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WAPITI VALLEY FAUNAS: EARLY AND MIDDLE EOCENE FOSSIL VERTEBRATES FROM THE NORTH FORK OF THE SHOSHONE RIVER, PARK COUNTY, WYOMING

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Abstract.— Five local faunas of Eocene age (designated Wapiti I-V) are described from Wapiti Valley on the North Fork of the Shoshone River in northwestern Wyoming. These faunas were recovered from about 500 meters of stratigraphic section in the Willwood and overlying Aycross formations. The Willwood Formation in Wapiti Valley encompasses two or three land-mammal subages: the Lysitean(?) and Lostcabinian subages of the Wasatchian land-mammal age (early Eocene), and the Gardnerbuttean subage of the Bridgerian land-mammal age (middle Eocene). The Aycross Formation in Wapiti Valley spans two land-mammal subages: Bridger A(?) and Bridger B of the Bridgerian land-mammal age (middle Eocene).

The Wapiti II, III, and V faunas are the best sampled. The Wapiti II fauna in the Willwood Formation includes associated *Pristichampsus*, *Loveina* (*Loveina wapitiensis*, new species), *Heptodon*, *Lambdotherium*, and *Eotitanops*, indicating a Lostcabinian late Wasatchian age. The Wapiti III fauna in the Willwood Formation includes associated *Smilodectes mcgrewi*, *Palaeosyops fontinalis* and *Trogosus* sp., indicating a Gardnerbuttean early Bridgerian age. The Wapiti V fauna in the Aycross Formation contains *Smilodectes gracilis*, *Washakius laurae* (new combination), and *Trogosus latidens*, indicating a Bridger B middle Bridgerian age. Faunal and sedimentological evidence shows a change from lacustrine environments at the base of the Willwood section here to meandering stream systems through most of the overlying Willwood and Aycross formations. Widespread Absarokan volcanism started in Bridger A time and continued through the middle Eocene. Wapiti Valley faunas augment limited evidence concerning the composition of basin margin faunas and the distribution of faunas across different habitat types.

INTRODUCTION

Eocene sediments of the fluvial Willwood Formation and volcaniclastic Aycross Formation are exposed in valleys of the North and South forks of the Shoshone River on the northwestern flank of the Bighorn Basin (Van Houten, 1944). The best exposures are in Wapiti Valley on

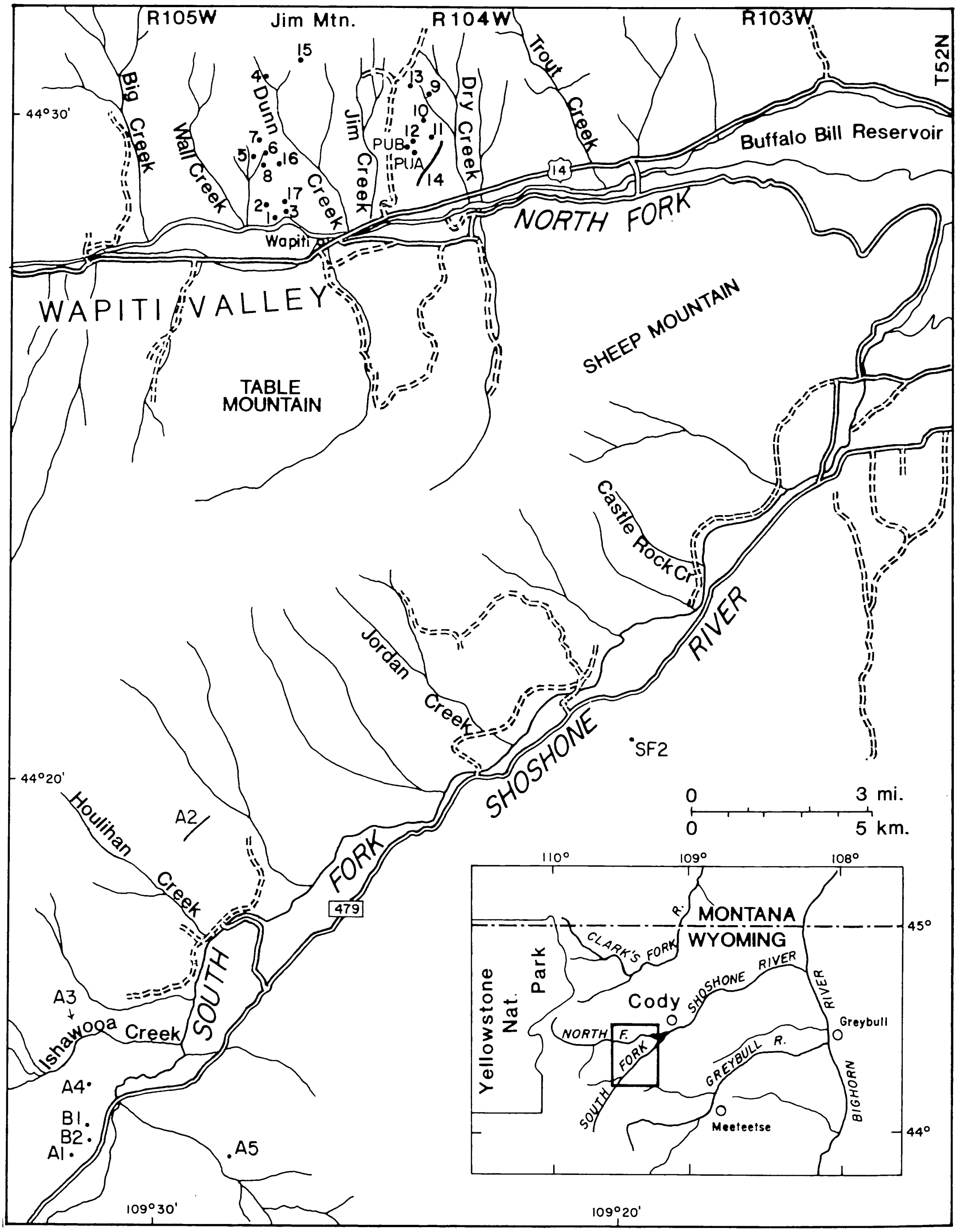

FIG. 1— Fossil vertebrate localities on the North Fork and South Fork of the Shoshone River in northwestern Wyoming. Inset map shows location of Wapiti Valley between the Bighorn Basin and Yellowstone Park. Numbers 1-17 in Wapiti Valley show location of University of Michigan North Fork [NF] localities and PUA and PUB [PU-A and PU-B] show Princeton University localities in the Willwood and Aycross formations of Wapiti Valley. SF2 [SF-2] is a University of Michigan locality and A1 to A5 and B1 to B2 are Princeton localities on the South Fork of the Shoshone River.

the north side of the North Fork of the Shoshone River, some 25-30 km west of the town of Cody, Wyoming. A locality map is provided in Figure 1. In Wapiti Valley the red-banded Willwood Formation rests unconformably on marine Cody Shale of Cretaceous age, and fine-grained brown-to-green Aycross Formation rests unconformably on Willwood Formation. The Aycross Formation is overlain in turn by a thick sequence of coarse cliff-forming Wapiti Formation volcanics and volcaniclastics.

Vertebrate fossils were first collected from the Willwood Formation in Wapiti Valley in 1937 by a field party from Princeton University (Jepsen, 1939). Jepsen found mammalian fossils identified as the perissodactyls *Homogalax* and *Lambdotherium*, and he initially thought that much of the Wasatchian land-mammal age (early Eocene) was probably represented in Wapiti Valley. Jepsen's fossils were never described. The stratigraphy of Wapiti Valley was restudied during the summer of 1982, when a special effort was made to recover fossil vertebrates from both the Willwood and Aycross formations. Stratigraphic results have been published by Torres and Gingerich (1983) and Torres (1985). Vertebrate fossils from Wapiti Valley are described in this report.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

AMNH — American Museum of Natural History, New York
UM — University of Michigan Museum of Paleontology, Ann Arbor
USNM — U.S. National Museum of Natural History, Washington
YPM-PU — Princeton collection at Yale Peabody Museum, New Haven

FOSSIL LOCALITIES

The Willwood and Aycross formations in Wapiti Valley are fossiliferous, but specimens are rare and often fragmentary. Most specimens are isolated teeth or jaw fragments of mammals, and fortunately these can often be identified to species. Seventeen fossiliferous localities were found in 1982 on the north side of the North Fork of the Shoshone River (Fig. 1). These University of Michigan localities, numbered sequentially, are prefaced by NF in the following text (e.g., NF-1). Two additional Princeton University localities in this area are labelled A and B (Fig. 1), and these are prefaced PU in the following text (e.g., PU-A). South Fork localities are shown in Figure 1, but these have not as yet yielded significant vertebrate fossils. Princeton University South Fork localities are labelled A-1 to A-5 and B-1 to B-2. The only University of Michigan South Fork locality of note is SF-2.

The stratigraphy of the Willwood and Aycross formations is summarized in Figure 2, based on investigations of Torres and Gingerich (1983) and Torres (1985). The Willwood Formation is approximately 300 m thick in Wapiti Valley, with about 20 m of lacustrine sediments at the base, overlain by 50 m of thick channel sandstones and 230 m of red-banded fluvial sediments. The Aycross Formation is about 200 m thick in Wapiti Valley, and this is predominantly fine-grained brown-to-green fluvial volcaniclastics. These are described in greater detail in Torres (1985).

It is useful to anticipate a conclusion of this study: Wapiti Valley fossil vertebrates can be grouped into five successive faunas, labelled, from lowest to highest (oldest to youngest) Wapiti I through Wapiti V. Localities belonging to each fauna are listed in Table 1. The age of each is discussed at the end of the paper.

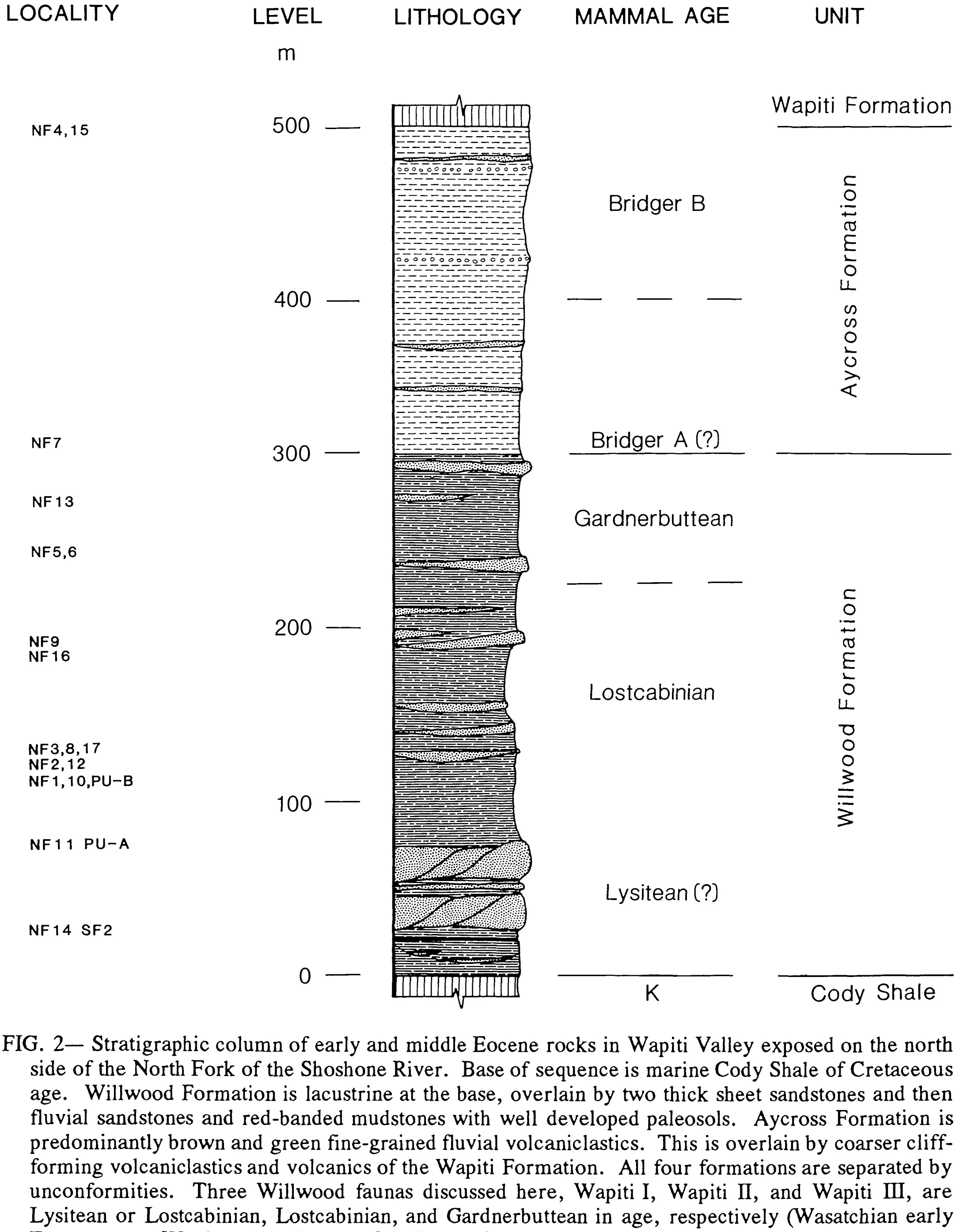

FIG. 2— Stratigraphic column of early and middle Eocene rocks in Wapiti Valley exposed on the north side of the North Fork of the Shoshone River. Base of sequence is marine Cody Shale of Cretaceous age. Willwood Formation is lacustrine at the base, overlain by two thick sheet sandstones and then fluvial sandstones and red-banded mudstones with well developed paleosols. Aycross Formation is predominantly brown and green fine-grained fluvial volcaniclastics. This is overlain by coarser cliff-forming volcaniclastics and volcanics of the Wapiti Formation. All four formations are separated by unconformities. Three Willwood faunas discussed here, Wapiti I, Wapiti II, and Wapiti III, are Lysitean or Lostcabinian, Lostcabinian, and Gardnerbuttean in age, respectively (Wasatchian early Eocene zone Wa-6 or Wa-7, zone Wa-7, and Bridgerian middle Eocene zone Br-1). Aycross Formation faunas Wapiti IV and Wapiti V are Bridger A(?) and Bridger B in age (Bridgerian middle Eocene zones Br-1 and Br-2). General succession and relative spacing of localities is determined by superposition, but meter levels are sometimes imprecise because the base of the Willwood Formation is not always well exposed.

