OVERVIEW OF MAMMALIAN BIOSTRATIGRAPHY IN THE PALEOCENE-EOCENE FORT UNION AND WILLWOOD FORMATIONS OF THE BIGHORN AND CLARKS FORK BASINS

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Abstract. — Some 2200 fossil vertebrate localities are known from the Paleocene Fort Union Formation and from the Paleocene and lower Eocene Willwood Formation of the Bighorn and Clarks Fork basins in northwestern Wyoming. Many localities yield faunas adequate to enable reference to one of the twenty distinct land-mammal zones representing the Puercan, Torrejonian, Tiffanian, Clarkforkian, and Wasatchian land-mammal ages spanning Paleocene and early Eocene time here. These are grouped biostratigraphically and plotted on a map of the two basins combined. Range charts of mammalian genera are compared for (1) the Polecat Bench–Sand Coulee area in the Clarks Fork and northern Bighorn basins, (2) the Foster Gulch–McCullough Peaks area in the northern Bighorn Basin, (3) the central Bighorn Basin, and (4) the southern Bighorn Basin. These show that mammalian biostratigraphy is similar in all four areas, with parts of the stratigraphic record being better developed in some areas than in others. The Paleocene and earliest Eocene are best known from the Clarks Fork Basin and from the northern Bighorn Basin, whereas middle and late early Eocene faunas are principally known from the west side of the northern and central parts of the Bighorn Basin. East-west asymmetry in the distribution of mammalian faunas reflects overthrusting from the west as strata and their contained fossil faunas accumulated and were buried.

INTRODUCTION

The Bighorn and Clarks Fork basins of northwestern Wyoming, drained by the Bighorn and Clarks Fork rivers, respectively (Fig. 1), are distinct parts of a single foreland depositional basin that accumulated continental sedimentary rocks during uplift of the Rocky Mountains. These basins preserve a thick sequence of continental sedimentary rocks representing Paleocene and early Eocene time. Two formations of particular interest, the Fort Union and Willwood formations, together rest conformably or unconformably on marine to continental upper Cretaceous strata. The highest of the Cretaceous strata belong to the dinosaur-bearing Lance Formation of latest Cretaceous age.

The first formation of interest here, the Fort Union Formation (*Tfu* in Fig. 1), is as much as 1700 m thick in places. It consists of thin-bedded, light-colored fluvial sandstones and conglomerates, with drab to olive-brown shales, carbonaceous shales, and thin beds of lignite and coal. Paleosols are generally hydromorphic and yellow to orange in color. Carbonates are present as thin, laterally-persistent, orange to brown marl or limestone bands. The Fort Union Formation is Paleocene in age and yields a vertebrate fauna dominated by champsosaurs, turtles, crocodilians, and mammals.

The second formation of interest, the Willwood Formation (*Twl* in Fig. 1), can be as much as 1400 m thick. It consists of immature fluvial sandstones and sometimes conglomerates, and conspicuously-varicolored mudstones. Paleosols are highly

In: Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming (P. D. Gingerich, ed.), *University of Michigan Papers on Paleontology,* 33: 1-14 (2001).

oxidized and often bright orange, red, and purple in color. Carbonates are generally present as dispersed nodules that formed within ancient soils. Carbonaceous shales are relatively rare. The Willwood Formation is predominantly Eocene in age and yields a vertebrate fauna dominated by turtles, crocodilians, and mammals.

The Tatman Formation (*Tta* in Fig. 1) overlying the Fort Union and Willwood formations is a relatively thin lacustrine unit of brown, papery, carbonaceous and calcareous shales interbedded with drab clays and sandstones. Vertebrate fossils are rare, and the Tatman Formation is mentioned here because it covers a substantial area of Willwood Formation along the southwestern margin of the Bighorn Basin. The Tatman Formation is considered early-to-middle Eocene in age.

The Fort Union and Willwood formations together provide evidence of a single major Laramide orogenic cycle. During this cycle there was a subtle change in the balance between basin subsidence and sediment accumulation. Initially, during deposition of the Fort Union Formation, subsidence exceeded accumulation, the water table was generally at or above the land surface, the environment was largely forested and wet, and great masses of vegetation were buried. Later, during deposition of the Willwood Formation, accumulation exceeded subsidence, the land surface was generally higher than the water table, the environment was more open and dryer, and much less organic material was buried.

Cycles are present on finer scales as well. There is always a tectonically-controlled 'allocyclic' component causing some parts of a basin to subside faster, and hence accumulate sediment faster, than others. The axis, for example, generally subsides faster than a basin margin, and hiatuses in sediment accumulation are more likely to be found on basin margins. There is also a more stochastic 'autocyclic' component that controls architecture on a finer scale (documented in the Fort Union by Gingerich, 1969, and in the Willwood by Neasham and Vondra, 1972, and Bown, 1979). Sediment accumulation in an orogenic setting like the Bighorn and Clarks Fork basins often involves a geometry of bounded wedges and fans rather than simple parallel layering.

The Fort Union and Willwood formations of the Bighorn and Clarks Fork basins have long been known for their mammalian fossils, which are relatively common in thick sequences of superposed strata that can be traced and examined in badland outcrops extending for kilometers with little interruption. These fossils are interesting because they enable evolutionary lineages to be traced through time in unusual detail, and they document episodes of biotic change, sometimes abrupt, that appear to require explanation in terms of broader environmental change. Mammals are particularly useful for evolutionary studies, for study of biotic and environmental change, and for constraining depositional history. This is because mammals evolved rapidly, their teeth and bones preserve well in the fossil record and are informative about the mammals they represent, and mammalian fossils generally have been more intensively studied than other fossil remains.

Study of mammalian fossils in stratigraphic context means that episodes of faunal change affecting mammals can be related directly to change in other vertebrates, invertebrates, and plants preserved in the same strata. Change affecting mammals can also be related directly to environmental proxies such as stable isotopes of carbon and oxygen. Further, change affecting any of these systems can be constrained in time by interpolation between paleomagnetic polarity reversal events recorded in the strata themselves. In some cases, as at the Paleocene-Eocene boundary where artiodactyls, perissodactyls, and modern primates first appear, faunal change can now be explained in terms of oceanic and atmospheric events altering climate and favoring biogeographic dispersal (see, e.g., Bowen et al., this volume). Finally, it is worth mentioning that the geographic and stratigraphic distribution of faunas in the Bighorn and Clarks Fork basins is the principal evidence we have for interpreting the depositional history and hence the timing of tectonic deformation during development of the combined basins.

The purpose of this contribution is to provide an overview of the geographic distribution of some 2200 known Bighorn and Clarks Fork basin fossil mammal localities (Fig. 1), and to provide an overview of the stratigraphic distribution of mammalian faunas of different ages (Figs. 2-5).

DEVELOPMENT OF A MAMMALIAN BIOSTRATIGRAPHY

The Western Interior basins of North America are rich in late Mesozoic (latest Cretaceous) and early Cenozoic (Paleocene and Eocene) vertebrate fossils. The animals that these fossils represent lived, died, and were buried during the Laramide Orogeny, when the Rocky Mountains were uplifted and thick wedges of fresh sediment accumulated in intervening depositional basins. Explorers in the middle nineteenth century (principally F. V. Hayden) recognized a Laramie formation or series of strata thought to be late Cretaceous in age, a Wasatch Formation thought to be early Eocene, an intermediate Wind River Formation, and a higher Bridger Formation thought to be middle Eocene. There was at the time no intervening Paleocene epoch.

