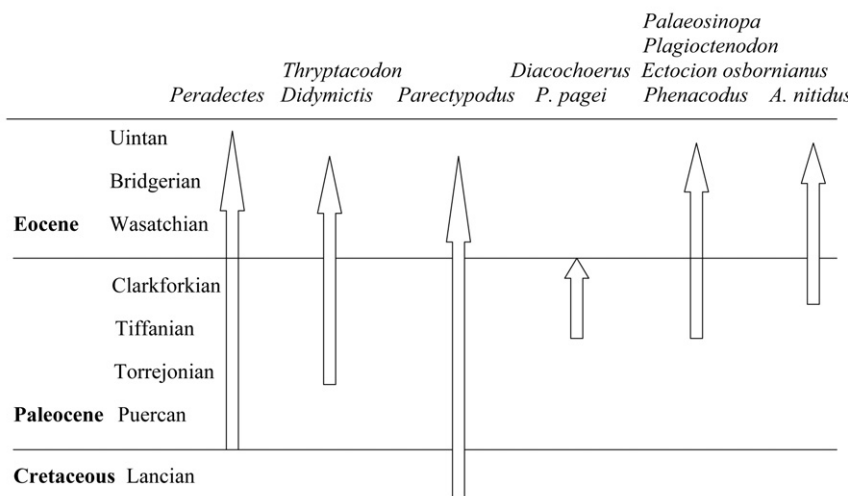


FIGURE 1 | Mark’s Locality dates to the late Paleocene and occurs in the upper part of the Fort Union Formation in the Great Divide Basin. Mammalian fossils from this locality show similarities to typical early (Cf1) and middle (Cf2) Clarkforkian faunas from the Bighorn Basin of northern Wyoming. Note that the figure is not to scale and boundaries are approximate. PE and KT boundary dates from Gradstein et al., 2004. North American Land Mammal Ages (NALMAs) from Wood et al., 1941.

ance in North America of the rodent *Paramys*, the tillodont *Esthonyx*, the pantodont *Coryphodon*, and the condylarth *Haplomytus*. It ends with the first appearances of the perissodactyl *Hyracotherium*, the artiodactyl *Diacodexis*, the adapiform primate *Cantius*, the omomyid primate *Teilhardina*, and the hyaenodontid creodonts. All of these taxa are generally considered to be immigrants to North America, most likely of Asian origin. In addition, Rose divided the Clarkforkian age into three biostratigraphic zones, comprising from oldest to youngest, the *Plesiadapis gingerichi* Zone, the *Plesiadapis cookei* Zone, and the *Phenacodus-Ectocion* Zone. In modern usage, the first two of these can be considered Lineage Zones, and are based on the first and last appearances of index fossils, after which the zones are named (Lofgren et al., 2004; Woodburne, 1987d). The third is currently considered an Acme Zone, since it “is based on the simultaneous abundance of the phenacodontid condylarths *Phenacodus* and *Ectocion*” (Lofgren, 2004, p. 86).

The current conception of the Clarkforkian land mammal age has been best articulated in the articles by Archibald et al. (1987) and Lofgren et al. (2004) in two volumes edited by Woodburne (1987a, 2004). Both of these works are based heavily on the contribution of Rose (1981), and incorporate much recent paleontological and geochronological work, both in and outside of the type area of the Clarkforkian, in a rigorous attempt to formalize the named mammal ages of the Paleocene in North America. In the most recent Woodburne (2004) volume, Lofgren et al. (2004) define the beginning of the Clarkforkian by the first appearance of Rodentia, and its end (i.e., the onset of the Wasatchian) by the simultaneous first appearance of adapid and omomyid euprimates, hyaenodontid creodonts, perissodactyls and artiodactyls (Archibald et al., 1987; Robinson et al., 2004). Following Rose (1981) and Archibald et al. (1987), Lofgren et al. (2004) also divide the Clarkforkian mammal age into an early (Cf1), middle (Cf2) and late (Cf3) zone. The early Clarkforkian or Cf1 is defined as the Rodentia/*Plesiadapis cookei* subzone of the *P. gingerichi*/*P. cookei* Lineage Zone, which includes the latest Tiffanian (Ti6) and earliest Clarkforkian (Cf1). This subzone begins with the first appearance of Rodentia and ends with the first appearance of *P. cookei*. The middle Clarkforkian (Cf2) is the *Plesiadapis cookei* Lineage Zone, and is defined by the presence of the Cf2 index fossil *P. cookei*. Finally, the late Clarkforkian (Cf3) is the *Phenacodus-Ectocion* Acme Zone (Lofgren et al., 2004), defined by the absence of *P. cookei*, the first appearances of *Esthonyx grangeri* and *Phenacolemur praecox*, and abundant remains of *Phenacodus*, *Ectocion*, *Didymictis*, and *Prodinoceras*.

Species of the primatomorph genera *Plesiadapis* and *Carpolestes* have long played an important role in the

biostratigraphic zonation of the late Paleocene. Gingerich (1976) erected five zones of the Tiffanian based on an evolving lineage of species of *Plesiadapis*, and the Carpolestidae play an important role in Rose’s (1981) discussion of middle and late Paleocene mammal biostratigraphy. Recently Bloch and Gingerich (1998) named a new species of *Carpolestes* and, with the benefit of a wealth of new and very complete specimens from the Bighorn Basin, presented a revised interpretation of the biostratigraphy of *Carpolestes* species during the late Paleocene. They suggested *C. nigridentis* as an index fossil of the Cf1 faunal zone, where it is typically found alongside *Plesiadapis dubius* and *P. gingerichi*. They also suggested that *C. simpsoni*, the new species they named in this paper was “almost completely restricted to the Cf2 faunal zone” (Bloch and Gingerich, 1998, p. 154), where it co-occurs with *P. dubius* and *P. cookei*. The exception was a single occurrence at University of Michigan locality SC-29, an earliest Cf3 locality from which the type specimen of *C. simpsoni* was recovered but which yielded no evidence of *P. cookei*, in spite of a reasonably large sample.