North Fork (Wapiti Valley) localities are as follows (see Figs. 1-2):

NF-1. Wapiti II, Willwood Formation. SE¼, Section 14, R104W, T52N, Park County, Wyoming. Locality is just north of the Shoshone River, eight meters above the top of a prominent multistory sandstone. The fossiliferous bed is a laterally extensive, one meter-thick, cream colored sandy siltstone. Six meters above this bed, an elongate lens of medium sandstone yielded additional vertebrates. The sandstone consists of superimposed, fining upward sequences with a total thickness of 1.85 meters. Tabular and trough cross-bedding, ripples, and horizontal laminations are present. Fossils appear to be concentrated in the thickest sets of trough cross-beds, and consist mostly of isolated teeth of large and medium sized forms, with some small jaws, crocodilian teeth, turtle bones, gar scales, and abraded pieces of bone. Turtle remains are noticeably larger than mammalian remains. This sandstone bed may represent a small point-bar deposit. NF-1 is the locality of our camp in 1982.

NF-2. Wapiti II, Willwood Formation. Southwest corner of NE¼, Section 14, R104W, T52N, Park County, Wyoming. Locality is 110 meters above the base of the section. This site is in a slump block, but its original stratigraphic position can be reconstructed by matching variegated beds with the undisturbed sediments on an adjacent wall. The lithology consists of 12.2 meters of red and gray mudstones. Fossils all appear to come from a laterally extensive and distinctive red unit. NF-2 is at the same stratigraphic level as NF-3, NF-12, and NF-17. The variegated gray-over-red mudstones of this and other Willwood localities are interpreted as paleosol horizons (Bown and Kraus, 1981).

NF-3. Wapiti II, Willwood Formation. Southwest side of quarter-section corner between Sections 13 and 14, R104W, T52N, Willwood Formation, Park County, Wyoming. Locality is 120 meters above the base of the section. It is on a low isolated butte capped by a small remnant of gray mudstone. Fossils occur in the purple mudstone immediately beneath the gray mudstone cap and in variegated beds below this level. This site yielded large postcranial elements of *Coryphodon*, turtles, and crocodilians, but also small isolated mammalian teeth and jaws. Some fossils are coated with iron oxide, and soil nodules are abundant. The environment of deposition appears to have been a floodplain with well developed soils.

NF-4. Wapiti V, Aycross Formation. Northwest corner of SE¼, Section 2, R104W, T52N, Park County, Wyoming. This locality is far up the slope of Jim Mountain and close to the top of the formation. NF-4 is located above a conspicuous, steeply dipping conglomerate. The fossil bearing strata are blue-green volcanic mudstones. Complete jaws and some large mammalian teeth were recovered along with large fragments of turtle shell and crocodilian teeth.

NF-5. Wapiti III, Willwood Formation. North center of SW¼, Section 11, R104W, T52N, Park County, Wyoming. Locality is 240 meters above the base of the section. Variegated sediments in the form of red, gray, and brown mudstones, drab sandy siltstone, and medium to fine grained sandstones are the dominant lithologies. Turtle remains are most common, but a fragment of a large mammal tooth was also recovered. These sediments represent paleosols developed on a floodplain associated with small channels.

NF-6. Wapiti III, Willwood Formation. Center of Section 11, R104W, T52N, Park County, Wyoming. Locality is 240 meters above the base of the section. Located on an isolated low butte with the same lithology as NF-5. Large turtle and mammalian bones, and fragments of mammalian teeth are present in these deposits.

NF-7. Wapiti IV, Aycross Formation. Center of Section 11, R104W, T52N, Park County, Wyoming. Locality is in the lower part of the Aycross Formation near its basal contact with the Willwood Formation. This locality is in a slumped block of green and white siltstone and sandstone. The structural position of the block can be reconstructed by matching its lithology to beds up-slope on the south face of the valley. Small fossil fragments were collected from a lens of coarse, pale gray sandstone. These deposits are similar to those at NF-4.

NF-8. Wapiti II, Willwood Formation. East center of SW¼, Section 11, R104W, T52N, Park County, Wyoming. Locality is approximately 120 meters above the Cody Shale here (composite section). This site is located in mudstones above two massive sandstones interbedded with drab mudstones. Fossils recovered here consist of turtles, gar scales, and a fragment of rodent incisor. The site is interpreted as a floodplain, proximal to large tributary channels.

NF-9. Wapiti II, Willwood Formation. Southeast corner of SE¼, Section 6, R103W, T52N, Park County, Wyoming. Locality is 193 meters above the base of the section. NF-9 is located in the first yellow sandstone within a thick mudstone interval above the basal massive sandstones. The fossil bearing unit is a 1.7 meter-thick fining-upward sandy siltstone to medium planar-bedded sandstone sequence. Fossils appear to be preserved in the planar-bedded sandstone. Fossils found here include small teeth and bone fragments of mammals and reptiles. The depositional environment is interpreted as that of a small tributary channel, or perhaps, a crevasse splay.

NF-10. Wapiti II, Willwood Formation. Center of NE¼, Section 7, R103W, T52N, Park County, Wyoming. Locality is 108 meters above the Cody Shale. This locality is in a series of variegated mudstones above the basal massive sandstones. Fossiliferous beds are tuffaceous and have a paleosol developed in them. Fossils vary greatly in size and are often coated with iron oxide or partially contained in concretions. This site is at the same stratigraphic level as NF-12, and either or both are probably equivalent to Jepsen (1939) and Van Houten's (1944) B-1 (PU-B) locality along the North Fork of the Shoshone River.

NF-11. Wapiti I, Willwood Formation. South center of NE¼, Section 7, R103W, T52N, Park County, Wyoming. Locality is 72 meters above the base of the section. NF-11 is located in the middle of a 5.4 meter thick shoestring sandstone, between two massive buff sandstones. The single fossil from this locality is a large mammalian tibia. The specimen was collected from a medium- to coarse-grained sandstone. This locality may correspond to Jepsen's "*Homogalax* site" (PU-A, see below). Massive sandstones at NF-11 probably represent the master streams of the local depositional basin. NF-11 appears to represent an upper point-bar environment.

NF-12. Wapiti II, Willwood Formation. North center of SE¼, Section 7, R103W, T52N, Park County, Wyoming. Locality is 110 meters above the contact with the Cody Shale. NF-12 consists of variegated red, purple, and gray mudstones above massive sandstones. Specimens collected here exhibit a wide range of sizes, the largest fossils representing turtles, and smaller remains including gar scales, and crocodilian and mammalian teeth. Fossils appear to be associated with paleosol horizons.

NF-13. Wapiti III, Willwood Formation. Northern half of boundary line between east and west halves of Section 7, R103W, T52N, Park County, Wyoming. Locality is 270 meters above the base of the section. Variegated mudstones are the dominant lithology here. Fossils consist of large postcranial elements of reptiles, crocodilian teeth, and gar scales. These appear to be preserved in paleosols developed on a floodplain.

NF-14. Wapiti I, Willwood Formation. This locality is exposed just above lacustrine beds of the basal Willwood Formation and it contains abundant fossil plants. The best exposures (3-4 km long) are in Dry Creek, from the northeastern corner of Section 7 to the southwestern corner of Section 18, R103W, T52N. The plant-bearing layer seems to be present wherever the local base of the Willwood Formation crops out. Fossils are primarily leaves preserved in clay, silt, and sandstone above lenticular coal beds. The best fossils occur in clay beds, below low angle, very large-scale tabular cross-bedded fine sandstones. These deposits appear to represent swampy delta plain and delta front environments.

NF-15. Wapiti V, Aycross Formation. Southeast part of NW¼, Section 1, R104W, T52N, Park County, Wyoming. Locality is near the top of the section. This locality is developed

TABLE 1— Wapiti Valley faunas, formations, and localities.

Fauna	Formation[1]	Interval[1]	Localities
Wapiti V	Upper Aycross	400 m - 500 m	NF-4, NF-15
Wapiti IV	Lower Aycross	300 m - 400 m	NF-7
Wapiti III	Upper Willwood	200 m - 300 m	NF-5, NF-6, NF-13
Wapiti II	Middle Willwood	100 m - 200 m	NF-1, NF-2, NF-3, NF-8, NF-9, NF-10, NF-12, NF-16, NF-17, PU-B
Wapiti I	Lower Willwood	0 m - 100 m	NF-11, NF-14, PU-A, SF-2

[1]Upper, middle, lower, and approximate meter levels refer to relative position locally in Wapiti Valley section.

in steeply dipping (to the north), cream-colored volcaniclastics. Fossils include isolated mammalian teeth and turtle fragments. There is a large size range, and bones are often abraded. It has been suggested that portions of the Aycross Formation were deposited by braided streams (Bown, 1982), but exposures at NF-4 and NF-15 are too poor to allow an accurate depositional interpretation for the Aycross Formation in Wapiti Valley.

NF-16. Wapiti II, Willwood Formation. Center of SE¼, Section 11, R104W, T52N, Park County, Wyoming. Locality is 180 meters above the contact with the Cody Shale (composite section), 110 meters above the top of the multistory massive sandstones. This site is contained in a red mudstone between two massive sandstones. No mammals were recovered from these beds, but large turtle fragments, crocodilian teeth, and gar scales are present. The paleoenvironment appears to have been that of a floodplain.

NF-17. Wapiti II, Willwood Formation. Southeast corner of NE¼, Section 14, R104W, T52N, Park County, Wyoming. Locality is in a slumped block, 250 meters north of NF-3 and possibly at the same stratigraphic level. The lithologies and the fossil bearing strata in both localities are the same. Specimens recovered here include postcranial fragments of turtles, and isolated mammalian and crocodilian teeth associated with floodplain paleosols (as at NF-3).

PU-A. Wapiti I, Willwood Formation. Princeton University sites could not be relocated with certainty. Jepsen's notes indicate that this locality, his "*Homogalax* site," is in the Dry Creek area "70 feet above the base of a massive buff sandstone." PU-A is probably close to NF-11 geographically and temporally.

PU-B. Wapiti II, Willwood Formation. PU-B denotes a locality in the same general area as PU-A, but 240 feet above the base of the sandstone and at least partially contained in gray mudstone.

One UM locality on the South Fork of the Shoshone River is worthy of note:

SF-2. Wapiti I, Willwood Formation. Southwest corner of Section 35, R104W, T50N, Park County, Wyoming. This locality is between the basal lacustrine deposits and the first sheet sandstone bed of the Willwood Formation. The South Fork thrust fault cuts strata above the locality level. Fossils recovered are fragmentary reptile bone and one *Hyracotherium* tooth. The site is in a purple mudstone bed interpreted as a paleosol and a lateral equivalent of the plant-bearing beds at NF-14.

Van Houten (1944) studied several sites along the South Fork of the Shoshone River. His localities A-2 through A-6 occur in the "Early Acid Breccia", and locality B-1 is a site 500 feet above the base of the "Early Acid Breccia." All of these were probably in the Aycross Formation and the few specimens known from the Aycross Formation along the South Fork of the Shoshone River are discussed by Bown (1982).

SYSTEMATIC PALEONTOLOGY

Wapiti Valley faunas, taken together, include at least one species of fish, eight species in five different families of reptiles, and 40 species representing 18 families of mammals. These are reviewed systematically here, and interpreted in the following discussion. Measurements given here are in mm. Tooth measurements are given as length × width.

Class OSTEICHTHYES
Order LEPISOSTEIFORMES
Family LEPISOSTEIDAE
Lepisosteus Lacepede, 1803
Lepisosteus sp.

Referred specimens.—Uncataloged scales from various localities.

Occurrence.—Wapiti II (NF-1, NF-8, NF-10, NF-12, NF-16); Wapiti III (NF-5, NF-6, NF-13); Wapiti V (NF-4).

Discussion.—Gar scales are common throughout the North Fork early and middle Eocene. Most of the scales are isolated, often occurring in red overbank mudstones, suggesting postmortem transportation. The largest scales exceed two centimeters in length, indicating the presence of very large individual gars.

Class REPTILIA
Order TESTUDINES
Family TRIONYCHIDAE
Trionychidae indet.

Referred specimens.—Numerous uncataloged shell fragments.

Occurrence.—Wapiti II (NF-1, NF-2, NF-3, NF-8, NF-9, NF-10, NF-12); Wapiti III (NF-5, NF-6, NF-13); Wapiti V (NF-15).

Discussion.—Fragmentary remains of trionychids are abundant throughout the North Fork section. There is enough variation in form among these specimens to suggest the presence of at least two trionychid taxa in the North Fork region during the late Wasatchian and early Bridgerian. Many of these specimens represent very large individuals similar to those reported from the Bridger A of southwestern Wyoming (Gaffney, 1979; Gunnell and Bartels, in press), while others represent a second, highly sculptured, smaller taxon. These remains are generically indeterminate due to their fragmentary nature, as well as to uncertainties in fossil soft-shell turtle taxonomy (see Gaffney, 1979, Meylan, 1987).

Family EMYDIDAE
Emydidae indet.

Referred specimens.—UM 80421, UM 80641, partial carapaces; and several uncataloged shell fragments.

Occurrence.—Wapiti II (NF-1, NF-2, NF-3, NF-9, NF-10, NF-12, NF-17); Wapiti III (NF-6, NF-13), Wapiti V (NF-15).

Description.—Included here are very fragmentary and indeterminate remains of one or more emydid turtles. The most complete specimen (UM 80641, NF-6) possesses long neural elements, relatively thick carapace elements, costal elevations lateral to the vertebral/costal scute sulci, and close confluence of the neural/costal sutures with the vertebral/pleural scute sulci, all characteristic of the genus *Echmatemys*, particularly *E. testudinae*, a poorly understood Wasatchian form (see Hay, 1908; Hutchinson, 1980). This specimen is unusual, however, in the possession of an octagonal third neural, "reversed" fourth neural, and possibly an octagonal fifth neural.

Discussion.—Generalized aquatic emydids (such as *Echmatemys*) are common throughout most of the Eocene of Wyoming (Hutchinson, 1980), and their very fragmentary remains are abundant in most North Fork deposits. The more complete specimens resemble well preserved Bridgerian specimens from southwestern Wyoming.

Family TESTUDINIDAE
Hadrianus Cope, 1874
Hadrianus sp.

