Portrait of a Late Paleocene (Early Clarkforkian) Terrestrial Ecosystem: Big Multi Quarry and Associated Strata, Washakie Basin, Southwestern Wyoming

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In-depth understanding of past climatic and biotic change requires the study of ancient ecosystems. However, terrestrial plants and vertebrates are preferentially preserved under very different taphonomic conditions, and diverse fossil floras and faunas are rarely found in close association. Big Multi Quarry and associated strata in the uppermost Fort Union Formation of the Washakie Basin, southwestern Wyoming, provide a uniquely detailed record of terrestrial fauna, flora, and climate during the early Clarkforkian. The Clarkforkian Land Mammal Age, approximately the last million years of the Paleocene, was an interval of global warming that had profound biotic consequences.

The mammalian fauna of Big Multi Quarry, consisting of 41 species, is the most diverse known from a single Clarkforkian locality. Unlike most other Clarkforkian faunas, this assemblage is not significantly biased against small forms. Lipotyphlan insectivores were dominant, and arboreally adapted taxa were abundant and diverse. The closely associated and well-preserved fossil plant assemblage was overwhelmingly dominated by a single species belonging to the birch family. Floral richness, heterogeneity, and evenness were as low as in the Tiffanian of the same region, showing that forest structure remained monotonous even as climate warmed and mammals diversified in the Clarkforkian. The plant assemblage more closely resembles middle than early Clarkforkian floras of northern Wyoming, suggesting northward migration of the ranges of plant taxa coincident with warming.

A great deal of research has focused on the unusually warm interiors of continents in the terminal Paleocene and early Eocene. Multiple lines of evidence from our study, including sedimentological indicators, analyses of the nearest living relatives and functional analogues of the fossil plants and animals, size and margin analysis of fossil leaves, and cenogram analysis of the mammalian fauna, indicate that southwestern Wyoming had a humid subtropical climate with little or no seasonal frost or marked dry season, well before the terminal Paleocene.

INTRODUCTION

The Clarkforkian North American Land Mammal Age (NALMA), approximately the last million years of the Paleocene (Butler et al., 1981; Berggren et al., 1995), was an interval of global warming that linked the cooler earlier Paleocene with the hothouse of the early Eocene (Savin, 1977; Corfield and Cartlidge, 1992; Zachos et al., 1994; Wing et al., 1995, in press). As a result of this sustained warming trend, at least three successive waves of Asian endemic mammals were able to disperse into North America across a high-latitude filter that probably coincides with present-day Beringia (Beard, 1998). The first of these waves, consisting of archaic herbivorous mammals known as uintatheres (Dinocerata) and arctostylopids, arrived in the latter part of the preceding Tiffanian NALMA (zone Ti5 of Archibald et al., 1987). The second and third waves of immigrants bracket the Clarkforkian NALMA itself. The beginning of the Clarkforkian is defined by the first North American appearances of rodents, coryphodontids (Pantodonta), and tillodonts. The Clarkforkian is also associated with a floral immigration in the Northern Rockies, where many arriving taxa had modern subtropical to tropical affinities and were predominantly evergreen, including members of the cycad, ginger, laurel, and tea families (Hickey, 1980; Wing, 1998). The beginning of the succeeding Wasatchian NALMA is defined by the arrival of the third wave of immigrants, which included even-toed and odd-toed ungulates (Artiodactyla and Perissodactyla, respectively), lemur-like and tarsier-like primates, and the carnivorous hyaenodontids. Immigrant plant genera in the earliest Wasatchian of the Northern Rockies included *Platycarya, Alnus* (alder), the scrambling fern *Lygodium,* the aquatic fern *Salvinia,* and the tree fern *Cnemidaria* (Hickey, 1977; Wing, 1998; Wing et al., in press).

The Clarkforkian, therefore, records part of this iterative pattern of immigration and the initial response of the native North American biota, both of which were mediated by climatic warming.

Despite the importance of the Clarkforkian for understanding the mechanisms and effects of global warming on land, nearly all work to date on a fine stratigraphic scale has focused on a single area, the Bighorn Basin of northwestern Wyoming (Hickey, 1980; Gingerich et al., 1980; Rose, 1980, 1981a; Archibald et al., 1987; Bown et al., 1994; Wing, 1998; Wing et al., 1995, in press). This geographic restriction limits our ability to understand whether patterns seen in the Bighorn Basin reflect local, regional, or global processes. Moreover, biogeographic consequences of climate change can only be understood by examining records from more than one area.

The most significant Clarkforkian mammal locality outside of the Bighorn Basin is Big Multi Quarry, located in the Washakie Basin (Fig. 1), about 350 km south of the classic Clarkforkian sections in the Bighorn Basin (Gingerich et al., 1980; Rose, 1981a). Fossil mammals from Big Multi Quarry comprise the most diverse Clarkforkian mammal fauna yet obtained from a single locality. Because of unusually thorough faunal sampling, Big Multi Quarry is ideally suited for reconstruction of ancient climate and habitats using methods that rely on faunal data. Furthermore, the fauna is associated with a well-preserved fossil plant assemblage, both in the bedding planes immediately above the quarry and throughout a well-exposed local section of 18 m. The plant assemblage is sufficient for reconstruction of paleoclimate and paleoecology, and sedimentological data provide additional information on paleoclimate and paleoenvironment.

The purpose of this paper is to integrate these different lines of evidence regarding the Clarkforkian biota, climate, and environment of southwestern Wyoming. The picture that emerges is the most complete portrait now available of a Clarkforkian terrestrial "ecosystem". At the same time, the record from Big Multi Quarry and associated strata broadens the geographic coverage of our understanding of this important interval.

Setting

The study area is located near the settlement of Bitter Creek, Sweetwater County, Wyoming, in the northwestern Washakie Basin, a sub-basin of the greater Green River Basin (Fig. 1). Today this area is an arid and windy high desert, with less than 30 cm of annual rainfall, January mean temperature near −10°C, and only about 100 frost-free days per year (Knight, 1994). Big Multi Quarry lies in the uppermost part of the Fort Union Formation, which crops out around the trace of the Rock Springs Uplift (Love and Christiansen, 1985). Along the eastern flank of the Rock Springs Uplift, the thickness of the Fort Union Formation varies from about 420 to 750 m (Roehler, 1979; Winterfeld, 1982; Hettinger and Kirschbaum, 1991). Fort Union strata in this region do not provide a continuous record of Paleocene deposition. Rather, stratigraphic unconformities correspond to temporal hiatuses across the Cretaceous/Tertiary boundary and within the early and middle Paleocene (Roehler, 1979; Winterfeld, 1982; Kirschbaum and Nelson, 1988; Kirschbaum et al., 1994).
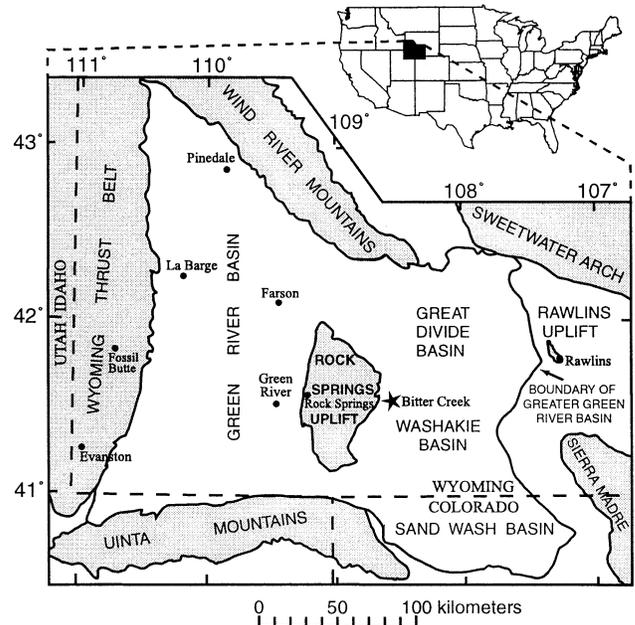

FIGURE 1—The greater Green River Basin of southwestern Wyoming, redrawn after Roehler (1992), showing major subbasins and uplifts (gray). Big Multi Quarry is located in the northwestern Washakie Basin, near Bitter Creek (starred).

Fossil mammals demonstrate local Fort Union deposition during the late Torrejonian (To3) and latter Tiffanian (Ti4-Ti5) NALMAs (Winterfeld, 1982), in addition to the Clarkforkian interval emphasized here. The overlying Wasatch Formation contains vertebrates representing the Wasatchian NALMA (Gazin, 1962; Savage et al., 1972; Savage and Waters, 1978; Williams and Covert, 1994). The Fort Union-Wasatch contact is locally covered by alluvium, approximately 80 m above Big Multi Quarry.

Big Multi Quarry occurs in a 0.5-m-thick, purple-gray, blocky mudstone near the base of our 23.4-m measured section (Figs. 2, 3). The vertebrate-bearing horizon is laterally continuous and traceable for at least 100 m. The local section is well-exposed by ephemeral drainages but bounded by covered intervals. Lithologies consist of coarsening-up packages of dark coal, rooted and drab underclay, carbonaceous shale, siltstone, progressively coarser grades of muscovitic sandstone, including cross-bedded strata, and limy siltstones. The limy siltstones are the most resistant units, and their weathered and fractured remains typically cap small buttes in the area. There are no mature paleosols, downcut channels, or any other indications of significant unconformities in the local section. Redbeds are absent, and rocks in general are drab-colored. The only exceptions are the purple coloration of the mudstone comprising Big Multi Quarry, an orange-stained goethitic sandstone immediately above the quarry, and yellow coloration from natrojarosite associated with coals. Paleosols in the area are thin, rooted underbeds lacking differentiated horizons as well as carbonate nodules. Poorly preserved fossil wood is common as talus. The lithologies observed in our section are typical of the upper Fort Union Formation throughout its outcrop zone around the Rock Springs Uplift (Roehler, 1973, 1979; Kirschbaum, 1987; Hettinger and Kirschbaum, 1991).
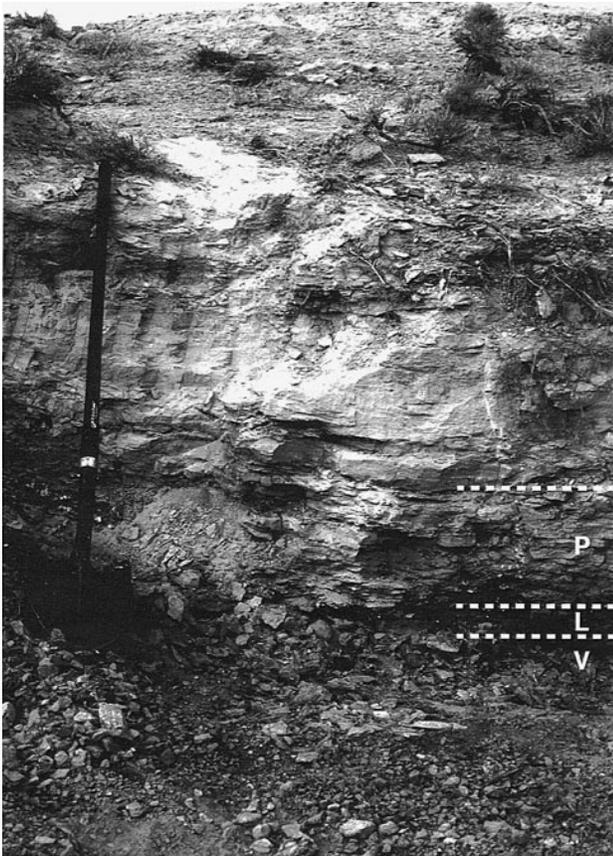
FIGURE 2—Big Multi Quarry. The shovel rests on the vertebrate-bearing mudstone (V), above which is a thin lignite (L) and a horizon bearing abundant fossil plants (P).