THE FIRST CLARKFORKIAN MAMMALS FROM THE GREAT DIVIDE BASIN

Geological setting and Stratigraphy of the Mark’s locality

Our paleontological fieldwork in Sweetwater County has led to the recovery of the first assemblage of Clarkforkian mammals from the Great Divide Basin of southwestern Wyoming (Anemone et al., 1999, 2000) at a site we call Mark’s Locality (WMU locality 110; UTM: 12TXB986(E)339(N)). The locality is in the NW section 3, Township 21 N, Range 99 W, on the Twelvemile Well 1:24,000 Quadrangle map, just west of the Bitter Creek road approximately 30 km north of Bitter Creek Station and nearly 350 km south of the Clarks Fork Basin (Fig. 2). It is the most productive of a very small number of localities we have identified in the relatively unfossiliferous upper Fort Union formation stretching along the Bitter Creek road from a few miles north of Interstate-80 to the flowing well known as Twelvemile Well in Section 28, Township 22 N, Range 99 W.

WMU 110 is in the upper Fort Union Formation (Fm), close to the mapped but locally unexposed contact between the Fort Union and the overlying Wasatch formation (Love and Christenson, 1985) that parallels the Bitter Creek Road north of Interstate-80. The Fort Union Fm in the Twelvemile Well area consists of olive gray silty mudstones, muddy sublithic to quartz arenites, and carbonaceous mudstones deposited in fluvial and floodplain environments (Fig. 3). The sands represent channel and

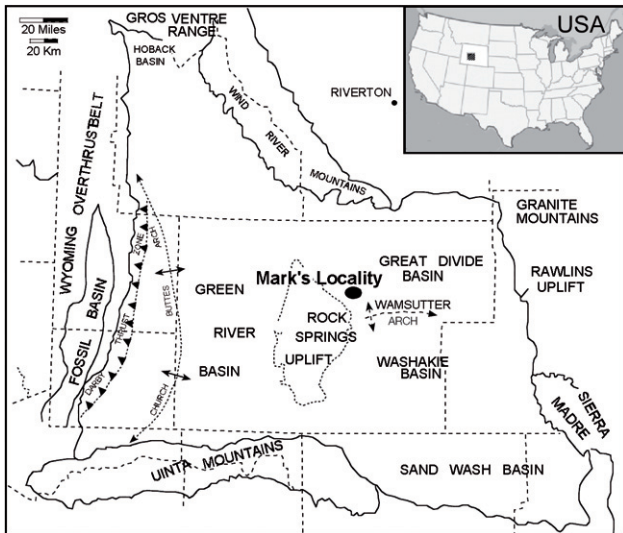


FIGURE 2 | Mark's Locality is in the Great Divide Basin, approximately 30 km north of Bitter Creek, in Sweetwater County, southwestern Wyoming. The Great Divide Basin is bounded on the north by the Wind River Mountains, on the east by the Rawlins Uplift and the Granite Mountains, on the south by the Wamsutter Arch, and on the west by the Rock Springs Uplift (After Sullivan, 1980).

avulsion deposits. Carbonaceous mudstones are clay-rich and often contain well-preserved plants. Mammals are concentrated at two levels in the grey-green silty mudstones, representing overbank deposits. The upper fossil-bearing unit is approximately 6 meters up-section from the lower unit.

Sampling and material

The Mark's Locality site was first located and identified in 1994 during systematic paleontological surveying (on foot) of the extensive but rarely fossiliferous deposits of the Fort Union formation along the Bitter Creek Road. The fossils represent mostly small to medium sized mammals, and include mostly isolated teeth, a number of disarticulated postcrania, and a few jaws. The locality has been surface collected during five different field seasons and screen washed. Wet screen washing (with .3 cm screen) of the upper fossil-bearing unit in the field resulted in the retrieval of approximately 20 kg of fossil-bearing matrix. This matrix was subsequently examined under a low-power dissecting microscope in the first author's lab at Western Michigan University, yielding approximately 1-2 mammalian fossils (mostly tiny isolated teeth) per kilogram of matrix. Surface collecting at Mark's Locality has always involved careful crawling of both levels of the locality in search of fossils in the small to tiny size range. As a result of these collecting techniques, we are confident that small taxa are not underrepresented in our collections. The mammal collection now stands at 170 specimens from 16 taxa.

The faunal assemblage

The mammalian fauna from Mark's Locality is dominated by condylarths and primatomorphs, including several taxa that are important biostratigraphic indicators (Table 1). The most common condylarth is the hyopsodontid *Apheliscus nitidus* (N=36), followed by *Ectocion osbornianus* (N=9). Both *Apheliscus* and *Ectocion* have been recovered from both the lower and upper fossil-bearing deposits at Mark's Locality. A single specimen each of *Thryptacodon* sp. and *Phenacodus* sp. complete the condylarth sample, which totals 42% of the entire mammalian assemblage in terms of specimens (NISP) and 27% of the individuals (MNI). Three different families of Primatomorpha comprise 45% of the total specimens and 42% of the individuals represented at this locality. Plesiadapidae include at least two species of *Plesiadapis*, namely *Plesiadapis cookei* (N=20) and *P. dubius* (N=18). Paromomyidae is represented by 5 specimens of *Phenacolemur* cf. *pagei*, while Carpolestidae includes 7 specimens of