Referred specimens.—UM 80719, partial carapace and plastron; several uncataloged shell fragments.

Occurrence.—Wapiti II (NF-3, NF-8, NF-16, NF-17); Wapiti III (NF-5).

Discussion.—Included here are fragmentary specimens representing a large testudinid referable to *Hadrianus*. The most complete specimen (UM 80719) preserves only a small portion of the shell, making specific assignment difficult. *Hadrianus* is the oldest known testudinid, first appearing near the base of the Lysitean (Hutchinson, 1980).

Order SQUAMATA
Suborder LACERTILIA
Family ANGUIDAE
Subfamily Glyptosaurinae
Xestops Cope, 1873
Xestops sp.
Fig. 3A-B

Referred specimens.—YPM-PU 17067, partial right maxilla and osteoderms; UM 83139, UM 83140, osteoderms.

Occurrence.—Wapiti II (PU-B, NF-10, NF-12).

Description.—A single incomplete maxilla with associated osteoderms (YPM-PU 17067) and a few isolated body osteoderms are the only lizard specimens recovered from North Fork Eocene deposits. The maxilla is similar in form to, but rather smaller than, previously reported *Xestops* specimens (see Meszoely et al., 1978). The associated osteoderms bear the dorsal keel and prominent rugose lateral bevels characteristic of *Xestops*. Several of the isolated osteoderms are larger and more robust than those found with YPM-PU 17067, and may belong to another glyptosaurine taxon.

Discussion.—*Xestops* is a small, primitive glyptosaur characterized by unfused frontals and fully developed tuberculate osteodermal sculpturing (Meszoely et al., 1978). It may be distinguished from large Eocene glyptosaurine lizards, such as *Melanosaurus* or *Glyptosaurus*, by its smaller size, less bulbous and more isodont dentition, and by its more gracile mandible. It can be distinguished from the small Eocene glyptosaur *Proxestops* by its larger size, lack of vermiculate-tuberculate osteodermal sculpturing, and by its possession of body osteoderms with well-developed rugose lateral bevels and dorsal keels (Gauthier, 1982). Originally described from the middle Eocene (Bridger B) Bridger Formation of Wyoming (Marsh, 1872), *Xestops* has also been reported from late Paleocene Clarkforkian (Bartels, 1983), early Eocene Wasatchian (Meszoely et al., 1978), and early middle Eocene Bridger A (Gunnell and Bartels, in press) horizons of Wyoming.

Order CROCODYLIA
Family CROCODYLIDAE
Crocodylidae indet.

Referred specimens.—UM 83135, isolated tooth; UM 83138, isolated teeth; uncataloged teeth, cranial, and postcranial fragments.

Occurrence.—Wapiti II (NF-2, NF-3, NF-10, NF-12, NF-16, NF-17); Wapiti V (NF-4, NF-15).

Discussion.—All of the material referred here is very fragmentary, consisting of isolated teeth, and partial posterior cranial and mandibular elements. The teeth are subisodont, being long and conical anteriorly and low and spatulate posteriorly. Each bears anterior and posterior carinae, and a very fine rugose sculpturing. All specimens represent large individuals that are probably assignable to either a generalized leidyosuchine or a more derived crocodilid such as "*Crocodylus*" *affinis* (Gunnell and Bartels, in press).

Subfamily Pristichampsinae
Pristichampsus Gervais, 1853
Pristichampsus vorax (Troxell, 1925)
Fig. 3C-E

Referred specimens.—UM 80639, UM 83133, isolated teeth.

Occurrence.—Wapiti II (NF-9); Wapiti III (NF-5).

Description.—Included in the North Fork sample are three serrated crocodilian teeth, two of which are associated. All teeth are laterally compressed, slightly recurved posteriorly and medially, have a longer anterior edge, and bear prominent anterior and posterior carinae with serrated margins (Fig. 3C-E). The isolated specimen (UM 83133, Fig. 3C) preserves the middle portion of a large, presumably, anterior tooth. It is asymmetrical in cross-section and possesses about four serrations along each millimeter of tooth margin. The associated teeth (UM 80639) are only slightly asymmetric (Fig. 3D-E) and have 7-8 serrations per millimeter of tooth margin. The less complete of these (Fig. 3E) appears to be the upper portion of an anterior caniniform tooth. Its sides are somewhat faceted, giving it a polygonal appearance in cross-section. The complete tooth (Fig. 3D) is short and spatulate, suggesting a posterior origin in the dental series. Unlike its anterior companion, this tooth has smooth sides. The carinal serrations in this posterior tooth run from the apex to a position about 1.2 mm above its base, indicating that, when fully erupted, the serrations in these teeth did not contact the soft tissues of the mandibles.

These *Pristichampsus* teeth agree in form with late Bridgerian *Pristichampsus vorax* specimens (Langston, 1975), but are somewhat more blade-like. This difference is probably due to individual and/or positional variability, and is not considered taxonomically significant.

Measurements—UM 80639 (anterior): length = 4.8, width = 2.3, estimated height = 12.0+. UM 80639 (posterior): length = 4.5, width = 2.3, height = 6.7. UM 83133: length = 8.1, width = 4.3, estimated height = 20.0+.

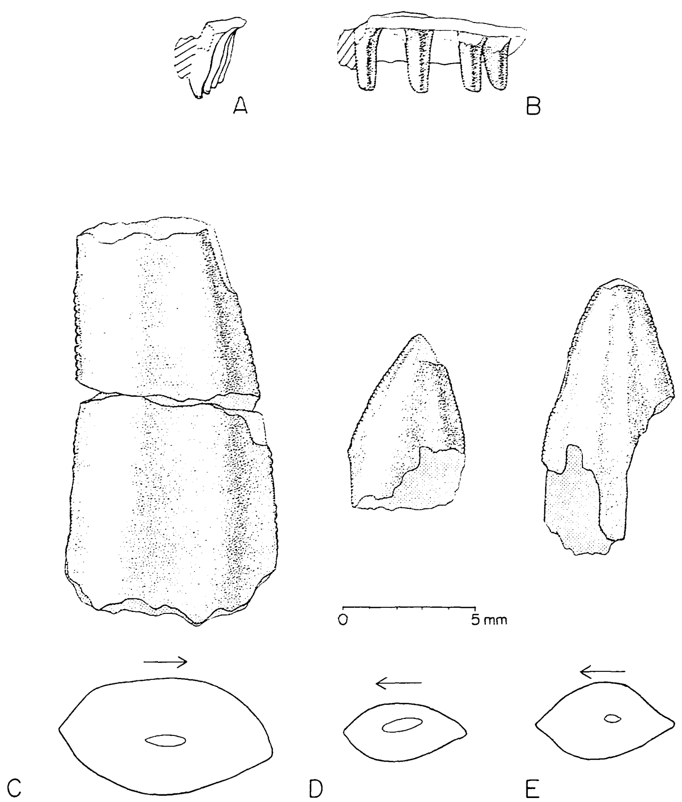

FIG. 3— Squamata and Crocodylia from Wapiti Valley. A, YPM-PU 17067, *Xestops* sp., right maxilla in anterior view; B, same in lateral view. Note the relatively gracile construction and small size of the maxilla and the laterally compressed tooth crowns. C-E, *Pristichampsus vorax*, lingual views and cross-sectional outlines of teeth (arrows point anteriorly). C, UM 83133, anterior tooth. D, UM 80639, posterior tooth. E, UM 80639, anterior tooth. Note serrated margins and irregular, almost faceted, tooth sides and cross-sections.

Discussion.—Langston (1975) first recognized the occurrence of eusuchian dinosaur-toothed (ziphodont) crocodilians in North America. Based on *Crocodylus vorax* (Troxell, 1925) from the early Bridgerian of Wyoming, *Pristichampsus vorax* is also known from the Tiffanian, late Paleocene (Douglass Quarry, UM 99019), basal Wasatchian (Gingerich, 1989), Bridger A (Gunnell and Bartels, in press), and latest Bridgerian (earliest Uintan?, Langston, 1975). Other possible pristichampsine records include a questionable tooth (which may belong to a reworked dinosaur) from the earliest Paleocene of the Bighorn Basin (Bartels, 1980), and *Orthogenysuchus olseni* (Mook, 1924) from the Wasatchian of the Bighorn Basin (Langston, personal communication, 1979).

Family ALLIGATORIDAE
Allognathosuchus Mook, 1921
Allognathosuchus sp.

Referred specimens.—UM 83137, UM 83141, UM 83142, isolated teeth.

Occurrence.—Wapiti II (NF-1, NF-16); Wapiti III (NF-13).

Description.—Included here are several teeth belonging to *Allognathosuchus*, a primitive alligatorid characterized by a heterodont dentition, including an anterior canine and spatulate, bulbous posterior teeth. Each tooth possesses anterior and posterior carinae and fine striations radiating from their apices. The posterior molariform teeth are often heavily worn.

Discussion.—*Allognathosuchus* is a common element in virtually all Paleocene and Eocene faunas of western North America (Mook, 1921). The systematic relationships among the various *Allognathosuchus* species are poorly understood (see Bartels, 1988). Many of the teeth described here probably belonging to the ill-defined *Allognathosuchus heterodon/polyodon* morphological group distinguished by their small size, gracile form, and modest development of heterodonty and tooth margin undulations (see Bartels, 1983). Two teeth (UM 83137 and UM 83141) from Wapiti Valley may represent a very large and robust undescribed alligatorid present in the Wasatchian of the northern Bighorn Basin (UM 65283).

Diplocynodon Pommel, 1847
Diplocynodon sp.

Referred specimen.—UM 83134, osteoderms.

Occurrence.—Wapiti II (NF-3).

Discussion.—*Diplocynodon* is a large, primitive caiman. It is the most common crocodilid in Eocene deposits of Europe (Berg, 1966), but is quite rare in North American deposits of similar age. *Diplocynodon* has been reported from the Clarkforkian Paleocene and Bridgerian Eocene of Wyoming (Bartels, 1983; Gunnell and Bartels, in press; Mook, 1960). The single specimen referred here includes several bipartite ventral osteoderms characteristic of *Diplocynodon* in particular, and caimans in general.

Class MAMMALIA

Order INSECTIVORA
Family DORMAALIIDAE

Scenopagus McKenna and Simpson, 1959
Scenopagus curtidens (Matthew, 1909)
Fig. 4A-B

Referred specimens.—YPM-PU 17315, right dentary with P_4-M_2; YPM-PU 17320, right dentary with P_4-M_3.

Occurrence.—Wapiti II (PU-B).

Description.—These specimens share similar morphology and are identical in size with *Scenopagus curtidens* samples described by Krishtalka (1976).

Measurements—YPM-PU 17135: $P_4 = 1.7 \times 1.1$, $M_1 = 1.8 \times 1.4$, $M_2 = 1.7 \times 1.4$. YPM-PU 17320: $P_4 = 1.7 \times 1.0$, $M_1 = 1.7 \times 1.3$, $M_2 = 1.8 \times 1.4$, $M_3 = 1.9 \times 1.1$.

Discussion.—*Scenopagus curtidens* is known from Wasatchian through early Uintan localities in Wyoming, New Mexico, Colorado, and California (Krishtalka, 1976).

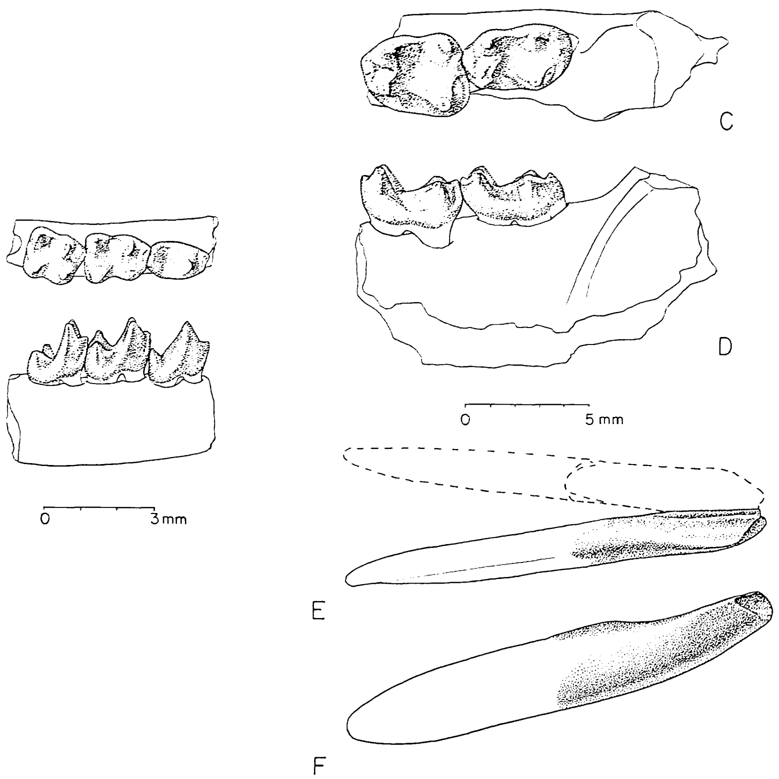

FIG. 4— Insectivora and Proprimates from Wapiti Valley. A, *Scenopagus curtidens*, YPM-PU 17315, right dentary with P_4-M_2 in occlusal view; B, same in buccal view. C, *Microsyops scottianus*, YPM-PU 17321, left dentary with M_{2-3} in occlusal view; D, same in buccal view. E, cf. *Elwynella oreas*, YPM-PU 23946, right I_1 in occlusal view with left I_1 shown in outline. F, right I_1 in buccal view.

Order PROPRIMATES
Superfamily MICROSYOPOIDEA
Family MICROSYOPIDAE
Microsyops Leidy, 1872
Microsyops scottianus Cope, 1881
Fig. 4C-D

Referred specimens.—UM 80423, left dentary with roots of I_1-P_3; UM 80718, isolated right P^4, M_1, left I_1; YPM-PU 17321, left dentary with M_{2-3}.

Occurrence.—Wapiti II (NF-1, NF-10, PU-B).

Description.—The specimens referred to *M. scottianus* from Wapiti Valley are similar in size to samples of *M. scottianus* from the Lostcabinian in the Wind River and Bighorn basins (Gunnell, 1989).

Measurements—UM 80718: $P^4 = 3.70 \times 4.20$, $M_1 = 4.20 \times 3.20$. YPM-PU 17321: $M_2 = 4.40 \times 3.50$, $M_3 = 4.40 \times 2.80$.