Plant compression-impression megafossils, primarily of leaves, are abundant in carbonaceous shales, siltstones, and sandstones throughout the local section (Fig. 3), especially at two stratigraphic levels: (1) immediately above Big Multi Quarry in gray and orange siltstone and sandstone (Fig. 2); and (2) in a 0.5-m-thick carbonaceous shale and 0.5-m siltstone unit that occurs from 18 to 19 m above Big Multi Quarry, where plant species diversity is highest and preservation is best (hereafter referred to as the "18-m level"). The latter is interpreted as a swamp deposit; it is laterally extensive and bears fossil plants over a distance of 1.3 km along strike. Given the conformable and floristically uniform nature of the local section, it is reasonable to assume that the 18 m of section from Big Multi Quarry to the best fossil plant horizon covers a very short interval of geologic time and that the fossil vegetation can be combined for analysis. The 18 m represents less than 40 ky if sedimentation rates recently calculated for the Clarkforkian of the Clark's Fork Basin are roughly applicable (Wing et al., 1999).

Previous Work

Big Multi Quarry was discovered in 1976 by a field party from the University of California Museum of Paleontology (UCMP) under the direction of Dr. Donald E. Savage (UCMP loc. V76134). According to Rose (1981a: p.
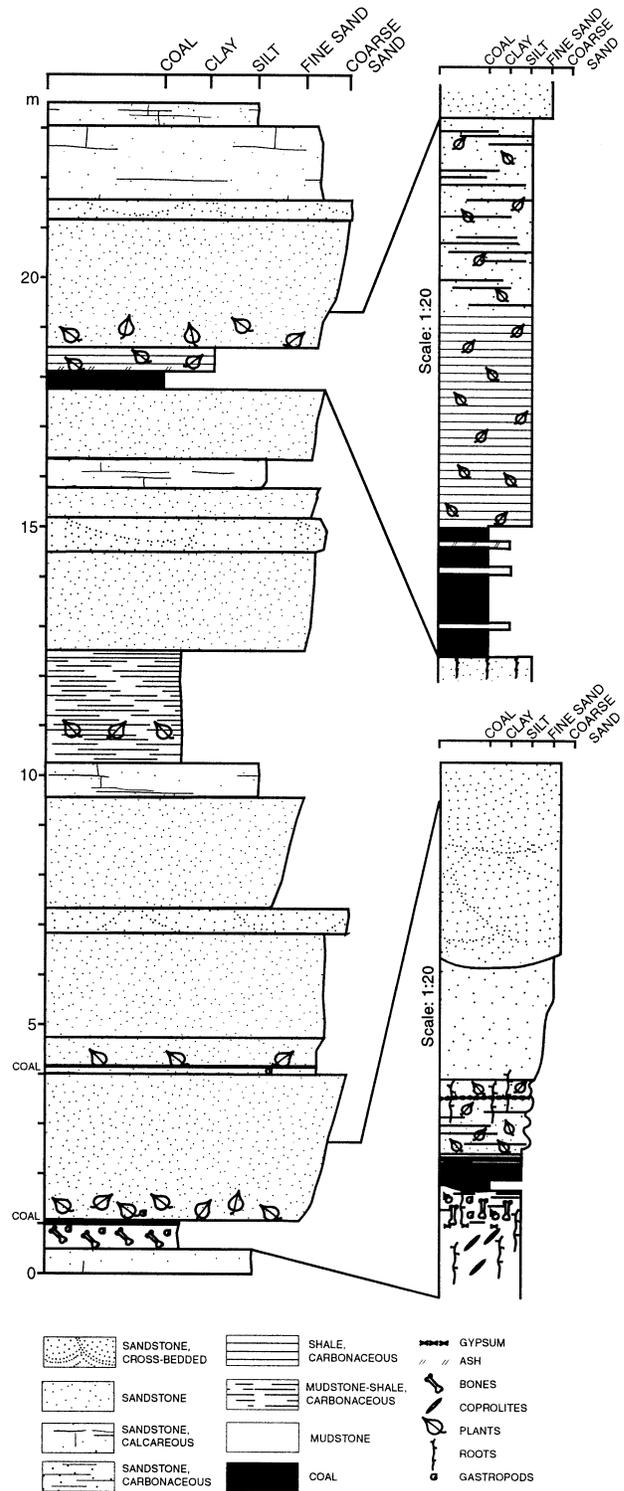

FIGURE 3—Measured section and expanded sections through Big Multi Quarry and plant bearing beds. The lower expanded section is through Big Multi Quarry (Fig. 2); the upper is adjacent to the most diverse fossil plant localities, USNM locs. 41270 and 41274, which are not on the main line of section.

131), the locality derives its name from the discovery of a large multituberculate (?*Neoliotomus*) during initial field work. The relevant specimens were placed in storage soon thereafter, and the exact identity of the large multituberculate remained a mystery for many years. The original multituberculate specimens were recently relocated in the UCMP collections and can now be provisionally referred to *N. conventus.* Based on the 1970s collections, Rose (1981a, p. 131–132) provided an annotated faunal list for Big Multi Quarry consisting of some 25 species of mammals. Citing the presence of *Plesiadapis cookei,* Rose (1981a) correlated the assemblage with the middle Clarkforkian (Cf2) *Plesiadapis cookei* Zone of the Bighorn Basin. However, we regard the occurrence of *P. cookei* at Big Multi Quarry as questionable because we have not found specimens of *P. cookei* in either the Berkeley or subsequent collections.

In 1992, field parties from the Carnegie Museum of Natural History (CM) resumed work at Big Multi Quarry, which has now been excavated intensively for six consecutive field seasons (CM loc. 2433). This new phase of research has significantly expanded our knowledge of the fauna, which now consists of 41 species of mammals. Two new species of rodents from Big Multi Quarry, among the oldest known from North America, were described by Dawson and Beard (1996). These included the first North American species of the primitive rodent family Alagomyidae, otherwise known only from early Cenozoic localities in Mongolia and China (Dashzeveg, 1990; Meng et al., 1994; Tong and Dawson, 1995). Systematic study of the remainder of the mammalian fauna is ongoing.

Plant fossils have occasionally been reported from the upper Fort Union Formation of the Rock Springs Uplift (Brown, 1962; Roehler, 1979; Kirschbaum, 1987), but few paleobotanical publications have treated this area and time period in any depth. Most research has been systematic (Manchester and Chen, 1996; Manchester and Dilcher, 1997). Gemmill and Johnson (1997) recently published a paleoecological analysis of a Tiffanian plant assemblage from the nearby Great Divide Basin. Their work was conducted at similar spatial scales to ours, consisting of ten localized sediment samples collected over a limited total area, thus providing a useful temporal antecedent to this study. Field crews from the U.S. National Museum of Natural History (USNM) conducted the paleobotanical field work for this study during the 1994–1996 field seasons.

Kirschbaum et al. (1994) showed that prevailing paleocurrents in the area were southerly, with the crystalline Wind River Mountains to the north supplying lithic sand, and that these drainages eventually joined northward-flowing drainages from the Uinta Mountain Front before flowing east. The Rock Springs Uplift in the latest Paleocene was flattened by erosion and did not impede this drainage pattern (Kirschbaum et al., 1994). The only previous paleoclimatic report is that of Roehler (1979), who suggested, on the basis of lithologic observations and preliminary collections of fossil leaves, pollen, and vertebrates from correlative rocks in the adjacent Sand Butte Rim NW Quadrangle, that ". . . the (Fort Union) rocks were deposited in a subtropical climate in swamps and on forested floodplains, probably not more than 900–1300 ft. above sea level."

TABLE 1—Total organic carbon content (TOC) for selected beds.

Sample	Meter level	Lithology/fossils	% TOC
USNM loc. 41272	18	fissile siltstone/plants	5.5
USNM loc. 41272	18	fissile siltstone/plants	5.8
USNM loc. 41272	18	carbonaceous shale-siltstone/plants	7.6
USNM loc. 41269	18	carbonaceous shale/plants	7.8
USNM loc. 41269	18	lignite	84
USNM locs. 41275-76	11	mudstone/plants	5.8
USNM loc. 41264	4	sandstone/plants	5.2
USNM loc. 41263	1	sandstone/plants	3.8
Big Multi Quarry	0.5	mudstone/vertebrates	5.8
Big Multi Quarry	0.5	organic mudstone/vertebrates	8.6
Big Multi Quarry	<0.5	gray mudstone/vertebrates	6.2

METHODS

Sedimentological Analysis

The section shown in Figure 3 was measured from below the base of the vertebrate-bearing mudstone, to USNM loc. 41264 (4-m level), USNM loc. 41276 (11-m level), and USNM loc. 41271 (18-m level), ending at the siltstone cap on the butte containing the latter locality. In addition, detailed sedimentological logs were taken of the major fossiliferous layers at Big Multi Quarry and four localities along the strike of the 18-m plant bed, one of which is shown in Figure 3. These logs identified beds on the centimeter scale to detect minor changes in lithologies and deposition. Each bed was assessed for thickness, type of boundary with adjacent beds, Munsell color, grain size, sedimentological features, structure, presence and type of organic material, and coloration by secondary and pedogenic minerals. Representative samples from each of the fossil-bearing beds were collected for analysis of total organic carbon content (TOC; Table 1). These were taken from well below the weathered surface to avoid errors associated with the introduction of modern organic material. To evaluate TOC, we used low-temperature combustion methods (Wilde et al., 1979), where TOC is equal to the weight of carbon divided by the dry weight.