Wortman, Fisher, and Loomis

The first search for vertebrate fossils in the Bighorn Basin was carried out by J. L. Wortman in 1880 and 1881, who was employed privately by E. D. Cope. Wortman entered the Bighorn Basin from the south, from Fort Washakie in the Wind River Basin, and found it to yield abundant fossil mammals. The fossils were described by Cope (1880, 1882). These were found in 'Wasatch beds' characterized by the preponderance of red clay and containing 'small limestone nodules of a rusty

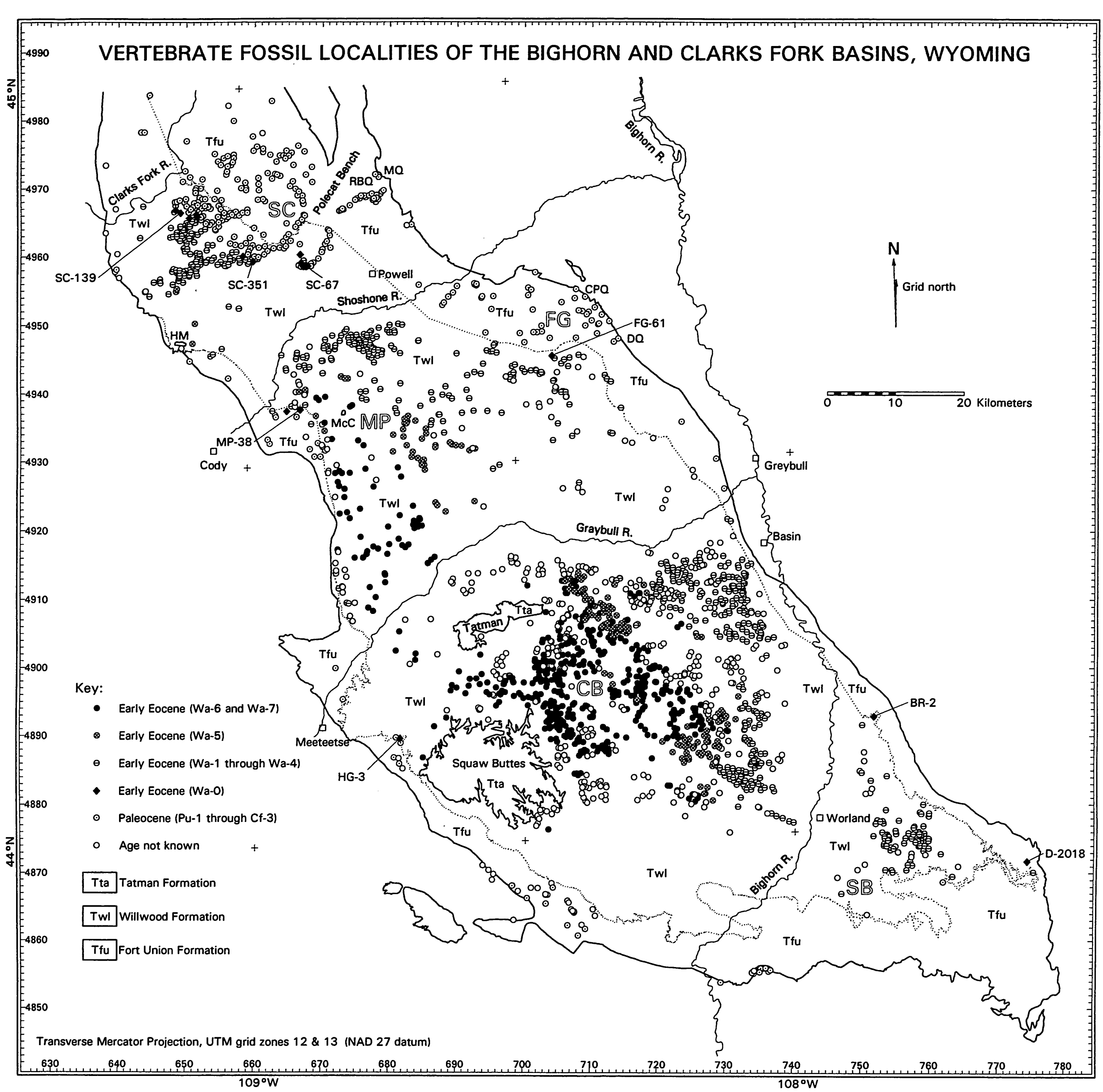

FIGURE 1 — Map of the Bighorn and Clarks Fork basins in northwestern Wyoming showing the distribution of 2224 Paleocene and lower Eocene vertebrate fossil localities in relation to principal rivers and geological formations. Four regions discussed separately here are: (1) the Polecat Bench–Sand Coulee (*SC*) area in the Clarks Fork and northern Bighorn basins, north of the Shoshone River; (2) the Foster Gulch (*FG*)–McCullough Peaks (*MP*) area in the northern Bighorn Basin south of the Shoshone River and north of the Graybull River; (3) the central Bighorn Basin (*CB*) south of the Graybull River and north and west of the Bighorn River; and (4) the southern Bighorn Basin (*SB*) east of the Bighorn River. Heart Mountain (*HM*) and McCullough Peaks (*McC*) are peaks supported by allochthonous detached blocks of Paleozoic limestone that reached their present positions on top of the Willwood Formation by gravity-sliding. Fossil localities are from Bown (1979), Rose (1981), Gingerich and Klitz (1985), Hartman (1986), Leite (1992), and Bown et al. (1994a), Clyde (1997, this volume), Strait (this volume). Geology is from Love et al. (1978a,b, 1979) and Pierce (1997).

brown appearance'(Wortman, 1882). The perissodactyl *Lambdotherium* was not found in the Bighorn Basin, and this absence was considered an important distinction from the fauna of the Wind River Formation.

A second field investigation of the Bighorn Basin was carried out by Wortman in 1891, now working for the American Museum of Natural History. This time Wortman entered the Bighorn Basin from the north, from the then-new railhead at Red Lodge. He traversed the Clarks Fork Basin, where he was the first to establish the presence of Wasatchian mammals, and followed the old Bridger Trail on his way to Wasatch exposures south of the Graybull River. The new fossils were described by Osborn (1892) and by Wortman (e.g., 1896). Wortman (1892) concluded: (1) that Puerco and Laramie strata (Paleocene and latest Cretaceous) are absent and do not underlie the Bighorn Wasatch, which lies on older Mesozoic rocks; and (2) that Wind River beds in the Wind River Basin are distinct from those of the Bighorn Wasatch, and were deposited in a later-filling lake.