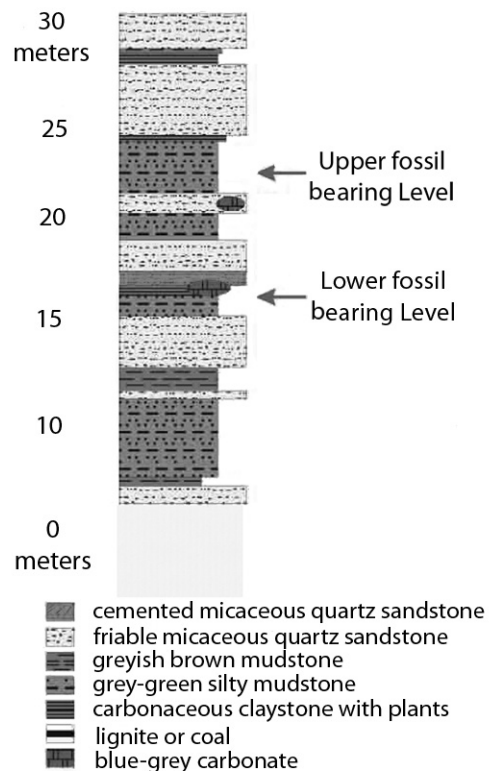


FIGURE 3 | Measured stratigraphic section of Mark's Locality. Note that both fossil-bearing levels are in the grey-green silty mudstone facies. All of the primatomorph taxa represented at this site (i.e., *Carpolestes nigridentis*, *Plesiadapis cookei* and *P. dubius*, and *Phenacolemur* cf. *pagei*), as well as the condylarths *Apheliscus nitidus* and *Ectocion osbornianus*, have been recovered from both the upper and lower sampling levels of Mark's Locality.

TABLE 1 | Faunal list from Mark's Locality, Great Divide Basin, Sweetwater County, WY. Fifty six unidentifiable mammalian specimens were excluded from these calculations to yield a sample size (TNS) of 114: the total number of mammals recovered from Mark's Locality is 170, and the minimum number of individuals (MNI) represented is 36.

Taxon	TNS ¹	MNI ²	%TNS	%MNI
Multituberculata				
Neoplagiulacidae				
<i>Parectypodus</i> sp.	1	1	1%	3%
Ptilodontidae				
<i>Prochetodon</i> sp.	2	2	2%	6%
Marsupialia				
Didelphidae				
<i>Peradectes</i> sp.	2	1	2%	3%
Primates				
Plesiadapidae				
<i>Plesiadapis cookei</i>	20	5	18%	15%
<i>Plesiadapis dubius</i>	18	4	16%	12%
cf. <i>Plesiadapis</i>	2	1	1%	3%
Paromomyidae				
<i>Phenacolemur</i> cf. <i>pagei</i>	5	2	4%	6%
Carpolestidae				
<i>Carpolestes nigridentis</i>	7	4	6%	6%
Carnivora				
Viverravidae				
<i>Didymictis</i> sp.	1	1	1%	3%
Cimolesta				
Pantolestidae				
<i>Palaeosinopa</i> sp.	1	1	1%	3%
Condylarthra				
Arctocyonidae				
<i>Thryptacodon</i> sp.	1	1	1%	3%
Hyopsodontidae				
<i>Apheliscus nitidus</i>	36	5	32%	15%
Phenacodontidae				
<i>Ectocion osbornianus</i>	9	2	8%	6%
<i>Phenacodus</i> sp.	1	1	1%	3%
Lipotyphla				
Erinaceidae				
<i>Diacchoerus</i> sp.	3	2	3%	6%
Nyctitheriidae				
<i>Plagiactenodon</i> sp.	2	1	2%	3%
Rodentia				
Ischyromyidae				
<i>Ischyromys</i> sp.	2	1	2%	1%
Totals³	114	36	100%	100%

¹ Total number of specimens

² Minimum number of individuals

Carpolestes nigridentis. Each of the four primate taxa has been recovered at both upper and lower levels of Mark's Locality. The rest of the mammalian groups recovered from Mark's Locality are rare, typically represented by one to three specimens each. They include Multituberculata (upper level only), Marsupialia (upper level only), Rodentia, Cimolesta, Lipotyphla (upper level only), and Carnivora. Several of these taxa (e.g., Multituberculata, Marsupialia, Cimolesta, and Lipotyphla) have only been recovered from the upper fossil bearing level as a result of screen washing operations: all other taxa have been recovered from both fossil bearing levels.

DISCUSSION

Biostratigraphic significance of the Clarkforkian Mark's Locality fauna

The mammalian fauna from Mark's Locality is clearly Clarkforkian or latest Paleocene in aspect. The evidence in support of a Clarkforkian age includes the presence of *Plesiadapis cookei* (Fig. 4) and *P. dubius* (Fig. 5), ischyromyid rodents, and *Carpolestes nigridentis* (Fig. 6), as well as the absence of the four groups that define the onset of the Wasatchian (i.e. artiodactyls, perissodactyls, euprimates and hyaenodontids). The stratigraphic position of Mark's Locality in the upper Fort Union formation further supports this age assignment. Determining which zone of the Clarkforkian this fauna should be attributed to is problematic, however, because of the co-occurrence of *P. cookei* and *C. nigridentis* at Mark's Locality. This association is surprising because, while *P. cookei* is generally considered to be an index fossil of Cf2 (Rose, 1981; Archibald et al., 1987; Lofgren et al., 2004), *C. nigridentis* is thought to be an index of Cf1 (Bloch and Gingerich, 1998). Thus the question remains as to whether Mark's Locality contains an early (Cf1) or middle (Cf2) Clarkforkian faunal assemblage. The unexpected combination of taxa that are generally restricted to different biostratigraphic ages or zones has been called an example of "anachronism" (Gunnell and Bartels, 2001). The nature of the anachronism at Mark's Locality is restricted to the two primate taxa mentioned above: *P. cookei* and *C. nigridentis*. As Fig. 1 indicates, none of the other taxa recovered at this site are particularly useful for determining the proper zone within the Clarkforkian in which to place this assemblage, since they all range through the entire Clarkforkian, often appearing first in the Tiffanian and generally extending into at least the Wasatchian.