Specimen Collection and Processing

The most complete specimens of fossil vertebrates were invariably collected by small-scale quarrying, either by hand or using hand-held tools. However, in order to sample the fauna as thoroughly as possible and to remove collecting biases against the recovery of small taxa, virtually all fossiliferous rock was screen-washed subsequent to initial quarrying. Some specimens were also obtained by surface-prospecting, amounting to fewer than 1% of all specimens recovered.

Plant megafossils were collected from 15 quarries at four stratigraphic levels (Fig. 3, Table 2). Each quarry comprised only 1–2 m³ of sediment in order to allow investigation of small-scale variation in vegetation. Collections representing the full range of morphological variation found for each species at each locality have been deposited

TABLE 2—Floral list, with presence-absence data and previously known range in the Tiffanian to Lostcabinian of the Bighorn Basin (from Wing, 1998). *f* = frequency. Ranges: Ti, Tiffanian; Cf1-3, Clarkforkian Zones 1–3; GB, Graybullian; LC, Lostcabinian. Organs: A, axis; F, foliage; C, cone; Ca, calyx; Fr, fruit. ''sl'' = found at same stratigraphic level as the quarry, usually within 20 m, but not at the quarry itself.

Taxon	Organ	62 (1)	63 (1)	64 (4)	75 (11)	76 (11)	65 (18)	66 (18)	67 (18)	68 (18)	69 (18)	70 (18)	71 (18)	72 (18)	73 (18)	74 (18)	f	Range, Ti-LC
							USNM loc. 412- (meter level)											
Sphenopsida																		
Equisetum sp.	A	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	1	Cf1-LC
Polypodiopsida																		
BLECHNACEAE																		
Woodwardia gravida Hickey	F	—	—	—	—	—	—	—	x	—	x	—	x	—	—	—	3	GB-LC
?POLYPODIACEAE																		
Allantodiopsis erosa Lesquereux	F	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	4	Cf1-LC
Pinopsida																		
TAXODIACEAE																		
Glyptostrobus europaeus (Brogniart) Heer	F,C	x	x	x	—	—	x	—	x	x	x	x	x	x	x	x	12	Ti-LC
Metasequoia occidentalis Newberry	F,C	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	1	Ti-GB
Liliopsida																		
ARECACEAE																		
Amesoneuron sp. Goeppert	F	—	—	—	—	—	—	—	x	—	—	—	—	x	—	—	2	Cf1-LC
ZINGIBERACEAE																		
Zingiberopsis isonervosa Hickey	F	—	—	x	—	—	—	—	x	—	—	—	—	—	—	—	2	Cf1-LC
Magnoliopsida																		
BETULACEAE																		
Corylites sp. Gardner	F	x	x	—	—	—	x	x	x	x	x	x	—	x	x	x	11	Cf1-GB
Palaeocarpinus aspinosa Manchester and Chen	Fr	x	x	—	—	—	x	—	x	x	x	x	—	—	—	x	8	Cf2-3
?CERCIDIPHYLLACEAE																		
aff. Cercidiphyllaceae FW09	F	x	x	—	—	—	—	—	x	—	x	—	—	x	sl	x	6	
CORNACEAE																		
Cornus hyperborea Heer	F	—	x	—	—	—	—	—	—	—	—	x	—	x	—	x	4	Cf1-GB
JUGLANDACEAE																		
"*Carya*" *antiquorum* Newberry	F	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	1	Ti-GB
LAURACEAE																		
"*Cinnamomum*" *sezannense* Watelet	F	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	2	Cf1-Cf3
aff. *Ocotea* FW03	F	—	—	—	—	—	—	—	x	x	—	x	—	x	x	x	6	
Persites argutus Hickey	F	x	x	—	x	x	—	x	x	—	—	x	x	x	—	x	10	Cf1-GB
?LAURACEAE																		
"*Ficus*" *planicostata* Lesquereux	F	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	Cf2-GB
MAGNOLIACEAE																		
Magnoliaceae sp. FW07-22-46	F	—	—	—	—	—	—	—	x	—	x	—	—	—	—	x	3	
MYRTACEAE																		
Paleomyrtinaea sp. Pigg, Stockey, and Maxwell	Fr	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	1	
?PLATANACEAE																		
"*Ficus postartocarpoides*" FW06	F	—	—	—	—	—	—	—	—	—	x	x	—	—	—	x	3	Cf1-3
?VITACEAE																		
"*Ampelopsis*" *acerifolia* (Newberry) Brown	F	—	—	—	—	—	x	x	x	x	—	x	x	—	x	x	8	Ti-GB
INCERTAE SEDIS																		
Averrhoites affinis (Newberry) Hickey	F	—	—	x	—	—	sl	—	—	—	—	x	—	x	—	—	3	Cf1-LC
Calycites sp. FW13	Ca	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	1	
aff. "*Viburnum*" *antiquum* (Newberry) Hollick FW40	F	—	—	—	—	—	—	—	—	—	—	x	—	—	—	x	2	
FW05	F	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	1	
FW18	F	—	—	—	—	—	—	x	—	—	—	—	—	x	—	—	2	
FW23	F	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	1	
FW24	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	1	
FW25	F	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	1	
FW27	F	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	1	
FW31 ?aquatic herb	F	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	1	
FW58	?Fr	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	1	
fertilized catkin FW65	Fr	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	1	
FW68	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	1	
Site richness (nonreproductive)		6	7	3	1	1	5	4	9	6	6	12	4	11	5	14		

Notes. "aff." = strong morphological similarity. Quotation marks = assignment thought to be invalid. Morphotype numbers (FW) shown for undescribed forms. *Woodwardia gravida* material is sterile; assignment based on fertile material found in nearby Clarkforkian rocks in the Sand Butte Rim NW Quadrangle (Wilf, unpublished data). "*Ficus postartocarpoides*" = "*F.*" *artocarpoides, sensu* Wing (1998). The modified name is used to separate the morphotype from nomenclatural issues involving "*F.*" *artocarpoides* Lesquereux and "*F.*" *preartocarpoides* Brown (see Johnson, 1996). FW40 is consistently narrower and less cordate than "*Viburnum*" *antiquum* as usually defined but shares other architectural features. Figured descriptions and additional references for the species designated with author names can be found in Brown (1962), Hickey (1977), Pigg et al. (1993), and Manchester and Chen (1996).

FIGURE 4—Relative abundance of mammals in three different size classes at Big Multi Quarry and a modern woodland assemblage from the Ohio River valley. Body size for the fossil mammal species was estimated using regressions of body size versus M_1 area in extant mammalian groups (see Table 3 and text). The distribution of body size in the extant woodland sample was adapted from Gunnell (1994) and references therein. Size categories are as follows: I, less than 0.5 kg; II, 0.5 kg–10 kg; III, greater than 10 kg.

at USNM under accession no. 420051. Fossil plants were segregated into morphospecies (Table 2) based on previous descriptive work and detailed analysis of the leaf architecture of undescribed forms (Hickey, 1973, 1979; Hickey and Wolfe, 1975).

Paleoecology

Both the vertebrate and plant assemblages appear to be parautochthonous and, therefore, well suited for paleoecological study. The frequent preservation of delicate, yet relatively complete microvertebrate fossils strongly indicates minimal transport. This interpretation is consistent with the fine-grained sediments comprising the vertebrate-bearing bed, which imply a low-energy depositional environment. The relative abundance of mammals in small, medium, and large size classes closely approximates that in a modern woodland assemblage (Fig. 4), suggesting that sampling bias against any particular size class is negligible. Most other Clarkforkian mammal assemblages are dominated by medium- and large-bodied taxa (Rose, 1981a). Also, it is widely acknowledged that fossil assemblages produced by surface collecting, including the vast majority of Clarkforkian assemblages currently known, are systematically biased against the recovery of small taxa (e.g., Winkler, 1983). Our collecting methods were designed to allow the small mammal component to be sampled especially thoroughly. Hence, we ar-

gue that the Big Multi Quarry assemblage provides the most unbiased approximation of a Clarkforkian mammalian community currently available.

Preservation of plant fossils is good to excellent. Fine details of leaf architecture are commonly preserved, often including the highest orders of venation. Cuticular preservation occurs on many specimens. Leaves from the 18-m level are of many different sizes on the same slab, indicating little taphonomic sorting. Davies-Vollum and Wing (1998) have shown that plant fossils found in fine-grained sediments of backswamp environments similar to those at the 11-m and 18-m levels preserve parautochthonous floral assemblages. Plant fossils found in coarser-grained sediment in the section, such as at the 1-m and 4-m levels, may have been transported short distances under higher energy fluvial conditions. The coarse-grained rocks indicate environments that were subject to more frequent sediment influx, as individual leaf layers tend to be separated vertically by sand, while the finer-grained sediments at the 18-m level preserved more leaf mats. However, even in these coarser-grained sediments the preservation of fine detail and the lack of mechanical damage indicate that there was not substantial transport prior to deposition. In addition, the presence of roots below plant beds throughout the section shows that standing phytomass was present (Fig. 3). For the fossil leaves to be derived from a distant source, they would have to be transported into the area in large numbers and also displace the leaf litter of existing forests.

All mammal specimens identifiable to the species level were tabulated (Table 3), yielding measures of relative abundance of the mammalian fauna in the form of total number of specimens (TNS) and minimum number of individuals (MNI). It is widely thought that MNI overestimates the abundance of rare species but underestimates the abundance of common forms (e.g., Rose, 1981b, and references therein). Although estimates of relative abundance based on TNS and MNI varied somewhat, these differences were typically minor (Fig. 4, Table 3). Diversity indices were calculated for comparison with similar data for other Paleocene and early Eocene North American mammal faunas taken from the literature (Table 4).

For the plants, the primary paleoecological technique was field censusing (Table 5). Our methodology was very similar to that of Gemmill and Johnson (1997) and Davies-Vollum and Wing (1998). Actualistic study in modern forests by Burnham et al. (1992) has shown that there is a strong positive correlation between the leaf mass of species recovered from litter baskets and the stem basal area of the source forest, that a correlation nearly as strong exists when leaf area is used instead of leaf mass, and that leaf count is a good proxy for leaf area. This study and others have shown that individual, highly local litter samples reflect the species composition of a source area of no more than about 20 m radius (Burnham, 1996, 1997). Burnham et al. (1992) suggested that, for minimally transported samples of fossil vegetation, censuses of 350–400 leaves would provide a useful approximation of the relative stem biomass of the ancient plant species in the immediate vicinity and would probably recover most of the species that shed leaves into the depositional site. The goal in this study was at least 350 leaves per site, but this number was lowered slightly if site richness was very low or raised if

TABLE 3—Mammalian faunal composition at Big Multi Quarry. For purposes of cenogram analysis, the natural logarithm of body mass was calculated from measurements of lower first molar area in each species, according to regression equations published by Legendre (1989). See text for discussion regarding estimates of body mass in multituberculates and palaeanodonts.