A third phase of field work in the Bighorn and Clarks Fork basins started in 1904 when C. A. Fisher of the U. S. Geological Survey and F. B. Loomis of Amherst College initiated independent investigations. Fisher's work was carried out in connection with construction of the Buffalo Bill Dam on the Shoshone River and development of the then new Shoshone Irrigation District. Fisher (1906) mapped what we today call Paleocene strata as part of his Cretaceous 'Laramie and succeeding formations' (p. 31), representing 'possibly in its upper portions the Fort Union beds' (p. 32). Absence of distinctive fossils was cited as a cause for some uncertainty about age. Fisher mapped extensive deposits of 'Wasatch Formation' that were already well known to be Wasatch or early Eocene in age. Both Fisher and Loomis concluded that the Wasatch deposits of the Bighorn Basin were fluvial because of : (1) association with erosional truncation of underlying formations around the basin margin (Fisher, 1906, p. 42); (2) the dominance of terrestrial rather than aquatic vertebrates found in them (Loomis, 1907, p. 358); and (3) an abundance of lenticular bedforms, poor sorting, and red color indicating subareal oxidation (Loomis, 1907, p. 361).

Loomis (1907) published the first detailed stratigraphic section of Wasatch deposits in the Bighorn Basin, starting from the Owl Creek Mountains near Meeteetse in the west and carrying the section northward and eastward through the Buffalo Basin area to reach the top of Tatman Mountain, covering a distance of some 27 km. He worked from a camp near the head of Fifteen Mile Creek, possibly in or near Hole-in-the-Ground (e.g., HG-3 on the map in Fig. 1), which was presumably on or near his line of section. Loomis found that the mammalian fauna in the Buffalo Basin area lacked the perissodactyl *Homogalax* ('*Systemodon*') characteristic of the Wasatch fauna, but included the perissodactyls *Heptodon* and *Lambdotherium* characteristic of the Wind River fauna. Thus he concluded that both faunas, Wasatch and Wind River, are present, one above the other, in the Bighorn Basin.

Sinclair and Granger

The reports on the Bighorn Basin by Fisher and Loomis inspired three extended collecting trips in 1910-1912 led by W. J. Sinclair of Princeton University and W. Granger of the American Museum of Natural History. There was also a followup trip in 1913 when neither leader was present. Sinclair and Granger's first field work focused on Loomis' results, and then took advantage of Fisher's geological map to trace beds of interest around the margin of the Bighorn Basin. In their first report, Sinclair and Granger (1911) subdivided the Bighorn 'Wasatch' into three faunal intervals (numbered 1, 2, and 3), and specified that the *Lambdotherium* beds of the Bighorn 'Wind River' formation might include both faunal intervals represented in the Wind River Basin (named Lysite and Lost Cabin, respectively; the latter, with *Lambdotherium*, was known to be present).

After their second season of field work, Sinclair and Granger (1912) changed the name of the 'Wasatch' beds in the Bighorn Basin to 'Knight' formation, and described a new 'Ralston' fauna from the top of the Fort Union Formation. They confirmed the presence of a distinct Lysite fauna with *Heptodon* but lacking *Homogalax* ('*Systemodon*') and *Lambdotherium*, and they proposed a new Tatman Formation younger than the Bighorn 'Wind River' formations.

Granger (1914) revised stratigraphic nomenclature still further. 'Ralston' was found to have been used elsewhere, and Granger proposed calling these Clark Fork beds, with the Clark Fork fauna being characterized by the predominance of phenacodontid condylarths and an absence of perissodactyls, artiodactyls, rodents, and primates (rodents were later found in these beds). Discovery of *Heptodon* in the type area of the Knight Formation in southwestern Wyoming required that a new name be given to the Bighorn 'Knight' beds, and Granger proposed that these be called Gray Bull beds. Lower, middle, and upper Gray Bull thus replaced Knight faunas 1, 2, and 3. Finally, the name Sand Coulee beds was proposed for an interval of red-banded shales above the Clark Fork beds and below the Gray Bull beds that yield the perissodactyl *Hyracotherium* ('*Eohippus*') but lack *Homogalax* ('*Systemodon*'). Granger (1914, p. 207) assigned the Clark Fork beds to the Paleocene, and Sand Coulee and higher beds to the Eocene. (The earliest references we can find using *Paleocene* for the 'basal Eocene' of Osborn (1910) and others are by Sinclair (1912) and Scott (1913).)

Thus at the end of their effort, Sinclair and Granger recognized the following sequence of mammalian faunas and 'formations' in the Bighorn Basin: (1) a Clark Fork fauna, faunal zone, and 'formation,' lacking perissodactyls, and 'perhaps representing the top of the Paleocene Series' (Granger, 1914, p. 204); (2) a Sand Coulee fauna, faunal zone, and 'formation,' with *Hyracotherium* ('*Eohippus*') but lacking *Homogalax* ('*Systemodon*'), representing the lowest interval in the lower Eocene; (3) lower, middle, and upper faunas from the Gray Bull faunal zone and 'formation,' with both *Hyracotherium* ('*Eohippus*') and *Homogalax* ('*Systemodon*'); (4) a Lysite fauna, faunal zone, and 'formation,' with *Hyracotherium* ('*Eohippus*') and *Heptodon*, but lacking *Homogalax* ('*Systemodon*') and *Lambdotherium*; (5) a Lost Cabin fauna, faunal zone, and 'formation,' with *Hyracotherium* ('*Eohippus*'), *Heptodon*, and *Lambdotherium*, but again lacking *Homogalax* ('*Systemodon*'); and finally (6) a Tatman 'formation' with scraps of bone and with invertebrates suggesting a Bridger middle Eocene age. Sinclair and Granger recognized a sequence of Clark Fork, Sand Coulee, and Graybull faunas, with no Lysite or Lost Cabin fauna, in the Clarks Fork Basin; while all five mammalian faunas were thought to be present in the Bighorn Basin when the northern and central parts are considered together.

Sinclair and Jepsen

W. J. Sinclair of Princeton University started field work in Gray Bull beds of the central Bighorn Basin again in 1927, accompanied this time by graduate student G. L. Jepsen. A new Paleocene fauna had just been discovered from the Fort Union Formation of Bear Creek in southern Montana (Simpson, 1928, 1929a,b), and it is not surprising that in 1928 Jepsen moved northward from the central Bighorn Basin toward Bear Creek and started to investigate the Fort Union Formation on Polecat Bench. There he found the proprimate *Plesiadapis* and pantodont *Titanoides*, both characteristic of Paleocene faunas.

Jepsen returned to the Bighorn and Clarks Fork basins in 1929, when he found: (1) the type specimen of *Plesiadapis cookei*, which became an important index fossil for the Clarkforkian land-mammal age (latest Paleocene); (2) Princeton Quarry of Tiffanian age (late Paleocene); (3) Rock Bench Quarry of Torrejonian age (middle Paleocene); and (4) Mantua Quarry of Puercan age (early Paleocene)— all in one superposed Polecat Bench–Sand Coulee sequence of strata (Jepsen, 1930, 1940; Gingerich, this volume). Jepsen was a member of the Wood committee on nomenclature and correlation of North American faunas (Wood et al., 1941), and Puercan, Torrejonian, Tiffanian, Clarkforkian, and Wasatchian are the names given to North American provincial land-mammal ages (see Archibald et al., 1987, and Krishtalka et al., 1987, for updates).

Jepsen carried on research in the Bighorn and Clarks Fork basins virtually every year from 1930 until he died in 1974. Many students were trained in the process, and Princeton collections formed the backbone of theses on Paleocene and early Eocene mammals published by Van Houten (1944, 1945), Simons (1960), Wood (1967), Gingerich (1975, 1976b), Rose (1975, 1981), Krause (1980, 1982), Gunnell (1989), and Thewissen (1990).