Microsyops cf. *M. elegans* (Marsh, 1871)

Referred specimens.—UM 80630, broken right P_4; UM 80716, right P^4.

Occurrence.—Wapiti III (NF-6); Wapiti V (NF-15).

Description.—Wapiti Valley specimens referred to *Microsyops elegans* are somewhat larger than samples of *M. elegans* from the Bridger Basin, but do not approach the size of *Microsyops annectens* (Gunnell, 1989). P^4 (UM 80716) exhibits the dilambdodonty typical of *M. elegans* (Gunnell, 1989).

Measurements—UM 80630: $P^4 = 4.00 \times 4.50$.

Microsyops cf. *M. annectens* (Marsh, 1872)

Microsyops, Jepsen, 1939, p. 1914.

Referred specimen.—YPM-PU 14693, left M^1.

Occurrence.—Van Houten (1944) Locality B-1, Aycross Formation.

Description.—A single upper molar from Wapiti Valley may represent *Microsyops annectens*. This tooth corresponds in size and morphology to samples of *M. annectens* from the Bridger Basin (Gunnell, 1989).

Measurements—YPM-PU 14693: $M^1 = 4.6 \times 5.4$.

Discussion.—*M. annectens* is known only from the late Bridgerian (Bridger C-D) in the Bridger Basin, but it has been reported from earlier sediments (Bridger A-B) at Carter Mountain (Eaton, 1982). Both Wapiti Valley and Carter Mountain represent basin margin areas. It is possible that *M. annectens* was more common in upland environments away from the basin floor, reflecting habitat preference among *Microsyops* species (Gunnell, 1989).

Superfamily PLESIADAPOIDEA
Family PAROMOMYIDAE
Cf. *Elwynella* Rose and Bown, 1982
Cf. *Elwynella oreas* Rose and Bown, 1982
Fig. 4E-F

Referred specimen.—YPM-PU 23946, right I_1.

Occurrence.—Wapiti II (PU-B).

Discussion.—The referred incisor is elongate, resembling *Phenacolemur praecox* (see Bown and Rose, 1976; Simpson, 1955), but has mesial and distal cristids and the characteristic dorsomedial surface of *E. oreas* (Rose and Bown, 1982). This species is known from the early Bridgerian Aycross Formation.

Order PRIMATES
Superfamily TARSIOIDEA
Family OMOMYIDAE
Subfamily Omomyinae
Tribe Washakiini
Loveina Simpson, 1940
Loveina wapitiensis new species
Fig. 5A-D

Holotype.—YPM-PU 17317 (right dentary with P_3-M_3).

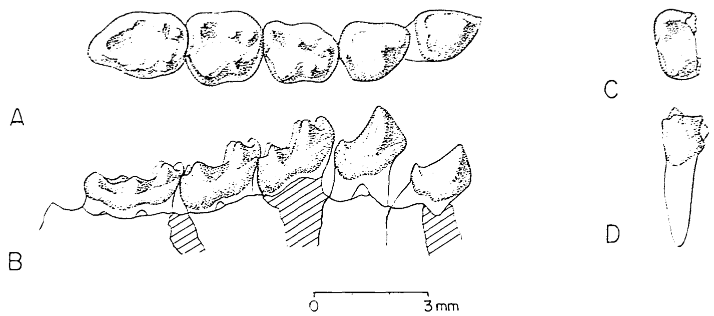

FIG. 5— Primates from Wapiti Valley: *Loveina wapitiensis*, new species. A, YPM-PU 17317 (holotype), right dentary with P_3-M_3 in occlusal view; B, same in buccal view. C, UM 79492, M_2 talonid in occlusal view; D, same in buccal view. Note lack of buccolingual inflation on P_3, open trigonid on P_4, and incipient metastylids on $M_{2\text{-}3}$.

Referred specimens.—UM 79492, (talonid of right M_2).

Occurrence.—Wapiti II (NF-1, PU-B).

Diagnosis.—*Loveina wapitiensis* differs from *Loveina zephyri* in having P_3 less buccolingually inflated; in having P_3 with a lower, relatively smaller paraconid and less bulging metaconid; in having P_4 with less differentiated paraconid and metaconid and a less distinct metacristid causing the trigonid to be more open; and in having small, but distinct metastylids on $M_{2\text{-}3}$.

Discussion.—It is evident that *Loveina* is closely related to the washakiin genera *Shoshonius*, *Washakius*, and *Dyseolemur* (Szalay, 1976; Honey, 1990). *Loveina wapitiensis* resembles these genera in having metastylids on $M_{2\text{-}3}$, but differs in lacking a metastylid on M_1. *L. wapitiensis* shares a buccolingually distended P_4 with *L. zephyri*, as well as lingually closed talonids on lower molars. Other washakiins lack premolar distention, have a distinct talonid notch, and have relatively deeper talonid basins (Szalay, 1976; Honey, 1990). *Loveina* lacks the buccolingually constricted molar trigonids typical of *Shoshonius* and has mesiodistally restricted trigonids with a more lingual paraconid (especially on $M_{2\text{-}3}$) than either *Washakius* or *Dyseolemur*.

Loveina wapitiensis is derived compared to *Loveina zephyri*. YPM-PU 17317 (Fig. 5A-B) is slightly larger than the type of *L. zephyri* (AMNH 52517) and has metastylids on $M_{2\text{-}3}$. The incipient metastylids of *L. wapitiensis* are intermediate in size and development between *Loveina zephyri* (no metastylids) and other washakiins.

Measurements—YPM-PU 17317: $P_3 = 1.70 \times 1.30$, $P_4 = 1.90 \times 1.80$, $M_1 = 2.30 \times 1.80$, $M_2 = 2.20 \times 2.00$, $M_3 = 2.80 \times 1.80$.

Washakius Leidy, 1873
Washakius laurae (Simpson, 1959)
Fig. 6A-B

Shoshonius? *laurae* Simpson, 1959 (in McGrew), p. 153, fig. 10A-B.
Washakius insignis (in part), Szalay, 1976, p. 303, fig. 95; Szalay and Delson, 1979, p. 243; Honey, 1990, p. 215.

Holotype.—AMNH 55672, left dentary with $M_{1\text{-}3}$.

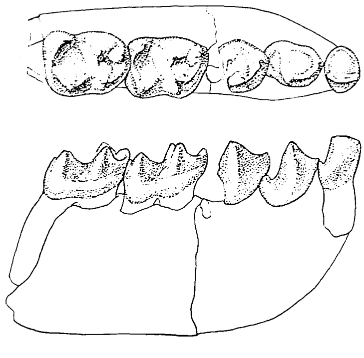

FIG. 6— Primates from Wapiti Valley: *Washakius laurae*. A, UM 80652, right dentary with P_2-M_2 in occlusal view; B, same in buccal view. Note relatively closed trigonid with lingually placed paraconid, straight cristid obliqua, and small hypoconulids on lower molars.

Type locality.—American Museum/University of Wyoming Locality 10, Morrow Creek Member, Green River Formation, Sublette County, Wyoming.

Referred specimen.—UM 80652, right dentary with P_2-M_2.

Occurrence.—Wapiti V (NF-4).

Emended diagnosis.—Washakius laurae differs from *Washakius insignis* in having P_4 metaconid high on the flank of the protoconid and not well differentiated; in having more closed trigonids on lower molars with paraconids positioned lingually; in having a straight cristid obliqua on lower molars; in having less distinct and less posteriorly projecting hypoconulids on M_{1-2}; and in being somewhat smaller. *W. laurae* differs from *W. izetti* in having less distinct P_4 paraconid and metaconid; in having P_4 paraconid more lingually placed; in having a better developed metastylid on M_1; in having lower molar trigonids with lingually positioned paraconid. *W. laurae* differs from *W. insignis*, *W. woodringi*, and *W. izetti* in having less well developed enamel crenulations and differs from *W. woodringi* in being larger.

Description.—UM 80652 contains P_{2-4}, teeth not preserved in the holotype. P_2 of *Washakius laurae* is similar to that of *W. insignis* except that it is not as lingually expanded and has an anteroposteriorly deeper protoconid. Both species have a small, centrally placed P_2 paraconid and no metaconid. *W. laurae* has a P_3 with a lingually placed paraconid and a curving paracristid. The paraconid is more buccally placed with a shorter, straight paracristid in *W. insignis*. P_3 in *W. laurae* lacks a lingual cingulum, has a smaller talonid shelf, and is less lingually inflated than in *W. insignis*.

The P_4 metaconid of *W. laurae* is higher and less well separated from the protoconid compared to *W. insignis* and *W. izetti*. The paraconid is just buccal of the metaconid in *W. laurae*, but is well buccal of the metaconid in *W. insignis* and *W. izetti* (due to the lingually placed metaconid).

Measurements—UM 80652: $P_2 = 1.20 \times 1.2$, $P_3 = 1.70 \times 1.30$, $M_1 = 2.30 \times 1.70$, $M_2 = 2.50 \times 1.90$.

Discussion.—Simpson (1959, in McGrew) originally assigned *Washakius laurae* questionably to *Shoshonius*. Simpson based his diagnosis on the morphology of M_3, noting that "*S*?" *laurae* was similar to *Shoshonius cooperi*, but differed in having a more symmetrical M_3 talonid with a "more distinctly incipient third lobe," and in having a "vaguely twinned hypoconulid." Simpson differentiated "*S*?" *laurae* from *Washakius insignis* by its somewhat smaller size and less well developed M_3 hypoconulid lobe.

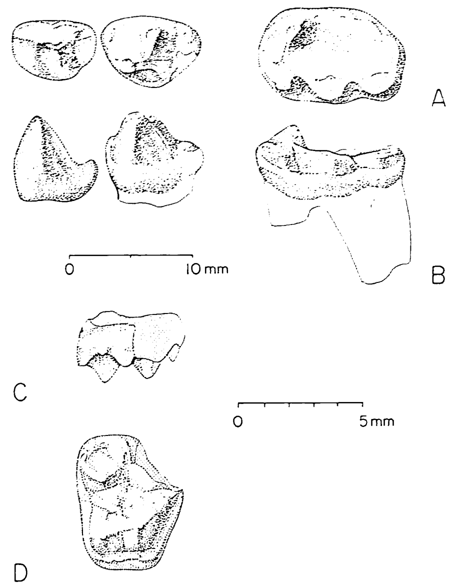

FIG. 7— Primates from Wapiti Valley: *Smilodectes*. A, *S. mcgrewi*, UM 80644, left $P_{3\text{-}4}$ and M_3 in occlusal view; B, same in buccal view. C, *S. gracilis*, UM 80673, right M^1 in buccal view; D, same in occlusal view.

Szalay (1976) synonymized *S*? *laurae* with *Washakius insignis*, noting that the M_3 of *S*? *laurae* is, in fact, quite similar to *Washakius* (both have a twinned hypoconulid). *S*? *laurae* also lacks the constricted molar trigonid typical of *Shoshonius* (this feature is normally less well developed in *Washakius*, although it is variable).

Comparisons of UM 80652 with the type of *Washakius laurae* indicate that both represent the same taxon. It is interesting to note that both areas where *Washakius laurae* is now known represent basin margin environments, as is also the case for *W. izetti*. *Microsyops annectens* (see above), *W. laurae*, and *W. izetti* evidently preferred habitats away from the basin floor. The scarcity, at present, of localities that sample basin margin areas prevents a more definitive understanding of ecological and habitat differences among these taxa.

Superfamily ADAPOIDEA
Family ADAPIDAE
Subfamily Notharctinae
Smilodectes Wortman, 1903
Smilodectes mcgrewi Gingerich, 1979
Fig. 7A-B

Referred specimen.—UM 80644, left $P_{3\text{-}4}$, M_3.

Occurrence.—Wapiti III (NF-6).

Discussion.—Species of *Smilodectes* are based on size (Gingerich, 1979). North Fork specimens have the same dimensions as the type of *S. mcgrewi* reported by Gingerich (1979). This species is known from Bridger A faunas in Bridger Basin, and from the Gardnerbuttean in Huerfano Basin.

Measurements—UM 80644: $P_3 = 3.60 \times 2.60$, $P_4 = 4.20 \times 2.80$, $M_3 = 6.10 \times 4.00$.

Smilodectes gracilis (Marsh, 1871)
Fig. 7C-D

Referred specimen.—UM 80673, right M^1.

Occurrence.—Wapiti V (NF-4).

Discussion.—The paracone of this tooth is broken, but its square outline is clearly visible. There is a strong mesostyle and hypocone. These features are diagnostic of *Smilodectes* (Gingerich, 1979). UM 80673 is smaller than *S. mcgrewi* (Gingerich, 1979), and is referred to *S. gracilis*. This species is known from the middle Bridgerian.

Measurements—UM 80673: $M^1 = 4.40 \times 5.60$.

Order CONDYLARTHRA
Family HYOPSODONTIDAE
Hyopsodus Leidy, 1870
Hyopsodus miticulus Leidy, 1870

Referred specimens.—UM 80426, right M_2, left P^3; UM 80624, right dentary with P_4, M_2; UM 80626, left dentary with M_{1-2}; UM 80648, right M_2; UM 80844, five isolated teeth.

Occurrence.—Wapiti II (NF-1, 3, 12).

Discussion.—Three species of *Hyopsodus* are recognized from the Lostcabinian, *H. wortmani*, *H. miticulus*, and *H. walcottianus* (Gazin, 1968). These referred specimens from North Fork are assigned to *H. miticulus* based solely on size. Gazin (1968) was not able to recognize any consistent morphological differences distinguishing the three Lostcabinian species of *Hyopsodus*.

Measurements—UM 80426: $P^3 = 2.30 \times 3.60$, $M_2 = 4.60 \times 4.00$. UM 80624: $P_4 = 3.40 \times 2.40$, $M_2 = 4.10 \times 3.40$. UM 80626: $M_1 = 3.90 \times 3.00$, $M_2 = 4.00 \times 3.10$. UM 80844: $M^1 = 3.30 \times 4.50$, $M_2 = 4.20 \times 3.20$, $M_3 = 4.60 \times 3.10$.

Hyopsodus paulus Leidy, 1870

Referred specimen.—UM 80648, right M_2.

Occurrence.—Wapiti III (NF-6).