Taxon	TNS/MNI	%TNS	%MNI	ln (M, area, mm^2)	ln (body mass, g)	Regression model
Multituberculata						
Microcosmodon conus	70/13	4.19	4.98	0.24	2.66	All Mammal
Neoliotomus conventus	3/1	0.18	0.38	2.45	6.42	All Mammal
Ectypodus powelli	124/16	7.42	6.13	−0.057	2.15	All Mammal
Parectypodus laytoni	4/3	0.24	1.15	−0.39	1.59	All Mammal
Marsupialia						
Peradectes protinnominatus	175/21	10.47	8.05	0.24	3.24	Marsupial
Lipotyphla						
Palaeoryctes sp., cf. *P. punctatus*	12/3	0.72	1.15	0.96	3.08	Refined Insectivore
Leipsanolestes n. sp.	340/48	20.33	18.39	1.23	3.59	Refined Insectivore
Plagioctenodon sp. A	73/16	4.37	6.13	0.12	1.53	Refined Insectivore
Plagioctenodon sp. B	81/12	4.84	4.60	0.78	2.76	Refined Insectivore
Wyonycteris sp.	93/14	5.56	5.36	0.32	1.90	Refined Insectivore
Limaconyssus sp.	26/6	1.56	2.30	0.73	2.67	Refined Insectivore
Ceutholestes sp.	13/3	0.78	1.15	0.73	2.66	Refined Insectivore
cf. *Mckennatherium,* n. gen., n. sp.	5/2	0.30	0.77	0.74	2.68	Refined Insectivore
Diacocherus minutus	2/1	0.12	0.38	1.01	3.18	Refined Insectivore
Placentalia, incertae sedis						
Labidolemur kayi	13/2	0.78	0.77	0.74	2.68	Refined Insectivore
Palaeosinopa sp.	7/1	0.42	0.38	2.45	6.43	All Mammal
Planetetherium n. sp.	13/2	0.78	0.77	2.07	5.77	All Mammal
Primatomorpha						
Chiromyoides n. sp.	11/3	0.66	1.15	1.99	6.13	Primate
Plesiadapis dubius	3/1	0.18	0.38	1.95	6.07	Primate
Plesiadapidae, large sp.	2/1	0.12	0.38	3.37	8.50	Primate
Carpolestes nigridens	88/11	5.26	4.21	0.89	4.23	Primate
Phenacolemur simonsi	37/4	2.21	1.53	0.74	4.01	Primate
Phenacolemur pagei	41/4	2.45	1.53	1.56	5.41	Primate
cf. *Ignacius,* n. gen., n. sp.	21/6	1.26	2.30	2.07	6.27	Primate
Arctodontomys simplicidens	18/4	1.08	1.53	1.95	6.07	Primate
Arctodontomys n. sp.	19/5	1.14	1.92	0.80	4.10	Primate
Tinimomys n. sp.	38/7	2.27	2.68	−0.13	2.51	Primate
Chalicomomys n. sp.	5/1	0.30	0.38	−0.11	2.56	Primate
"Condylarthra"						
Phenacodus intermedius	8/1	0.48	0.38	4.75	10.80	Ungulate
Ectocion osbornianus	27/4	1.61	1.53	3.74	9.27	Ungulate
Apheliscus nitidus	114/11	6.82	4.21	1.84	5.39	All Mammal
Aletodon sp., cf. *A. conardae*	5/1	0.30	0.38	2.74	6.92	All Mammal
Chriacus sp.	6/1	0.36	0.38	3.32	7.91	All Mammal
Dinocerata						
Probathyopsis sp., cf. *P. harrisorum*	2/1	0.12	0.38	5.00	10.78	All Mammal
Pantodonta						
Cyriacothenum psamminum	1/1	0.06	0.38	3.54	8.28	All Mammal
Tillodontia						
Azygonyx xenicus	2/1	0.12	0.38	3.81	8.74	All Mammal
Rodentia						
Paramys adamus	94/13	5.62	4.98	0.79	3.48	Refined Rodent
Alagomys russelli	58/10	3.47	3.83	−0.31	1.54	Refined Rodent
Palaeanodonta						
Palaeanodon sp., cf. *P. parvulus*	1/1	0.06	0.38		6.62	All Mammal
Carnivora						
Viverravus sp.	8/2	0.48	0.77			
Didymictis sp.	9/3	0.54	1.15			
Total	1672/261					

TABLE 4—Diversity indices for Paleocene and early Eocene mammalian assemblages from the western United States. Comparative data for localities other than Big Multi Quarry are from Gunnell (1994) and references therein. Diversity indices as in Rose (1981a).

Locality/Zone	Simpson (D)	Shannon (H′)	Whittaker (E)
Rock Bench Quarry (To3)	0.954	3.40	33.3
Douglass Quarry (Ti1)	0.952	3.40	35.2
Scarritt Quarry (Ti2)	0.811	2.03	11.2
Cedar Point Quarry (Ti3)	0.877	2.64	18.1
Chappo Type Locality (Ti3)	0.904	2.77	16.6
Princeton Quarry (Ti5)	0.937	2.97	24.6
Clarkforkian Zone Cf1	0.865	2.59	17.5
Big Multi Quarry	**0.937**	**3.13**	**24.3**
Clarkforkian Zone Cf2	0.866	2.62	16.6
Clarkforkian Zone Cf3	0.878	2.62	17.1
Wasatchian Zone Wa0	0.940	3.20	31.9
Wasatchian Zone Wa1	0.925	2.85	24.1
Wasatchian Zone Wa2	0.921	2.90	21.6
Wasatchian Zone Wa3	0.928	2.89	21.4

Simpson Index (D) = $1 - \Sigma \, [n_i(n_i - 1)]/[N(N-1)]$, where

n_i = number of individuals in species i

N = total number of individuals in sample.

Shannon Index (H′) = $- \Sigma \, p_i \, (\ln p_i)$, where

p_i = proportion of individuals in species i

Whittaker Index (E) = $s/(\log p_1 - \log p_s)$, where

s = number of species

p_1 = proportion of individuals in the most common species

p_s = proportion of individuals in the rarest species.

the site was more diverse. Non-dicots were not counted because their foliage was fragmentary. Diversity indices were calculated for the censused quarries (Table 5). To the extent that leaf counts reflect relative dominance of species in the source forest, diversity indices based on leaf counts directly reflect evenness and concentration of dominance within the original biomass.

Paleoenvironmental and Paleoclimatic Analysis from Fossils

Vertebrates

Data from fossil vertebrates can be used to infer aspects of ancient environments and climates, although paleobotanical data are frequently regarded as more reliable indicators. We used two different methods. The first relies on assessment of the habitat preferences and/or requirements of nearest living relatives (NLRs); the second is a semi-quantitative approach known as cenogram analysis.

The NLR approach has greatest potential when phylogenetic relationships are well established, identification of fossils is nonproblematic, and the living relatives of fossil forms remain diverse and widespread, with environmental requirements that are well documented (e.g., Markwick, 1994). We assume that the precision and accuracy of the NLR approach decreases as a function of the age of the fauna under analysis. However, even when phylogenetic affinities with living taxa are either remote or poorly established, as is typically the case for Paleocene mammals, it may still be possible to draw paleoenvironmental inferences on the basis of reconstructed functional or ecological attributes of fossil taxa. For example, taxa that are thought to have been arboreal for purely anatomical reasons imply the presence of forested or at least woodland conditions.

The cenogram method is based on the empirical observation that the distribution of body size among non-carnivorous and non-volant species comprising modern mammalian faunas varies in specific ways with respect to environmental moisture and habitat regime (Legendre, 1989). Several workers have applied cenogram analysis to Paleogene mammal faunas (e.g., Gingerich, 1989; Legendre, 1989; Gunnell, 1994, 1997; Gunnell and Bartels, 1994). Because cenogram analysis is based on body-size distribution across the entire mammalian fauna, its application to fossil assemblages is only appropriate when most or all of the ancient fauna is believed to have been sampled and when a variety of collecting methods have been employed to minimize the problem of taphonomic bias (cf. Gunnell, 1994). Given its unusually high diversity of mammalian species and the variety of sampling procedures used, the Big Multi Quarry sample probably comes closer to meeting these criteria than most Paleocene mammal assemblages in North America.

Cenograms are dependent on accurate estimates of body mass, which are typically obtained using regressions of body mass versus lower first molar (M_1) area in various

TABLE 5—Dicot leaf census data: raw leaf counts and diversity indices (formulae in Table 4).

Taxon	USNM loc. 412- 63	65	70	72	Total
"*Ampelopsis*" *acerifolia*	0	6	269	11	286
"*Cinnamomum*" *sezannense*	109	0	0	0	109
aff. Cercidiphyllaceae	7	0	0	0	7
Cornus hyperborea	0	0	13	0	13
Corylites sp.	180	274	284	327	1065
Magnoliaceae sp.	0	0	19	0	19
aff. *Ocotea*	0	0	12	22	34
Persites argutus	2	0	22	3	27
aff. "*Viburnum*" *antiquum*	0	0	2	0	2
FW18	0	0	0	1	1
FW25	0	1	0	0	1
#Specimens	298	281	621	364	1564
Simpson (mean 0.336)	0.502	0.049	0.602	0.189	0.498
Shannon (mean 0.620)	0.794	0.127	1.13	0.427	1.052

mammalian groups (Legendre, 1989). Many North American Paleocene mammal taxa belong to extinct groups having uncertain phylogenetic relationships. Hence, it is frequently unclear which of these different regression models is most appropriate. In such cases, we usually employed Legendre's (1989) most generalized, "all mammal" regression model (Table 3). However, unique problems arise in estimating the body mass of extinct taxa, such as multituberculates and palaeanodonts, that are dentally highly specialized and for which the scaling properties of M_1 area with respect to body mass remain entirely unknown. Gunnell (1994) excluded multituberculates from his cenogram analyses of Paleocene mammal faunas in North America because of difficulties in relating M_1 area to body mass. While we are fully aware of this problem, we have nonetheless included multituberculates in our cenogram analysis, on the hypothesis that using an imperfect estimate of body mass in multituberculates is preferable to ignoring such a significant component of the mammalian fauna altogether. Body mass in multituberculates was estimated using Legendre's (1989) "all mammal" regression of body mass versus M_1 area, with M_1 area in multituberculates adjusted by a factor of 0.5 to compensate for the hypertrophy of M_1 in this taxon. Similarly, body mass of *Palaeanodon* sp., cf. *P. parvulus* was estimated as 750 g by comparison with its larger relative *Brachianodon westorum,* the body mass of which was estimated by Gunnell and Gingerich (1993) to lie between 1.0 and 2.7 kg.