The Van Houten (1944) paper deserves special mention because this is where the 'Bighorn Wasatch' of earlier authors was described in detail, and the name 'Wasatch' here replaced by Willwood Formation. Willwood is a small agricultural settlement at the northern edge of the McCullough Peaks badlands in the northern Bighorn Basin, making this de facto the type area of the formation.

Simons, Radinsky, and Ongoing Investigations

E. L. Simons and L. Radinsky of Yale University initiated the present phase of detailed mammalian biostratigraphy in the Bighorn and Clarks Fork basins. The two worked together in Wyoming for Jepsen and Princeton University in 1960, and then initiated the first of a long series of Yale University expeditions to the central Bighorn Basin in 1961. These were carried forward by Simons. The objectives initially were clarification of the temporal successions of Wasatchian species of *Coryphodon* as an extension of Simons' dissertation research on pantodonts, and the temporal succession of the tapiroids *Homogalax* and *Heptodon*, as part of Radinsky's dissertation. Radinsky measured a stratigraphic section documenting a 15 m zone of overlap of *Homogalax* and *Heptodon* (Radinsky, 1963, p. 77) at the base of the Lysitean. Extension of the Radinsky stratigraphic section by G. E. Meyer formed the basis for later evolutionary analyses of *Hyopsodus*, *Cantius* ('*Pelycodus*'), and *Haplomylus* (Gingerich, 1974, 1976a; Gingerich and Simons, 1977).

During the 1960s two other stratigraphic projects were active in the Willwood Formation of the central Bighorn Basin. The first, by Rohrer and Gazin on the Willwood Formation of Tatman Mountain, led to publication of two geological maps (Rohrer (1964a,b) and a brief text (Rohrer and Gazin, 1965). The second, by Neasham and Vondra (1971), is important in demonstrating that red beds in the Willwood Formation are due to soil formation on the higher and better drained parts of alluvial floodplains.

The Bighorn and Clarks Fork basins have been sites of active paleontological investigation from the 1970s to the present, with many of the investigators being students of Simons (or now second- and third-generation students of Simons). Notable theses and publications contributing to our understanding of mammalian biostratigraphy include Gingerich (1975, 1976b, 1982, 1983, 1989, 1991, 2000, this volume), Bown (1979), Schankler (1980, 1981), Rose (1981), Winkler (1983), Hartman (1986), Badgley and Gingerich (1988), Badgley (1990), Leite (1992), Bown et al. (1994a), Gunnell (1998), Clyde (this volume), and Strait (this volume). Results are summarized in the following charts (Figs. 2-5), where Tiffanian land-mammal age zones are abbreviated Ti-1 through Ti-6, Clarkforkian zones are abbreviated Cf-1 through Cf-3, and Wasatchian zones are abbreviated Wa-0 through Wa-7 (following Gingerich, 1983, 1989, 1991, and this volume). In the Wasatchian, Wa-0 through Wa-2 correspond to Granger's Sandcouleean subage, Wa-3 through Wa-5 correspond to Granger's Graybullian subage, Wa-6 is equivalent to Sinclair and Granger's Lysitean subage, and Wa-7 is equivalent to Sinclair and Granger's Lostcabinian subage.

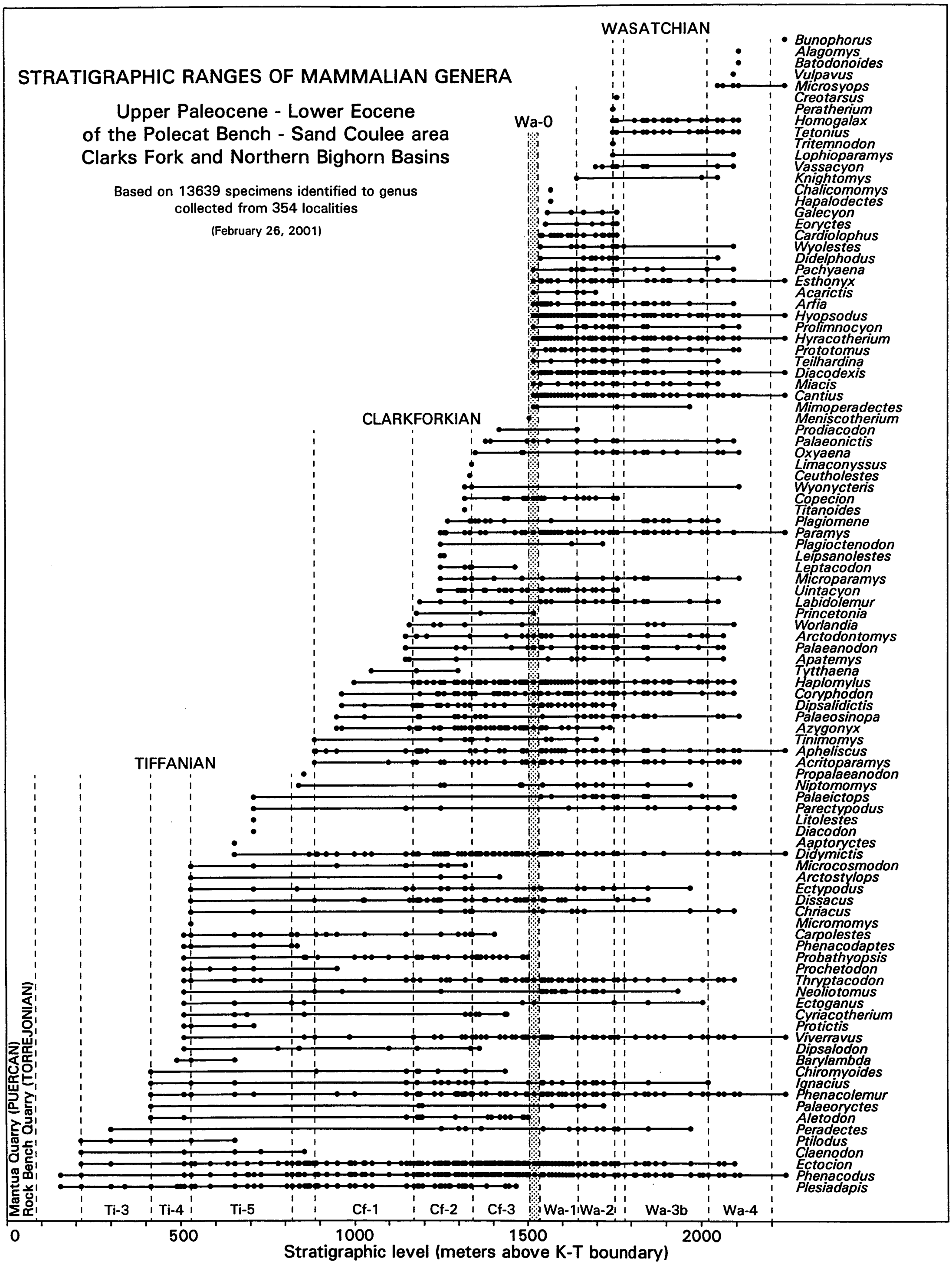

FIGURE 2 — Stratigraphic ranges of late Paleocene and early Eocene mammalian genera in the Polecat Bench–Sand Coulee area of the Clarks Fork and northern Bighorn basins. Dashed lines separate zones of the Tiffanian, Clarkforkian, and Wasatchian land-mammal ages (labeled Ti-3, etc., at the bottom of the chart). Stippled column is Wa-0. Chart is based on a University of Michigan database of stratigraphic occurrences maintained by the senior author.

