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# A Wyoming succession of Paleocene mammal-bearing localities bracketing the boundary between the Torrejonian and Tiffanian North American Land Mammal “Ages”

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## **ABSTRACT**

A succession of fossil localities from the Hanna Basin, south-central Wyoming, brackets the boundary between Torrejonian and Tiffanian North American Land Mammal “Ages” (NALMAs). Unusually high rates of deposition in mid-Paleocene time in the Hanna Basin led to a greatly expanded section relative to classic mid-Paleocene sedimentary accumulations. Outcrops of the Hanna Formation, in an area of badlands in the northeast corner of the Hanna Basin called “The Breaks,” yield abundant vertebrate fossils. Mammalian fossils from a 550 m-thick interval in The Breaks document the latest Torrejonian (To3) through middle Tiffanian (Ti3) NALMAs. A 55 m-thick overlap zone between faunas typical elsewhere of To3 or earliest Tiffanian (Ti1) lies centrally within this interval.

The entire overlap zone in The Breaks represents the earliest parts of Ti1 as based upon presence of *Plesiadapis praecursor* and *Nannodectes intermedius*, index taxa for the Tiffanian. This does not affect the traditional definition of the To–Ti boundary. It does, however, extend ranges of several mammals typically considered exclusively Torrejonian into early Tiffanian time.

The mammalian fauna from The Breaks is one of the most diverse earliest Tiffanian faunas yet described, with 72 species of mammals recognized. The high diversity facilitates correlation with less diverse faunas of western North America. This is especially valuable for faunas of late Torrejonian or early Tiffanian age that lack critical index taxa (i.e., members of the Plesiadapidae) necessary for assigning a definitive age to the fauna. Furthermore, recognition of an overlap zone, the fauna of which is formally defined as The Breaks local fauna, within earliest parts of Ti1 provides greater age resolution for faunas near the Torrejonian–Tiffanian boundary. The greater detail about first and last appearances of mammalian species near the To–Ti boundary has resulted in complications to biostratigraphic zonation that have been undetectable elsewhere in thinner sections.

**KEY WORDS:** Torrejonian, Tiffanian, North American Land Mammal “Ages”, Hanna Basin, Wyoming, vertebrate paleontology.

## **INTRODUCTION**

### **Geologic Setting**

The Hanna Basin is a small but complex structural basin that formed in south-central Wyoming during the Laramide orogeny (Late Cretaceous through early Eocene; Lillegraven and Eberle, 1999; Fig. 1). The Hanna Basin lies on the southeastern

flank of the Sweetwater arch, structural subdivisions of which mark the northern boundary of the basin (Burris, 2001). Rocks ranging in age from Pennsylvanian into early Tertiary (Paleocene and earliest Eocene), and also some remnants of younger depos-

its that may be Neogene in age (Lillegraven and Snoke, 1996), lie within the Hanna Basin. The total thickness of Phanerozoic strata is nearly 13 kilometers, with all but about one kilometer representing Cretaceous and younger deposits (Lillegraven and Snoke, 1996). The three kilometer-thick Hanna Formation is the result of uplift and erosion of mountain ranges adjacent to the subsiding Hanna Basin during the peak of local Laramide tectonism (Lillegraven and Snoke, 1996). Organic-rich floodplain deposits and fine-grained facies of alluvial fans dominate its strata (Knight, 1951; Hansen, 1986), which represent deposition from middle Paleocene to late Paleocene or early Eocene (Lillegraven and Snoke, 1996). The present research focuses on the Hanna Formation from its local base to a stratigraphic level of about 1,980 m (6,500 ft; Fig. 2). This part of the Hanna Formation

is well exposed in the northeastern corner of the Hanna Basin in an area of badlands known as The Breaks.

Near the middle of the section exposed in The Breaks is a zone in which numerous vertebrate fossil localities have been discovered. This zone, termed the Vertebrate Fossil-Bearing Zone (VFBZ), begins about 975 m (3,200 ft) above the local base of the Hanna Formation. The VFBZ is approximately 550 m (1,800 ft) thick and is traceable laterally for approximately five kilometers within The Breaks. There is no obvious lithologic explanation for this stratigraphically restricted distribution of vertebrate fossils. However, there is evidence for loss of vertebrate fossils through the diagenetic activity of uranium roll-front geochemical cells in groundwater (Higgins, 1999).

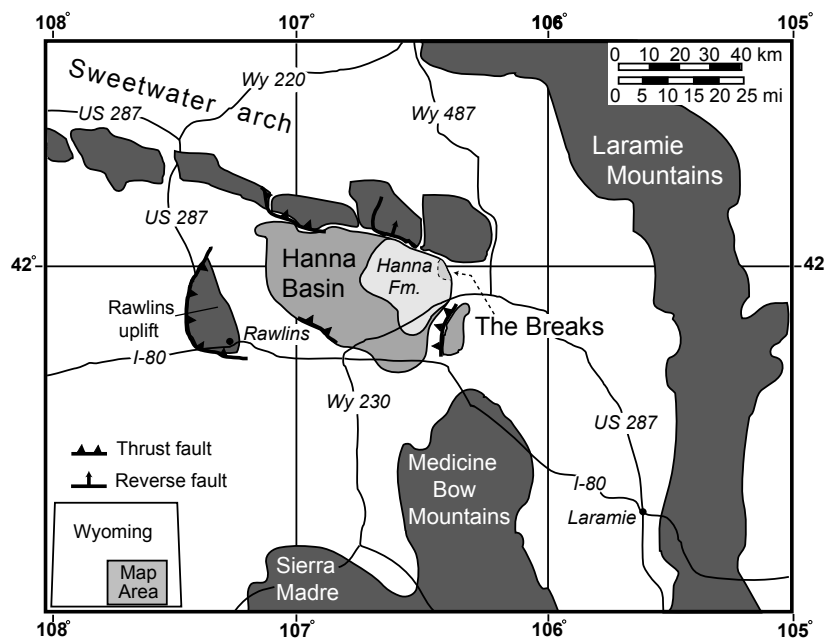
One hundred and forty vertebrate-fossil localities have been recorded from the VFBZ; of these,

61 have yielded mammalian fossils identifiable to the generic or specific level. Early analysis of the mammalian fossils by Secord (1996) suggested that the fauna from The Breaks lies close to the boundary between the Torrejonian (To) and Tiffanian (Ti) North American Land Mammal "Ages" (NALMAS). The present study documents that mammalian faunas from The Breaks indeed bracket the To-Ti boundary.

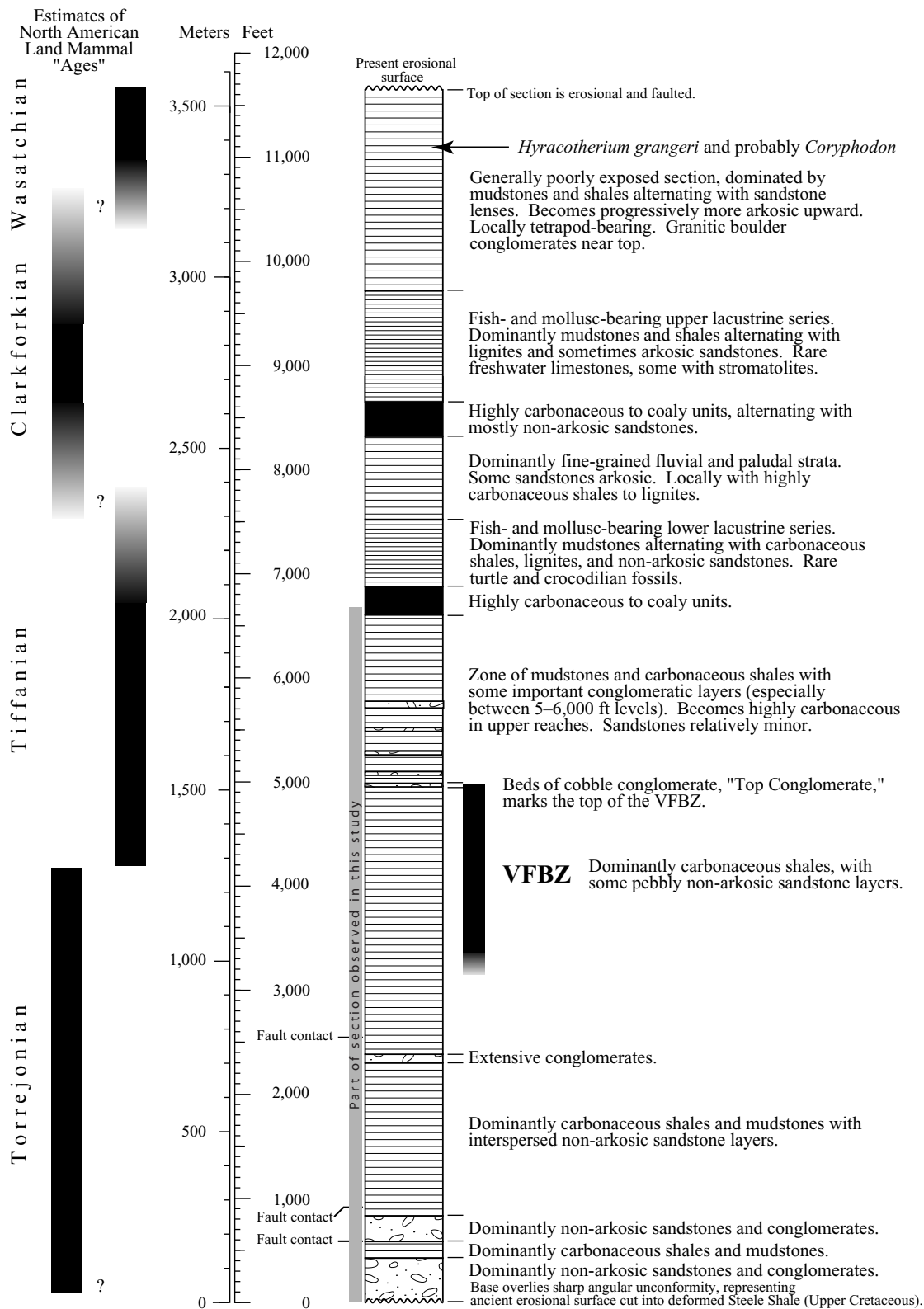
### Previous Analyses of To-Ti Transition

The Torrejonian and Tiffanian NALMAS were originally defined based upon mammalian faunas collected from the San Juan Basin (Wood et al., 1941). Subsequently, Archibald et al. (1987) and Williamson (1996) have revised the definitions of the Torrejonian NALMA and its subdivisions. Williamson (1996) established six biochronologic divisions of the Torrejonian based upon faunas from the San Juan Basin. The sixth, and youngest, he termed the M-zone, which he defined as the interval beginning with the first appearance of *Mixodectes pungens*. Williamson (1996) noted that no fossil vertebrates have been discovered in the Nacimiento Formation above the M-zone. For this reason, he did not define the top of the M-zone, nor did he define the To-Ti boundary on a paleontological basis within his measured sections. He suggested that the top of the M-zone is open for redefinition using fossils from overlying tongues of the Animas Formation in the northern San Juan Basin.

Gingerich (1976) described transitional faunas of To-Ti age from the Crazy Mountains Basin, Montana that yielded highly abundant fossils of plesiadapid



**Figure 1.** Location map for south-central Wyoming showing position of The Breaks and Hanna Basin.



**Figure 2.** Generalized composite section of Hanna Formation in vicinity of The Breaks. Note approximate placement of boundaries between adjacent NALMAs (shading indicates uncertainty). VFBZ = strata comprising Vertebrate Fossil-Bearing Zone (described in text). Adapted from Lillegraven and Snoke (1996) and Burris (1998).

primates. Based on the stratigraphic relationships among species, he devised a plesiadapid phylogeny. He used this phylogeny to propose a faunal zonation of latest Torrejonian through earliest Tiffanian with seven zones, two in the Torrejonian and five in the Tiffanian, each with an estimated duration of about one million years. Gingerich (1976) used the presence of *Plesiadapis* to indicate localities that were Tiffanian in age. Archibald et al. (1987) revised the definition of the Tiffanian NALMA “. . . to include faunas that occur during the time between the first appearance of the plesiadapid primate, *Plesiadapis*, and the first appearance of the Rodentia.”

Ideally, such single-taxon definitions make it simple and objective to determine the biostratigraphic position of a fossil locality relative to a particular biostratigraphic boundary (e.g., the To–Ti boundary; Woodburne, 1987, 1996). In practice, however, index taxa may be absent from a locality for reasons other than the age of the locality, making assignment of the correct NALMA difficult. Other taxa may be used to recognize the relative age of a locality. However, when dealing with a stratigraphically superposed succession of localities, the defining taxon is needed to absolutely identify the actual boundary between adjacent NALMAs.