Anachronistic faunas in the North American Cenozoic: Meaning and explanation

The notion of anachronistic associations of taxa in the biostratigraphy of the North American Cenozoic has been most seriously explored by Gunnell and Bartels (2001) but its roots go back at least to the middle 1960s. Robinson et al. (1964) reported on a late Eocene fauna from near Badwater Creek in the Wind River Basin of central Wyoming that included several multituberculates thought to have gone extinct in the early Eocene. Black (1967) described a similar fauna from Montana known as Shoddy Springs, in which a multituberculate, a dermopteran, and several other small and rare taxa thought to have become extinct in the early Eocene were recovered in late Eocene rocks. Black (1967) argued that the biostratigraphy of much of the middle Eocene was based on collections that may not be truly representative of the diversity of mammals then living. He states that "most of our knowledge of middle Eocene mammals has come from the lowland, a limited area of uniform

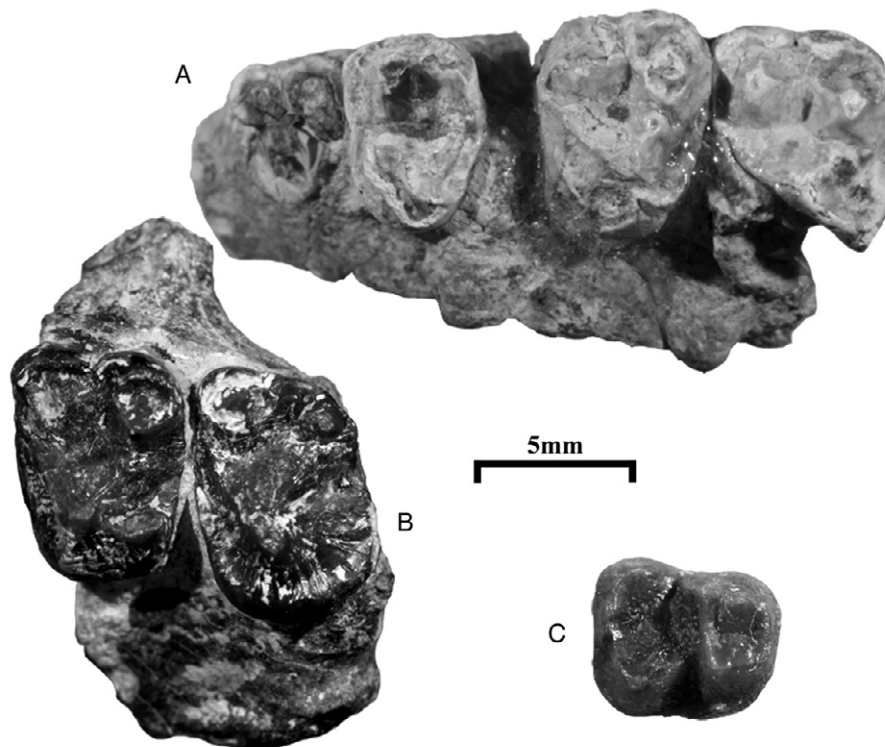


FIGURE 4 | *Plesiadapis cookei* from Mark's Locality. A) Left maxilla with P3-M2/ (WMU-VP 916). B) Left maxilla with M2-3/ (WMU-VP 917). C) Right M2 (WMU-VP 329). All views are occlusal.

vegetation, low relief, and probably little annual climatic fluctuation" (Black, 1967, p. 63), while late Eocene collections come from more diverse ecological and geographic settings that perhaps reflect a greater degree of endemism. Late Eocene collections may preserve small, rare mammals (like multituberculates and dermopterans) unknown in the middle Eocene because they are sampling uplands and other microhabitats far from the typical middle Eocene depositional settings. Black (1967, p. 64) concludes his paper with the prediction that uplands and basin margin habitats may preserve "mammalian communities quite different from those presently known for the middle Eocene".

Gunnell and Bartels (2001) tested these ideas of Black (1967) in their analysis of anachronistic associations within Bridgerian vertebrate faunas from the South Pass region of Wyoming. In this paper they formalized the concept of "basin margins" in terms of "geographic, physiographic, ecologic, and geologic components" (Gunnell and Bartels, 2001: 408). Basin margins were conceptualized as essentially uplands areas (at the time of deposition) along the geographic boundaries of sedimentary basins, characterized by a great diversity of microhabitats resulting from topographic diversity and climatic variability. Geologically, basin margins are regions of higher energy fluvial deposition and less mature and coarser sedimentary deposits. From the per-

spective of Eocene mammals themselves, Gunnell and Bartels (op. cit.) suggest that basin margin habitats would have provided more challenging and diverse habitats, with perhaps greater chances for allopatric speciation than in the typical, more homogeneous lowland basin centers where most of our knowledge of middle Eocene mammals originates. In their analysis of nearly 2,000 Bridgerian mammals from South Pass, they suggested four faunal indicators of the presence of basin margin environments. These indicators, all of which are present in the South Pass assemblage, included common forms that were rare in typical Bridgerian basin center depositional settings ("distinctive taxa"), unique taxa not found in the basin centers ("unique taxa"), morphologically distinct forms of common taxa found both in the basin centers and basin margins ("taxa of unique morphological form"), and taxa that do not occur at the same biostratigraphic interval in the basin centers, often representing ancestor-descendant pairs ("anachronistic taxa") (Gunnell and Bartels, 2001: 410).