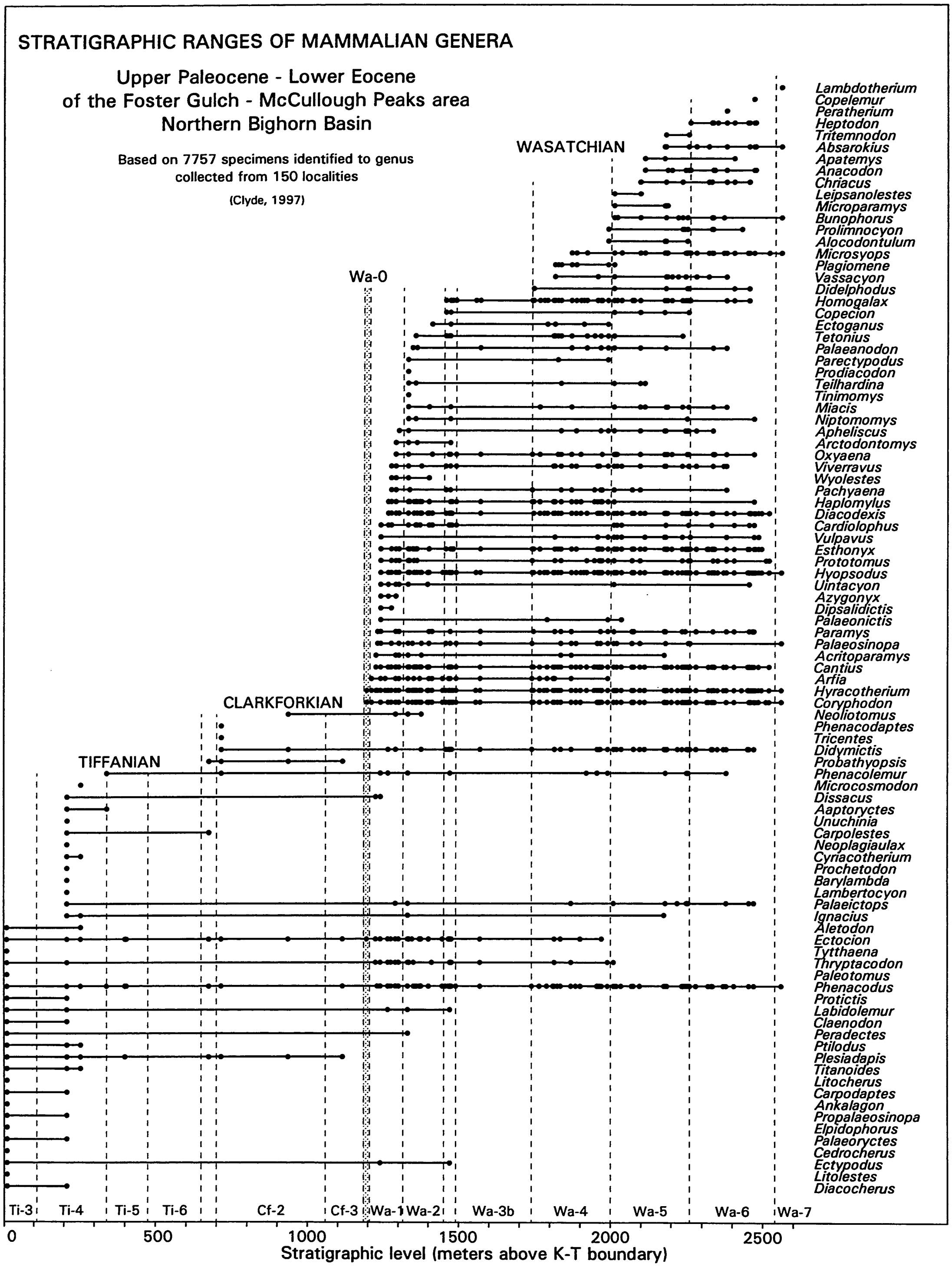

FIGURE 3 — Stratigraphic ranges of late Paleocene and early Eocene mammalian genera in the Foster Gulch–McCullough Peaks area of the northern Bighorn Basin. Dashed lines separate zones of the Tiffanian, Clarkforkian, and Wasatchian land-mammal ages (labeled Ti-3, etc., at the bottom of the chart). Stippled column is Wa-0. Chart is based on the Southeast McCullough Peaks composite stratigraphic section of Clyde (1997, this volume), fossil identifications of Clyde (1997), and the University of Michigan database of stratigraphic occurrences maintained by the senior author.

STRATIGRAPHIC DISTRIBUTION OF PALEOCENE–EOCENE MAMMALS

The combined Clarks Fork and Bighorn basins can be divided into four geographical regions: (1) the Polecat Bench–Sand Coulee area in the Clarks Fork and northern Bighorn Basin north of the Shoshone River (*SC* in Fig. 1); (2) the Foster Gulch–McCullough Peaks area in the northern Bighorn Basin south of the Shoshone River and north of the Graybull River (*FG* and *MP* in Fig. 1); (3) the entire central Bighorn Basin south of the Graybull River and north of the Bighorn River (*CB* in Fig. 1); and (4) the southern Bighorn Basin south and east of the Bighorn River (*SB* in Fig. 1). Each of these regions has yielded an important sequence of mammalian faunas, which are discussed in turn.

Polecat Bench–Sand Coulee Area

The most complete sequence of mammal-bearing Paleocene strata is on Polecat Bench, starting with the Mantua and Rock Bench quarries (Puercan and Torrejonian, respectively; *MQ* and *RBQ* in Fig. 1) discovered and described by Jepsen (1930, 1940). Both are in the lower 60 m of the Fort Union Formation on Polecat Bench (Gingerich, this volume). The remainder of the Polecat Bench–Sand Coulee stratigraphic section, from 150 m to 2240 m, yields Tiffanian to Clarkforkian faunas from the Fort Union Formation, and Clarkforkian to middle Wasatchian faunas from the Fort Union and Willwood formations (the formational boundary here is lower than the Clarkforkian-Wasatchian boundary). A range chart of Tiffanian, Clarkforkian, and Wasatchian genera is shown in Figure 2, based on the University of Michigan database of stratigraphic occurrences maintained by the senior author.

The Tiffanian land-mammal age starts with the appearance of *Plesiadapis* and *Phenacodus*. Tiffanian zones Ti-3 through Ti-6 are well represented in the Polecat Bench–Sand Coulee section, with each being recognized by the presence of distinctive species of *Plesiadapis* (Gingerich, 1975, 1976b, this volume). A new study of all Tiffanian localities in the Clarks Fork and northern Bighorn basins is underway (Secord, in prep.), and a clearer understanding of faunal change through the Tiffanian, and from the late Tiffanian into the early Clarkforkian, will soon be forthcoming.

The Clarkforkian land-mammal age starts with appearance of the first Rodentia (here *Acritoparamys*), which are presently known from as low as the 885 m level. *Apheliscus*, *Azygonyx*, *Coryphodon*, and *Haplomylus* appear at or near the beginning of the Clarkforkian as well. Clarkforkian zones Cf-1 through Cf-3 correspond to the early, middle, and late Clarkforkian of Rose (1981; see also Gingerich, this volume), with the first two again being characterized by the presence of distinctive species of *Plesiadapis*.