Such is the case for the To–Ti boundary. The Torrejonian and Tiffanian NALMAs were defined based on faunas from the San Juan Basin, from which the genus *Plesiadapis* is not known. Simpson (1935b) described the mammalian species from the Tiffany beds (the type Tiffanian) in the northern San Juan Basin and included in his faunal list *Plesiadapis gidleyi*. This species since has been reassigned to the genus

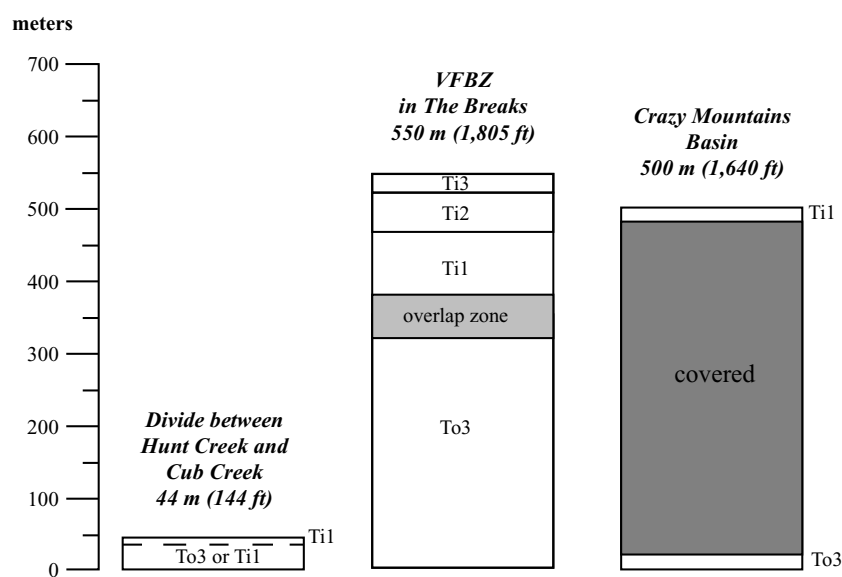
*Nannodectes* by Gingerich (1975). No other species of *Plesiadapis* has been identified from the San Juan Basin, thus the To–Ti boundary, as defined by Archibald et al. (1987), cannot be recognized there on that basis alone (Williamson, 1996). Thus direct correlations are difficult between the type Torrejonian and Tiffanian of the San Juan Basin and the Torrejonian and Tiffanian sections in Wyoming and Montana, where *Plesiadapis* is present.

### Significance of The Breaks

Definition of the To–Ti boundary is confounded by the fact that few sections have been recognized that document the faunal transition from the Torrejonian to the Tiffanian. No such section has been identified in the San Juan Basin, but a few have been described from elsewhere. One of the best sections exposing this transition is on the divide between Hunt Creek and Cub Creek near the

Wyoming–Montana border. This section is 44 m thick (compared to the 550 m thickness of the VFBZ) and has yielded only six mammalian species from seven localities (Archibald et al., 1987; Butler et al., 1987; Fig. 3). In the Crazy Mountains Basin, faunas of latest Torrejonian age (Gidley and Silberling quarries) are separated from faunas of earliest Tiffanian age (Locality 68 and Douglass Quarry) by a covered interval about 300–500 m thick (Archibald et al., 1987). This is comparable in thickness to the VFBZ in The Breaks, but few fossils have been collected from the covered interval.

Seventy-two mammalian species have been identified from localities in the VFBZ. Because of its great thickness, abundant fossil localities, and diverse mammalian fauna, the VFBZ provides an opportunity to develop a high-resolution biostratigraphy of the Torrejonian–Tiffanian boundary. The great diversity of the fauna of the VFBZ makes it eminently



**Figure 3.** Comparative thicknesses of three sections bracketing To–Ti boundary. Hanna Formation in The Breaks is thicker, with a more abundant and diverse fauna than any other previously known section.

correlatable to other To-Ti faunas in western North America. With documentation of the To-Ti boundary in the VFBZ, recognition of the To-Ti boundary at localities in which the faunal diversity is lower may be facilitated, especially where critical taxa such as *Plesiadapis* are not present (e.g., the San Juan Basin).

### **NALMA Boundaries and Nature of Transitions Between NALMAs**

Paleontologists recognize that using a single-taxon definition of a NALMA boundary is probably not realistic, as a single species of mammal may never have existed at a specific locality or may make its first appearance at different times at different localities (Woodburne, 1987, 1996; Walsh, 1998). Multiple-taxon definitions of NALMA boundaries attempt to solve this problem. Two or more species may be selected that have overlapping geographic ranges plus evidence of association in the same fauna. If all species appeared at about the same time, each independently could mark the beginning of the NALMA. But multiple-taxon definitions are not without problems, because different taxa tend not to make their first appearances everywhere at the same time. Problems also arise when several index taxa are present in one area or stratigraphic section. A paleontologist must decide, for example, whether a NALMA begins with the appearance of any one of the index species, when any three are present, or when they all are, and so forth. One might be forced to decide if the presence or absence of one species is more important than that of another. The VFBZ, because of the abundance of fossils and the distribution of localities, provides an excellent opportunity to investigate in detail the nature of a faunal transition from one NALMA to the next, specifically, the To-Ti boundary.

## **METHODS OF STUDY**

### **Identification**

All specimens used in this study are housed at the University of Wyoming (UW) Collection of Fossil Vertebrates, held by the Department of Geology and Geophysics. Specimens consist mostly of isolated teeth or tooth fragments, with some partial or complete jaws. No postcranial material was used for biostratigraphic interpretation. Most specimens were mounted on pins and examined using a dissecting microscope. Measurements for smaller specimens were recorded to the nearest

thousandth of a millimeter through use of an Ehrenreich Photo-Optical Industries Shopscope™. Larger specimens, and others which could not be measured with the microscope, were measured to the nearest hundredth of a millimeter using Helios™ calipers. Most identifications were based on comparisons with specimens and casts in the UW collections. Some identifications were made during visits to collections at The American Museum of Natural History and the State University of New York at Stony Brook. Published drawings, photographs, and measurements also were used in the process of identification. Identifications were made before knowing the relative stratigraphic levels of the localities from which the specimens were collected to avoid bias based on preconceived notions about mammalian biostratigraphy in the VFBZ.

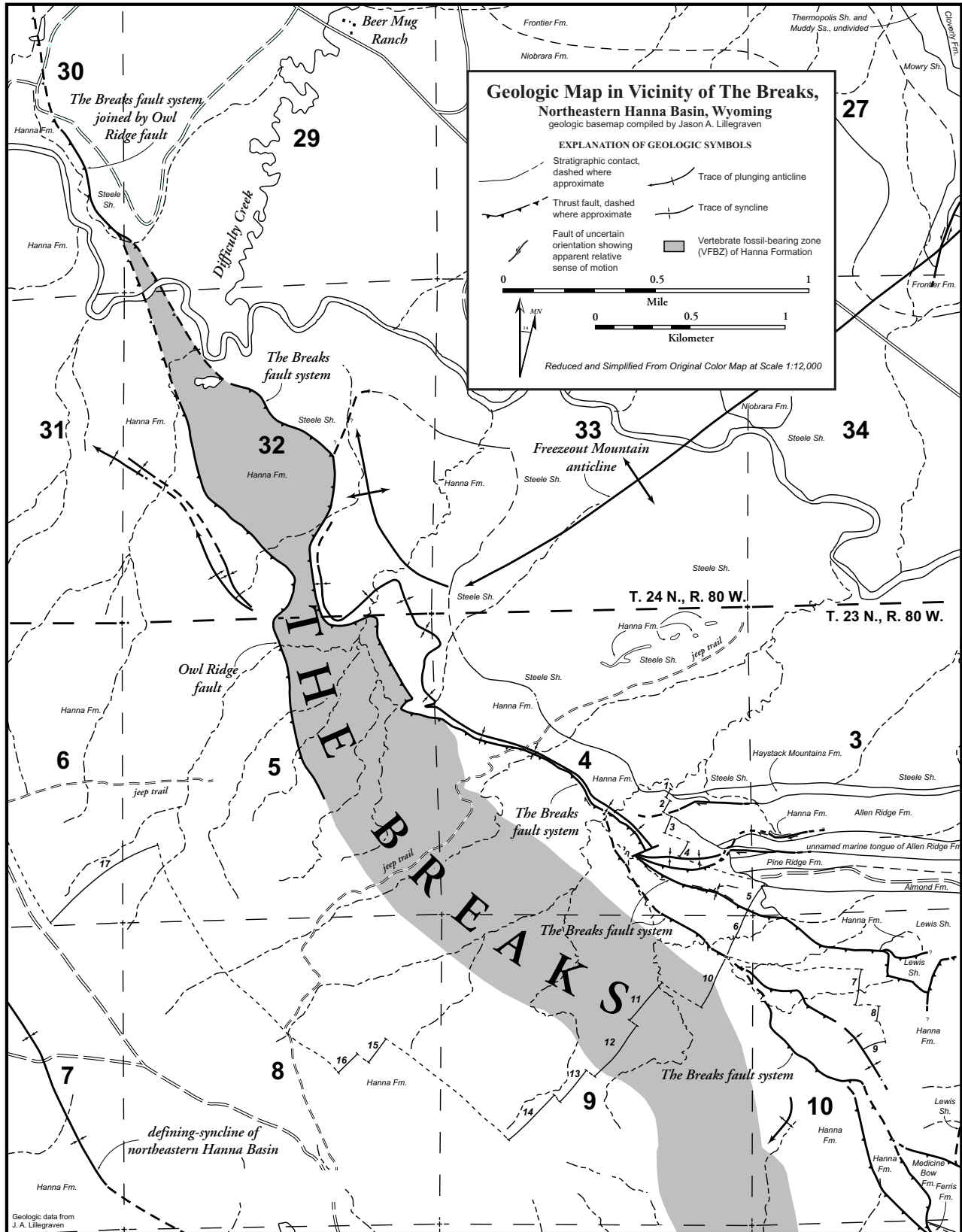
### **Correlation**

Lillegraven and Snoko (1996) compiled a detailed geologic map of The Breaks, on the topographic base of the Como East, Como West, and Difficulty USGS 7.5 minute quadrangle maps (Fig. 4). All University of Wyoming fossil localities (denoted V-) were plotted in the field and recorded on computerized copies of this map. Figure 5 shows the relative stratigraphic positions and lateral correlations of all fossil localities from The Breaks. This diagram was compiled using data from four different sections measured through the VFBZ for this study. A fifth section, measured by Jason A. Lillegraven (Lillegraven and Snoko, 1996; Fig. 4), also was used. All localities were correlated to the nearest measured section by walking out beds. Occasionally, ground cover prevented walking out beds and correlation had to be made by following structural trends in the field or on the geologic map, and/or by tracing beds on enlarged color aerial photographs. The four new measured sections were then correlated to the section measured by Lillegraven (Lillegraven and Snoko, 1996) by the same methods. The accuracy of the measured stratigraphic level above the base of the Hanna Formation for localities is estimated to be approximately  $\pm 6$  m (20 ft). Lateral correlation is very approximate (based upon measurements made from 7.5 minute quadrangle maps) and is intended only to give a general sense of the lateral distribution of fossil-bearing localities.

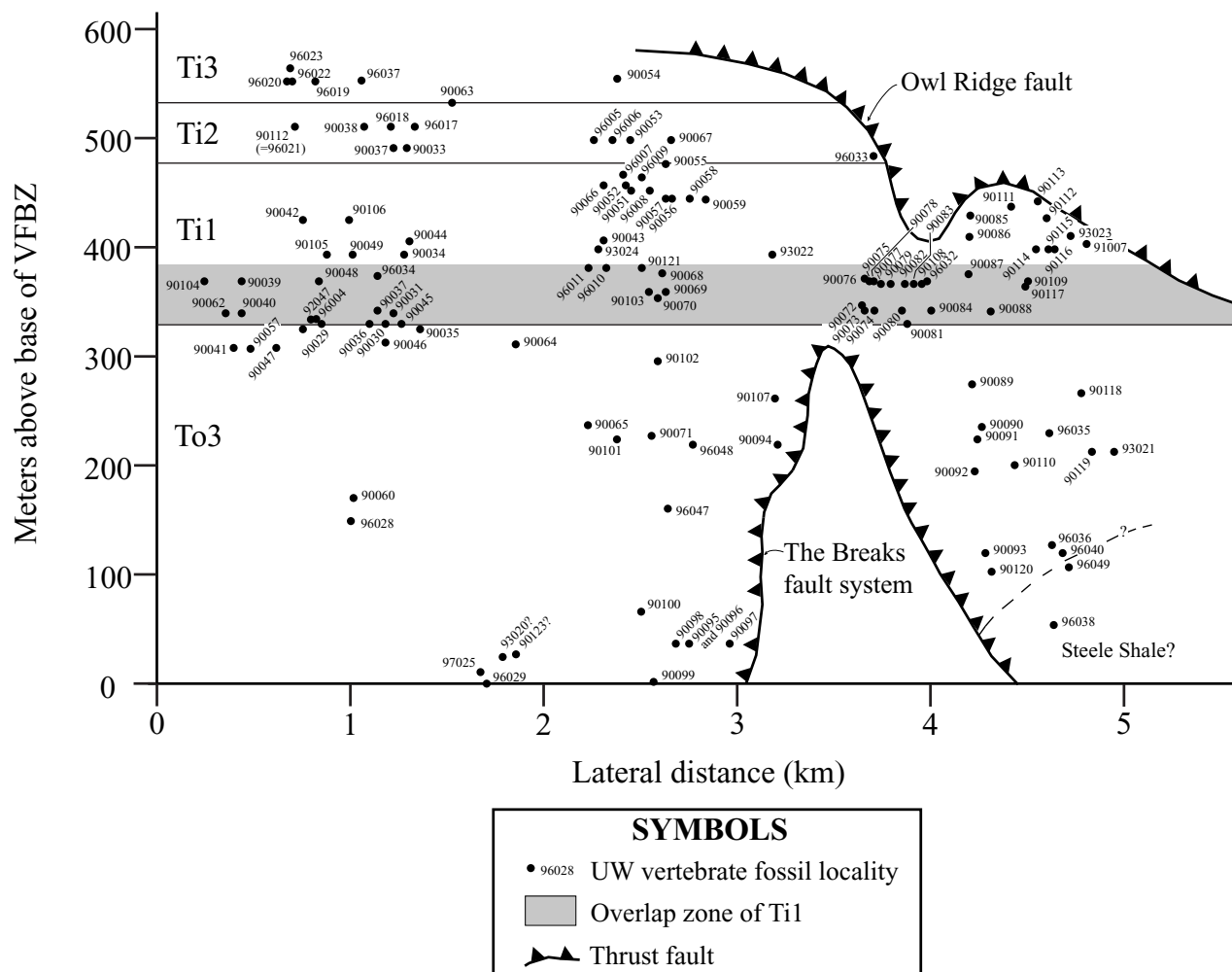
### **Results**

Figure 6 illustrates the approximate correlations of biostratigraphic units and the geologic time scale.