Clarkforkian biostratigraphy is heavily based on the faunal collections from the Clarks Fork Basin of northwestern Wyoming, and the concept of faunal anachronism in the Clarkforkian must be understood relative to the biostratigraphic standard developed in the type area. As a result, the Clarkforkian age suggests more severe

constraints with respect to the lack of diversity of the faunal collections on which this biostratigraphic unit is based than the middle and late Eocene settings discussed by Black (1967) and Gunnell and Bartels (2001). The relevant question with respect to the fauna from Mark's Locality concerns whether or not the anachronistic association of *P. cookei* and *C. nigridentis* can be explained by the basin margin hypothesis. For a variety of reasons, we do not think that Mark's Locality represents a basin margin assemblage. For example, our anachronistic taxa are not an ancestor-descendant pair, and there seem to be no unique or distinctive taxa compared to typical Clarkforkian assemblages from northern Wyoming. Furthermore, the geographic (and paleo-geographic) position of this locality is within the broadly-defined basin center, far from the Rock Springs Uplift and the other uplands surrounding the Great Divide Basin. Finally, the sedimentary environments of the Fort Union formation in the Great Divide Basin involve typical fluvial, braided stream and alluvial fan deposition as is common in other basin centers.

A similar situation occurs in another Clarkforkian mammal locality from southwestern Wyoming that may shed some light on the anachronistic fauna from Mark's Locality. Big Multi Quarry is located in the northern Washakie Basin, approximately 30 km south of Mark's Locality, in similar strata from the uppermost part of the Fort Union Fm (Wilf et al., 1998). First discovered by University of California Museum of Paleontology

(UCMP) crews under the direction of DE Savage in the late 1970s, it has since 1992 been the focus of intensive quarrying by Carnegie Museum of Natural History (CM) crews under the direction of KC Beard (Rose, 1981; Wilf et al., 1998). With the largest and most diverse mammalian fauna from any Clarkforkian locality (NISP=1672 representing 41 taxa, Wilf et al., 1998), Big Multi Quarry provides another independent comparison to the biostratigraphic picture presented by the Clarkforkian faunas from the type area in northern Wyoming. Although Big Multi Quarry clearly contains a Clarkforkian assemblage of mammals (e.g., presence of rodents, tillodonts, and certain plesiadapiforms), controversy exists concerning its zonation within the Clarkforkian. While the presence of *Plesiadapis cookei* (confirmed by PD Gingerich -pers. comm., 2006- and KC Beard -pers. comm., 2006-, but contrary to Wilf et al., 1998) indicates middle Clarkforkian (Cf2) age, several other taxa are typical of the early Clarkforkian (Cf1), in particular *Microcosmodon conus*, *Planetetherium* sp., and *Carpolestes nigridentis* (Wilf et al., 1998). Wilf et al. (1998) argue for an early but not earliest Clarkforkian age (Cf1) for this assemblage, and offer an interesting ecological scenario to explain this anachronistic assemblage. Since their analysis of the fossil plant assemblage from Big Multi Quarry suggests greater affinities with the middle Clarkforkian (Cf2) and later floral communities of the Bighorn Basin, they suggest an interpretation involving northward dispersal of floral communities with increased warming in the late Paleocene. These floral changes, including the dominance

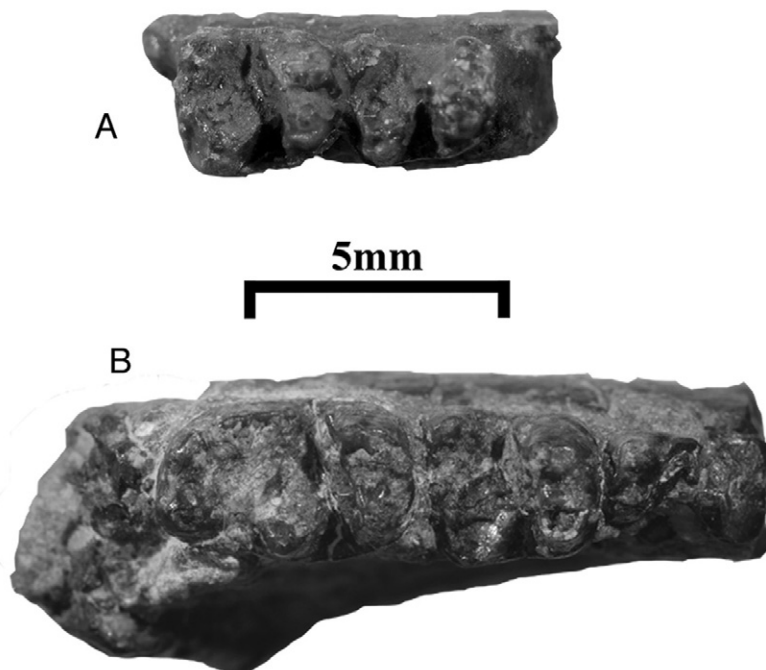


FIGURE 5 | *Plesiadapis dubius* from Mark's Locality. A) Right mandible with M/1-2 (WMU-VP 275). B) Right mandible with M/1-3 (WMU-VP 925). Both views are occlusal.