Discussion.—Gazin (1968) recognized two species of *Hyopsodus* from the early Bridgerian, *H. minusculus* (smaller) and *H. paulus* (larger). UM 80648 most closely resembles *H. paulus* in size.

Measurements—UM 80648: $M_2 = 4.60 \times 3.80$.

Hyopsodus minusculus Leidy, 1873
Fig. 8A-B

Referred specimens.—UM 80634, left dentary P_1-M_3; UM 80650, right P_4, M_2, M^3, left M_3, P^2, M^3.

Occurrence.—Wapiti V (NF-4).

Discussion.—These specimens fall within the size range of *H. minusculus* (Gazin, 1968), the smaller of the two *Hyopsodus* species from the early Bridgerian.

Measurements—UM 80634: $P_1 = 1.3 \times 1.2$, $P_2 = 2.0 \times 1.4$, $P_3 = 2.3 \times 1.7$, $P_4 = 2.9 \times 2.1$, $M_1 = 3.4 \times 2.7$, $M_2 = 3.5 \times 2.9$, $M_3 = 3.9 \times 2.4$. UM 80650: $P^2 = 2.0 \times 2.1$, $M^3 = 2.2 \times 3.0$.

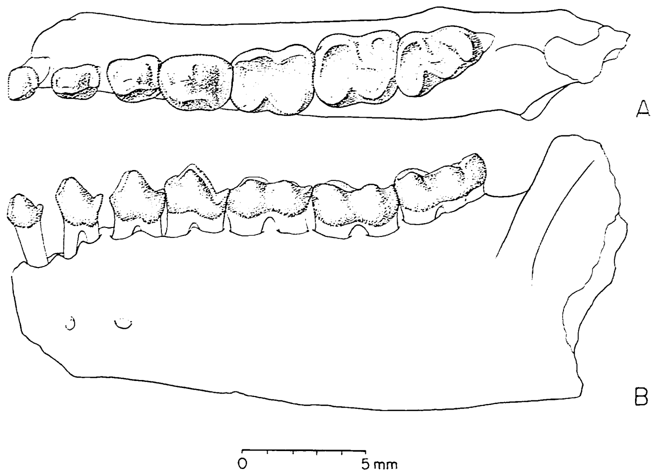

FIG. 8— Condylarthra from Wapiti Valley: *Hyopsodus minusculus*. A, UM 80634, left dentary with P_1-M_3 in occlusal view; B, same in buccal view.

Family PHENACODONTIDAE
Ectocion Cope, 1882
Ectocion cf. *E. superstes* Granger, 1915

Referred specimens.—YPM-PU 23947, left dentary with M_1; YPM-PU 23948, right dentary with P_3 talonid and P_4.

Occurrence.—Wapiti II (PU-B).

Description.—These specimens were found in miscellaneous collections from PU-B. P_3 has a strong, centrally placed hypoconid. P_4 is submolariform with a well developed entoconid and well separated protoconid and metaconid. These premolar characteristics are consistent with those developed in *E. superstes* (Thewissen, 1990). The teeth are smaller than samples of *E. superstes* from the Wind River Basin, but are larger than most specimens of *E. osbornianus* from the Bighorn Basin.

Measurements—YPM-PU 23948: $P_4 = 7.50 \times 5.20$.

Phenacodus Cope, 1873
Phenacodus vortmani (Cope, 1880)

Referred specimens.—UM 80843, left M_1; UM 80845, right M^2, left M^3, and a fragment of P_4.

Occurrence.—Wapiti II (NF-1, NF-9).

Discussion.—Two different sized species of *Phenacodus* occur in the Wapiti II fauna. *P. vortmani* is the smaller of the two (Thewissen, 1990).

Measurements—UM 80845: $M^2 = 7.70 \times 9.50$.

Phenacodus intermedius Granger, 1915

Referred specimens.—UM 80847, right M^2, incisor; miscellaneous teeth from PU-B including left P_4.
Occurrence.—Wapiti II (NF-1, PU-B).
Discussion.—These specimens were assigned to *Phenacodus intermedius* in a recent revision of phenacodontids by Thewissen (1990).
Measurements—P_4 = 13.60 × 8.60.

Order PANTODONTA
Family CORYPHODONTIDAE
Coryphodon Owen, 1845
Coryphodon sp.

Referred specimen.—UM 80622, right lower canine, and fragments of right P_3 and P^4.
Occurrence.—Wapiti II (NF-3).
Discussion.—*Coryphodon* is the largest mammalian taxon from North Fork. *Coryphodon* ranges throughout the Wasatchian in Wyoming, Colorado, and New Mexico.
Measurements—UM 80622: C_1 = 30.2 × 26.3, P_3 = 19.4 × 12.9.

Order TILLODONTIA
Family ESTHONYCHIDAE
Esthonyx Cope
Esthonyx cf. *E. acutidens* Cope, 1881

Referred specimen.—UM 80663, fragment of right P^4 and lower incisor.
Occurrence.—Wapiti II (NF-1).
Discussion.—The P^4 fragment most closely resembles that of the *E. spatularius- E. bisulcatus-E. acutidens* group (Gingerich and Gunnell, 1979). UM 80663 is larger than specimens of *E. spatularius* and *E. bisulcatus* and is provisionally referred to *E. acutidens*, which is known from Lostcabinian through early Bridgerian.

Trogosus Leidy, 1871
Trogosus sp.

Referred specimen.—UM 80645, fragment of I_2.
Occurrence.—Wapiti III (NF-6).
Discussion.—This incisor fragment belongs to one of the small species of *Trogosus*, perhaps *T. hillsii* or *T. castoridens* (Gazin, 1953). Measurement: I_2 length = 11.00.

Trogosus latidens (Marsh, 1873)
Figs. 9-10

Referred specimens.—UM 80651, left and right P_3 and M_1, left P^3, and fragments of left M^{1-3}; YPM-PU 16134, right I_2, P_4, M_3.
Occurrence.—Wapiti V (NF-4), Locality A-4 (South Fork) of Van Houten (1944).

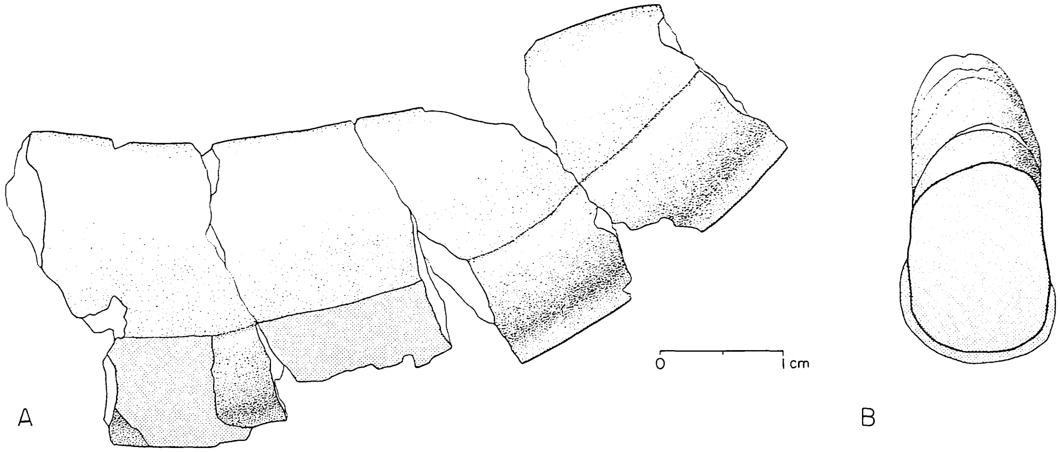

FIG. 9— Tillodontia from Wapiti Valley: *Trogosus latidens*. A, YPM-PU 16134, right I_2 in lateral view; B, same in mesial view.

Description.—These specimens are assigned to *T. latidens*, based on their large size. The preserved portions resemble the type of *T. ?latidens* (Gazin, 1953). The P_3 (Fig. 10F-G) paraconid and metaconid are small folds of enamel on the lingual flank of the protoconid. The talonid basin is deep but narrow anteroposteriorly, and is bordered by the protocristid and cristid obliqua, both of which lack cusp development. M_1 (Fig. 10D-E) is heavily worn, as is generally the case with tillodonts. P^3 (Fig. 10A-B) has a small hypocone and preprotocrista.

Measurements—UM 80651: P^3 = 16.5 × 17.6, P_3 = 13.6 × 9.8, M_1 = 21.2 × 17.6. YPM-PU 16134: I_2 mesial length = 19.1, distal length = 27.2, P_4 = 18.6 × 16.5, M_3 = 29.0 × 17.2.

Discussion.—*T. latidens* is poorly known. It has been previously reported from the Bridger Formation (Gazin, 1953; McGrew and Sullivan, 1970), from the western Bighorn Basin (Bown, 1982), from the *Palaeosyops borealis* Zone (Gardnerbuttean) in the Wind River Basin (Stucky and Krishtalka, 1983), and from a coal mine near the town of Princeton in southeastern British Columbia (Russell, 1935).

Order PERISSODACTYLA
Family EQUIDAE
Hyracotherium Owen, 1840
Hyracotherium sp. (small)

Referred specimen.—UM 83889, left P^2.

Occurrence.—Wapiti I (SF-2).

Discussion.—This specimen is similar to *Hyracotherium vasacciense* and *H. angustidens*. Both species have a P^2 of similar size (Kitts, 1956), and there are few morphological differences that distinguish them. This specimen is from South Fork, collected between the plant bearing beds (NF-14 equivalent) and the basal sheet-like sandstone (PU-A equivalent).

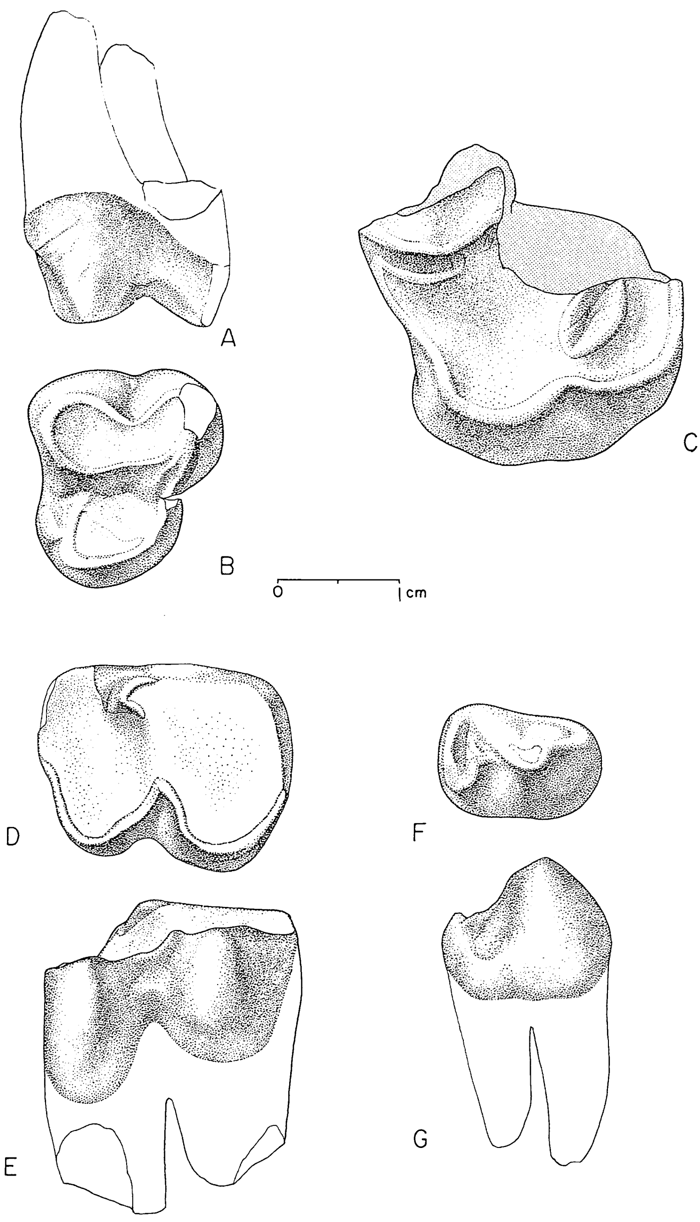

FIG. 10— Tillodontia from Wapiti Valley: *Trogosus latidens*. A, UM 80651, left P^3 in buccal view; B, same in occlusal view. C, UM 80651, left M^1 in occlusal view. D, UM 80651, right M_1 in occlusal view; E, same in buccal view. F, UM 80651, right P_3 in occlusal view; G, same in buccal view.

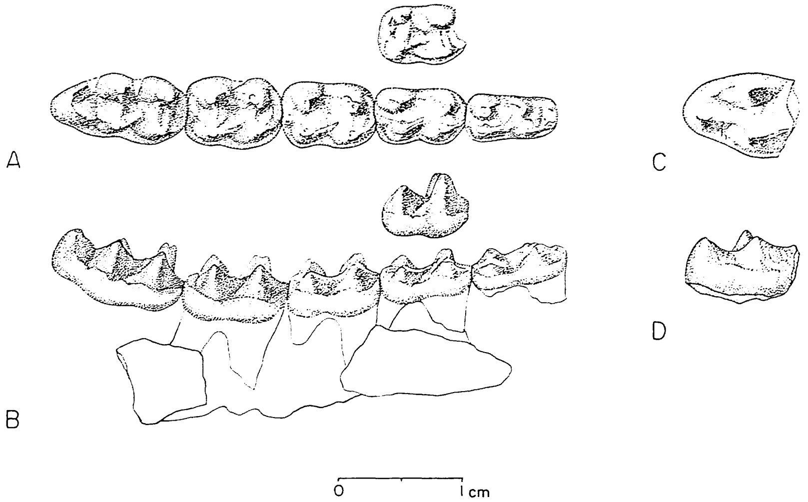

FIG. 11— Perissodactyla from Wapiti Valley: *Hyracotherium*. A, *Hyracotherium* cf. *H. venticolum*, YPM-PU 17319, right $dp_{3\text{-}4}$, right P_4 (above), and $M_{1\text{-}3}$ in occlusal view; B, same in buccal view. C, *H. craspedotum*, UM 80628, right M_3 talonid in occlusal view; D, same in buccal view.