**Figure 4.** Simplified geologic map of The Breaks and immediate surroundings. Shaded area is VFBZ. Adapted from Lillegraven and Snoke (1996).



**Figure 5.** Distribution of vertebrate fossil localities in VFBZ. This diagram represents all vertebrate localities in VFBZ, placed with respect to stratigraphic positions and approximate lateral distributions. Parts of VFBZ section were lost through motion along Owl Ridge fault and Breaks fault system. Two localities (V-96049 and V-96038) occur in beds that are questionably on Steele Shale; both are anthill localities and have yielded only shark teeth of Cretaceous origin.

Figure 7 summarizes the known ranges of genera and species from the VFBZ used for biostratigraphic interpretation. P-P, P-E, E-A, A-P, P-M, and M represent Williamson's (1996) biostratigraphic zonation of the Torrejonian in the San Juan Basin. Archibald et al. (1987) divided the Torrejonian into three major divisions, To1-3. To3 is equivalent to Williamson's (1996) P-M plus M zones; therefore, taxa reported from To3 are indicated in both P-M and M. Additionally, for convenience To2 is considered to include both E-A and A-P and To1 is considered to include both P-P and P-E. Further research is needed to examine the exact relationships among the biostratigraphic zonations of Williamson (1996) and Archibald et al. (1987). OZ and Ti1-6 denote divisions of the Tiffanian (Fig. 6), Ti1-6 being the

divisions of the Tiffanian defined by Archibald et al. (1987) and OZ (the "Overlap Zone") representing an early part of Ti1 that will be discussed fully later in this paper. Figure 7 was constructed based on faunal data from 35 localities in western North America (Fig. 8) ranging in age from the late Torrejonian (To3) through the middle Tiffanian (Ti3). All references on which Figure 7 is based are provided in Table 1. Taxa known to appear in nonconsecutive zones are assumed also to have been present through the intermediate zones, denoted by grey boxes. Range extensions of taxa recognized after biostratigraphic analysis of the fauna from the VFBZ were appended later and are shown as cross-hatched boxes.

**Table 1 (continued on the following two pages). Primary references for various localities referred to in text. First column lists number by which each locality is identified on Figure 8. Faunas are placed in approximate order from oldest to youngest, then from south to north.**

<b>Age, Locality Name</b>	<b>No.</b>	<b>Author</b>
Pu1–Tb3, Nacimiento Formation, San Juan Basin, New Mexico	33–35	Williamson, 1996
Tb1, Dragon local fauna, North Horn Formation, central Utah	32	Williamson, 1996 Robison, 1986
Tb2, KU locality 13, Nacimiento Formation, San Juan Basin, New Mexico	34	Sloan, 1981
Tb3, KU locality 9, Nacimiento Formation, San Juan Basin, New Mexico	35	Sloan, 1981
Tb3, Little Muddy Creek faunule, Evanston Formation, Fossil Basin, Wyoming	29	Gazin, 1969
Tb3, Swain Quarry, Fort Union Formation, Washakie Basin, Wyoming.	31	Williamson, 1996 Rigby, 1980
Tb3, Rock Bench Quarry, Fort Union Formation, northern Bighorn Basin, Wyoming	19	Williamson, 1996 Rose, 1981
Tb3, Gidley Quarry, Fort Union Formation, Crazy Mountains Basin, Montana	14	Williamson, 1996 Rose, 1981
Tb3, Silberling Quarry, Fort Union Formation, Crazy Mountains Basin, Montana	14	Douglass, 1908 Simpson, 1937 Russell, 1967
Tb3, Medicine Rocks I, Fort Union Formation, Williston Basin, Montana	12	Gingerich, 1976 Krause, 1982
Tb3, Ti4–Cf, Fort Union Formation, Rock Springs uplift, Wyoming	30	Winterfeld, 1982
Pu, Tb3–Ti1, Fort Union Formation, southern Bighorn Basin, Wyoming	21	Hartman, 1986
Tb3–Ti3, The Breaks local fauna, Hanna Formation, Hanna Basin, Wyoming	27	Higgins, this report
Ti1, Schiebout-Reeves Quarry, Black Peaks Formation, Big Bend National Park, Texas	36	Schiebout, 1974 Archibald et al., 1987
Ti1, Shotgun local fauna, Fort Union Formation, Wind River Basin, Wyoming	22	Gunnell, 1989
Ti1*, Carbon Basin fauna, Hanna Formation, Carbon Basin, Wyoming	28	Secord, 1996, 1998
Ti1, Bangtail Locality, Fort Union Formation, Bangtail Plateau, Crazy Mountains Basin, Montana	16	Gingerich et al., 1983
Ti1, Douglass Quarry, Fort Union Formation, Crazy Mountains Basin, Montana	14	Krause and Maas, 1990 Krause and Gingerich, 1983
Ti1, Cochrane 1, Porcupine Hills Formation, Alberta, Canada	4	Fox, 1990
Ti1, Cochrane 2, Porcupine Hills Formation, Alberta, Canada	4	Fox, 1990
Ti2, Saddle Locality, Fort Union Formation, Bison Basin, Wyoming	26	Gazin, 1956a



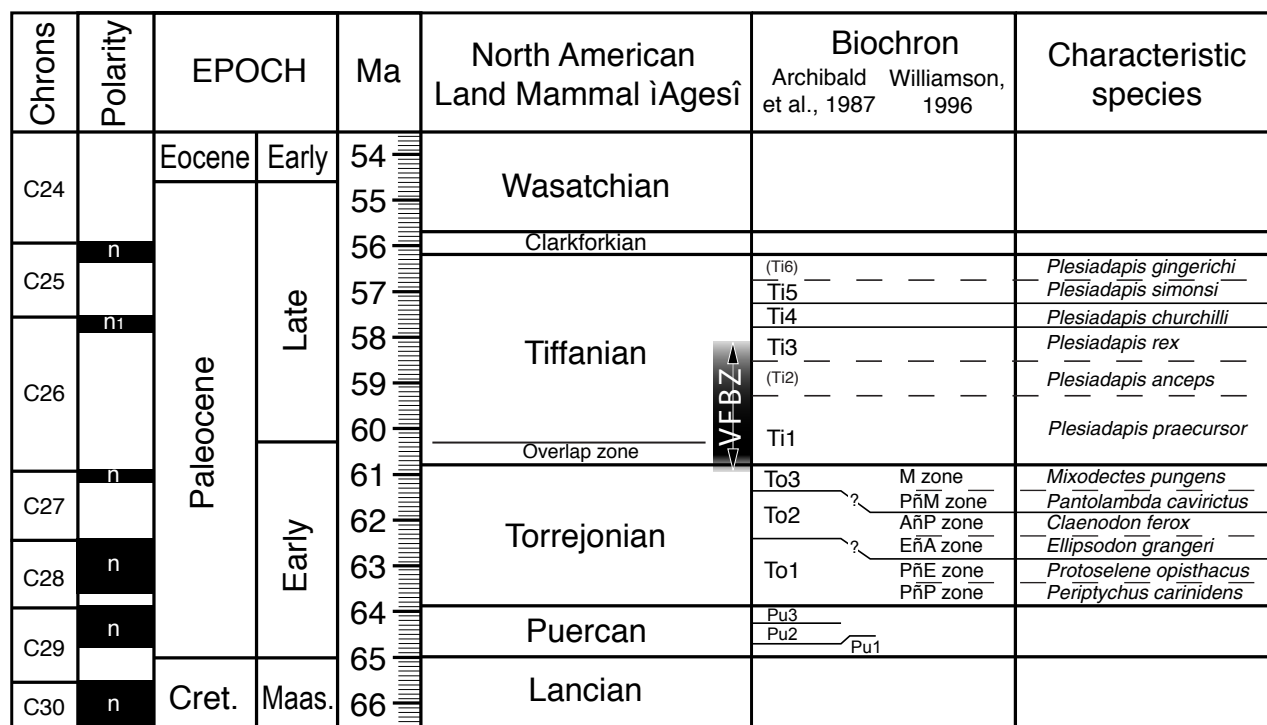
**Table 1 (continued). Primary references for various localities referred to in text.**

<b>Age, Locality Name</b>	<b>No.</b>	<b>Author</b>
Ti2, Scarritt Quarry, Fort Union Formation, Crazy Mountains Basin, Montana	15	Rose, 1981
Ti2, Highway Blowout, eastern Montana	11	Krause, 1982 Archibald et al., 1987
Ti3?, eastern Tornillo Flats washing site, Black Peaks Formation, Big Bend National Park, Texas	36	Rose, 1981
Ti3, Ray's Bonebed, Black Peaks Formation, Big Bend National Park, Texas	36	Schiebout, 1974
Ti3, Battle Mountain local fauna, Hoback Formation, Hoback Basin, Wyoming	24	Dorr, 1958 Russell, 1967 Gingerich, 1983
Ti3, Twin Creek locality, Evanston Formation, Fossil Basin, Wyoming	29	Gazin, 1956b Russell, 1967
Ti3, Ledge locality, Fort Union Formation, Bison Basin, Wyoming	26	Gazin, 1956a
Ti3, False Lance (V-76022), Fort Union Formation, southwestern Bighorn Basin, Wyoming	20	Leite, 1992
Ti3, Cedar Point Quarry, Polecat Bench Formation, northern Bighorn Basin, Wyoming	18	Rose, 1981
Ti3, Seaboard Well, Fort Union Formation, northern Bighorn Basin, Wyoming	18	Krause, 1982 Archibald et al., 1987
Ti3, Localities 11 and 13, Fort Union Formation, Crazy Mountains Basin, Montana	15	Simpson, 1937 Gingerich, 1976
Ti3, Brisbane and Judson localities, Fort Union Group, Williston Basin, North Dakota	9–10	Holtzman, 1978
Ti3, Birchwood locality, Paskapoo Formation, near Drayton Valley, Alberta, Canada	2	Webb, 1996
Ti3, Blindman River locality DW-2, Paskapoo Formation, Alberta, Canada	3	Fox, 1990
Ti3, Joffre Bridge roadcut lower level, Paskapoo Formation, Alberta, Canada	3	Fox, 1990 Webb, 1996
Ti3–Ti4, Chappo type locality, Wasatch Formation, Green River Basin, Wyoming	25	Gunnell, 1994
Ti3 or Ti4, Police Point locality, Ravenscrag Formation, Alberta, Canada	5	Fox, 1990
Ti4, Mason Pocket, San Jose Formation, San Juan Basin, Colorado.	33	Savage and Russell, 1983
Ti4, Malcolm's locality, Fort Union Formation, Wind River Basin, Wyoming	23	Krause, 1982 Archibald et al., 1987
Ti4, Croc Tooth Quarry, Fort Union Formation, northern Bighorn Basin, Wyoming	18	Krause, 1982 Archibald et al., 1987
Ti4, Divide Quarry, Fort Union Formation, northern Bighorn Basin, Wyoming	18	Krause, 1982 Archibald et al., 1987
Ti4?, Riverdale locality, Fort Union Group, Williston Basin, North Dakota	8	Krause, 1982 Archibald et al., 1987
Ti4, Swan Hills site 1, Paskapoo Formation, Alberta, Canada	1	Fox, 1990

**Table 1 (continued). Primary references for various localities referred to in text.**

Age, Locality Name	No.	Author
Ti4, Roche Percée, Ravenscrag Formation, Saskatchewan, Canada	6	Fox, 1990 Krause, 1982
Ti5, Joe's Bonebed, Black Peaks Formation, Big Bend National Park, Texas	36	Schiebout, 1974
Ti5, Titanoides locality, Fort Union Formation, Bison Basin, Wyoming	26	Gazin, 1956a
Ti5, Princeton Quarry, Fort Union Formation, northern Big-horn Basin, Wyoming	18	Rose, 1981

\*Secord (1998) considered this fauna latest Torrejonian (To3).



**Figure 6.** Chart illustrating correlation among geochronologic units, polarity chrons, and mammal “ages” of Paleocene age, modified from Woodburne and Swisher (1995). Includes divisions of Torrejonian and Tiffanian NALMAs and species that mark beginning of each division. Divisions of Tiffanian are those of Gingerich (1976) and Archibald et al. (1987). Divisions of Torrejonian are those of Archibald et al. (1987) and Williamson (1996). Abbreviations: Cret. = Cretaceous; Maas. = Maastrichtian; and VFBZ = Vertebrate Fossil-Bearing Zone in The Breaks.

The stratigraphic distribution of mammalian species in the VFBZ is shown in Figure 9. Localities are grouped by 12 m (40 foot) intervals to account for the uncertainty in the measured stratigraphic level of each locality. Figure 9 shows all localities discovered by University of Wyoming crews; however, not all localities have yielded mammalian fossils. Localities that have not yielded mammalian specimens identifiable to genus or species may yet

do so, because many contain good material of other vertebrates including sharks, turtles, crocodiles, and gar.

The biostratigraphy was developed using approximately 800 specimens identified to the level of genus or species. Interpretation of the biostratigraphic divisions of the VFBZ was based upon comparisons of associations of species presented in Figure 7.