Plants

Fossil plants have long been recognized for their potential to indicate past climates (e.g., Lesquereux in Hayden, 1871, p. 374). We employed two approaches: (1) analysis of the climatic preferences of the NLRs of the fossil vegetation, and (2) the uniformitarian application of the correlation of the sizes and shapes of modern leaves to prevailing climatic conditions. The relative advantages and disadvantages of each approach have been exhaustively compared elsewhere (e.g., Wing and Greenwood, 1993; Herman and Spicer, 1997), and the potential pitfalls inherent in the NLR approach, discussed above with respect to fossil vertebrates, apply to plants as well. In contrast to the use of NLRs, quantitative methods based on dicot leaf size and shape are theoretically independent of taxonomy (Wolfe, 1979, 1993). The two strongest leaf-climate relationships currently known are the positive correlations of (1) mean annual temperature (MAT) and the proportion of woody dicot species with entire (untoothed) margins (Wolfe, 1979; Wilf, 1997), and (2) mean annual precipitation (MAP) and leaf area (Givnish, 1984; Wilf et al., 1998). Use of these correlations to estimate past mean annual temperature and mean annual precipitation is known as leaf-margin analysis and leaf-area analysis, respectively, and these two methods are employed here (Table 6). The equation for leaf-margin analysis is Wing and Greenwood's (1993) quantification of Wolfe's (1979) East Asian dataset:

$$\text{MAT} = 30.6P + 1.14,$$

where P is the proportion of species of woody dicotyledons that have entire margins. The same equation has been used for recent paleo-MAT estimates from Clarkforkian

TABLE 6—Leaf-margin and leaf-area data. T, toothed margin; E, entire margin; Na, Nanophyll, Mi, Microphyll; No, Notophyll; Me, Mesophyll; Ma, Macrophyll (Webb, 1959).

Taxon	Margin	Area
"Ampelopsis" acerifolia	T	Mi-Me
Averrhoites affinis	E	Mi-Me
"Carya" antiquorum	T	Mi-No
aff. Cercidiphyllaceae	T	Mi-No
"Cinnamomum" sezannense	E	Mi-Me
Cornus hyperborea	E	Mi-Me
Corylites sp.	T	Mi-Me
"Ficus postartocarpoides"	T	Mi-No
"Ficus" planicostata	E	Me
Magnoliaceae sp.	E	Mi-Ma
aff. *Ocotea*	E	Mi-Me
Persites argutus	E	Na-Me
aff. *"Viburnum" antiquum*	T	Mi-No
FW05	T	No
FW18	T	Mi
FW23	E	Mi
FW24	E	Mi
FW25	E	Mi-Me
FW27	E	No-Me
FW68	E	Mi
Proportion entire margins	0.600	
MAT estimate, °C	19.5 ± 3.35	
MlnA	7.58	
MAP estimate, cm	137 + 59.2, − 41.4	

Notes. MAT estimate from leaf-margin analysis (Wolfe, 1979; Wing and Greenwood, 1993); error shown is binomial sampling error which is a minimum error of the estimate (Wilf, 1997). MlnA = mean natural log of the species' leaf-areas (Wilf et al., 1998); MAP estimate from leaf-area analysis (Wilf et al., 1998); error bars of one standard regression error are asymmetrical because they were converted from logarithmic units.

floras of the Bighorn Basin, allowing a firm basis of comparison (Wing et al., 1999). The equation for leaf-area analysis is

$$\ln (\text{MAP}) = 0.548 \, \text{MlnA} + 0.768,$$

standard error = 0.359, where MAP is in centimeters and MlnA is the mean of the natural logs of the species' leaf areas, area measured in square millimeters (Wilf et al., 1998).

Our leaf-margin and leaf-area data are based on the 20 presumably woody dicot leaf types found in the local section. To ascertain whether these taxa were a representative sample of the fossil flora over a broader area or a locally biased assemblage, we examined 22 roughly contemporaneous quarries of the uppermost Fort Union Formation on the east and south flanks of the Rock Springs Uplift (Wilf, unpublished data), adding several thousand specimens. Remarkably, these additional sites added only three leaf types (two toothed, one untoothed). The Big Multi local section, therefore, holds most of the dicot richness that can be recovered in the region and is clearly representative. For leaf-area analysis, we used the full range of leaf area found for each local taxon over the entire late Paleocene of the Rock Springs Uplift in order to take advantage of the additional sampling (Wilf, unpublished data). After Wilf et al. (1998), we calculated MlnA using the Raunkiaer-Webb system of discrete leaf areas (Webb, 1959). No upward adjustment in MlnA was made for pos-

sible removal of large leaves prior to deposition (Greenwood, 1992; Gregory and McIntosh, 1996), for several reasons. First, all of the samples were intensively collected over a large area, so that at least for common species, the largest leaves are likely to have been recovered. Second, analyses of leaf fossil-sediment relationships and comparison with recent taphonomic studies (Davies-Vollum and Wing, 1998) strongly indicate that most of the plant fossils were minimally transported. Third, there is no correction factor that has been shown to improve estimates of original leaf area.

BIOTA

Composition and Richness

With 41 species, Big Multi Quarry is richer than any other Clarkforkian mammalian assemblage (Table 3). Composition generally conforms with that of other well-sampled Clarkforkian faunas (Rose, 1981a, 1981b; Krause, 1986). Small insectivorous taxa dominate the assemblage, but relatively large herbivorous forms such as *Phenacodus* and *Probathyopsis* are also represented. As is typical of Paleocene mammal faunas in North America, most taxa belong to archaic groups without clear phylogenetic ties to modern orders. The marsupial *Peradectes,* the rodents *Paramys* and *Alagomys,* the carnivorans *Didymictis* and *Viverravus,* and the hedgehog *Leipsanolestes* are among the only mammals that can be unambiguously referred to modern higher taxa, although distant relatives of living Southeast Asian flying lemurs (order Dermoptera) are represented by *Phenacolemur,* cf. *Ignacius, Tinimomys, Chalicomomys,* and various plesiadapoid genera (Beard, 1990, 1993a, 1993b). Several groups that occur elsewhere in the western U.S. during this interval have not yet been recorded at Big Multi Quarry. These taxa include mesonychids, arctostylopids, oxyaenid creodonts, the hyopsodontid condylarth *Haplomylus,* and the pantodont *Coryphodon.* Mesonychids, arctostylopids, and oxyaenids are rare elements of penecontemporaneous mammalian faunas (Rose, 1981a, 1981b). Their absence at Big Multi Quarry may be an artifact of sampling, despite intensive efforts to overcome this problem.

A diverse herpetofauna, including salamanders, turtles, lizards, a champsosaur, and crocodilians, has been recovered from Big Multi Quarry, but these taxa have not yet been studied in detail. Among the crocodilians, both *Allognathosuchus* and *Ceratosuchus* have been identified (Rose, 1981a, p. 139).

Plant species richness is comparable to other localized plant assemblages in the late Paleocene of the Rocky Mountains. Gemmill and Johnson (1997) reported 28 leaf morphotypes for the Tiffanian Bison Basin florule from the Great Divide Basin, versus 27 in our sample, with a maximum at any one quarry of 14 leaf types, versus 13 in our section (Table 2). The Almont assemblage of North Dakota (Crane et al., 1990), which is probably Clarkforkian in age, was also collected over a small area and yielded a total of 24 leaf types. The overlying and presumably Clarkforkian Bear Den Member of the Golden Valley Formation, collected over a large area, has produced fewer than 25 leaf types (Hickey, 1977). The most speciose locality in the early Clarkforkian of the Clark's Fork Basin,

Double Kill Hill, yielded 25 species (Wing et al., 1995). The low species richness in our section is therefore typically Paleocene and not a taphonomic artifact.

Fossil vegetation from the coarsening-up sequence immediately above Big Multi Quarry is not particularly species-rich (Table 2). Families that can be recognized with reasonable confidence are the Betulaceae (birch family), Cornaceae (dogwood family), Lauraceae (laurel family), Zingiberaceae (ginger family), Taxodiaceae (bald cypress family), and a probable member of the Cercidiphyllaceae (katsura family). *Palaeocarpinus aspinosa* co-occurs with its presumed leaf type, *Corylites* (Manchester and Chen, 1996). *"Cinnamomum" sezannense, "Ficus" planicostata,* FW27, and *Calycites* sp. are the only forms restricted to this part of the section, most local to the mammal quarry.

When the upper part of the section is added (Table 2), the additional elements include leaf types of the Magnoliaceae (magnolia family) and Juglandaceae (walnut family), the guava berry *Paleomyrtinaea* (Pigg et al., 1993), undoubtedly a food source for vertebrates, and several non-dicots, including fragmentary palm leaves (*Amesoneuron*), *Metasequoia,* the ferns *Allantodiopsis erosa* and *Woodwardia gravida,* and a horsetail (*Equisetum*).

Insect-feeding damage on fossil leaves is ubiquitous throughout the section and exhibits some host specificity. Types of damage observed are two types of hole feeding, margin feeding, at least two galling types, window feeding, skeletonization, and at least four types of mines, some with well-preserved frass trails (terminology *sensu* Beck et al., 1998). Gastropod shells are abundant within the mudstone bearing the mammals (Fig. 3). A single terrestrial pulmonate examined has been identified as cf. Charopidae (B. Roth, pers. comm. 1996).