Hyracotherium cf. *H. venticolum* (Cope, 1881)
Fig. 11A-B

Referred specimens.—UM 80419, right M_3, left $P^{3\text{-}4}$, and fragments; UM 80628, right M_1, P^3, left P^3, M^2, M_3; UM 80662, right M^1's (2), left M_1, P^4, M^3; UM 80842, right M^3; YPM-PU 17319, right $dP_{3\text{-}4}$, P_3-M_3.

Occurrence.—Wapiti II (NF-1, NF-2, NF-3, NF-9, PU-B).

Description.—The lower first molars resemble the type of *H. venticolum* (AMNH 4832). In the upper series, the premetaconule crista connects with the metacone, there is no mesostyle, the enamel is smooth, and the cingula are moderate. In general, these teeth fall into the small end of the size range of *H. venticolum* teeth from the Wind River Formation (Kitts, 1956). This taxon is restricted to the Lostcabinian.

Measurements—YPM-PU 17319: P_4 length = 6.80, M_1 = 7.60 × 5.50, M_2 = 7.90 × 5.75, M_3 = 10.65 × 5.60. UM 80628: P^3 = 6.3 × 7.8, M_1 = 8.5 × 5.9. UM 80662: P^4 = 7.3 × 8.9, M^3 = 8.5 × 9.8, M_1 = 8.3 × 6.0. UM 80419: P^3 = 7.3 × 7.8, P^4 = 7.9 × 8.7, M_3 = 11.4 × 5.8.

Hyracotherium cf. *H. craspedotum* Cope, 1880
Fig. 11C-D

Referred specimens.—UM 80662, right P_3; UM 80628, right M_3 fragment.

Occurrence.—Wapiti II (NF-1, NF-3).

Description.—These *Hyracotherium* teeth have crenulated enamel and large cingulids. Their size corresponds to *H. craspedotum* from the Lost Cabin Member of the Wind River Formation (Kitts, 1956).

Measurements—UM 80662: P_3 = 7.60 × 5.00.

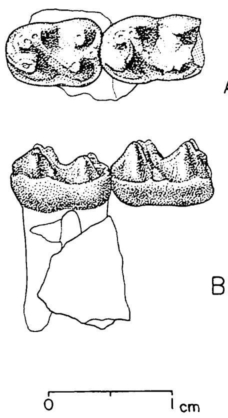

FIG. 12— Perissodactyla from Wapiti Valley: *Orohippus pumilus*. A, UM 80643, left dentary with M_{2-3} in occlusal view; B, same in buccal view.

Orohippus Marsh, 1872
Orohippus pumilus Marsh, 1871
Fig. 12A-B

Referred specimens.—UM 80643, left M_{2-3}; UM 80646, right proximal femur and left astragalus.

Occurrence.—Wapiti III (NF-6).

Description.—Tooth measurements of UM 80643 fall within the range of *O. pumilus* (Kitts, 1957). The astragalus (UM 80646) has trochlear ridges oblique to the long axis of the bone, typical of *Orohippus* (Kitts, 1957). The astragalus has a medial trochlear ridge that extends distally to join the dorsal margin of the distal navicular facet. This ridge does not extend as far distally and is separated from the distal navicular facet by a groove in *Hyracotherium*. The long axis of the navicular facet is oriented more dorsoplantarly than in *Hyracotherium* where this facet is oriented more mediolaterally. *Orohippus pumilus* is known from Bridger A and B (Gunnell and Bartels, in press).

Measurements—UM 80643: $M_2 = 7.80 \times 5.40$.

Family ISECTOLOPHIDAE
Cardiolophus Gingerich, 1991
Cf. *Cardiolophus semihians* (Cope, 1882)
Fig. 13A-B

Homogalax sp., Jepsen, 1939, p. 1914. Torres and Gingerich, 1983, p. 205.
Homogalax semihians, Torres, 1985, p. 91.

Referred specimens.—YPM-PU 17323, left dentary with P_4 alveolus and crowns of M_{1-3}; UM 80425, right tibia.

Occurrence.—Wapiti I (PU-A, NF-11).

Description.—YPM-PU 17323 represents a small isectolophid with a slender jaw, imperfect lophodonty, metaconid undivided, hypoconulid distinct, and talonid basin partially closed by an entocristid. The dimensions of M_{1-3} are slightly larger than those for typical *C. semihians*.

The dental morphology of YPM-PU 17323 resembles that of UM 64168 (*C. semihians*) from the late Graybullian (middle Wasatchian) of the Bighorn Basin. The latter is a dentary with

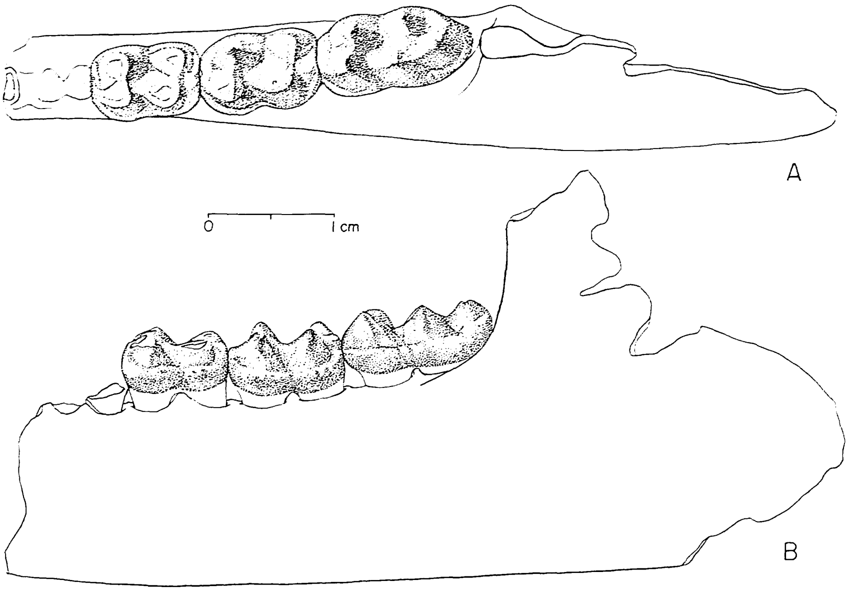

FIG. 13— Perissodactyla from Wapiti Valley: Cf. *Cardiolophus semihians*. A, YPM-PU 17323, left dentary with M_{1-3} in occlusal view; B, same in buccal view. This is possibly a lophodont *Hyracotherium* (the spacing of diastemata between C_1 and P_2 must be known for certain identification).

P_1(alveolus)-M_3, bearing the distinctive P_{1-2} diastema of *Cardiolophus* and *Homogalax* (Gingerich, 1991).

Measurements—YPM-PU 17323: $M_1 = 9.10 \times 6.35$, $M_2 = 9.50 \times 6.85$, $M_3 = 14.25 \times 6.80$.

Discussion.—Radinsky (1963) included only *Homogalax* (early Eocene) and *Isectolophus* (middle to late Eocene) in the family Isectolophidae. Gingerich (1991) proposed the genus *Cardiolophus* for early Eocene isectolophids that differed significantly from *Homogalax protapirinus*. The major distinguishing features between *Cardiolophus* and *Homogalax* are wider anterior diastemata (between canine and first premolar and between first and second premolars), weaker cheek tooth lophodonty, and transversely narrower upper cheek teeth in *Cardiolophus*.

The type specimen of *Cardiolophus semihians* (AMNH 4485) was collected by Wortman in the central Bighorn Basin, most likely from Graybullian or Lysitean beds (Gingerich, 1980, 1991). *C. semihians* is similar to YPM-PU 17323, except for the bilobate metaconid on M_1 and smaller size. The stratigraphic range of *Cardiolophus semihians* includes the late Graybullian (Wa-5) through Lysitean (Wa-6) and possibly Lostcabinian (Wa-7).

Family HELALETIDAE
Heptodon Cope, 1882
Heptodon posticus (Cope, 1882)
Fig. 14A-D

Referred specimen.—UM 79493, right M_x trigonid, mandibular symphysis.
Occurrence.—Wapiti II (NF-2).

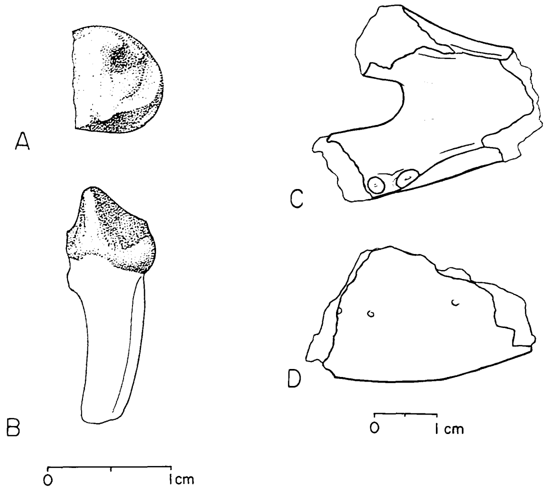

FIG. 14— Perissodactyla from Wapiti Valley: *Heptodon posticus*. A, UM 79493, right M_x trigonid in occlusal view; B, same in buccal view. C, UM 79493, symphysis in occlusal view; D, same in buccal view.

Description.—The trigonid of the molar has a notched protolophid. The paralophid is reduced and curves anteriorly forming a V shaped basin. UM 79493 compares favorably in size with the type of *H. posticus* (AMNH 4687). The alveolus of P_2 (UM 79493) is 8.60 mm in length, much longer than *H. calciculus*, and more like *H. posticus*, the larger of the two recognized *Heptodon* species (Radinsky, 1963).

Hyrachyus Leidy, 1871
Hyrachyus modestus (Leidy, 1870)
Fig. 15

Referred specimens.—UM 80638, right M^1 protoloph; UM 80657, talonid of P_4, M_2, trigonid of M_3.

Occurrence.—Wapiti III (NF-5) and Wapiti IV (NF-7).

Discussion.—UM 80638 is similar in size to *Hyrachyus modestus* from the Bridger Basin (Radinsky, 1967). It is larger than Bridger A specimens of *Hyrachyus* (McGrew and Sullivan, 1970), and smaller than *H. modestus* from the southeastern Absaroka Range (Bown, 1982). The preservation of this specimen is identical to UM 80657, the only specimen from NF-7. NF-7 is in the same drainage and a few meters above NF-5. It is possible that these two specimens are parts of the same individual.

Measurements—UM 80638: M_1 width = 13.60. UM 80657: M_2 width = 13.40.

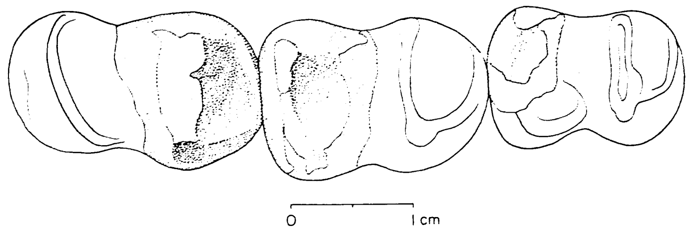

FIG. 15— Perissodactyla from Wapiti Valley: *Hyrachyus modestus*. A, UM 80657, right P_4 talonid, M_1 talonid, and M_2 trigonid in occlusal view. Even shading indicates broken tooth surface, white outline is reconstructed.

Family BRONTOTHERIIDAE
Lambdotherium Cope, 1880
Lambdotherium popoagicum Cope, 1880
Fig. 16A-D

Lambdotherium, Jepsen, 1939, p. 1914.

Referred specimens.—UM 80625, left M_2 talonid, fragments; UM 80661, unassociated left M_2, two M_3's, P^x, M^2; UM 83888, left M^1; YPM-PU 17316, left P_4, $M_{2\text{-}3}$; YPM-PU 17318, right M_3.

Occurrence.—Wapiti II (NF-1, NF-2, NF-3, PU-B).

Description.—These teeth agree in size and morphology with Wind River Basin *Lambdotherium* specimens (Osborn, 1929).

Measurements—UM 80661: $M^2 = 15.0 \times 16.1$, $M_2 = 13.1 \times 9.4$. YPM-PU 17316: $P_4 = 9.3 \times 7.2$, $M_2 = 12.3 \times 8.8$, $M_3 = 17.0 \times 8.6$. YPM-PU 17318: $M_3 = 16.7 \times 8.8$.

Discussion.—Although several species have been proposed for this genus, *Lambdotherium popoagicum* is presently considered to be the only valid species (Robinson, 1966; Stucky, 1982). *L. popoagicum* is restricted to the Lostcabinian and defines the *Lambdotherium* Range Zone in the Wind River Basin.

Eotitanops (Cope, 1880)
Eotitanops borealis (Cope, 1880)
Fig. 16E-H

Referred specimens.—UM 80659, right $M^{2?}$ fragment; UM 80627, left M^x fragment.

Occurrence.—Wapiti II (NF-2, NF-3).

Description.—UM 80659, probably an M^2 (Fig. 16G-H), preserves the paracone, parastyle, and a strong anterior cingula distinctive of *E. borealis* (Osborn, 1929). This specimen is larger than *E. gregoryi* (= *E. borealis* of Osborn, 1913), and most closely resembles the type of *E. borealis* both in size and morphology (Osborn, 1929). UM 80627 (Fig. 16E-F) is the lingual half of an upper molar, probably M^1. It is similar to *Eotitanops borealis* (AMNH 14887, Osborn, 1929).

Measurements—UM 80627: width across paracone and hypocone = 16.00.