## BIOSTRATIGRAPHY

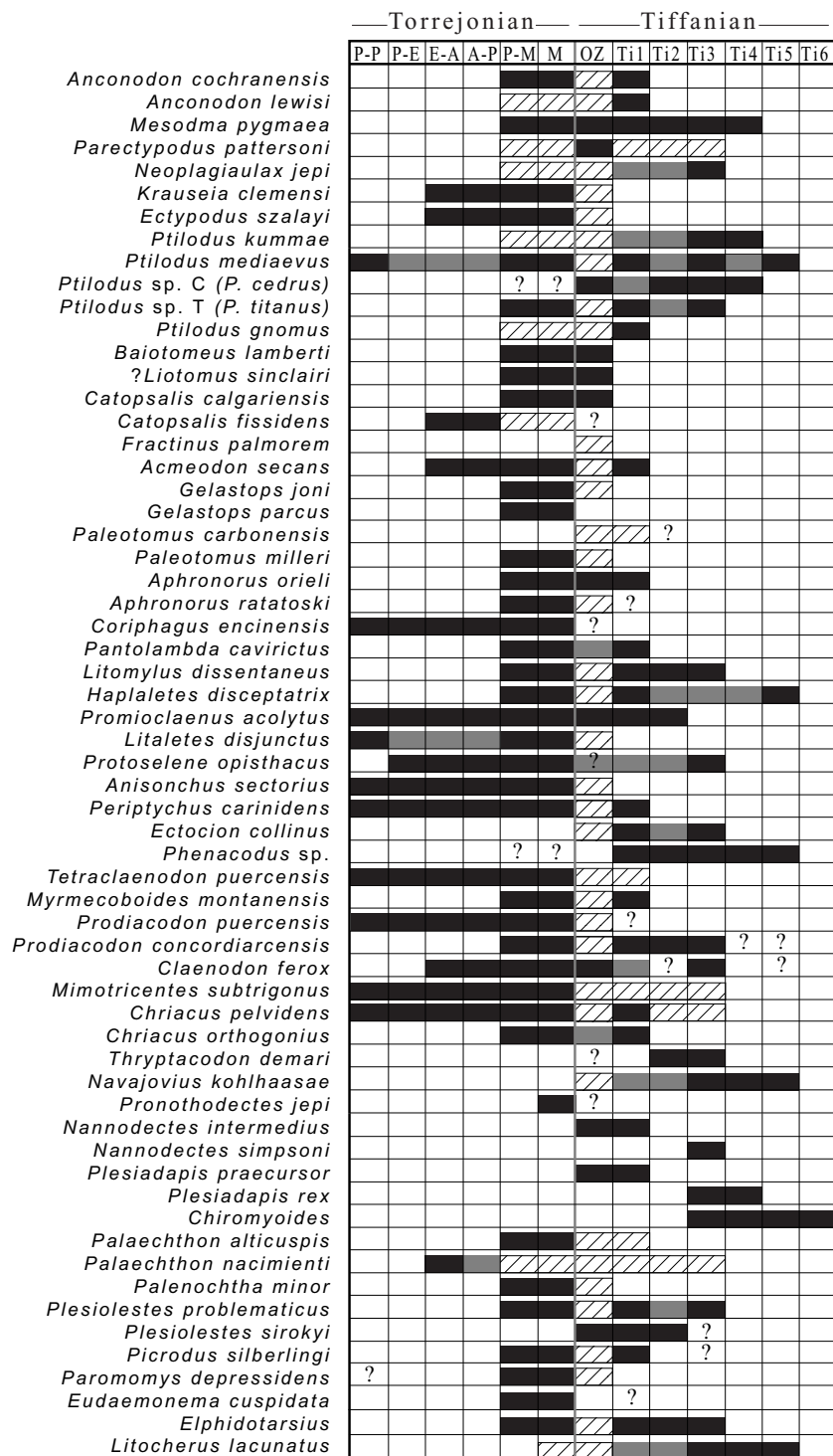
## Tiffanian in VFBZ

The current definition of the beginning of the Tiffanian (Archibald et al., 1987) is the first appearance of *Plesiadapis*. This definition is retained because single-taxon definitions are advantageous in allowing the potential for synchronicity in correlation (Woodburne, 1987, 1996).

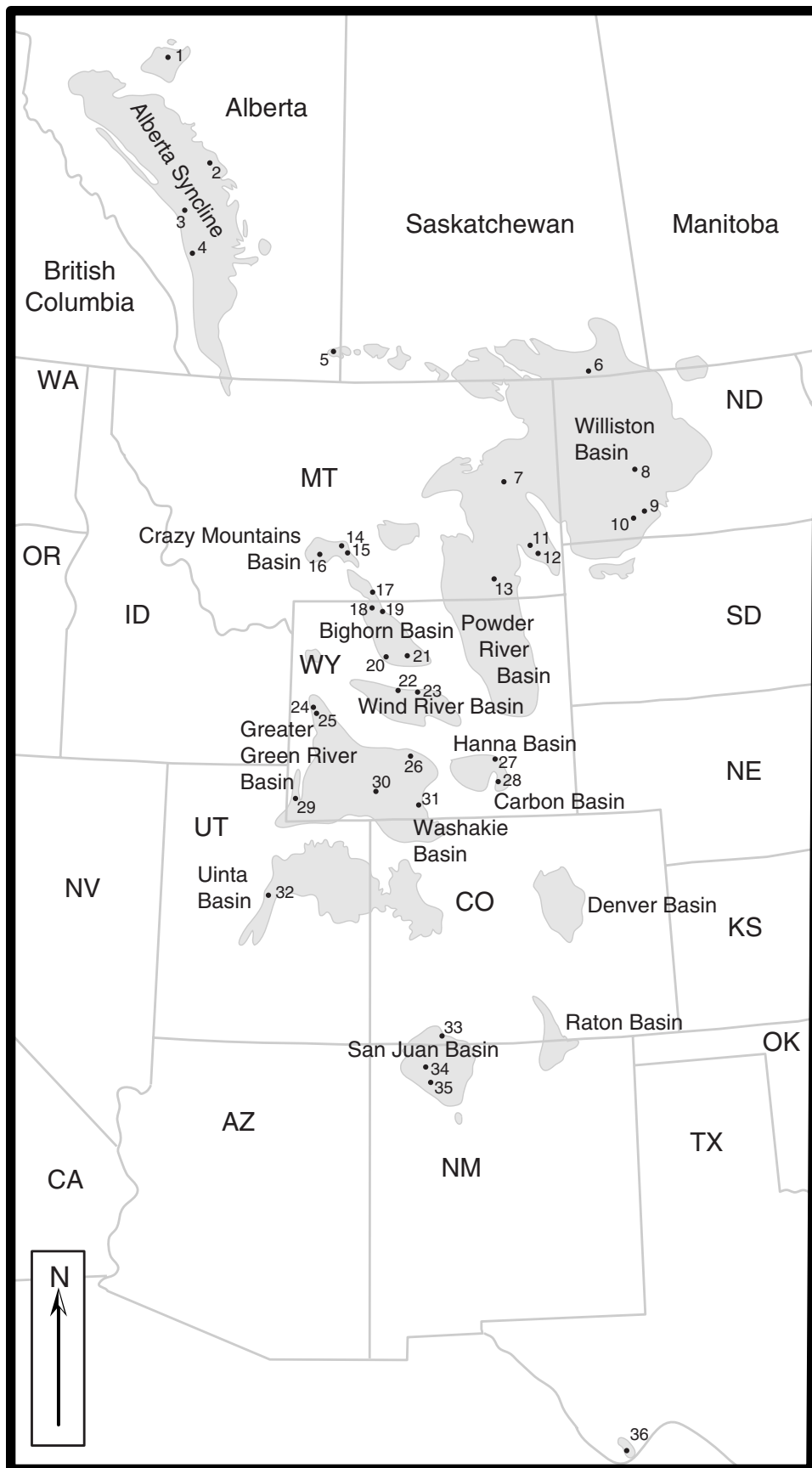
The stratigraphically lowest occurrence of *Plesiadapis* in The Breaks is about 325 m (1,070 ft) above the base of the VFBZ. Prior to the current study, several other species that occur in the VFBZ also were restricted only to strata of Tiffanian age (Fig. 7). These are: *Ectocion collinus*, *Phenacodus* sp., *Thryptacodon demari*, *Navajovius kohlhaasae*, *Nannodectes* sp., *Chiromyoides* sp., *Plesiolestes siroyki*, and *Litocherus lacunatus*. Using the first occurrence of *Plesiadapis* to define the beginning of the Tiffanian, *Ectocion collinus*, *Thryptacodon demari*, *Nannodectes* sp., *Chiromyoides* sp., and *Plesiolestes siroyki* remain restricted to the Tiffanian. *Phenacodus* sp., *Navajovius kohlhaasae*, and *Litocherus lacunatus*, however, appear in part of the VFBZ stratigraphically below the first appearance of *Plesiadapis*. As will be discussed later, this does not necessarily mean that these occurrences are in strata of Torrejonian age.

## Divisions of Tiffanian

The fauna above the first appearance of *Plesiadapis* represents Tiffanian time (Gingerich, 1976; Archibald et al., 1987). Species of *Plesiadapis* and the closely related genus *Nannodectes* can be used to further define subdivisions of the Tiffanian (Ti1–Ti6; Gingerich, 1976; Archibald et al., 1987). In the VFBZ, Ti1 is recog-

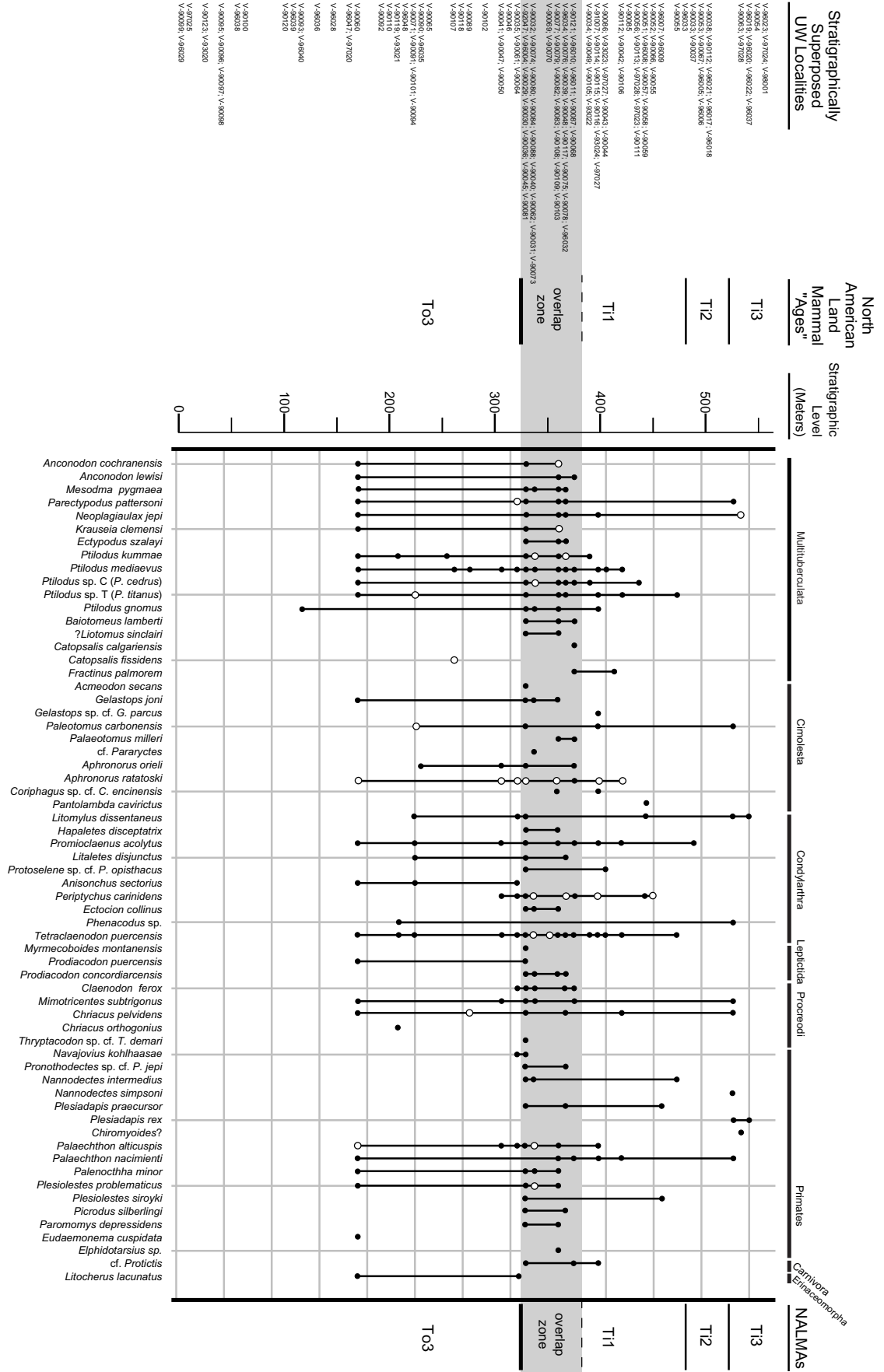


**Figure 7.** Known temporal distribution of species collected from The Breaks. Divisions of Torrejonian (P-P, P-E, E-A, A-P, P-M, and M) from Williamson (1996); Tiffanian divisions (Ti1–Ti6) of Archibald et al. (1987); OZ is overlap zone in VFBZ (described in text). Gray boxes indicate intervals from which a species has not been identified but is known both before and after that interval. Hatched boxes represent range extensions resulting from observations in The Breaks. Tentative identifications denoted by question marks.