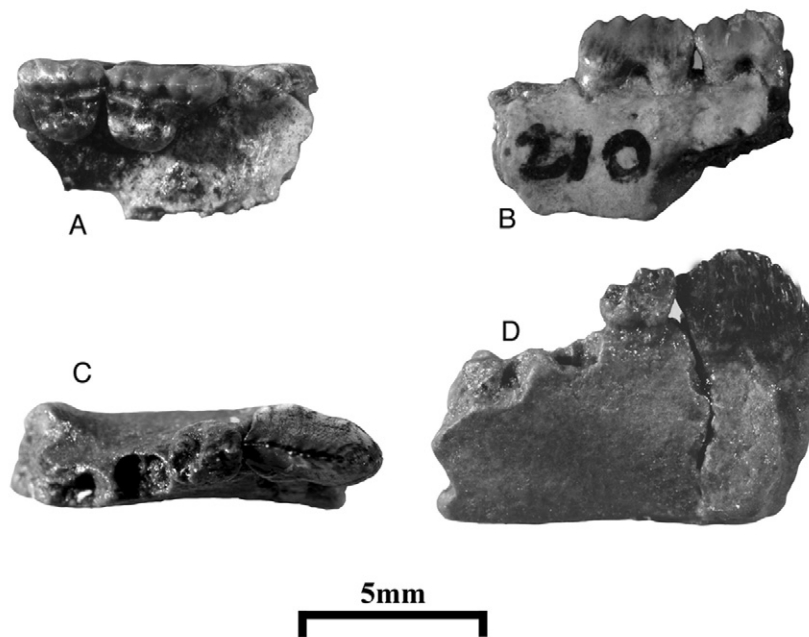


FIGURE 6 | *Carpolestes nigridentis* from Mark's Locality. Right maxilla with P3-4/ (WMU-VP 210) in occlusal (A) and lateral view (B). Left mandible with P/4-M1 (WMU-VP 1680) in occlusal (C) and lateral (D) views.

of the *Palaeocarpinus aspinosa* tree, would have occurred in southern Wyoming earlier than in the type area of the Clarkforkian, leading to evolutionary change in southern mammalian lineages preceding those in the north (Wilf et al., 1998).

The hypothesis of a latitudinal/climatic effect on faunal and floral evolution between southern and northern Wyoming, at a time of increasing global warming in the early Paleogene, has clear implications for the study of biostratigraphic assemblages. Most importantly, it suggests that faunal zones may not be completely synchronous between different basins in the American West. This is not surprising, since any biostratigraphic system based on intercontinental dispersals of mammals, as the North American Land Mammal Ages are (Woodburne, 2004), must in principal accept some degree of diachrony, especially as geographic distances between assemblages increase and at times of climate change. We suggest that the anachronistic faunal associations seen at Mark's Locality may similarly reflect a latitudinal/climatic difference between southern and northern Wyoming, with middle Clarkforkian (Cf2) faunal elements (i.e., *Plesiadapis cookei*) appearing slightly earlier than they generally do in the north, alongside mammals (i.e., *Carpolestes nigridentis*) typically restricted to the early Clarkforkian (Cf1). In a sense, this hypothesis suggests that Mark's Locality can be considered to be a

transitional fauna between early and middle Clarkforkian stages. Further testing of this hypothesis would require the location and analysis of additional Clarkforkian assemblages at differing latitudinal positions throughout the American West, a more general consideration of the nature and frequency of anachronistic faunal associations, and closer collaboration between climatologists, paleobotanists, and paleomammalogists in the analysis of climate change and associated biotic evolution in the Paleogene.

An alternative explanation of anachronistic mammalian associations at Mark's Locality might be that the fauna is a time-averaged assemblage sampling both early and middle Clarkforkian faunal zones. We tentatively reject this hypothesis for several reasons. The two stratigraphic levels from which fossils have been recovered are less than ten meters apart in the vertical dimension, and both *P. cookei* and *C. nigridentis* have been found at both the lower (16 m) and higher (22 m) levels. Furthermore, if the assemblage were truly time-averaged, we would expect a greater number of anachronistic associations, rather than the one that we have identified. While time-averaging cannot be ruled out at this point in time, we prefer the hypothesis that Mark's Locality represents a transitional Cf1 – Cf2 fauna reflecting the biotic effects of climatic warming occurring earlier in southern than in northern Wyoming.

CONCLUSIONS

A new and interesting Clarkforkian fauna from Fort Union deposits far from the type area of the Clarkforkian NALMA is described and analyzed.

Although the mammalian fauna from Mark's Locality is small in number of specimens and of taxa, the rarity of Clarkforkian faunas in the Rocky Mountain Interior makes this fauna an important datum in studies of biostratigraphy and faunal turnover during the transition from the latest Paleocene to the earliest Eocene.

The coexistence of typical early (Cf1) and middle (Cf2) Clarkforkian elements in the mammalian fauna from Mark's Locality is reminiscent of the concept of an "anachronistic fauna" in the sense of Black (1967) and Gunnell and Bartels (2001). Our analysis of the anachronistic association of primatomorph taxa at Mark's Locality suggests that biostratigraphic zones established mainly on the basis of fossils from northern Wyoming may not provide an unambiguous guide to faunal change in the basins of southern Wyoming. This is especially true at times of major global climate change, like the transition between the Paleocene and Eocene. While anachronistic faunas at South Pass (Gunnell and Bartels, 2001) or in the Wind River Basin (Black, 1967) may result from the sampling of basin margin faunas, anachronistic elements in the mammalian fauna from Mark's Locality in the Great Divide Basin are best explained by gradual climatic warming and the associated northward range expansion of floral and faunal elements.