Paleoecology

Among the mammals, the species diversity and abundance of small lipotyphlan insectivores is remarkable, even when the assemblage is compared with other Clarkforkian micromammal assemblages such as University of Michigan locality SC-188 in the Clark's Fork Basin (Krause, 1986, Table 3; Fig. 5). By far the most common species is a hedgehog belonging to the genus *Leipsanolestes.* Eleven species of basal primatomorphs (early relatives of primates and flying lemurs) are known from Big Multi Quarry. This is an extraordinarily high species richness for this group at a single site, but their combined abundance is comparable to that at other Clarkforkian and late Tiffanian localities (Fig. 5). Only one species of marsupial occurs, *Peradectes protinnominatus,* but this species is exceptionally abundant in comparison to total marsupial abundance at sites of roughly similar age in the Rocky Mountain region (Fig. 5). Multituberculates are reasonably abundant and diverse (four species), whereas this group is unknown from the early Clarkforkian Bear Creek fauna of southern Montana. Interestingly, the relative abundance of multituberculates in two of the best-sampled Clarkforkian mammal assemblages (Big Multi Quarry and SC-188) is similar to or greater than that from an assemblage that antedates the dispersal of rodents into North America (Princeton Quarry, from late Tiffanian zone Ti5; Fig. 5). This finding conflicts with the notion that the immigration of rodents severely affected North Amer-
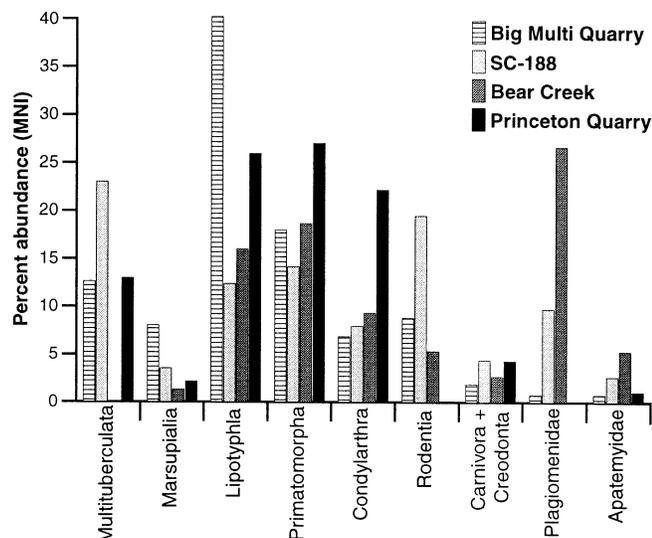
FIGURE 5—Relative abundance of major groups of mammals at Big Multi Quarry and penecontemporaneous localities in the northern Bighorn Basin, based on minimum number of individuals (MNI). Comparative data for Bighorn Basin localities are derived from Rose (1981a) and Krause (1986).

ican multituberculates (Krause, 1986). In contrast to the primarily surface-collected Clarkforkian sites in the Clark's Fork Basin, large mammal taxa are not disproportionately represented at Big Multi Quarry, although some large-bodied forms are present. These include the uintathere *Probathyopsis,* the pantodont *Cyriacotherium,* the condylarths *Phenacodus* and *Ectocion,* and the carnivoran *Didymictis.* Diversity indices indicate greater mammalian faunal heterogeneity and evenness than for primarily surface-collected Clarkforkian assemblages from the Clark's Fork Basin (Table 4).

For the plants, both frequencies of occurrence (Table 2) and census results (Table 5) demonstrate the overwhelming dominance of *Corylites* leaves both in the near-channel environment found above Big Multi Quarry (USNM loc. 41263) and in the backswamps preserved at the 18-m level. *Corylites* was found at 11 of the 15 localities and constituted 1065 of the 1564 leaves in the four censuses combined. It was common at the plant localities from the 18-m level to find 20–30 *Corylites* leaves in a single block and no other species, a possible result of synchronous abscission of leaves (i.e., deciduousness). The fact that all extant Betulaceae are deciduous supports this hypothesis. However, even if deciduousness exaggerated the leaf counts in favor of *Corylites,* the lopsidedness of the census results leaves no doubt that the tree bearing *Corylites* leaves and *Palaeocarpinus aspinosa* fruits (Manchester and Chen, 1996) dominated the areas nearest to depositional centers.

The only challenges to *Corylites* dominance were the strong showings of "*Ampelopsis*" *acerifolia* at USNM loc. 41270 and of "*Cinnamomum*" *sezannense* above Big Multi Quarry. However, *Glyptostrobus europaeus,* although not censused, occurred at the greatest number of localities (Table 2). From qualitative observations, *G. europaeus* foliage was clearly not as abundant as *Corylites* but was nevertheless very common. *Persites argutus* was also ubiquitous, occurring at ten localities, but it was not a dominant

element in any of the censuses. Similarly, aff. Cercidiphyllaceae occurred at seven localities but at very low abundance.

The overall dominance pattern is very similar to that described by Gemmill and Johnson (1997) for the Tiffanian Bison Basin plant assemblage. There, the two leading rank dominants are *Corylites* sp., also in association with *Palaeocarpinus aspinosa,* and *Archeampelos acerifolia* (probably the same species as our "*Ampelopsis*" *acerifolia*), while the third is *Metasequoia occidentalis,* a taxodiaceous conifer that may have occupied a niche similar to *Glyptostrobus europaeus.* However, at our sites, *Corylites* is even more dominant in the leaf counts, comprising 68.1% of total dicot leaves vs. 49.3% in the Bison Basin.

Diversity indices are shown for the censused quarries in Table 5. The site immediately above Big Multi Quarry, USNM loc. 41263, has the second highest values. Diversity indices from ten Tiffanian quarries in the Bison Basin are comparable although slightly higher (Simpson: cumulative 0.559, mean 0.484; Shannon: cumulative 1.02, mean 0.880; Gemmill and Johnson, 1997, Appendix 1, adjusted for dicots only). The greater percentage of *Corylites* leaves at our sites is a primary cause of the lower index values at our sites than in the Bison Basin. The low values of diversity indices in both the Bison Basin and Big Multi assemblages could reflect the biological and preservational limitations on species richness and evenness that can be recovered from individual fossil plant localities of floodplain environments (Wing and DiMichele, 1995). However, these index values are well below those from early Eocene assemblages from similar depositional settings in the nearby Great Divide Basin, strongly supporting the argument for originally low evenness in the late Paleocene (Wilf, unpublished data).

Low-diversity forests are typical of the early and middle Paleocene worldwide (e.g., Crane et al., 1990; Wing and Sues, 1992), and in western North America, these conditions have been documented as late as the Tiffanian (Hickey, 1980; Gemmill and Johnson, 1997). The monotony of Paleocene forests stands in sharp contrast to the contemporaneous radiation of mammals (Wing and Fleming, 1995; Alroy, 1996). Our data show that even in the Clarkforkian, during a period of warming associated with the immigration of exotic mammals and plants, the overall structure of basin forests remained monotonous in southern Wyoming, not to be reorganized until the early Eocene (Wilf, unpublished data).

Biostratigraphic Correlation

Assignment of the Big Multi Quarry mammalian assemblage to the Clarkforkian NALMA is secure, based on the occurrence of both rodents and tillodonts in the fauna (Rose, 1980, 1981a; Archibald et al., 1987). In the Clark's Fork Basin, finer biostratigraphic zonation of the Clarkforkian is based on species of plesiadapids that have not been adequately documented at Big Multi Quarry. However, many of the mammals occurring at Big Multi Quarry imply correlation with the early part of the Clarkforkian NALMA, and correlation with zone Cf1 is advocated here. For example, the multituberculate *Microcosmodon conus* and the plagiomenid *Planetetherium* have never been found in strata as young as middle Clarkforkian (Cf2) in

the Clark's Fork Basin, suggesting an earlier age for Big Multi Quarry. Taxa that seemingly corroborate this age assignment include (1) *Carpolestes nigridens,* (2) a species of *Chiromyoides* that is smaller and more primitive than *C. major,* and (3) a species of *Aletodon* that is similar to and possibly conspecific with *A. conardae* (late Tiffanian) but smaller and more primitive than *A. gunnelli* (middle and late Clarkforkian). On the other hand, it seems unlikely that Big Multi Quarry is as old as the Bear Creek, Montana, mammalian assemblage, the best sampled early Clarkforkian fauna available for comparison, because *Leipsanolestes* n. sp. from Big Multi Quarry is more derived than *L. siegfriedti* from Bear Creek in having a more nearly molariform P_4. On the basis of the entire mammalian assemblage, we correlate Big Multi Quarry with early, but not earliest Clarkforkian strata in the Clark's Fork Basin. Thus Big Multi Quarry antedates the latest Paleocene thermal maximum, which is considered to be synchronous with the Clarkforkian/Wasatchian boundary (Kennett and Stott, 1991; Koch et al. 1992; Thomas and Shackleton, 1996).

The plant assemblage (Table 2) is completely consistent with published megafloral zonations for the Clarkforkian of the Bighorn Basin (Hickey, 1980; Wing, 1998). That is, almost none of the Big Multi plants also found in the Bighorn Basin has a pre-Clarkforkian LAD (last appearance datum) or post-Clarkforkian FAD (first appearance datum) in the Bighorn Basin, as shown in Table 2. The only exception, *Woodwardia gravida,* is known from the Clarkforkian of North Dakota (Hickey, 1977). This result is encouraging for careful application and further development of megafloral zonations tied to NALMAs.

At a finer scale, the local plant assemblage more closely resembles middle Clarkforkian and later floras of the Bighorn Basin, which, given the early Clarkforkian age determined from the fauna, suggests northward floral migration coincident with climatic warming. The *Persites-Cornus* Zone (PCZ; Hickey, 1980), named for the conjunction of *Persites argutus* and *Cornus hyperborea,* has been correlated to Clarkforkian and earliest Wasatchian strata in the Bighorn Basin (Hickey, 1980; Wing, 1998). Recently, the PCZ has been divided into lower and upper parts (Wing, 1998), with an approximate boundary between the parts within Cf 2 time. Using this zonation, the Big Multi plant assemblage clearly falls into the upper part because two diagnostic characteristics of the upper PCZ are: (1) *Corylites* sp. is dominant at many localities and co-occurs with its presumed fruits, *Palaeocarpinus aspinosa* (Manchester and Chen, 1996), as in our assemblage (Tables 2, 5); (2) three taxa that are characteristically abundant in the lower PCZ are uncommon or extinct in the upper PCZ. Two are definitely not present in our study area: "*Viburnum*" *asperum* Newberry, and "*Viburnum*" *cupanioides* (Newberry) Brown. The third, "*Viburnum*" *antiquum* (Newberry) Hollick appears to be absent, although the morphotype FW40 is possibly a variant form of this taxon (Table 2). All three "Viburnums" have long pre-Clarkforkian Paleocene ranges throughout the Rocky Mountains and Great Plains (Brown, 1962; Hickey, 1980), including the Fort Union Formation of the Rock Springs Uplift (Brown, 1962; Gemmill and Johnson, 1997; Wilf, unpublished data).