**Figure 8, left.** Location map showing geographic positions of faunas of Torrejonian through middle Tiffanian (Ti3) age used to create Figure 7. 1, Swan Hills; 2, Birchwood locality; 3, Blindman River and Joffre Bridge roadcut localities; 4, Cochrane localities; 5, Police Point; 6, Roche Percée; 7, Circle locality; 8, Riverdale locality; 9, Judson locality; 10, Brisbane locality; 11, Highway Blowout; 12, Medicine Rocks; 13, Olive quarry; 14, Douglass quarry; 15, Silberling, Gidley, and Scarritt quarries; 16, Bangtail locality; 17, divide between Hunt Creek and Cub Creek; 18, Princeton, Cedar Point, Croc Tooth, and Divide quarries, and Seaboard Well; 19, Rock Bench quarry; 20, False Lance locality; 21, vicinity of Cedar Mountain, southern Bighorn Basin, Wyoming; 22, Shotgun local fauna; 23, Malcolm's locality; 24, Battle Mountain; 25, Chappo type locality; 26, Bison Basin; 27, The Breaks; 28, Carbon Basin; 29, Twin Creek and Little Muddy Creek; 30, Black Butte Coal Mine, Rock Springs uplift, Wyoming; 31, Swain quarry; 32, Dragon local fauna; 33, Mason Pocket; 34, KU locality 13 (= Big Pocket); 35, KU locality 9 (= Little Pocket); and 36, Big Bend National Park.

**Figure 9, facing page.** Documented relative stratigraphic occurrences of mammalian species in The Breaks, plotted against thickness of strata above base of VFBZ. Open circles indicate questionable identifications.





nized by the presence of *Plesiadapis praecursor* and *Nannodectes intermedius*. Ti3 is recognized in the VFBZ by presence of *Plesiadapis rex*, *Nannodectes simpsoni*, and a molar tentatively identified as *Chiromyoides*. Outside of the Hanna Basin, *Plesiadapis anceps* and *Nannodectes gazini* are index species used to recognize Ti2 (Gingerich, 1976; Archibald et al., 1987). Neither of these species is present in the VFBZ. Ti2, therefore, is inferred in the 55 m section between the highest occurrence of *N. intermedius* and the lowest occurrence of *Plesiadapis rex*. A complete discussion of the specimens of plesiadapids from The Breaks can be found in Higgins (2000).

### Recognizing To-Ti Boundary in Absence of *Plesiadapis*

Plesiadapids are critical for interpreting the age of a fauna that lies near the To-Ti boundary. As noted above, *Plesiadapis* and *Nannodectes* are index taxa for the Tiffanian and its subdivisions. *Pronothodectes*, a plesiadapid considered ancestral to both *Plesiadapis* and *Nannodectes*, is considered an index fossil for the Torrejonian (Gingerich, 1986; Archibald et al., 1987). If a fauna lacks important plesiadapids such as *Plesiadapis*, *Nannodectes*, and *Pronothodectes*, and contains many species considered restricted to the Torrejonian, it will most likely be assigned a Torrejonian age. For this reason, Secord (1996, 1998) assigned an age of latest Torrejonian (To3) to two faunas (Halfway Hill and Grayson Ridge) in the Carbon Basin of south-central Wyoming. The current research suggests that these faunas more probably represent the earliest Tiffanian (Ti1).

The mammalian fauna at each stratigraphic level in the VFBZ was examined in terms of what age might be assigned to it if plesiadapid fossils were absent. The To-Ti boundary probably would have been placed within the VFBZ about 55 m (180 ft) higher in the section than the first appearance of *Plesiadapis*, based on the presence of *Tetraclaenodon puercensis*, *Mimotricentes subtrigonus*, *Gelastops joni*, *Paleotomus milleri*, *Litaletes disjunctus*, *Palaechthon nacimienti*, *Palaechthon alticuspis*, *Palenochtha minor*, *Paromomys depressidens*, *?Liotomus sinclairi*, *Baiotomeus lamberti*, *Ectypodus szalayi*, *Krauseia clemensi*, and *Catopsalis calgariensis*, all of which previously have been restricted to the Torrejonian (Fig. 7). Furthermore, teeth of the plesiadapid *Pronothodectes*, also considered restricted to the Torrejonian, were collected from the same locality (V-90029) yielding the lowest occurrence of *Plesiadapis* and from a second locality (V-90039) 38 m

higher in the section that also yields *Plesiadapis*. This suggests that the part of the VFBZ beginning with the first appearance of *Plesiadapis* and ending 55 m higher in the section could be considered either Torrejonian or Tiffanian, depending on which taxa are emphasized.

This interval, in which species characteristic of the Tiffanian (including *Plesiadapis* and *Nannodectes*) occur at the same level as species characteristic of the Torrejonian (including *Pronothodectes*), is referred to as the "overlap zone." The overlap zone is considered earliest Tiffanian because of the presence of *Plesiadapis* and *Nannodectes*.

### Torrejonian Mammals in Overlap Zone

Several species observed in the overlap zone are well known elsewhere from several Torrejonian localities (*Gelastops joni*, *Litaletes disjunctus*, *Palaechthon alticuspis*, *Palenochtha minor*, *Paromomys depressidens*, *?Liotomus sinclairi*, *Baiotomeus lamberti*, *Ectypodus szalayi*, *Krauseia clemensi*, and *Catopsalis calgariensis*). Their appearance in the overlap zone represents a temporal range extension to include at least earliest parts of the Tiffanian.

For other species, reasonable explanations exist (i.e., possible synonymy with a Tiffanian species or poor knowledge of the species) to explain a range extension into strata of Tiffanian age. *Paleotomus milleri* and *Palaechthon nacimienti* were known previously from only one locality apiece, both of which are Torrejonian (Rigby, 1980; Wilson and Szalay, 1972). Therefore, range extensions for these two species to include the early Tiffanian are not unexpected. *Mimotricentes subtrigonus* had been identified with confidence only from faunas of latest Torrejonian age. The only exception is a questionable identification from the earliest Tiffanian Shotgun local fauna (Ti1; Gunnell, 1989). The observations from the VFBZ extend the range of *M. subtrigonus* into the middle Tiffanian (Ti3). Secord (1998) suggested the possibility that the similar *Mimotricentes fremontensis* may be a junior synonym of *M. subtrigonus* because of the wide range of variation of both species. *Mimotricentes fremontensis* is known from faunas of early to middle Tiffanian age. Further research on the possible synonymy of *M. subtrigonus* and *M. fremontensis* is warranted.

### Biostratigraphic Significance of *Tetraclaenodon puercensis*

*Tetraclaenodon puercensis* has been used as an index species for the Torrejonian (Archibald et al.,

1987; Thewissen, 1990). *Phenacodus*, a younger relative of *Tetraclaenodon*, has been considered an index taxon for the Tiffanian (Archibald et al., 1987; Thewissen, 1990). Forty-five specimens collected from the VFBZ resemble either of these genera. Two of these specimens are identified as *Phenacodus* on the basis of size. The others all appear to represent a single species. All are identified as *T. puercensis* because the teeth are indistinguishable from specimens of *T. puercensis* in The University of Wyoming Collection of Fossil Vertebrates and at The American Museum of Natural History. Also, measurements of specimens fall within the size ranges for *T. puercensis* reported by Thewissen (1990). Distribution of the 20 localities yielding *T. puercensis* covers much of the VFBZ, from 169 to 503 m above the base of the VFBZ. Specimens identified as *Tetraclaenodon* collected from the VFBZ extend the temporal range of this genus into the earliest Tiffanian (Ti1). Only five localities yielding *Tetraclaenodon* are stratigraphically below the first appearance of *Plesiadapis*.

Previously, *Tetraclaenodon* has been reported only from faunas of Torrejonian age, and it is considered an index fossil of the Torrejonian (Archibald et al., 1987). However, given that isolated molars of *Tetraclaenodon* and *Phenacodus* are difficult to differentiate, and the apparent range extension of *Tetraclaenodon* into the Tiffanian in The Breaks, it does not seem reasonable to assume that all occurrences of *Tetraclaenodon* are definitive of a Torrejonian age.

### Nature of VFBZ Below First Occurrence of *Plesiadapis*

The overall abundance of vertebrate fossils and fossil localities decreases below the first occurrence of *Plesiadapis*. Three factors contribute to this decrease: geochemical alteration by roll fronts (described below) increases; pebble conglomerate abundance decreases; and the abundance of coal and carbonaceous mudstone increases.

Roll fronts are pods of geochemical alteration through groundwater associated with uranium ore deposition. These reduction-oxidation cells are capable of eliminating, by way of oxidation, pyrite, calcite, and organic material from the rock through which they move. Oxidation of pyrite produces sulfuric acid, which is known to react rapidly to dissolve the mineral apatite (Toy and Walsh, 1987; Greenwood and Earnshaw, 1997). Apatite is the major constituent of mammalian bones and teeth. With increased roll-front alteration, the chances of vertebrate fossil preservation are decreased. Hig-

gins (1999) described the chemistry of destruction of vertebrate fossils by roll fronts.

Most vertebrate-bearing localities throughout the VFBZ occur in pebble conglomerate. The fossils themselves are of similar size as the pebbles and probably were transported as part of the bed load of the small streams that were common during deposition of the Hanna Formation. A decrease in pebble conglomerate lower in the VFBZ, with a concurrent increase in mudstone, reflects less suitable conditions for transport and deposition of vertebrate remains. Furthermore, depositional environments for carbonaceous mudstone and coal, which increase lower in the section, tend to be too acidic for preservation of vertebrate bone and tooth material. Some vertebrate localities in the VFBZ do occur in carbonaceous mudstone, but fossil material from these localities is generally poorly preserved, etched, and pitted.

It is possible that the lack of *Plesiadapis* below its first recorded occurrence in the VFBZ is due to non-preservation related to the above factors. Therefore, the To–Ti boundary may be stratigraphically lower in the VFBZ than the first occurrence of *Plesiadapis*. It follows that although *Navajovius kohllaasae*, *Phenacodus*, and *Litocherus* occur in the part of the VFBZ below the first occurrence of *Plesiadapis*, their true distribution may still be restricted to the Tiffanian. If the To–Ti boundary remains set at the first known occurrence of *Plesiadapis*, the overlap zone is 55 m thick in the VFBZ. The uncertainty in absolute placement of the To–Ti boundary stratigraphically within the VFBZ does not, however, diminish the significance of recognition of the overlap zone between the Torrejonian and Tiffanian, as moving the boundary lower in the VFBZ only increases the thickness of the overlap zone.

### Overlap Zone: Result of Reworking?

The mixture of Tiffanian mammals with those previously considered strictly Torrejonian raises the question of whether the overlap zone represents a period of time when these animals coexisted, or alternatively is an example of reworking of Torrejonian fossils into Tiffanian sediments. Indeed, Burris (1998, 2001) demonstrated that Cretaceous shark teeth in vertebrate localities of the VFBZ were reworked from nearby Cretaceous strata. Shark teeth are locally abundant in Cretaceous rocks around margins of the Hanna Basin. Torrejonian fossils, however, are less abundant in lower parts of the VFBZ (see above). An enormous volume of Torrejonian sediment would have had to have been reworked

to account for the amount of Torrejonian mammals found in the overlap zone, making reworking an unlikely scenario.

It is possible, however, that reworking occurred prior to geochemical alteration of sediments low in the VFBZ and in the rest of the Hanna Formation below, at a time when Torrejonian mammalian remains were abundant. Torrejonian fossils of the overlap zone could have been emplaced either from greater depths in the Hanna Formation as the result of vertical incision of surface streams near their final depositional site, or from erosion at the margins of the basin and transport by surface streams. The typical river channel preserved in The Breaks is quite small, usually less than two meters in depth. Vertical incision by such a small stream cannot explain an overlap zone that is over 55 m thick.

Deposition occurred rapidly in the Hanna Basin as Laramide tectonism reached its peak (Lillegraven and Snoke, 1996). Strata in The Breaks lie in a part of the basin close to its deepest point, thus probably represent some of the most rapid deposition. Depositional rates were calculated by dividing the total thickness of an interval by the estimated duration of that interval (from Sloan 1987). Sediment compaction was not considered; therefore these rates represent rock accumulation rates. Rates of deposition calculated based on thickness of Ti1 (including or excluding the overlap zone) and/or Ti2 are the most reliable because the beginning and end of both intervals are recognized in the VFBZ.

Rates that include Ti1 were calculated both including and excluding the OZ to allow for the possibility that the approximate duration of Ti1 presented by Sloan (1987) may not have included what I have recognized as the overlap zone. Best estimates for the depositional rate of the Hanna Formation during Ti1–Ti2 (with or without the OZ) range from 0.14 to 0.36 mm per year, averaging about 0.23 millimeters per year. Williamson (1996) estimated depositional rates for the Nacimiento Formation in the San Juan Basin to be from 0.03 to 0.05 mm per year. Although not explicitly stated, these probably are also rock accumulation rates. Rates of rock accumulation for the VFBZ are approximately five to seven times faster than those of the Nacimiento Formation. At this rate, reworking of fossils would be highly improbable as the Hanna Basin would be dominantly an aggradational depositional system.

The final possibility is that Torrejonian fossils were eroded from along the flanks of the Hanna Basin and redeposited in early Tiffanian sediments, as was the case for the Cretaceous shark

teeth throughout the Hanna Formation (Burris, 1998, 2001). Rapid uplift of the Sweetwater arch resulted in the erosion of much, if not all, of the Phanerozoic strata on that structure, resulting in clasts of Cretaceous through Pennsylvanian rocks within conglomerates of the Hanna Formation. It is unlikely that remains of a mammal that died on the Sweetwater arch could have been preserved and transported, a half-million years later, to the environment of deposition inside the Hanna Basin before being destroyed by natural decay. Pulses of uplift might have resulted in some reworking of the Hanna Formation near the margins of the basin. The Breaks, however, being near the deepest point in the Hanna Basin, and therefore near the point of most rapid deposition, was far from the depositional margins of the Hanna Basin and probably was not affected by pulses of tectonic activity. Any reworked fossils probably would not have moved far from their original point of deposition.