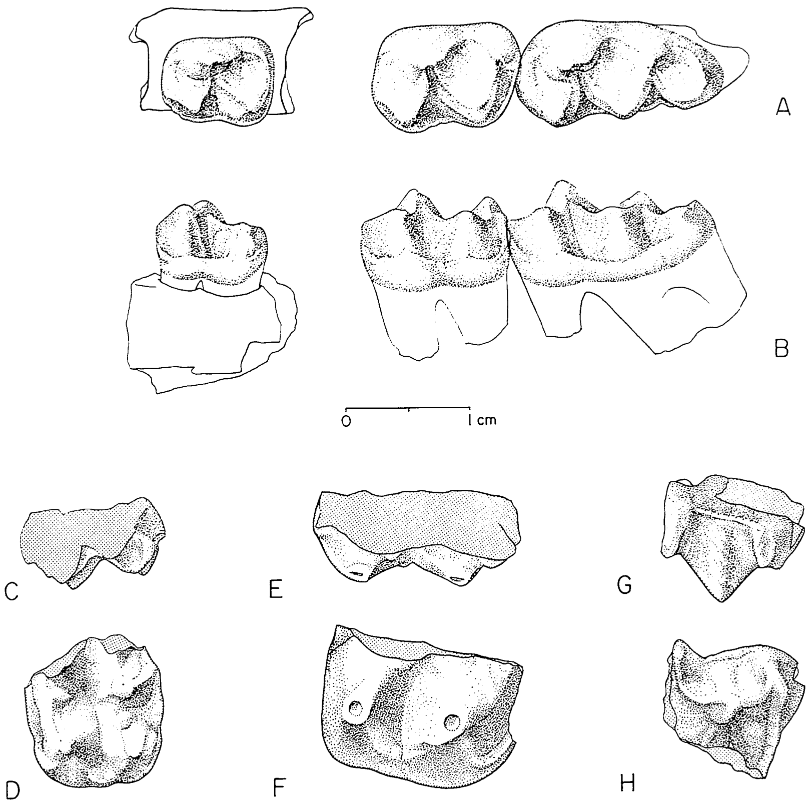

FIG. 16— Perissodactyla from Wapiti Valley. *Lambdotherium popoagicum*: A, YPM-PU 17316, left P_4 and $M_{2\text{-}3}$ in occlusal view; B, same in buccal view. C, UM 83888, broken left M^1 in buccal view; D, same in occlusal view. *Eotitanops borealis*: E, UM 80627, broken left M^x in buccal view; F, same in occlusal view. G, UM 80659, broken right M^2(?) in buccal view; H, same in occlusal view.

Palaeosyops Leidy, 1870
Palaeosyops fontinalis (Cope, 1873)
Fig. 17A-B

Referred specimen.—UM 80642, left and right broken M_3 fragments.

Occurrence.—Wapiti III (NF-6).

Description.—Two broken lower third molars represent *Palaeosyops*. One M_3 is well preserved, missing only the protoconid. It resembles *P. fontinalis* from the Huerfano Formation (Robinson, 1966), except the enamel is smoother and the overall size is smaller. This species is known from the Gardnerbuttean in Huerfano Basin and from Bridger A in the Bridger Basin (Gunnell and Bartels, in press).

Measurements—UM 80642: $M_3 = 36.30 \times 18.30$.

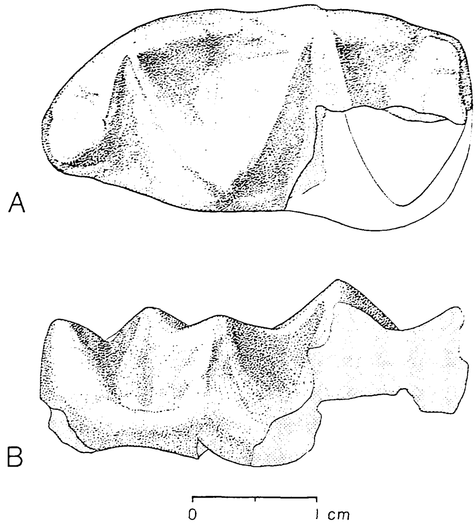

FIG. 17— Perissodactyla from Wapiti Valley: *Palaeosyops fontinalis*. A, UM 80642, broken right M_3 in occlusal view; B, same in buccal view. Even shading represents broken tooth surface, white outline is reconstructed.

Order ARTIODACTYLA
Family DICHOBUNIDAE
Diacodexis Cope, 1882
Diacodexis cf. *D. secans* (Cope, 1881)

Referred specimen.—UM 80756, left P_4, broken right M_1.

Occurrence.—Wapiti II (NF-1).

Description.—These teeth are within the size range of *Diacodexis secans*. Both P_4 and M_1 are relatively wide, a diagnostic character of *D. secans* (Guthrie, 1971). *Diacodexis* is known from the early Wasatchian (Sandcouleean) to Bridger B (Stucky, 1984b).

Measurements—UM 80756: $P_4 = 5.10 \times 3.00$.

Bunophorus Sinclair, 1914
Bunophorus sinclairi Guthrie, 1966

Referred specimens.—UM 80418, left P^4, right M_1; UM 80664, broken M_x and fragments.

Occurrence.—Wapiti II (NF-1, NF-9).

Description.—There are two *Bunophorus* species of similar size to these specimens, Lysitean *B. etsagicus* and Lostcabinian *B. sinclairi*. UM 80418 is similar to *B. sinclairi* in having incipient molar paraconids and in lacking a cristid obliqua (Stucky and Krishtalka, 1990).

Measurements—UM 80418: $M_1 = 7.50 \times 6.70$, $P^4 = 5.50 \times 6.60$.

Order CARNIVORA
Family VIVERRAVIDAE
Viverravus Marsh, 1872
Viverravus gracilis Marsh, 1872

Referred specimens.—UM 80623, right P_4; UM 80422, right dentary with M_1 talonid, M_2.

Occurrence.—Wapiti II (NF-3, NF-10).

Description.—These specimens match the size and morphology of *V. gracilis* from the Lost Cabin (Robinson, 1966). *V. gracilis* is known from the Lostcabinian and Bridgerian (Matthew, 1909).

Measurements—UM 80623: $P_4 = 5.20 \times 2.00$.

Didymictis Cope, 1875
Didymictis cf. *D. vancleveae* Robinson, 1966

Didymictis, Jepsen, 1939, p. 1914.

Referred specimen.—YPM-PU 14692, left M^2.

Occurrence.—Locality B-1 of Van Houten (1944), Bridgerian.

Description.—This upper molar is larger than *Didymictis altidens*, approaching *D. vancleveae* in size. M^2 has a distinct metacone as does the type of *D. vancleveae* (Robinson, 1966). The metacone is variably developed in *D. altidens*, and is normally quite small when present (Robinson, 1966).

Measurements—YPM-PU 14692: $M^2 = 7.2 \times 11.0$.

Family MIACIDAE
Vulpavus Marsh, 1871
Vulpavus cf. *V. australis* Matthew, 1915

Referred specimen.—UM 80427, right M^1 and M^x fragment.

Occurrence.—Wapiti II (NF-12).

Description.—UM 80427 is smaller than *V. canavus* (Guthrie, 1971) and is tentatively referred to *V. australis*. M^1 resembles *V. australis* (Gazin, 1962) in both morphology and size.

Measurements—UM 80427: $M^1 = 4.80 \times 6.80$.

Order RODENTIA
Family PARAMYIDAE
Subfamily Paramyinae
Paramys Leidy, 1871
Paramys copei, Leidy, 1907
Fig. 18A-D

Referred specimens.—YPM-PU 17322, left dentary with P_4-M_2; YPM-PU 23404, right M_2 and unassociated incisors; UM 80633, left P^4-M^3.

Occurrence.—Wapiti II (PU-B); Wapiti V (NF-4).

Description.—These specimens resemble *P. copei* (Wood, 1962) in size and morphology. The upper molars (Fig. 18C-D) are like those in *P. copei* in having hypocones on M^{1-2}, but

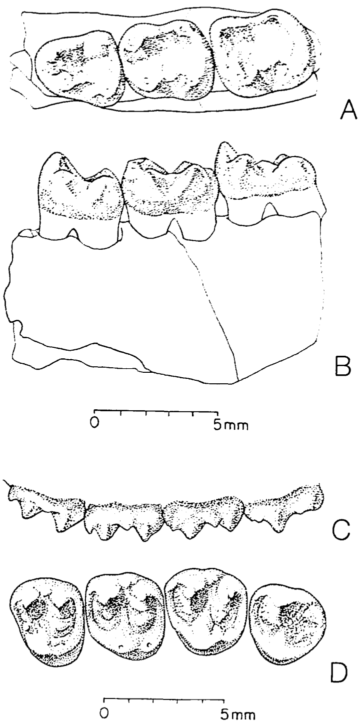

FIG. 18— Rodentia from Wapiti Valley: *Paramys copei*. A, YPM-PU 17322, left dentary with P_4-M_2 in occlusal view; B, same in buccal view. C, UM 80633, left P^4-M^3 in buccal view; D, same in occlusal view.

lacking this cusp on P^4 and M^3. The enamel has minor crenulations. The stratigraphic range of *P. copei* is Clarkforkian through Bridger B (Korth, 1984; Wood, 1962).

Measurements—YPM-PU 17322: $P_4 = 3.20 \times 3.00$, $M_1 = 3.50 \times 3.40$, $M_2 = 3.90 \times 3.30$. YPM-PU 23404: $M_2 = 3.70 \times 3.70$. UM 80633: $P^4 = 3.00 \times 3.50$, $M^1 = 3.40 \times 3.60$, $M^2 = 3.30 \times 3.70$, $M^3 = 3.20 \times 3.20$.

Paramys delicatus Leidy, 1873

Referred specimen.—UM 80647, incisor and left M^2.

Occurrence.—Wapiti III (NF-6).

Description.—UM 80647 is a large, square tooth of a typical *Paramys delicatus* pattern with a prominent hypocone and enamel surface pitting. The incisor is heavily built and convex labially with the enamel covering 1/3 of the distal side. UM 80647 falls within the upper size range of *Paramys delicatus* (Wood, 1962).

Measurements—UM 80647: $M^2 = 4.70 \times 5.00$.

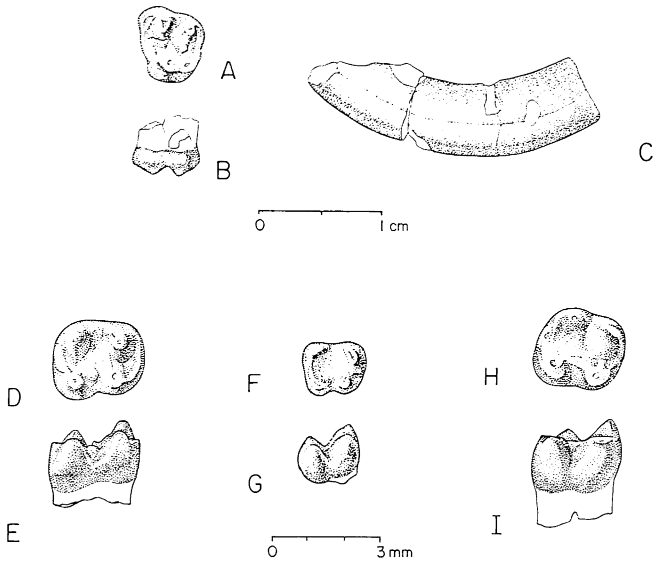

FIG. 19— Rodentia from Wapiti Valley. *Pseudotomus* cf. *P. robustus*: A, UM 80653, left M^2 in occlusal view; B, same in lateral view. C, UM 80653, lower incisor in lateral view. *Knightomys* cf. *K. huerfanensis*: D, UM 80654, right M_2 in occlusal view; E, same in buccal view. *Knightomys* cf. *K. depressus*: F, UM 80655, left P_4 (reversed) in occlusal view; G, same in buccal view. Reithroparamyinae indet.: H, UM 80636, right M_1 in occlusal view; I, same in buccal view.

Pseudotomus Cope, 1872
Pseudotomus cf. *P. robustus* (Marsh, 1872)
Fig. 19A-C

Referred specimens.—UM 80653, incisor and left M^2; UM 80715, right M_1.

Occurrence.—Wapiti V (NF-4, NF-15).

Description.—M^2 has an incipient hypocone, a single protoconule, and a double metaconule. M_1 has an incomplete metalophid and the entoconid is distinct and continuous with the posterior cingulum. The incisor is massive, convex labially, triangular in cross section, and has an enamel band extending one-quarter of the width up the lateral side (Wood, 1962).

Measurements—UM 80653: $M^2 = 5.20 \times 5.50$. UM 80715: $M_1 = 5.70 \times 5.70$.

Discussion.—*Pseudotomus* is quite similar to *Ischyrotomus* (Dawson, 1968; Bown, 1982; Eaton, 1982). However, these Wapiti Valley specimens are more comparable with *Pseudotomus*. M^2 is similar to cf. *Pseudotomus* sp. (Bown, 1982; Dawson, 1968). M_1 and the incisor are similar to *Pseudotomus robustus* (Wood, 1962). In the Bighorn Basin, *P. robustus* is known from the Aycross Formation (Bown, 1982), from the South Fork of the Shoshone River (Locality A-5, Van Houten, 1944; Bown, 1982), and from Carter Mountain (Eaton, 1982). *Pseudotomus* ranges through the Bridgerian.

Subfamily Reithroparamyinae
Reithroparamyinae indet.
Fig. 19H-I

Referred specimen.—UM 80636, right M_1.

Occurrence.—Wapiti V (NF-4).

Description.—This M_1 is somewhat similar to *Acritoparamys atwateri*, a reithroparamyine from the late Clarkforkian and early Wasatchian. It differs from *A. atwateri* in having a higher crown, in having a better developed cristid between the protoconid and hypoconid, and in having conspicuous ridges at the inner base of the protoconid (see Ivy, 1990).

Measurements—UM 80636: $M_1 = 2.30 \times 2.10$.

Family SCIURAVIDAE

Knightomys Gazin, 1961

Knightomys cf. *K. huerfanensis* (Wood, 1962)

Fig. 19D-E

Referred specimen.—UM 80654, right M_2.

Occurrence.—Wapiti V (NF-4).

Description.—UM 80654 is an unworn and characteristic tooth of *Knightomys*. It shares similar morphology and size with *K. huerfanensis* (Korth, 1984). Diagnostic features include: a cuspate crown, the separation of the anterior cingulum from the protoconid and metaconid, a well-developed but incomplete hypolophid, and a prominent posterior cingulum and mesoconid. *K. huerfanensis* is known from the Lostcabinian through Bridger B.

Measurements—UM 80654: $M_2 = 2.50 \times 2.00$.

Knightomys cf. *K. depressus* (Loomis, 1907)

Fig. 19F-G

Referred specimen.—UM 80655, left P_4.

Occurrence.—Wapiti V (NF-4).

Description.—This tooth is very similar to *Knightomys depressus* (Korth, 1984). It is large for *K. depressus*, but not out of the range exhibited among Wind River Basin specimens of that species (Korth, 1984).

Measurements—UM 80655: $P_4 = 1.70 \times 1.40$.

AGE AND CORRELATION OF WAPITI VALLEY FAUNAS

Five successive faunas appear to be represented in Wapiti Valley. These are numbered, from oldest to youngest, Wapiti I through Wapiti V (Table 1). Three of the faunas are still poorly known, but even these appear to have a distinctive taxon of some importance biostratigraphically.