Given the conflict between an early Clarkforkian faunal

age and floral composition similar to middle and late Clarkforkian floras of northern Wyoming, elements and abundance patterns of the local plant assemblage appear to be diachronous with those in northern Wyoming. This hypothesis needs to be tested with further study, but it is strongly supported by recent work in the Tiffanian of the nearby Great Divide Basin, where *Corylites* sp. is also overwhelmingly dominant and also co-occurs with *Palaeocarpinus aspinosa* (Manchester and Chen, 1996; Gemmill and Johnson, 1997). In addition, *P. aspinosa* is only known from the Fort Union Formation of the greater Green River and Bighorn basins of Wyoming, despite an extensive survey of Paleocene sites in the Rocky Mountains and Great Plains that yield *Palaeocarpinus* spp. by Manchester and Chen (1996). Therefore, the absence of *P. aspinosa* in the Tiffanian and early Clarkforkian of the Bighorn Basin is probably not a local biogeographic peculiarity of the Bighorn Basin among other basins north of our study area. This absence also seems unlikely to be an artifact of undersampling in the Bighorn Basin, where the megaflora has been heavily sampled and temporal hiatuses are rare throughout this time interval (Hickey, 1980; Wing et al., 1995). Finally, it is improbable that the lack of a pattern as obvious as *Corylites* dominance could be due to undersampling.

We suggest that the *P. aspinosa* tree, which dominated southern Wyoming floodplain forests in the Tiffanian and early Clarkforkian, spread to northern Wyoming in the early Clarkforkian, presumably in response to climatic warming, and dominated forests there in the middle and late Clarkforkian. This northward range extension of native flora stands in contrast to the more rapid and contemporaneous southward migration of exotic mammals, and possibly plants, that dispersed across high-latitude land bridges. Warming was also detrimental to long-lived taxa that were poorly adapted to these conditions. For example, the three "Viburnums" suffered decreases in abundance and then extinction, apparently in the warmer south before the cooler north.

PALEOENVIRONMENTAL AND PALEOCLIMATIC RECONSTRUCTION

Sedimentology and Depositional Environments

We interpret the coarsening-up sequences in our section (Fig. 3) as sequential overbank events associated with avulsion cycles of the local fluvial system. Each sequence records the increasing proximity of river channels and their subsequent avulsions onto low-lying, distal swamps. The swamps are represented by the carbonaceous shales and coals that occur at the bases of the sequences. Adjacent, vegetated areas of slight relief are represented by the rooted underclays. During coal and carbonaceous shale formation, distal areas were starved of sediment because of their distance from the main fluvial channels and the rarity of flood events capable of transporting sediment far out onto the floodplain. As channels migrated and relocated nearer to formerly distal areas, increasingly coarser grained and greater amounts of sediment were deposited there during flood events. This deposition is represented by the siltstones and fine sandstones of the middle parts of coarsening-up sequences. Finally, when channels avulsed

onto the lower parts of the floodplain, cross-bedded sandstones were deposited, which are observed at the upper parts of coarsening-up sequences. This system is similar to that described by Davies-Vollum (1996) and Davies-Vollum and Wing (1998) for deposits in the Bighorn Basin.

The lack of red beds and the predominantly drab colors of lithologies in the section indicate deposition under low-oxygen, probably waterlogged conditions that kept iron compounds in their reduced, gray-green colored state (e.g., Wilding and Rehage, 1985; Retallack, 1991). The orange coloration at the 1-m level is clearly secondary because it occurs preferentially at plant fossil layers and is due to infiltration of waters into the porous sandstone and redeposition of iron minerals. Natrojarosite, the yellow mineral that stains coal and carbonaceous shales, is secondary, occurring after pyrite (Bouma et al., 1990). Pyrite forms in slightly acidic, reduced conditions, and is also associated with waterlogging (Chague-Goff et al., 1996). The thin, featureless paleosols that occur as underclays below carbonaceous shales and coals are interpreted as periodically dry, hydromorphic soils of vegetated swamps that became permanently waterlogged at the onset of carbonaceous shale deposition (Atkinson, 1986; Davies-Vollum, 1996), similar to the wettest of the "simple paleosols" described by Kraus and Aslan (1993) from the Willwood Formation of the Bighorn Basin.

The presence of muscovite-rich sandstones is consistent with the interpretation of Kirschbaum et al. (1994) of south to southeast-flowing drainage on a nearly flat Paleocene floodplain. The drainage system flowed from the ancestral, crystalline Wind River Mountains to the north, the source for the muscovite. Volcanic activity is indicated by a laterally extensive, highly degraded ash deposit of unknown source near the base of the carbonaceous shale at the 18-m level (Fig. 3).

Although fossil plants and vertebrates are found in close stratigraphic proximity, they are not found in the same bed in any part of the section. This suggests that the two different kinds of fossils were preferentially preserved by different environmental or depositional conditions. The fossil mammal-bearing bed has a purple color, often associated with wet, oxygenated paleosols (Bown and Kraus, 1981). Oxidizing environments tend to degrade plant material and preclude fossilization. Conversely, the acidic conditions often associated with the reduced, swampy environments where plant fossils are typically preserved tend to destroy bone material before it can be fossilized. The two preservational regimes indicate variation in substrate chemistry, probably associated with changes in waterlogging that can be attributed to position on the floodplain relative to the main channel system.

Total organic carbon content for beds bearing vertebrates and plants varies between 3.8–8.6% (Table 1). Coarser-grained samples tend to have lower TOC, but higher TOC is not required for good preservation; many whole leaves came from the sandstone at the 1-m level, which has the lowest TOC studied, 3.8%. Influxes of relatively coarse sediment can "sandwich" layers of organic material, inhibiting the accumulation of organic mats but facilitating the preservation of individual, identifiable leaf fossils.

The drab color of all lithologies in our section, the dark color of coals, the hydromorphic nature of the paleosols,

and the absence of redbeds, differentiated soil horizons, and carbonate nodules all strongly indicate conditions that were moist year-round, without major seasonal variation in substrate moisture content and precipitation. Formation of paleosol carbonate nodules generally requires a moisture deficit, and the absence of such nodules implies soil saturation and a water table that was near the substrate surface with little seasonal fluctuation (Arkley, 1963; Sobecki and Wilding, 1982). Rooting in the underbeds, however, suggests that conditions were not so waterlogged as to inhibit plant colonization and growth. As the major topographic lows in the area at this time were further south, along the ancient Uinta Mountain Front (Kirschbaum et al. 1994), the coals in our section are not primarily tectonic but represent humid conditions.

Nearest Living Relatives and Functional Analogues

The presence of salamanders, turtles, a champsosaur, and alligatorid crocodilians at Big Multi Quarry implies relatively moist environmental conditions. The large-bodied and presumably piscivorous champsosaurs are consistent with fairly large bodies of standing water and/or medium-to-large streams and rivers (Bartels, 1983). This possibility is reinforced by the presence of the pantolestid mammal *Palaeosinopa.* Pantolestids have long been considered to have been semi-aquatic and otter-like in their adaptations (Matthew, 1909), a view that is strongly corroborated by functional analyses and fossilized gut contents of the middle Eocene European pantolestid *Buxolestes piscator* (Koenigswald, 1980; Pfretzschner, 1993). The occurrence of two species of alligatorids reflects warm and equable climatic conditions, "with coldest-month mean temperatures of $>7°C$, mean annual temperatures of $>16°C$, and mean annual temperature ranges of $<21.1°C$" (Markwick, 1994, p. 616).

The high species richness of basal Primatomorpha suggests the presence of forested, or at least woodland, conditions because most or all of these taxa were highly arboreal, and several of them show adaptations for gliding (Beard, 1990, 1991, 1993b). Other mammalian taxa that were likely to have been at least partly arboreal include the marsupial *Peradectes* (Szalay, 1994), the apatemyid *Labidolemur* (Koenigswald and Schierning, 1987), the arctocyonid condylarth *Chriacus* (Rose, 1987), and the rodent *Paramys* (Szalay, 1985).

The presence of palms and gingers strongly suggests frost-free conditions (e.g., Greenwood and Wing, 1995). All extant gingers are tropical, about 1300 species (Heywood, 1993). Palms are a widespread group of about 2800 species characterized, with only a handful of exceptions, by a profound physiological incapacity to withstand hard freezes (Sakai and Larcher, 1987; Heywood, 1993; Doughty et al., 1994; Greenwood and Wing, 1995). According to Greenwood and Wing (1995), palms are restricted to "climates with mean annual temperature $> 10°C$, cold month mean temperature $> 5°C$, and yearly minimum temperature $> -10°C$".

The nearest living relatives of some of the fossil plants are associated with continuously wet conditions, and none indicate dry environments. The most significant in this regard are the ferns and horsetails. These plants are characteristically found in moist areas because their life cycles
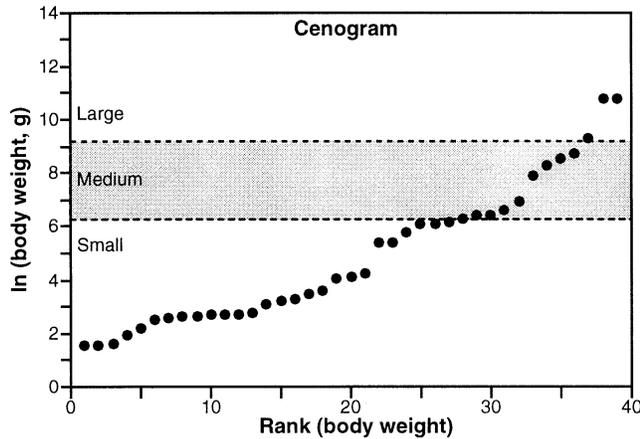
FIGURE 6—A cenogram for Big Multi Quarry. The gray area indicates the size range for medium-sized mammals, 0.5 kg to 10 kg. Vertical offset is calculated about the lower dashed horizontal line. Body weight data from Table 3. Slope of least squares regression line through data points for medium sized mammals is 0.35; vertical offset between data points on either side of the 0.5 kg threshold is 0.14.

include both free-living haploid generations, which are usually highly vulnerable to drying, and aqueous fertilization. Recent experimental work on horsetail spores has shown that their viability is irreparably compromised after only two weeks of desiccation (Lebkuecher, 1997). *Glyptostrobus* is probably another good indicator of damp to waterlogged environments, although its past distribution far exceeded its present range and could have once included better-drained environments (e.g., Wolfe, 1980).