ACKNOWLEDGMENTS

We would like to thank the organizers of the Climate and Biota of the Early Paleogene 2006 conference in Bilbao for a wonderfully stimulating scientific meeting and for inviting us to submit this paper. Colleagues who have graciously helped us with the analysis and interpretations offered here and with access to fossil collections include Chris Beard, Gregg Gunnell, Phil Gingerich, and Jon Bloch. We heartily thank all of our fieldcrew members who have prospected the Fort Union deposits along Bitter Creek Road, especially Ron Watkins, Brett Nachman, Ed Johnson, Bill Moore, John Van Regenmorter and Mark Brotherton, who found WMU Locality 110 and for whom it is named. We also thank John Van Regenmorter for his help with the figures and maps. We appreciate the comments of Jerry Hooker and Humberto Astibia, which helped improve this paper. Finally we thank the Wyoming Bureau of Land Management for their support of our fieldwork in the Great Divide Basin, and the Office of the Vice President for Research at Western Michigan University for financial support of this fieldwork.

REFERENCES

- Alroy, J., Koch, P., Zachos, J., 2000. Global climate change and North American mammalian evolution. *Paleobiology*, 26, 259-288.
- Anemone, R., Johnson, E., Nachman, B., Over, D., 2000. A new Clarkforkian primate fauna from the Great Divide Basin, SW Wyoming. *American Journal of Physical Anthropology*, Suppl. 30, p. 97.
- Anemone, R., Johnson, E., Rubick, C., 1999. Primates and other mammals from the Great Divide Basin, SW Wyoming: Systematics, geology, and chronology. *American Journal of Physical Anthropology*, Suppl. 28, p. 84.
- Archibald, J., Clemens, W., Gingerich, P., Krause, D., Lindsay, E., Rose, K., 1987. First North American land mammal ages of the Cenozoic era. In: Woodburne, M. (ed.). *Cenozoic Mammals of North America*. Berkeley, University of California Press, 24-76.
- Aubry, M.P., Lucas, S., Berggren, W. (eds.), 1998. *Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*. New York, Columbia University Press, 513 pp.
- Beard, K.C., 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In: Beard, K.C., Dawson, M. (eds.). *Dawn of the Age of Mammals in Asia*. Pittsburgh, Bulletin of Carnegie Museum of Natural History, 34, 5-39.
- Beard, K.C., Dawson, M. (eds.), 1998. *Dawn of the Age of Mammals in Asia*. Pittsburgh, Bulletin of the Carnegie Museum of Natural History, 34, 348 pp.
- Beard, K.C., Dawson, M., 1999. Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: Paleogeographic, paleoclimatic and biostratigraphic implications. *Bulletin de la Société Géologique de France*, 170, 697-706.
- Black, C.C., 1967. Middle and late Eocene mammal communities: A major discrepancy. *Science*, 156, 62-64.
- Bloch, J.I., Gingerich, P.D., 1998. *Carpolestes simpsoni*, new species (Mammalia, Proprimates) from the late Paleocene of the Clark's Fork Basin, Wyoming. *The University of Michigan, Contributions from the Museum of Paleontology*, 30, 131-162.
- Bowen, G.J., Alroy, J., Tsubamoto, T., Wang, Y., Clyde, W.C., Koch, P.L., Ting, S., 2002. Mammalian dispersal at the Paleocene/Eocene boundary. *Science*, 295, 2062-2065.
- Clyde, W.C., Gingerich, P.D., 1998. Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology*, 26, 1011-1014.
- Cornette, J., Lieberman, B., Goldstein, R., 2002. Documenting a significant relationship between macroevolutionary origination rates and Phanerozoic pCO₂ levels. *Proceedings of the National Academy of Science, USA*, 99, 7832-7835.
- Dukes, J., Mooney, H., 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, 14, 135-139.