The rapid rate of accumulation within the Hanna Basin resulted in an expanded section that made recognition of the overlap zone possible. The presence of Torrejonian taxa within localities of Tiffanian age could have been attributed to reworking, had sedimentation rates been lower and if the overlap zone were only a few meters thick. In fact, the overlap zone most likely would not have been recognized at all. While some Torrejonian fossils may have been reworked from the margins of the basin, these can not account for the great abundance in the overlap zone of species usually restricted to the Torrejonian. Therefore, the overlap zone assemblage probably is not the result of reworking; probably it does represent an interval during which mammalian species originally thought to never occur together actually did coexist.

### The Breaks Local Fauna

The overlap zone is considered part of Ti1 (Archibald et al., 1987) because of the presence of *Plesiadapis*. It is distinct from the younger part of Ti1 because it includes species that previously were considered restricted to the Torrejonian. No new division of the Tiffanian is defined at this time, however, because the younger boundary of the overlap zone at present cannot be defined based on the first appearance of a genus (i.e., following the standard convention with NALMAs).

Recognition of the overlap zone is based on the following criteria. It begins with the first appearance of *Plesiadapis*, the defining genus for the To–Ti boundary (Archibald et al., 1987). As discussed



above, the To–Ti boundary may occur somewhat lower than the first occurrence of *Plesiadapis* in the VFBZ, due to the paucity of fossils below this point. Species characterizing this interval include those restricted to the Tiffanian (*Plesiadapis praecursor*, *Nannodectes intermedius*, *Ectocion collinus*, *Plesiolestes sirokyi*) and species previously restricted to the Torrejonian (*Pronothodectes* sp. cf. *P. jepi*, *Tetraclaenodon puercensis*, *Mimotricentes subtrigonus*, *Gelastops joni*, *Paleotomus milleri*, *Litaletes disjunctus*, *Palaechthon alticuspis*, *Palaechthon nacimienti*, *Palenochtha minor*, *Paromomys depressidens*, ?*Liotomus sinclairi*, *Baiotomeus lamberti*, *Ectypodus szalayi*, *Krauseia clemensi*, *Catopsalis calgariensis*). This results in the overlap zone being earliest Tiffanian, while on the whole the overlap zone fauna is composed of species usually considered to be Torrejonian. The end of the overlap zone is recognized where species originally restricted (listed above) to the Torrejonian disappear from the section.

The fauna from the VFBZ is significant because it documents the nature of transition from Torrejonian to the Tiffanian NALMA. Of particular importance is evidence in the overlap zone that species previously considered restricted to the Torrejonian coexisted with species previously restricted to the Tiffanian. This warrants designation of a formalized local fauna: The Breaks local fauna. The Breaks local fauna includes all species present in the overlap zone of the VFBZ and excludes those species found only outside the overlap zone. Therefore, The Breaks local fauna is representative of the earliest part of the Tiffanian. Appendix 1 provides a complete listing of species (with their representative fossils in Appendix 2) known from the VFBZ.

Even though the Torrejonian and Tiffanian were defined based on faunas from the San Juan Basin, the boundary itself has yet to be defined there within a superposed stratigraphic sequence. *Plesiadapis*, vital to pinpointing the To–Ti boundary (Archibald et al., 1987; Gingerich, 1976), is lacking in southerly faunas such as those in the San Juan Basin and the Big Bend National Park, Texas. The challenge, therefore, is to designate criteria by which the To–Ti boundary may be recognized within areas in which *Plesiadapis* is absent. The diverse fauna of the VFBZ may make this goal possible.

One obvious solution to the problem is to include other taxa within definition of the boundary for use when *Plesiadapis* is absent. One taxon ideal for this is *Nannodectes*. *Nannodectes* has been listed as an index fossil for the Tiffanian (Archibald et al., 1987) and is considered by Gingerich (1976) to have been a descendent of *Pronothodectes*. Gingerich

(1976) also considered *Pronothodectes* to have been the ancestor of *Plesiadapis*. *Nannodectes gidleyi* is known from the Tiffany beds and from localities in Big Bend National Park and is important to recognition that these faunas are, in fact, of Tiffanian age (Schiebout, 1974; Gingerich, 1976; Archibald et al., 1987). These localities are classified as Ti4 according to the zonal definitions of Gingerich (1976) and Archibald et al. (1987).

Another possibility is to apply the Simpson Coefficient (Simpson, 1936) to faunas appearing to be either of latest Torrejonian or earliest Tiffanian age. The Simpson Coefficient is a simple statistic to compare resemblance between two faunas (Flynn, 1986). Its formula is  $(C/N1) \times 100$ , where C is the number of taxa at a specified taxonomic level, and N1 is the total number of taxa (within that same taxonomic level) present in the smaller of the two faunas. Table 2 shows calculated Simpson Coefficients comparing The Breaks local fauna to several Torrejonian and Tiffanian faunas throughout western North America.

A temporal equivalent to The Breaks local fauna is recognized in the combined faunas of two localities (Grayson Ridge and Halfway Hill) in the Carbon Basin of south-central Wyoming (20 genera and 22 species total; Secord, 1996, 1998). Secord (1996, 1998) originally assigned an age of latest Torrejonian (To3) to the Grayson Ridge and Halfway Hill localities because of their overwhelming Torrejonian character and lack of *Plesiadapis* (or any plesiadapid primate). At the generic level, however, these faunas have a 90 percent similarity with the fauna from the overlap zone, indicating that these two faunas are actually of earliest Tiffanian (Ti1) age.

Calculated values using Simpson Coefficients suggest that the Shotgun local fauna of the Wind River Basin (24 genera and 27 species total; faunal list from Gunnell, 1989) and the Douglass Quarry of the Crazy Mountains Basin (24 genera and 28 species total; faunal list from Krause and Maas, 1990) also may be correlative to The Breaks local fauna, each having a 75 percent similarity at the generic level. Both faunas have both *Plesiadapis praecursor* and *Nannodectes intermedius*, and therefore are definitely Tiffanian (Ti1) in age. The Shotgun local fauna shares a 52 percent similarity with The Breaks local fauna, slightly better than that for the Carbon Basin fauna, suggesting it probably is correlative to the overlap zone. The Douglass Quarry shares only a 32 percent similarity to The Breaks local fauna, indicating that while it is still Ti1, it probably is not directly correlative to the overlap zone.

**Table 2. Calculated Simpson coefficients comparing The Breaks Local Fauna to other known late Torrejonian through early Tiffanian faunas.**

Quarry		Percent Quarry Genera also Occurring in The Breaks Local Fauna	Percent Quarry Species also Occurring in The Breaks Local Fauna
The Breaks	Ti1	100	100
Dragon l. f.	To1	59	23
P-M zone	To3	50	40
(San Juan Basin)			
Swain Quarry	To3	59	42
Gidley Quarry	To3	63	32
Rock Bench Quarry	To3	61	37
M-zone	To3	55	38
(San Juan Basin)			
Carbon Basin	Ti1*	90	50
Shotgun l. f.	Ti1	75	52
Douglass Quarry	Ti1	75	32
Cochrane 2	Ti1	53	27
Scarritt Quarry	Ti2	44	6
Saddle locality	Ti2	83	36
Ledge locality	Ti3	77	27
Cedar Point Quarry	Ti3	48	6

\*Secord (1998) considered this fauna latest Torrejonian (To3).

### Biostratigraphic (Temporal) Range Extensions

The following is a summary of all biostratigraphic (temporal) range extensions of mammalian species observed through study of the fauna from the VFBZ (refer to Fig. 7). An asterisk (\*) denotes species that extend only into the overlap zone.

- First record in Tiffanian Biochron Ti3 of *Anconodon cochranensis*, extended from Tiffanian Biochron Ti1.
- First records in Tiffanian Biochron Ti1 of *Krauseia clemensi*\*, *Ectypodus szalayi*\*, *Gelastops joni*\*, *Paleotomus milleri*, *Pantolambda cavirictus*, *Litaletes disjunctus*\*, *Anisonchus sectorius*\*, *Periptychus carinidens*, *Tetraclaenodon puercensis*, *Prodiacodon puercensis*\*, *Palaechthon alticuspis*, *Palenochtha minor*\*, and *Paromomys depressidens*\*, all extended from the Torrejonian.
- Tentatively, first records in Tiffanian Biochron Ti1 of *Coriphagus encinensis* and *Pronothodectes jepi*, extended from the Torrejonian.
- First record in Torrejonian Biochron To3 and Tiffanian Biochrons Ti1 and Ti3 of *Palaechthon*

*nacimienti*, extended from Torrejonian Biochron To2.

- First record in Tiffanian Biochron Ti2 of *Pro-mioclaenus acolytus*, extended from Tiffanian Biochron Ti1.
- First records in Tiffanian Biochrons Ti2–Ti3 of *Mimotricentes subtrigonus* and *Chriacus pelvidens*, extended from the Torrejonian and Tiffanian Biochron Ti1.
- First records in Torrejonian Biochron To3 and Tiffanian Biochrons Ti2–Ti3 of *Parectypodus pattersoni* and *Paleotomus carbonensis*, both extended from Tiffanian Biochron Ti1.
- First record in Torrejonian Biochron To3 of *Anconodon lewisi*, extended from the Tiffanian.
- First record in Torrejonian Biochron To3 and Tiffanian Biochron Ti1 of *Ptilodus kummae*, extended from Tiffanian Biochrons Ti3–Ti4.
- First record in Torrejonian Biochron To3 and Tiffanian Biochrons Ti1–Ti2 of *Neoplagiaulax jepi*, extended from Tiffanian Biochron Ti4.
- First record in Tiffanian Biochron Ti1 of *Nava-jovius kohlhaasae*, extended from Tiffanian Biochrons Ti3–Ti5.



- First record in Tiffanian Biochron Ti1 of *Litocherus lacunatus*, extended from Tiffanian Biochrons Ti3–Ti5, although questionably known from To3 and Ti2.
- First record in Torrejonian Biochron To3 of *Catopsalis fissidens*, extended from Torrejonian Biochron To2, although questionably known from Ti1.

## BIOGEOGRAPHY

### Geographic Affinity

Figure 10 summarizes biogeographic relationships of most species in the mammalian fauna of the VFBZ. For simplicity, I have lumped together occurrences of tentatively identified species with more definitive representatives of their namesake. More northerly and southerly occurrences are grouped into two geographic categories to the north of Wyoming and three to the south. Inspection of Figure 10 reveals that fauna of the VFBZ has affinities both to northerly and southerly faunas; however, the mammalian fauna of the VFBZ has greater affinities with northerly faunas (56% of species are shared only with northerly faunas). Only 19 percent of species has southern affinities, and 25 percent is found both in northern and southern faunas. This is in contrast to the Puercan fauna from the Ferris Formation in the central Hanna Basin, which has clear southerly affinities (Eberle and Lillegraven, 1998).

Gingerich (1976, 1977a, 1977b) provided a possible explanation for this shift in affinity, noting that the beginning of the Tiffanian marks a shift from warm subtropical climate in North America to a period of cooler, temperate climate. This caused a southward shift in the geographic ranges of North American species adapted to the subtropical climate. Gingerich's (1976, 1977a, 1977b) hypothesis would suggest that Tiffanian faunas (including the VFBZ) in northern North America must be derived from as yet unknown, even more northerly faunas. Krause and Maas (1990) disagreed with Gingerich's (1976, 1977a, 1977b) hypothesis, however, because Tiffanian species can be phylogenetically derived from late Torrejonian forms of the same region.

Another explanation for this shift in affinity may be simply due to sampling bias (refer to Table 1 and Fig. 8). Early Tiffanian faunas are rare and yield scanty samplings of fossils in sites south of the Hanna Basin. In contrast, some of the most fossiliferous and best-described early Tiffanian faunas are known from Montana and Canada.

### Geographic Range Extensions

Occurrences of certain mammalian species in the VFBZ result in biogeographical range extensions for them, which are summarized below.