The Wasatchian land-mammal age starts with the first appearance of Perissodactyla (here *Hyracotherium* in zone Wa-0; Granger, 1914; Gingerich, 1989, this volume). *Diacodexis* representing Artiodactyla, *Cantius* and *Teilhardina* representing Primates, and *Prototomus* and *Prolimnocyon* representing hyaenodontid Creodonta appear at this time as well. Wasatchian zones Wa-0, Wa-1, and Wa-2 with *Hyracotherium* correspond to the Sandcouleean subage of Granger (1914); while zones Wa-3, Wa-4, and Wa-5 with *Homogalax* correspond to the Graybullian subage of Granger (1914). Wasatchian zones Wa-6 and Wa-7 are missing at the top of the Polecat Bench–Sand Coulee section in the Clarks Fork and northern Bighorn basins.

Foster Gulch–McCullough Peaks Area

The Foster Gulch–McCullough Peaks stratigraphic section is different from the Polecat Bench–Sand Coulee section because 34 km southeast of Mantua Quarry there is no Puercan, Torrejonian, or early Tiffanian at the base of the Fort Union section. Instead zone Ti-3, represented by Cedar Point Quarry 10 m above the base (*CPQ* in Fig. 1), rests disconformably on the upper Cretaceous Lance Formation. Ten km farther to the southeast zone Ti-4, represented by Divide Quarry a few meters above the base (at the 210 m level; *DQ* in Fig. 1), rests disconformably on the Lance Formation. Some 300 m of stratigraphic thickness and about 6 m.y. of geological time have been lost in moving 34 km along strike from Mantua Quarry to Cedar Point Quarry. An additional ca. 200 m of stratigraphic thickness and as much as 1 m.y. more of geological time have been lost in moving the additional 7 km southeast from Cedar Point to Divide Quarry. The Fort Union Formation clearly laps unconformably onto the Lance Formation along the eastern margin of the Bighorn Basin (Gingerich, 1983), showing how an uplifted basin margin bounded Fort Union fans during deposition.

The remainder of the Foster Gulch–McCullough Peaks stratigraphic section, from 210 m to 2560 m, yields Tiffanian and Clarkforkian faunas from the Fort Union Formation, and early-to-late Wasatchian faunas from the Willwood Formation (the formational boundary here coincides with the Clarkforkian-Wasatchian boundary). A range chart of genera is shown in Figure 3, based on the Southeast McCullough Peaks composite stratigraphic section of Clyde (1997, this volume), fossil identifications by Clyde (1997), and the University of Michigan database of stratigraphic occurrences maintained by the senior author.

The lowest zone of the Tiffanian land-mammal age is Ti-3, represented by Cedar Point Quarry, as mentioned above. Cedar Point Quarry has yielded a large mammalian fauna (summarized in Rose, 1981, with additions in Fig. 3 based on later publications). Similarly, Ti-4, represented by Divide Quarry, has yielded a large mammalian fauna (under study by R. Secord). The highest Tiffanian fauna here comes from the 405 m level. There are not as many Tiffanian localities or collecting levels in the McCullough Peaks area, nor is the Ti-3 through Ti-6 thickness as great (ca. 400-500 m vs. ca. 800 m), but the

Tiffanian in the McCullough Peaks area has yielded about the same number of genera as that in the Polecat Bench–Sand Coulee section.

The Clarkforkian land-mammal age starts at the 675 m level in the McCullough Peaks area and continues up to the 1115 m level, which is the highest level yielding *Plesiadapis* here. The Clarkforkian here is about the same thickness (ca. 500-600 m) as it is in the Polecat Bench–Sand Coulee section, but there are many fewer collecting levels and many fewer genera known. The difference is probably due to a difference in depositional environment, directly or indirectly, as there are many fewer sandstones and consequently relatively poor and less productive exposures.

The Wasatchian land-mammal age starts at the 1195 m level and continues to the 2560 m level. Wa-0 is represented by one locality at 1195 m that yields *Hyracotherium sandrae* and *Ectocion parvus* characteristic of the zone. *Homogalax protapirinus* marking the beginning of zone Wa-3 and the beginning of the Graybullian subage comes in at 1455 m, *Bunophorus etsagicus* marking the beginning of zone Wa-5 comes in at 2010 m, *Heptodon calciculus* marking the beginning of zone Wa-6 and the Lysitean subage comes in at 2260 m, and *Lambdotherium popoagicum* marking the beginning of Wa-7 and the Lostcabinian subage is known from one level at 2560 m above the base of the Foster Gulch–McCullough Peaks section. The Sandcouleean subage here (Wa-0 through Wa-2) is ca. 260 m thick, while the early and middle Gray-bullian subage (Wa-3 through Wa-4) is ca. 555 m thick. These thicknesses are about 25% greater than thicknesses for the same intervals in the Polecat Bench–Sand Coulee section (ca. 210 m and 450 m, respectively).

Central Bighorn Basin

The central Bighorn Basin has Torrejonian, Tiffanian, and Clarkforkian mammal localities, but these are all on the west side of the basin (Leite, 1992; Gingerich, unpublished), separated from late Wasatchian strata by a major disconformity (and in places a distinctly angular unconformity; e.g., Van Houten, 1944, pl. 3, fig. 1). The major stratigraphic sections incorporating mammals all start at the base of the Willwood Formation on the east side of the basin (e.g., those of Meyer and Radinsky, unpublished; Schankler and Wing in Schankler, 1980; and Bown et al., 1994a). There is a narrow band of strata mapped as Fort Union Formation here, but there is no mammalian control on age. The Willwood Formation covers a large area in the central Bighorn Basin and has yielded more than 100,000 fossil mammal specimens from about 1,500 localities (Bown et al., 1994a). The principal analysis of central Bighorn Basin faunas is by Schankler, who published a summary of his results in 1980. A range chart of Wasatchian genera is shown in Figure 4, based on information digitized from Schankler's range charts (Schankler, 1980; reanalyzed too by Bown and Kraus, 1993; see also Bown et al., 1994b).

There are ambiguities in interpretation of Schankler's ranges because he did not publish any systematic descriptions connecting his identifications of taxa to specimens in the Yale University collection. Bown and Kraus (1993) and Bown et al. (1994a) have revised the thicknesses of some of Schankler's zones, and Schankler's biozonation is different in some respects from that advocated by Granger (1914). Nevertheless, Schankler's central Bighorn Basin ranges of mammalian genera (Fig. 4) can be compared with those from the Polecat Bench–Sand Coulee and Foster Gulch–McCullough Peaks areas outlined here (Figs. 2 and 3).

There are almost certainly Wasatchian mammals of the Sandcouleean subage from Wa-1 and/or Wa-2 present in the lower 100 m of the central Bighorn Basin stratigraphic section, but these have not been described carefully enough to enable Wa-1 and Wa-2 to be distinguished. The beginning of zone Wa-3 and the beginning of the Graybullian subage are normally marked by the first appearance of the perissodactyl genus *Homogalax*, a genus missing from Schankler's chart. Stanley (1982) published a revised version of Schankler's chart that shows *Homogalax* originating at the 130 m level. Initiation of Wa-3 at this level appears reasonable in comparison to the Polecat Bench–Sand Coulee and Foster Gulch–McCullough Peaks faunal records, but the resulting thickness of Sandcouleean strata (ca. 130 m) is about one-half that in the Foster Gulch–McCullough Peaks area to the north, and the thickness of early and middle Graybullian strata here (ca. 400 m) is also less.