- Gingerich, P., 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Papers, on Paleontology, 15, 1-141.
- Gingerich, P., 2003. Mammalian responses to climate change at the Paleocene-Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming. In: Wing, S., Gingerich, P., Schmitz, B., Thomas, E. (eds.). Causes and Consequences of Globally Warm Climate in the Early Paleogene. Boulder, Geological Society of America, Special Paper, 369, 463-478.
- Granger, W., 1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bulletin of the American Museum of Natural History, 33, 201-207.
- Gunnell, G., 1998. Mammalian faunal composition and the Paleocene/Eocene Epoch/Series boundary: evidence from the northern Bighorn Basin, Wyoming. In: Aubry, M.P., Lucas, S., Berggren, W.A. (eds.). Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. New York, Columbia University Press, 409-427.
- Gunnell, G., Bartels, W., 2001. Basin margins, biodiversity, evolutionary innovation, and the origin of new taxa. In: Gunnell, G. (ed.). Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats. New York, Kluwer Academic/Plenum Publishers, 403-432.
- Hellberg, M., Balch, D., Roy, K., 2001. Climate-driven range expansion and morphological evolution in a marine gastropod. Science, 292, 1707-1710.
- Hooker, J., 1998. Mammalian faunal change across the Paleocene-Eocene transition in Europe. In: Aubry, M.P., Lucas, S.G., Berggren, W.A. (eds.). Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. New York, Columbia University Press, 428-450.
- Hooker, J., 2000. Paleogene mammals: crises and ecological change. In: Culver, S., Rawson, P. (eds.). Biotic Response to Global Change: The Last 145 Million Years. Cambridge, Cambridge University Press, 333-349.
- Hooker, J., Dashzeveg, D., 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene-Eocene boundary. In: Wing, S., Gingerich, P.D., Schmitz, B., Thomas, E. (eds.). Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America, Special Paper, 369, 479-500.
- Huber, B., MacLeod, K., Wing, S. (eds.), 2000. Warm Climates in Earth History. Cambridge, Cambridge University Press, 462 pp.
- Janis, C., 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. Annual Review of Ecology and Systematics, 24, 467-500.
- Jepsen, G., 1930. Stratigraphy and paleontology of the Paleocene of Northeastern Park County, Wyoming. Proceedings of the American Philosophical Society, 69, 463-528.
- Jepsen, G., 1940. Paleocene faunas of the Polecat Bench formation, Park County, Wyoming. Proceedings of the American Philosophical Society, 83, 217-331.
- Lofgren, D., Lillegraven, J., Clemens, W., Gingerich, P., Williamson, T., 2004. Paleocene biochronology: The Puercan through Clarkforkian Land Mammal Ages. In: Woodburne, M. (ed.). Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. New York, Columbia University Press, 43-105.
- Love, J., Christianson, A., 1985. Geological Map of Wyoming, U.S. Geological Survey.
- Mercer, J., Roth, V., 2003. The effects of Cenozoic global change on squirrel phylogeny. Science, 299, 1568-1572.
- Pounds, J., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature, 439, 161-167.
- Raia, P., Piras, P., Kotsakis, T., 2005. Turnover pulse or Red Queen? Evidence from the large mammal communities during the Plio-Pleistocene of Italy. Palaeogeography, Palaeoclimatology, Palaeoclimatology, 221, 293-312.
- Robinson, P., Black, C.C., Dawson, M.R., 1964. Late Eocene multituberculates and other mammals from Wyoming. Science, 145, 809-811.
- Robinson, P., Gunnell, G., Walsh, S., Clyde, W., Storer, J., Stucky, R., Froehlich, D., Ferrusquia-Villafranca, I., McKenna, M., 2004. Wasatchian through Duchesnean biochronology. In: Woodburne, M. (ed.). Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. New York, Columbia University Press, 106-155.
- Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C., Pounds, A., 2003. Fingerprints of global warming on wild animals and plants. Nature, 421, 57-60.
- Rose, K., 1981. The Clarkforkian land mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan, Papers on Paleontology, 26, 1-197.
- Sinclair, W.J., Granger, W., 1912. Notes on the Tertiary deposits of the Bighorn Basin. Bulletin of the American Museum of Natural History, 31, 57-67.
- Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Sciences, 103, 11223-11227.
- Stenseth, N., Mysterud, A., Ottersen, G., Hurrell, J., Chan, K., Lima, M., 2002. Ecological effects of climate fluctuations. Science, 297, 1292-1296.
- Sullivan, R., 1980. A stratigraphic evaluation of the Eocene rocks of southwestern Wyoming. Laramie. The Geological Survey of Wyoming, p. 50.
- Thomas, C., Franco, A., Hill, J., 2006. Range retractions and extinction in the face of climate warming. Trends in Ecology and Evolution, 21, 415-416.
- Vrba, E., 1993. Turnover-pulses, the red queen, and related topics. American Journal of Science, 293, 418-452.

- Vrba, E., 1995. On the connections between paleoclimate and evolution. In: Vrba, E., Denton, G., Partridge, T., Burckle, L., (eds.). *Paleoclimate and Evolution, With Emphasis on Human Origins*. New Haven, Yale University Press, 24-45.
- Vrba, E., 1996. Climate and human evolution. *Journal of Anthropological Research*, 52, 1-28.
- Vrba, E., Denton, G., Partridge, T., Burckle, L. (ed.), 1995. *Paleoclimate and Evolution, With Emphasis on Human Origins*. New Haven, Yale University Press, 547 pp.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesani, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416, 389-395.
- Wilf, P., Beard, K.C., Davies-Vollum, K.S., Norejko, J.W., 1998. Portrait of a late Paleocene (Early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, Southwestern Wyoming. *Palaaios*, 13, 514-532.
- Wing, S., Gingerich, P., Schmitz, B., Thomas, E. (eds.), 2003. *Causes and Consequences of Globally Warm Climate in the Early Paleogene*. Boulder, Geological Society of America Special Paper, 369, 614 pp.
- Wood, H., Chaney, R., Clark, J., Cobert, E., Jepsen, G., Reeside, J., Stock, C., 1941. Nomenclature and correlation of the North American continental Tertiary. *Bulletin of the Geological Society of America*, 52, 1-48.
- Wood, R., 1967. A review of the Clark Fork vertebrate fauna. *Breviora*, 257, 1-30.
- Woodburne, M., 1987a. *Cenozoic Mammals of North America*. Berkeley, University of California Press, 391 pp.
- Woodburne, M., 1987b. Introduction. In: Woodburne, M. (ed.). *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. Berkeley, University of California Press, 1-8.
- Woodburne, M., 1987c. Principles, classification, and recommendations. In: Woodburne, M. (ed.). *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. Berkeley, University of California Press, 9-17.
- Woodburne, M., 1987d. Mammal ages, stages, and zones. In: Woodburne, M. (ed.). *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. Berkeley, University of California Press, 18-23.
- Woodburne, M., 2004. *Late Cretaceous and Cenozoic Mammals of North America. Biostratigraphy and Geochronology*. New York, Columbia University Press, 391 pp.
- Zack, S., Penkrot, T., Krause, D., Maas, M., 2005. A new aphelesine "condylarth" mammal from the late Paleocene of Montana and Alberta and the phylogeny of "hyopsodontids". *Acta Palaeontologica Polonica*, 50, 809-830.

Manuscript received November 2007;
 revision accepted March 2008;
 published Online November 2008.