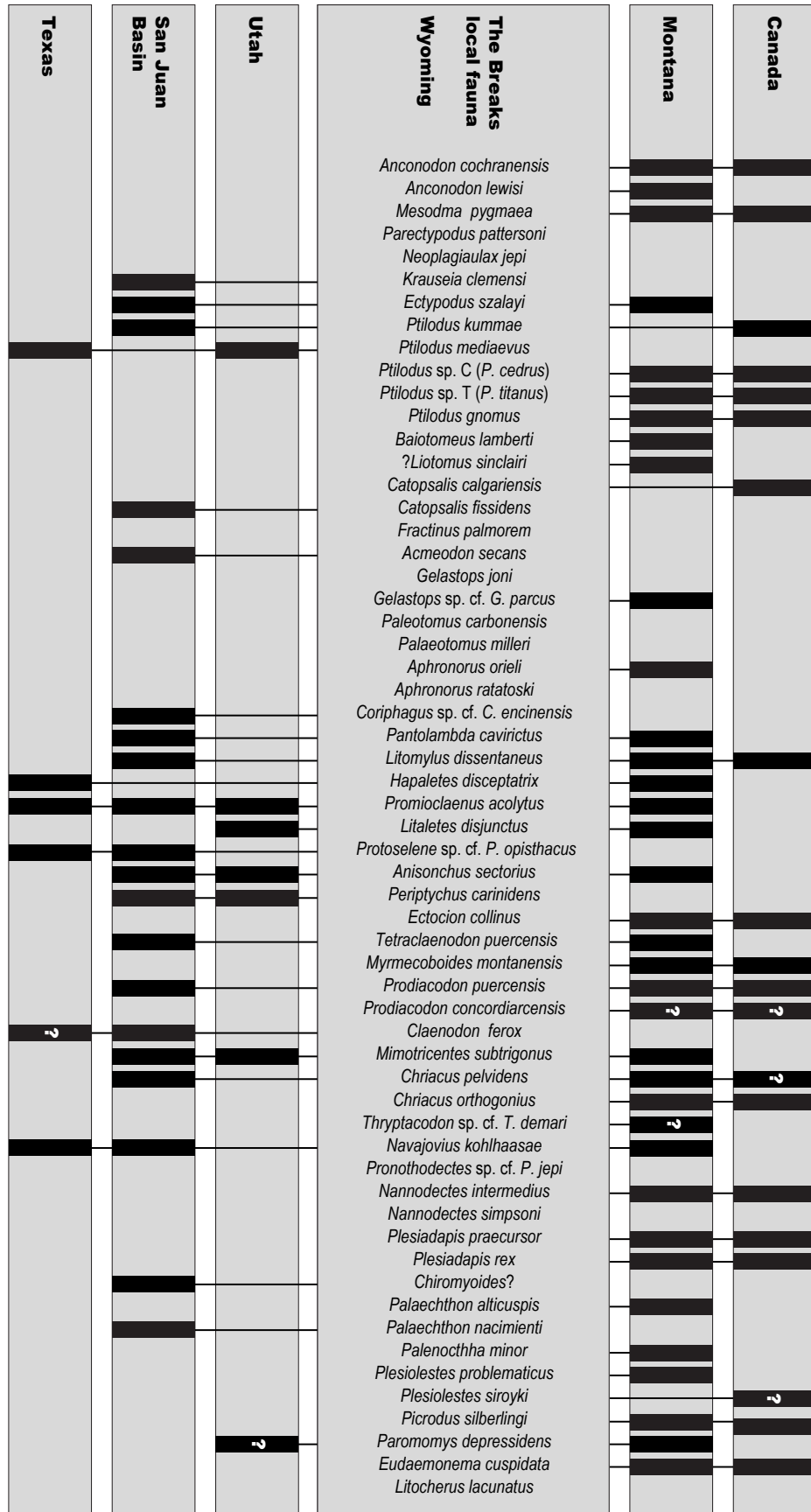
- Most southerly record of *Ptilodus* sp. T, extended from the Crazy Mountains Basin.
- Most southerly records of *Neoplagiaulax jepi* and *Eudaemonema cuspidata*, both extended from the northern Bighorn Basin.
- Most southerly records of *Anconodon cochranensis* and *Chriacus orthogonius*, both extended from the southern Bighorn Basin.
- Most southerly records of *Anconodon lewisi*, *Parectypodus pattersoni*, *?Liotomus sinclairi*, *Catopsalis calgariensis*, *Nannodectes intermedius*, *Plesiadapis praecursor*, and *Palaechthon alticuspis*, all extended from the Wind River Basin.
- Most northerly record of *Navajovius kohlhaasae*, extended from the southwestern Green River Basin.
- Most northerly records of *Krauseia clemensi*, *Ptilodus mediaevus*, *Gelastops joni*, and *Paleotomus milleri*, all extended from the Washakie Basin.
- Most northerly records of *Catopsalis fissidens* and *Palaechthon nacimienti*, both extended from the San Juan Basin.

## CONCLUSIONS

Biostratigraphic data from the Hanna Formation in The Breaks lend new insight into the nature of the boundary between the Torrejonian and Tiffanian NALMAs. The most important observation is the overlap zone, which yields a mixture of typically latest Torrejonian and earliest Tiffanian species, including *Tetraclaenodon puercensis*, *Plesiadapis praecursor*, and *Nannodectes intermedius*. *Plesiadapis* first appears at the base of the overlap zone, thus, by definition, marking the beginning of Tiffanian time (Archibald et al., 1987). The end of the overlap zone is recognized by the disappearance of several species that originally were thought to have been restricted to the Torrejonian. However, a new biochronologic term is not defined, as the end of the overlap zone cannot yet be defined by the first appearance of any known mammalian taxon. I define The Breaks local fauna as the assemblage of mammals within the overlap zone.

The unusually expanded stratigraphic section in The Breaks makes possible the recognition of an overlap zone. The diversity of The Breaks local fauna also allows the possibility of correlating the overlap zone to other faunas throughout western North

**Figure 10.** Geographic distribution of mammalian species known from The Breaks local fauna. Thick black bars indicate documented presence of species within indicated geographic region.



America. It is now possible to recognize faunas of earliest Tiffanian age that previously have been assigned to the Torrejonian due to the lack of critical index fossils. Faunas potentially correlatable to the overlap zone are recognized by an abundance of Torrejonian species alongside species definitive of the Tiffanian that may include *Plesiadapis* and *Nannodectes*. Several quarries outside of the Hanna Basin (i.e., the Halfway Hill and Grayson Ridge localities in the Carbon Basin and the Shotgun local fauna in the Wind River Basin) are now recognized as temporally equivalent to the overlap zone.

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**Appendix 1. Mammalian composition of Vertebrate Fossil-Bearing Zone (VFBZ). Following is a complete listing of all mammalian species known to occur in VFBZ. Double dagger (‡) denotes species present in VFBZ, outside of overlap zone, that are not included as part of The Breaks local fauna. Taxonomy follows McKenna and Bell (1997).**

Class Mammalia Linnaeus, 1758

  Infraclass Allotheria Marsh, 1880

    Order Multituberculata Cope, 1884b

      Cimolodontidae Marsh, 1889

*Anconodon* Jepsen, 1940

*Anconodon cochranensis* (Russell, 1929) Van Valen and Sloan, 1966

*Anconodon lewisi* Sloan, 1987

      Ptilodontidae (Cope, 1887) Simpson, 1927

*Mesodma* Jepsen, 1940

*Mesodma pygmaea* Sloan, 1987

*Parectypodus* Jepsen, 1930

*Parectypodus pattersoni* Sloan, 1987

*Neoplagiaulax* Lemoine, 1882

*Neoplagiaulax jepi* Sloan, 1987

*Neoplagiaulax?*

*Krauseia* Vianey-Liaud, 1986

*Krauseia clemensi* (Sloan, 1981) Vianey-Liaud, 1986

*Ectypodus* Matthew and Granger, 1921

*Ectypodus szalayi* Sloan, 1981

*Ptilodus* Cope, 1881d

*Ptilodus kummae* Krause, 1977

*Ptilodus mediaevus* Cope, 1881d

*Ptilodus* sp. C?

*Ptilodus* sp. T

*Ptilodus gnomus* Scott et al., 2002

*Ptilodus* sp.

*Baiotomeus* Krause, 1987

*Baiotomeus lamberti* Krause, 1987

*Baiotomeus* sp.

    Eucosmodontidae (Jepsen, 1940) Sloan and Van Valen, 1965

*Liotomus* Cope 1884c

        ? *Liotomus sinclairi* (Simpson, 1935a) Vianey-Liaud, 1986

    Taeniolabididae Granger and Simpson, 1929

*Catopsalis* Cope, 1882b

*Catopsalis calgariensis* Russell, 1926

        ‡ *Catopsalis fissidens?* Cope, 1884a

    Family indeterminate

*Fractinus* Higgins, *in press*

*Fractinus palmorem* Higgins, *in press*

  Infraclass Holotheria Wible et al., 1995

    Order Cimolesta McKenna, 1975

      Cimolestidae Marsh, 1889

*Acmeodon* Matthew and Granger, 1921

*Acmeodon secans* Matthew and Granger, 1921

*Gelastops* Simpson, 1935a

*Gelastops joni* Rigby, 1980

          ‡ *Gelastops* sp. cf. *G. parvus* Simpson, 1935a

*Paleotomus* Van Valen, 1967

*Paleotomus carbonensis* Secord, 1998

*Paleotomus* sp. cf. *P. carbonensis* Secord, 1998

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- Paleotomus milleri* Rigby, 1980  
 Palaeoryctidae (Winge, 1917) Simpson, 1931  
   cf. *Pararyctes* Van Valen, 1966  
 Pantolestidae Cope, 1884c  
   *Aphronorus* Simpson, 1935a  
     *Aphronorus orieli* Gazin, 1969  
     *Aphronorus ratatoski* Winterfeld, 1982  
     *Aphronorus* sp. cf. *A. ratatoski* Winterfeld, 1982  
     ? *Aphronorus*  
   *Coriphagus* Douglass, 1908  
     *Coriphagus* sp. cf. *C. encinensis* (Matthew and Granger, 1921) Simpson,  
       1937  
 Pantolambdidae Cope, 1883d  
   *Pantolambda* Cope, 1882c  
     *Pantolambda cavirictis* Cope, 1883c  
   Pantolambdidae gen. indet.  
 Order Condylarthra Cope, 1881e  
   Hyopsodontidae (Trouessart, ?1879) Nicholson and Lydekker, 1889  
     *Litomylus* Simpson, 1935a  
       *Litomylus dissentaneus* Simpson, 1935a  
       *Litomylus* sp.  
       ? *Litomylus*  
     *Haplaletes* Simpson, 1935a  
       *Haplaletes disceptatrix* Simpson, 1935a  
 Mioclaenidae Osborn and Earle, 1895  
   *Promioclænus* Trouessart, 1904  
     *Promioclænus acolytus* (Cope, 1882a) Wilson, 1956  
     ? *Promioclænus*  
   *Litaletes* Simpson, 1935a  
     *Litaletes disjunctus* Simpson, 1935a  
   *Protoselene* Matthew, 1897  
     *Protoselene* sp. cf. *P. opisthacus* (Cope, 1882f) Matthew, 1897  
 Periptychidae Cope, 1882e  
   *Anisonchus* Cope, 1881a  
     *Anisonchus sectorius* (Cope, 1881c) Cope, 1881a  
   *Periptychus* Cope, 1881a  
     *Periptychus carinidens* Cope, 1881b  
     *Periptychus* sp.  
 Phenacodontidae Cope 1881e  
   *Ectocion* Cope, 1882d  
     *Ectocion collinus* Russell, 1929  
   *Phenacodus* Cope, 1873  
     *Phenacodus* sp.  
   *Tetraclaenodon* Scott, 1892  
     *Tetraclaenodon puercensis* (Cope, 1881c) Matthew, 1937  
   Phenacodontidae gen. indet.  
 Order Leptictida McKenna, 1975  
   Leptictidae Gill, 1872  
     *Myrmecoboides* Gidley, 1915  
       *Myrmecoboides montanensis* Gidley, 1915  
     *Prodiacodon* Matthew, 1929  
       *Prodiacodon puercensis* (Matthew, 1918) Matthew, 1929  
       *Prodiacodon concordiaricensis* Simpson, 1935a  
       ? *Prodiacodon*  
 Order Procreodi Matthew, 1915  
   Arctocyonidae Blainville, 1841

- Claenodon* Scott, 1892  
*Claenodon ferox* (Cope, 1883b) Scott, 1892  
*Mimotricentes* Simpson, 1937  
*Mimotricentes subtrigonus* (Cope, 1881a) Van Valen and Sloan, 1965
- Oxyclaenidae Scott, 1892  
*Chriacus* Cope, 1883a  
*Chriacus pelvidens* (Cope, 1881f) Cope, 1883a  
*Chriacus orthogonius* Russell, 1929  
? *Chriacus*  
*Thryptacodon* Matthew, 1915  
*Thryptacodon* sp. cf. *T. demari* Gazin, 1956a
- Order Primates Linnaeus, 1758  
Microsyopidae Osborn and Wortman, 1892  
*Navajovius* Matthew and Granger, 1921  
*Navajovius kohlhaasae* Matthew and Granger, 1921
- Plesiadapidae Trouessart, 1897  
*Pronothodectes* Gidley, 1923  
*Pronothodectes* sp. cf. *P. jepi* Gingerich, 1975  
*Nannodectes* Gingerich, 1975  
*Nannodectes intermedius* (Gazin, 1971) Gingerich, 1975  
‡ *Nannodectes simpsoni* (Gazin, 1956a) Gingerich, 1975  
*Nannodectes*?  
*Plesiadapis* Gervais, 1877  
*Plesiadapis praecursor* Gingerich, 1975  
‡ *Plesiadapis rex* (Gidley, 1923) Simpson, 1937  
*Plesiadapis*?  
*Chiromyoides* Stehlin, 1916  
‡ *Chiromyoides*?
- Palaechthonidae (Szalay, 1969) Gunnell, 1989  
*Palaechthon* Gidley, 1923  
*Palaechthon alticuspis* Gidley, 1923  
*Palaechthon nacimienti* Wilson and Szalay, 1972  
*Palenochtha* Simpson, 1935a  
*Palenochtha minor* (Gidley, 1923) Simpson, 1935a  
*Plesiolestes* Jepsen, 1930  
*Plesiolestes problematicus* Jepsen, 1930  
*Plesiolestes sirokyi* Szalay, 1973
- Picrodontidae Simpson, 1937  
*Picrodus* Douglass, 1908  
*Picrodus silberlingi* Douglass, 1908
- Paromomyidae Simpson, 1940  
*Paromomys* Gidley, 1923  
*Paromomys depressidens* Gidley, 1923
- Plagiomenidae Matthew, 1918  
*Eudaemonema* Simpson, 1935a  
‡ *Eudaemonema cuspidata* Simpson, 1935a
- Carpolestidae Simpson, 1935a  
*Elphidotarsius* Gidley, 1923  
*Elphidotarsius* sp.
- Order Carnivora Bowdich, 1821  
Viverravidae Wortman and Matthew, 1899  
cf. *Protictis* (Matthew, 1937) MacIntyre, 1966
- Order Erinaceomorpha Gregory, 1910  
*Litocherus* Gingerich, 1983  
*Litocherus lacunatus* (Gazin, 1956a) Gingerich, 1983

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**Appendix 2. Listing, by taxon, of University of Wyoming cataloged specimens of fossil mammals used in study from localities in VFBZ.**