Continuing up-section, the first appearance of *Bunophorus* marks the beginning of zone Wa-5 in the late part of the Graybullian subage. The first appearance of *Heptodon* indicates the beginning of zone Wa-6 and the Lysitean subage. Finally, the first appearance of *Lambdotherium* marks the beginning of zone Wa-7 and the beginning of the Lostcabinian subage.

The meaning of Schankler's 'Biohorizon A' at the 200 m level in his central Bighorn Basin section has long been confusing (Badgley and Gingerich, 1988; Badgley, 1990). The clearest evidence on this is given not by Schankler (1980) but by Schankler (1981), who places 'Biohorizon A' at the time of disappearance of *Copecion* ('*Phenacodus*') *brachypternus*. This happens between zones Wa-3a and Wa-3b in the Polecat Bench–Sand Coulee section and in the Foster Gulch–McCullough Peaks section. *Copecion brachypternus* then reappears in Wa-5. Thus 'Biohorizon A' is evidently the faunal turnover separating Wa-3a from Wa-3b. The boundary between Wa-3b and Wa-4 coincides with the well-marked species-level replacement of *Hyracotherium aemulor* by *H. pernix*, noted by Froehlich (1996, p. 414) as being between the 250 and 300 m levels in the Schankler-Wing and Bown et al. sections in the central Bighorn Basin.

Schankler's zonation of the Wasatchian involves a *Haplomylus-Ectocion* range zone, a *Bunophorus* interval zone, and a *Heptodon* range zone. It is different from the zonation advocated by Granger (1914), involving a Sandcouleean subage, a Graybullian subage, a Lysitean subage, and a Lostcabinian

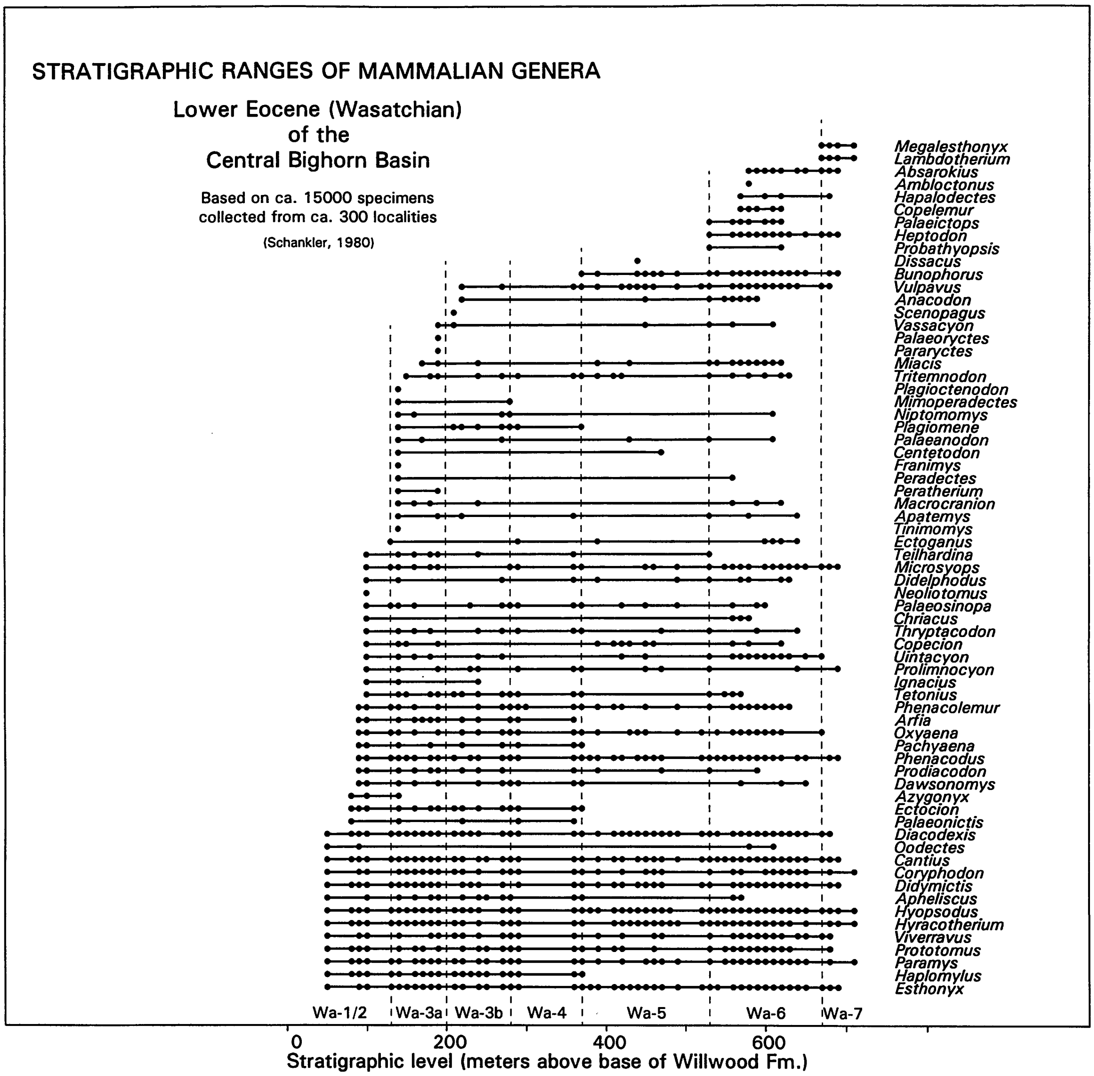

FIGURE 4 — Stratigraphic ranges of early Eocene mammalian genera in the central Bighorn Basin. Dashed lines separate zones of the Wasatchian land-mammal age (labeled Wa-1/2, etc., at the bottom of the chart). Chart is derived from Figure 3 in Schanker (1980). Generic names have been updated when possible; e.g., *Phenacodus brachypternus* is now placed in *Copecion brachypternus* (Gingerich, 1989).

subage, but the two are certainly comparable and probably even compatable. Granger had the advantage of a broader geographic and stratigraphic perspective based on his work in the Polecat Bench–Sand Coulee area and in the Foster Gulch–McCullough Peaks area as well as in the central Bighorn Basin, and his distinction of Sandcouleean from Graybullian faunas appears more representative of the general pattern of faunal evolution in the early Wasatchian than Schankler's lumping of everything into one or two thick units based on the parallel ranges of *Haplomylus* and *Ectocion*. Further clarification will come when the stratigraphic distribution of perissodactyls, so important to Granger's zonation, is studied in more detail in the central Bighorn Basin.