Wapiti I local fauna

The Wapiti I local fauna is the lowest stratigraphically in the Willwood Formation, and it is thus the oldest here. Wapiti I includes two mammalian species:

Hyracotherium sp. (small)
Cf. *Cardiolophus semihians*

Small *Hyracotherium* is common through much of the Wasatchian land-mammal age. *Cardiolophus semihians* has a stratigraphic range from middle through late Wasatchian (Gingerich, 1991). *Cardiolophus* is known from Lysitean-age faunas (Wasatchian zone Wa-6) in the Bighorn Basin, but it is not certain that the genus ranges into Lostcabinian (Wa-7) time.

Lostcabinian isectolophids are generally more lophodont than the Wapiti Valley specimen, and it is possible that the Wapiti I fauna is Lysitean in age instead of Lostcabinian, however it is also possible that this cf. *Cardiolophus* is really an unusually lophodont Lostcabinian *Hyracotherium*. *Cardiolophus* and *Hyracotherium* are sometimes difficult to distinguish without knowing the relative positions of anterior premolars and diastemata. NF-14, which lies below the beds yielding *Cardiolophus*, contains plants that closely resemble middle Eocene floras in both morphology and size (Wing, pers. comm., 1982). Considering the limited evidence available, Wapiti I is regarded as Lysitean or Lostcabinian in age.

Wapiti II local fauna

The Wapiti II local fauna from the Willwood Formation includes the following species:

Lepisosteus sp.
Trionychidae indet.
Emydidae indet.
Hadrianus sp.
Xestops sp.
Crocodylidae indet.
Pristichampsus vorax
Allognathosuchus sp.
Diplocynodon sp.
Scenopagus curtidens
Microsyops scottianus
Cf. *Elwynella oreas*
Loveina wapitiensis
Hyopsodus miticulus
Ectocion cf. *E. superstes*
Phenacodus vortmani
Phenacodus intermedius
Coryphodon sp.
Esthonyx cf. *E. acutidens*
Hyracotherium cf. *H. venticolum*
Hyracotherium cf. *H. craspedotum*
Heptodon posticus
Lambdotherium popoagicum
Eotitanops borealis
Diacodexis cf. *D. secans*
Bunophorus sinclairi
Viverravus gracilis
Vulpavus cf. *V. australis*
Paramys copei

Loveina wapitiensis is an advanced species, intermediate between *Loveina zephyri* and *Shoshonius*-*Washakius*. The co-occurrence of *Loveina*, *Coryphodon*, *Heptodon*, *Lambdotherium*, and *Eotitanops*, and the absence of *Palaeosyops*, *Trogosus*, and *Hyrachyus*, provide the best age information for this fauna.

The brontotheriid *Eotitanops borealis* (= *Palaeosyops borealis* of Stucky, 1984a) also occurs in the Wapiti II assemblage. In the Wind River Basin, *E. borealis* only occurs above *Lambdotherium* bearing beds, except at one enigmatic locality (USNM Locality 48FR65, see Stucky, 1984a, and also Gunnell, 1989). In the Wind River Basin, the lower boundary of the *Palaeosyops borealis* Assemblage Zone is marked by the first occurrence of *P. borealis*, *Trogosus*, and *Hyrachyus*. In Wapiti Valley, *Trogosus*, *Hyrachyus*, and *Palaeosyops fontinalis* first occur about 100 meters above *Eotitanops borealis* bearing beds. Two possibilities may explain the co-occurrence of *Eotitanops* and *Lambdotherium*: either *E. borealis* occurs in the Wasatchian of Wapiti Valley, or *Lambdotherium*, *Heptodon* (but not necessarily *Loveina*) range into the Bridgerian in Wapiti Valley. We take the first appearances of *Palaeosyops fontinalis*, *Trogosus*, and *Hyrachyus* to mark the lower boundary of the Bridgerian in Wapiti Valley, and assume that *E. borealis* appears in the latest Wasatchian. *Eotitanops* has also been found with *Loveina* at locality VII in the Huerfano Basin (Robinson, 1966), suggesting that *Eotitanops* occurs in the Wasatchian of Colorado as well.

Wapiti II faunas correlate with the lower faunal interval (locality VII) of the Huerfano Formation of southern Colorado (Robinson, 1966), the *Lambdotherium* Range Zone of Red Creek, Deadman Butte, and Buck Spring areas of the Wind River Basin (Stucky, 1984b), and Lost Cabin beds of the central Bighorn Basin (Schankler, 1980). The presence of *Eotitanops*, along with the advanced character of *Loveina wapitiensis*, indicates either that Wapiti II was younger than other typical Lostcabinian faunas or that basin margin faunas differed in composition from central basin faunas.

Wapiti III local fauna

The Wapiti III local fauna in the Willwood Formation includes:

Lepisosteus sp.
Trionychidae indet.
Emydidae indet.
Hadrianus sp.
Pristichampsus vorax
Allognathosuchus sp.
Microsyops cf. *M. elegans*
Smilodectes mcgrewi
Hyopsodus paulus
Trogosus sp.
Orohippus pumilus
Hyrachyus modestus
Palaeosyops fontinalis
Paramys delicatus

The Wapiti III fauna is interpreted as Gardnerbuttean (Bridgerian middle Eocene, zone Br-1), based on the first occurrence of *Trogosus*, *Palaeosyops* (in the sense of *Palaeosyops fontinalis*), *Hyrachyus*, and *Smilodectes*. *Microsyops elegans* replaces *Microsyops scottianus* in and above Wapiti III. *Smilodectes* is known from upper beds of the Huerfano Formation (Gardnerbuttean) in Colorado, and from Bridger A and B beds in southwestern Wyoming (*Smilodectes* has also been reported from the middle Wasatchian of New Mexico, represented by a single specimen, see Beard, 1988). *Smilodectes mcgrewi* appears in the Gardnerbuttean and Bridger A, and is replaced by *Smilodectes gracilis* in Bridger B (Gingerich, 1979). *Smilodectes mcgrewi* is represented in Wapiti III, and *Smilodectes gracilis* is present in the Wapiti V fauna.

Paramys delicatus, also found in Wapiti III, is a large, distinctive rodent restricted to the Bridgerian (Wood, 1962). *Orohippus pumilus* is known from various early Bridgerian sections: from the Aycross Formation in the Wind River Basin, from the Cathedral Bluffs Tongue of the Wasatch Formation, and from the Bridger Basin (Stucky, 1984b).

Wapiti IV local fauna

The Wapiti IV local fauna in the Aycross Formation includes a single species:

Hyrachyus modestus

Hyrachyus first appears in the earliest Bridgerian (Gardnerbuttean) and ranges through the Bridgerian in North America. The interpretation of the Wapiti IV fauna as Bridger A is based solely on relative stratigraphic position, with Wapiti IV being in a different formation lying above an unconformity that overlies the Gardnerbuttean Wapiti III fauna.

Wapiti V local fauna

The Wapiti V local fauna from the top of the Aycross Formation is separated from Wapiti IV by more than 100 meters of unfossiliferous strata. This fauna includes:

Lepisosteus sp.
Trionychidae indet.
Emydidae indet.
Crocodylidae indet.
Microsyops cf. *M. elegans*
Washakius laurae
Smilodectes gracilis
Hyopsodus minusculus
Trogosus latidens
Paramys copei
Pseudotomus cf. *P. robustus*
Reithroparamyinae indet.
Knightomys cf. *K. huerfanensis*
Knightomys cf. *K. depressus*

Smilodectes gracilis, *Washakius laurae*, *Trogosus latidens*, *Pseudotomus* cf. *P. robustus*, and *Knightomys* cf. *K. huerfanensis*, indicate a middle Bridgerian (Bridger B, Br-2) age for the Wapiti V fauna. *Washakius laurae* is also known from Bridger B near Tabernacle Butte (McGrew, 1959).

Figure 20 summarizes correlation of Wapiti Valley local faunas to faunas of similar age in the Huerfano Basin of Colorado and the Bridger, Wind River, and Bighorn Basins of Wyoming.

DISCUSSION

Wapiti Valley faunas are important because this is one of relatively few sections where the Wasatchian-Bridgerian transition from the early to middle Eocene has been studied. The Wapiti Valley section is not as fossiliferous as one might like, but it has yielded diagnostic late Wasatchian, early Bridgerian, and middle Bridgerian mammalian remains. This faunal succession shows that Willwood deposition extended into early Bridgerian middle Eocene time on the western margin of the Bighorn Basin, and it also shows that deposition of the Wapiti Formation did not begin here until middle Bridgerian time. We now know from mammalian stratigraphy that earliest middle Eocene (Early Bridgerian) Aycross Formation envelops blocks

<table>
<tr><th colspan="2">LAND MAMMAL AGE/SUBAGE</th><th>Huerfano Basin
Huerfano Fm.</th><th>Bridger Basin</th><th>Wind River Basin
Wind River Fm.</th><th>Bighorn Basin
Willwood Fm.</th><th>Wapiti Valley</th><th>Biostratigraphic Zone</th></tr>
<tr><td rowspan="3">BRIDGERIAN</td><td rowspan="2">Blacksforkian</td><td rowspan="2"></td><td>Bridger B
Bridger Fm.</td><td rowspan="2"></td><td rowspan="3"></td><td>Wapiti V
Aycross Fm.</td><td>Br-2</td></tr>
<tr><td>Bridger A
Bridger Fm.</td><td>Wapiti IV
Aycross Fm.</td><td rowspan="2">Br-1</td></tr>
<tr><td>Gardner-buttean</td><td>Upper Faunal Zone</td><td>Desertion Point Beds
Wasatch Fm.</td><td>Palaeosyops borealis Assemblage Zone</td><td>Wapiti III
Willwood Fm.</td></tr>
<tr><td rowspan="2">WASATCHIAN</td><td rowspan="2">Lostcabinian</td><td rowspan="2">Lower Faunal Zone</td><td rowspan="2"></td><td rowspan="2">Lambdotherium Range Zone</td><td rowspan="2">Upper Heptodon Range Zone</td><td>Wapiti II
Willwood Fm.</td><td>Wa-7</td></tr>
<tr><td>Wapiti I</td><td>Wa-6?</td></tr>
</table>

FIG. 20— Correlation chart of Wapiti Valley Faunas. Wapiti faunal horizons are compared to correlative horizons in the Huerfano Basin in southern Colorado (Robinson, 1966), the Bridger Basin in southwestern Wyoming (Gunnell and Bartels, in press), the Wind River Basin in south-central Wyoming (Stucky, 1984a,b), and the Bighorn Basin in northwestern Wyoming (Schankler, 1980).

of Paleozoic limestone constraining the age of the Heart Mountain detachment fault to be earliest middle Eocene as well (Torres, 1985).

Wapiti Valley faunas are also important because they are sampled from basin margin environments that remain poorly documented. Relatively few studies of the North American Eocene have included faunas in basin margin or upland environments (see, for example, McGrew, 1959; McKenna, 1980; Bown, 1982; Eaton, 1982; and Honey, 1990). These studies demonstrate that differences existed between basin floor and basin margin faunas, differences that have more to do with the distribution of animals in ecological zones than with any evolutionary difference. Studies of distal or high floodplain facies indicate that ecological differences and habitat preferences within basin floor environments also affect faunal composition (Winkler, 1983; Gingerich, 1989; Bown and Beard, 1990; Gunnell, 1993). The presence of *Loveina wapitiensis*, *Washakius laurae*, and *Microsyops annectens*, as well as the early appearance of *Eotitanops borealis*, in Wapiti Valley faunas may reflect such habitat preferences. Much more work on basin margin faunas will be required to understand the composition and distribution of faunas across habitat zones.

The Willwood Formation in Wapiti Valley is lacustrine, deltaic, and paludal at its base, and passes upward into fluvial deposits. Locality NF-14, an extensive plant site near the base of the Willwood, represents swamp and marsh beds developed on delta plains. The lowest vertebrate localities, PU-A and NF-11, are in massive multistory sheet sandstone bodies, interpreted as deposits of meandering streams within in a slowly subsiding basin. Overbank mudstones increase in thickness at higher levels in the Willwood Formation. Fossils occur preferentially in paleosols developed on overbank deposits (as at localities NF-2, NF-3, NF-5, NF-10, NF-12, NF-13, NF-16, and NF-17), or overbank deposits with clear influence of small (tributary?) channels (as at NF-1, NF-6, NF-8, and NF-9). Localities NF-11 and PU-A are interpreted as upper point-bar deposits. Individual channel sandstones high in the section are similar to those of the basal sheet sandstone complex (PU-A level). This suggests that the environment may have been constant through deposition of the fluvial Willwood but that sedimentation rates increased into the middle Eocene. Gardnerbuttean middle Eocene deposits of the upper Willwood Formation resemble those of the Lostcabinian lower Willwood lithologically, but the Gardnerbuttean beds are somewhat more strongly variegated, perhaps reflecting more mature paleosol development and lower sedimentation rates (Bown and Kraus, 1987).

Depositional interpretation of the Aycross Formation is difficult given the poor preservation of sedimentary structures. It is clear from included debris that Absarokan volcanism was prevalent at the time of Aycross deposition. Our general interpretation of Aycross fossil sites is that they represent braided stream deposits (NF-4, NF-7, and NF-15). The basal part (Bridger A?) of the Aycross Formation is characterized by green volcaniclastic sediments. The first appearance of Bridger B taxa occurs above a unfossiliferous interval over 100 meters thick. Bridger B sediments occur near the base of Jim Mountain in brown and green tuffaceous sandstones, mudstones, and conglomerates that suggest a fluvial volcaniclastic environment.

Paleoecological interpretation in Wapiti Valley is mostly derived from reptiles. The lower vertebrate portion of the Wapiti Valley fauna is dominated by large, aquatic taxa. The abundance and diversity of these forms (*Lepisosteus*, trionychids, emydids, *Diplocynodon*, and *Allognathosuchus*) suggest the presence of significant numbers of small lakes and large stream channels during the late early Eocene. Terrestrial lower vertebrates (lizards, testudinids, and perhaps *Pristichampsus*) are far less abundant, suggesting either the restriction of well drained environments or the existence of poor preservational conditions on the floodplain. Annual rainfall was probably high. The occurrence of both crocodiles and alligatorids suggest warm subtropical temperatures in the Lostcabinian and early Bridgerian (see Bartels, 1983).

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