Cenogram Analysis

A cenogram for Big Multi Quarry is presented in Figure 6. Alternative cenograms were constructed using different regression models for particular taxa, but these did not substantially affect paleoenvironmental interpretation. The slope of the least squares regression line through the cenogram points corresponding to medium-sized mammals (0.5–10 kg) has been related to environmental moisture, with many mammal species occupying the medium-size category (yielding lower slopes) in humid environments and fewer species occupying this size category (yielding higher slopes) in drier environments (Legendre, 1989; Gingerich, 1989; Gunnell, 1994, 1997; Gunnell and Bartels, 1994). The value obtained for this parameter for Big Multi Quarry is near the mean for modern faunas characterized as occurring in "subhumid" forests and savannas (Fig. 7A). Among other North American Paleocene assemblages, similar values for medium mammal slope have been documented at another Clarkforkian locality, SC-188 in the Clark's Fork Basin (Cf2), and at the Torrejonian Rock Bench Quarry, Bighorn Basin, by Gunnell (1994). In contrast, cenograms for Tiffanian localities analyzed by Gunnell (1994) uniformly yielded higher values for the medium mammal slope, suggesting drier conditions in the Tiffanian than in either the Torrejonian or the Clarkforkian.

The vertical offset between small and medium-sized mammals on a cenogram has been related to vegetational structure (Legendre, 1989; Gingerich, 1989; Gunnell,
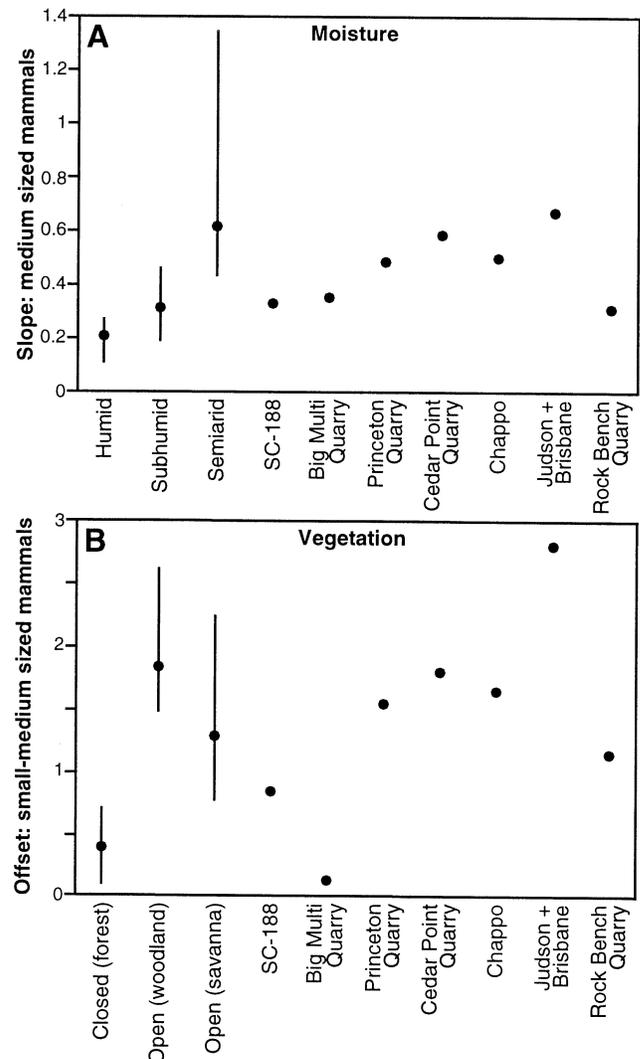

FIGURE 7—Paleoenvironmental results of cenogram analysis. (A) Variation in slope of the least squares regression line through cenogram data points for medium-sized mammals in Big Multi Quarry and selected fossil and extant faunas. This cenogram parameter is related to environmental moisture in extant mammal faunas. (B) Variation in values for the vertical offset between cenogram data points on either side of the 0.5-kg threshold for Big Multi Quarry and selected fossil and extant faunas. This cenogram parameter is related to vegetational regime in extant mammal faunas. Values for fossil faunas other than Big Multi Quarry are derived from Gunnell (1994); values for extant mammal faunas are derived from Gunnell and Bartels (1994), and references therein.

1994, 1997; Gunnell and Bartels, 1994). Many species traverse the gap separating small from medium-sized mammals in closed, forested settings, yielding smaller values for the vertical offset, while fewer species occupy this size range in more open vegetational settings, yielding higher values. Uniquely among North American Paleocene mammal assemblages analyzed to date, the cenogram for Big Multi Quarry shows a very small vertical offset, corresponding to closed forest conditions among modern mammal faunas (Fig. 7B). In contrast, cenograms for all other Paleocene mammal assemblages, including the Cf2 locality SC-188, yield much higher values for the vertical offset

(Gunnell, 1994). These values correspond to more open, woodland and/or savanna vegetational settings among modern faunas. Although Big Multi Quarry may actually sample a more closed, forested environment than do these other Paleocene mammal assemblages, we believe that an alternative possibility must also be considered: that the latter assemblages are relatively incomplete samples of the faunas from which they were derived. If this is the case, their vertical offsets are likely to be spuriously exaggerated in favor of "open" conditions. This line of reasoning is supported in the case of SC-188 by the previously discussed similarity in floral composition between the Big Multi plant assemblage and Cf2 floras of the Bighorn Basin.

Leaf Margin and Area Analysis

Leaf-margin analysis indicates mean annual temperatures approaching 20°C (Table 6). In comparison to the Bighorn Basin, this is warmer than leaf-margin temperatures near 13°C in Cf1 time and 16°C for Cf2 and Cf3 time (Wing et al., in press). This result is consistent with the more southerly location and also matches our floristic data that show late Clarkforkian floral elements of northern Wyoming to be present in southern Wyoming in the early Clarkforkian and before, suggesting that both a warmer climate and a thermophilic flora invaded northern Wyoming from the south during the Clarkforkian. Mean annual temperatures near 20°C, even in today's highly seasonal climate, are associated with winter temperatures far above freezing. Seasonal variation in temperature must have been present in the study area due to changes in light regime at middle latitudes, which may have been responsible for the inferred deciduous habit of some of the plants. However, frosts were rare and brief. Leaf-area analysis of the Big Multi plant assemblage yields estimated mean annual precipitation near 137 cm (Table 6).

Climatic Summary

The multiple lines of evidence presented above as well as Roehler's (1979) original paleoclimatic assessment are mutually consistent. The study area was a humid, subtropical, forested floodplain without significant frost or marked moisture deficits. Considerable emphasis has been placed on the exceptionally warm global conditions of the terminal Paleocene and early Eocene and on the enigma of warm continental interiors in the early Eocene (e.g., Sloan, 1994; Greenwood and Wing, 1995). Our data add to this enigma by documenting humid subtropical conditions in a continental area before the latest Paleocene thermal maximum. A plausible hypothesis for future study is that the climate of southern Wyoming was influenced by oceanic warmth that arrived via water vapor, possibly from a persistent Cannonball Sea (see Smith et al., 1994: Map 9).

ECOSYSTEM SYNTHESIS

The diverse fauna found at Big Multi Quarry lived on a humid subtropical floodplain with little relief, on which meandering streams and rivers flowed south across a flattened Rock Springs Uplift, carrying clay and muscovitic sand from the ancestral Wind River Mountains towards the Uinta Mountain Front and the Mississippi Embayment. Distal areas of the floodplain were occupied by sinking peat swamps, adjacent to periodically dry, forested soils. These swamps were filled in by overbank deposits from successive flood events as the main channel migrated closer, at first depositing clays and later increasing grain sizes until the channel itself occupied the site of the former swamp and deposited cross-bedded sand. The channel then migrated, allowing peat deposition at the start of a new fluvial cycle. The floodplain forest was frequently disturbed by this channel activity.

A single species of the birch family that presumably bore *Corylites* leaves and *Palaeocarpinus aspinosa* fruits was overwhelmingly dominant in all environments. *Glyptostrobus europaeus* was also common. The laurel family was well represented, and "*Ampelopsis*" *acerifolia, Cornus hyperborea,* and a cercidiphylloid dicot filled out much of the inferred phytomass. *Averrhoites affinis* and "*Cinnamomum*" *sezannense* were abundant in near-channel environments, while a variety of dicots as well as ferns and horsetails lived in the swampiest areas. Forest structure was homogeneous in comparison both to modern subtropical forests and to early Eocene forests in Wyoming (Davies-Vollum and Wing, 1998; Wilf, unpublished data).

These forested conditions supported a variety of arboreally adapted mammals. Taxonomically dominant among these were archaic relatives of living primates and flying lemurs, although squirrel-like rodents (*Paramys adamus*) and small arboreal marsupials (*Peradectes protinnominatus*) were also abundant. A species of hedgehog (*Leipsanolestes* n. sp.) was by far the most common mammal, although numerous additional species of tiny-to-small lipotyphlan insectivores occupied the forest floor. Mammalian herbivores of small-to-large size included hyopsodontid and phenacodontid condylarths, a tillodont, a pantodont, and a uintathere. The mammal assemblage also included an armadillo-like species (*Palaeanodon* sp., cf. *P. parvulus*), an otter-like form (*Palaeosinopa*), two species of carnivorans, and four species of multituberculates. Additional biota in the area included reptiles, amphibians, insects, and pulmonate gastropods.

CONCLUSIONS

Big Multi Quarry is the most diverse fossil vertebrate locality yet known from the Clarkforkian Land Mammal Age. The mammalian fauna can be correlated with early, but not earliest, Clarkforkian faunas of the Bighorn Basin, about 350 km to the north. The closely associated flora includes nearly all of the fossil plant species known from coeval rocks in the region. Floristic composition and abundance patterns better match middle and late than early Clarkforkian floras of northern Wyoming, suggesting a scenario of northward floral migration in step with the overall Clarkforkian warming trend. The well-exposed local section has also yielded reptiles, amphibians, gastropods, and insect feeding traces. These fossil organisms represent a forested floodplain ecosystem in a humid subtropical climate that existed before the latest Paleocene thermal maximum. Mean annual temperature was near 20°C and mean annual precipitation near 137 cm, with limited or no seasonal frost or marked dry season. Such warm and moist conditions are associated in the early Eo-

cene and today with moderately high plant species richness, mixed dominance, and spatial heterogeneity. However, plant communities in our study area were not species-rich, were strongly dominated by a single species, and were spatially homogeneous. These ecological conditions were typical of the cooler earlier Paleocene. Thus, the "temperate" ecology of Paleocene basin forests made its last stand in the area in the Clarkforkian as the earth warmed, mammalian diversity increased, and thermophilic plant taxa arrived. This scenario may have implications for understanding the resistance of modern temperate forests to perturbation by global warming.

Reconstructions of ancient environments are greatly strengthened by considering as wide a variety of evidence as possible. The uncertainties involved in the application of any single method are substantial, and analysis based on a preponderance of evidence from more than one methodology, applied at more than one spatial scale, greatly reduces the probability of incorrect conclusions and broadens interpretation.

ACKNOWLEDGMENTS

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