Southern Bighorn Basin

Three studies have been published on Paleocene-Eocene mammals from the southern Bighorn Basin. One deals with Puercan, Torrejonian, and Tiffanian mammals from a cluster of localities along the southern margin of the Fort Union Formation outcrop (Hartman, 1986), while the other two describe Wasatchian mammals at a considerable distance north and east of the Hartman localities (Bown, 1979; see also Bown et al., 1994a, and Strait, this volume). No Clarkforkian mammals have been found as yet in the southern Bighorn Basin, and the Paleocene mammals that have been found cannot be related stratigraphically to the Wasatchian mammals in the southern

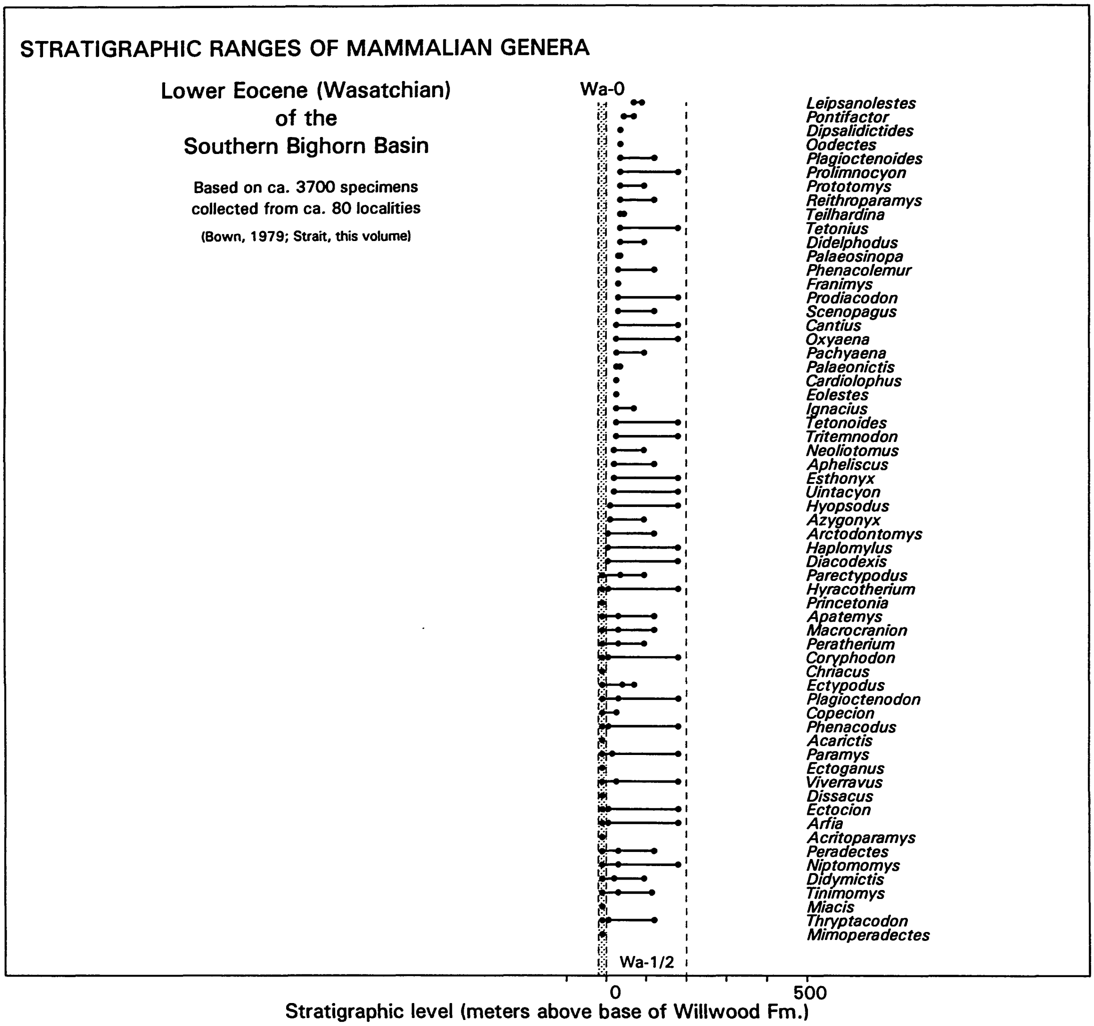

FIGURE 5 — Stratigraphic ranges of early Eocene mammalian genera in the southern Bighorn Basin. Dashed lines separate zones of the Wasatchian land-mammal age (labeled Wa-1/2, representing Wa-1 and/or Wa-2, at the bottom of the chart). Stippled column is Wa-0. Chart is derived from Strait (this volume), and from Bown (1979) and Bown et al. (1994a).

Bighorn Basin. A range chart of Wasatchian genera is shown in Figure 5.

The southern Bighorn Basin stratigraphic section clearly has Wa-0 mammals (Strait, this volume), overlain by Sandcouleean mammals (Bown, 1979), with no evidence of later Graybullian mammals. The total thickness of the Sandcouleean section here (Wa-0 through Wa-2) is ca. 220 m, which is more than double the Sandcouleean section in the central Bighorn Basin, and comparable to Sandcouleean sections farther north in the Polecat Bench–Sand Coulee and Foster Gulch–McCullough Peaks areas.

At the southeastern end of the Bighorn Basin the Fort Union Formation laps unconformably onto and over late Cretaceous formations (Love et al., 1979), and better mammalian age control here would enable estimation of the duration of the hiatus.

GEOGRAPHIC DISTRIBUTION OF PALEOCENE–EOCENE MAMMALS

Figure 1 shows the geographic distribution of Paleocene-Eocene mammals in the Bighorn and Clarks Fork basins. Localities are coded by faunal age, when known, to distinguish Paleocene, early Eocene Wa-0, early Eocene Wa-1 through Wa-4, early Eocene Wa-5, and early Eocene Wa-6 through Wa-7 localities. Paleocene strata are best exposed in the northern end of the depositional trough in the Clarks Fork and northern Bighorn basins, and at the southern end of the trough in the southern Bighorn Basin. There is a narrow band of Fort Union Formation encircling the rest of the basin with some potential to yield Paleocene mammals, though the Paleocene section is sometimes incomplete on the east side of the basin where it laps onto underlying Cretaceous strata and it is sometimes incomplete on the west side of the basin where it has been removed by erosion and overlapped unconformably by Eocene strata.

The map in Figure 1 also shows an asymmetry in the Foster Gulch–McCullough Peaks area and the central Bighorn basin, where older Wasatchian strata (Wa-0 through Wa-4) occupy the eastern one-third of the basin trough while younger Wasatchian strata (Wa-5 through Wa-7) occupy much of the western two-thirds. This is partly due to topography, because the entire area drains eastward into the Bighorn River, but it is also due to structural deformation of the basin during deposition. The western margin of the Clarks Fork and Bighorn basins is a high-angle overthrust involving basement rocks, and the basin itself is thus deepest along its western margin. The distribution of Wa-5 through Wa-7 strata is approximately the trace of the basin axis.

We hope that this summary of mammalian biostratigraphy in the Bighorn and Clarks Fork basins will encourage research in geographic areas and on geological and paleontological problems that have not been investigated thoroughly, and that development of a basin-wide reference map will encourage presentation and comparison of localized results in this broader context.

ACKNOWLEDGMENTS

This chapter summarizes more than a century of field and laboratory work on mammalian stratigraphy by colleagues mentioned above and listed in the following literature section. J. I. Bloch, G. F. Gunnell, R. Secord, and P. Wilf read the manuscript and provided many suggestions leading to its improvement.

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