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- Anconodon cochranensis*—From V-90029: UW 27051, Lp4, UW 27110, Rp4, UW 28261, Rp4, and UW 28379, Rp4 fragment; from V-90060: UW 27072, Rp4; and from V-90063: UW 28396, Lp4. Questionably, from V-90082: UW 31451, Lp4 fragment; and from V-90109, UW 27103, Rp4 fragment.
- Anconodon lewisi*—From V-90060: UW 27100, Lp4, UW 27105, Rp4 fragment, UW 28220 Lp4 fragment, and UW 28218, Lp4 fragment; from V-90082, UW 31465, Lp4 fragment; and from V-96010: UW 27068, Rp4.
- Mesodma pygmaea*—From V-90029: UW 27725, Rm1, UW 31699, m1 fragment, UW 31704, m1 fragment, UW 31705, m1 fragment, and UW 31706, m1 fragment; from V-90032: UW 28154, Lm1; from V-90039: UW 27124, Lm1, and UW 27131, LP4; from V-90060: UW 31218, Rm1, and UW 27140, LM1 fragment; from V-90082: UW 28099, LM1, UW 31349, Rm1, UW 28114, RM2, and UW 28138, RM2.
- Parectypodus pattersoni*—From V-90029: UW 27713, Lp4, UW 27876, Rm1, UW 27156, LP4, UW 27175, LP4, and UW 27176, RP4; From V-90039: UW 27135, LP4; from V-90060: UW 31192, Lp4, UW 27142, Rm2, UW 27141, LP4, UW 27149, LP4, and UW 31169, RP4; from V-90063: UW 28168, RP4; from V-90064: UW 27799, Rm1, and UW 28522, RP4 fragment; and from V-90082: UW 31435, Rp4 fragment, UW 28124, Lm1, UW 28110, Rm2, UW 28115, Lm2, UW 28137, Lm2, and UW 28105, LP4. Questionably, from V-90029: UW 27740, Lm1, and UW 28274, P4 fragment; and from V-97027: UW 28551, LP4 fragment.
- Neoplagiaulax jepi*—From V-90029: UW 27050, Lp4, UW 27052, Rp4, UW 27061, Lp4, UW 27092, Lp4 fragment, UW 28364, Lp4 fragment, UW 31115, Rp4 fragment, and UW 31667, Lp4 fragment; from V-90060: UW 27147, LP4, UW 28214, Lp4 fragment, and UW 28223, Rp4 fragment; from V-90063: UW 28403, LP4 fragment; from V-90082: UW 27087, RP4 fragment, and UW 31333, RP4 fragment; and from V-91007: UW 27069, RP4. Questionably, from V-90039: UW 27095, LP4 fragment; from V-90060: UW 31147, LP4 fragment; and from V-90082: UW 28092, RP4 fragment.
- Neoplagiaulax?*—From V-90029: UW 31684, P4 fragment; from V-90060: UW 31221, LP4 fragment; and from V-90082: UW 31304, Lp4 fragment, UW 31450, Rp4 fragment, UW 31313, LP4 fragment, UW 28094, RM2, and UW 28147, LM2.
- Krauseia clemensi*—From V-90029: UW 27066, Lp4, UW 31669, Lp4 fragment, and UW 31671, p4 fragment; from V-90032: UW 31768, Rp4 fragment; from V-90060: UW 27151, Rp4, and UW 31163, Rp4; and from V-90082: UW 31371, Rp4 fragment. Questionably, from V-90082: UW 31334, p4 fragment and UW 31369, Lp4 fragment.
- Ectypodus szalayii*—From V-90029: UW 27058, Lp4, and UW 31665, Lp4; from V-90039: UW 28633, Rm1 fragment; and from V-90082: UW 27067, Rp4, UW 28123, Rm1, and UW 28134, Lm1.
- Ptilodus kummae*—From V-90029: UW 27717, Rm1 fragment, UW 27841, Lm1, UW 31087, m1 fragment, and UW 31696, m1 fragment; from V-90049: UW 23097, Rp4 fragment; from V-90060: UW 27075, Lp4, UW 27076, Rp4, UW 27090, Lp4 fragment, UW 27144, LM1, and UW 28199, LM1 fragment; from V-90082, UW 31482, LM1 fragment; and from V-93021: UW 27113, Lp4 fragment. Questionably, from V-90029: UW 27112, Lp4 fragment, UW 27853, Rm1, UW 27872, Rm1, UW 27846, P3, UW 27849, P3, UW 27903, P3, UW 27906, P3, UW 27152, LP4, UW 27157, LP4, and UW 31082, LP4 fragment; from V-90048: UW 31500, Lp4; from V-90060: UW 28211, p4 fragment, UW 28213, Lp4 fragment, UW 28216, Lp4 fragment, UW 28224, Lp4 fragment, UW 28226, Lp4 fragment, and UW 27150, RM1 fragment; from V-90073: UW 27091, Lp4 fragment; and from V-90082: UW 27121, Rp4 fragment, UW 28100, Rm1 fragment, UW 28118, Lm1 fragment, and UW 31322, LM1 fragment.
- Ptilodus mediaevus*—From V-90029: UW 27038, Lp4, UW 27039, Lp4, UW 27045, Rp4, UW 27056, Lp4, UW 27060, Lp4 fragment, UW 28310, Rp4, UW 31074, Lp4 fragment, UW 31079, Lp4 fragment, UW 27861, Lm1 fragment, UW 27867, Rm1, UW 27869, Rm1, UW 31694, m1 fragment, UW 31698, m1 fragment, UW 27088, P3, UW 27718, P3, UW 27769, P3, UW 27870, P3, UW 27885, P3, UW 27886,



P3, UW 27890, P3, UW 27892, P3, UW 27893, P3, UW 27894, P3, UW 27895, P3, UW 27896, P3, UW 27905, P3, UW 27907, P3, UW 27934, P3, and UW 28254, P3; from V-90032: UW 28993, LP4; from V-90035, UW 28542, P3; from V-90039: UW 28625, Rp4, UW 27126, Lm1, UW 27128, P3, UW 28228, P3, and UW 28230, P3; from V-90040: UW 27080, Lp4 fragment; from V-90043: UW 28588, P3; from V-90047: UW 28460, P3; from V-90060: UW 28217, Lm1, UW 27148, P3, UW 28182, P3, UW 28184, P3, UW 28188, P3, UW 28189, P3, UW 28191, P3, UW 12196, P3, UW 28203, P3, UW 28219, P3, and UW 27139, LP4; from V-90061: UW 28658, RP4 fragment; from V-90063: UW 28417, m1 fragment; from V-90064: UW 27803, P3, and UW 28821, P3; from V-90073: UW 28173, P3; from V-90082: UW 27078, Lp4, UW 28088, Rm1, UW 28091, P3, UW 28093, P3, UW 28107, P3, and UW 28145, P3; from V-90084: UW 24329, P3; from V-90107: UW 27065, Rp4; from V-90112: UW 28803, Lm1 fragment, and UW 28807, P3; from V-91007: UW 28163, P3; from V-96010: UW 27089, P3, and UW 28969, P3. Questionably, from V-90029: UW 27857, Rm1, UW 27770, P3, UW 27840, P3, UW 28038, P3, UW 28300, P3, UW 27850, LP4, and UW 28083, RM1; from V-90047: UW 28755, RM1 fragment; from V-90060: UW 27137, Lm1, UW 28200, P3; from V-90082: UW 31398, Rm1 fragment; from V-90089: UW 24337, Lp4 fragment; from V-91007: UW 28164, P3; from V-93024: UW 27104, Rp4 fragment; from V-96010: UW 27077, Lp4, UW 27108, Lp4 fragment, and UW 28959, P3.

*Ptilodus* sp. C?—From V-90029: UW 27040, Lp4, UW 27043, Lp4, UW 27044, Rp4, UW 27055, Rp4, UW 27062, Rp4 fragment, UW 27114, Lp4 fragment, UW 27969, P3, UW 27037, LP4, UW 27177, LP4 fragment, UW 27733, LP4 fragment, UW 27764, LP4 fragment, UW 27847, LP4 fragment, UW 31672, RP4 fragment, UW 31674, LP4 fragment, UW 31680, LP4 fragment, UW 21758, RM1 fragment, UW 27174, LM1 fragment, UW 27179, LM1 fragment, and UW 27184, RM1 fragment; from V-90032: UW 28151, P3; from V-90039: UW 27127, LM1 fragment, and UW 27130, RM1; from V-90047: UW 28457, P3; from V-90048: UW 24322, Lp4 fragment; from V-90049: UW 23098, RP4 fragment; from V-90056: UW 27035, Rp4; from V-90057: UW 28546, RM1 fragment; from V-90060: UW 28185, P3, UW 28198, LP4 fragment, and UW 28204, LP4 fragment; from V-90064: UW 28511, LM1 fragment; from V-90082: UW 27101, Lp4 fragment, UW 28142, P3, UW 28117, LM1 fragment, and UW 31442, RM1 fragment; and from V-93022: UW 28699, Rp4.

*Ptilodus* sp. T—From V-90029: UW 27042, Rp4, UW 27856, Lm1 fragment, and UW 27171, RM2; from V-90039: UW 27085, Rp4 fragment; from V-90055: UW 28557, Lm2; from V-90060: UW 28221, RP4 fragment, and UW 28208, LM1 fragment; from V-90082: UW 31443, m1 fragment, and UW 28102, LM1; from V-90112: UW 27057, Rp4, and UW 28793, Rp4 fragment; and from V-91007: UW 27822, m1 fragment, UW 28159, LP4 fragment, UW 28162, RP4, and UW 27818, RM2. Questionably, from V-90029: UW 27899, P3, UW 27165, RM2, UW 27168, RM2, UW 27170, LM2, and UW 27871, RM2; from V-90060: UW 27145, RM2; from V-90071: UW 28476, Rp4 fragment; from V-90082, UW 28108, m1?, and UW 28143, Lm1; and from V-91007: UW 28160, LM2.

*Ptilodus gnomus*—From V-90029: UW 27041, Rp4, UW 27046, Rp4, UW 27049, Rp4, UW 27053, Lp4, UW 27059, Lp4, UW 27070, Rp4, UW 27096, Rp4, UW 27109, Rp4 fragment, UW 27117, Lp4 fragment, UW 27122, Lp3-p4, UW 31035, Lp4 fragment, UW 31666, Lp4 fragment, UW 27851, Lm1, UW 27860, Rm1, UW 31044, Lm1, UW 27838, Rm2, UW 27845, Rm2, UW 27862, Rm2, UW 28070, Rm2, UW 27153, LP4, UW 27163, LP4, UW 27164, LP4, UW 27178, LP4 fragment, UW 27868, RP4 fragment, UW 31062, RP4 fragment, UW 27159, RM1 fragment, UW 27160, RM1 fragment, UW 27161, LM1, UW 27181, LM1 fragment, UW 27183, RM1, UW 27873, RM1 fragment, UW 31709, LM1 fragment, and UW 31712, R?M1 fragment; from V-90032: UW 27074, Lp4, UW 27073, Rp4, UW 28150, LP4, and UW 28152, RP4; from V-90039: UW 31936, Lm1 fragment, and UW 27132, LM2; from V-90045: UW 23093, Lp4; from V-90060: UW 27138, Lm1; and from V-90082: UW 28089, Lm1, UW 28116, Lm2, UW 28130, RP4 fragment, UW 28095, LM1, and UW 28086, RM2. Questionably, from V-90047: UW 28753, RP4 fragment; from V-90064: UW 28526, Rm1 fragment; from V-96040: UW 28175, Lp4 fragment; and from V-97027: UW 28174, Rp4 fragment.

*Ptilodus* sp.—From V-90029: UW 27098, Rp4 fragment, UW 31036, Lp4 fragment, UW 31077, p4 fragment, UW 31117, p4 fragment, UW 31120, Rp4 fragment, UW 31129, Rp4 fragment, UW 31668, p4 fragment, UW 27848, Lm2 fragment, UW 27858, Rm2, UW 27945, Lm2, UW 27839, RP4 fragment, UW 27852, LP4 fragment, UW 27855, LP4 fragment, UW 27863, RP4 fragment, UW 27864, RP4 fragment,

UW 28368, LP4 fragment, UW 31086, P4 fragment, UW 27723, RM1 fragment; from V-90032: UW 28995, LP4 fragment, and UW 28996, RP4 fragment; from V-90039: UW 28232, Lp4 fragment, and UW 27134, Lm2; from V-90041: UW 27106, Lp4 fragment; from V-90043: UW 28607, Lp4 fragment; from V-90047: UW 28750, Rp4 fragment; from V-90048: UW 28272, LP4 fragment; from V-90060: UW 28225, Rp4 fragment, UW 28839, Rp4 fragment, UW 28181, Rm2, UW 28186, Lm2, UW 28190, Rm2, UW 28193, Rm2, UW 28201, Rm2, UW 28197, P3 fragment, UW 28187, LP4 fragment, UW 28195, RP4 fragment, UW 28202, RP4 fragment, UW 31158, LM1 fragment, UW 27143, RM2, and UW 28183, RM2; from V-90064: UW 28822, RP4 fragment; from V-90082: UW 28566, Rp4 fragment, UW 28567, Rp4 fragment, UW 31469, Lp4 fragment, UW 31473, Lp4 fragment, UW 31480, Rp4 fragment, UW 28104, Lm2, UW 28109, Rm2, UW 28148, Lm2, UW 31446, LP4 fragment, UW 31456, LP4 fragment, UW 28087, LM2, and UW 28096, LM2; from V-90112: UW 28792, Lp4 fragment; from V-91007: UW 28890, RP4 fragment, UW 28157, LM1 fragment, UW 28161, RM1 fragment, and UW 28158, RM2; from V-96007: UW 28465, Lp4 fragment, and UW 31536, Rp4 fragment; from V-96019: UW 28767, RP4 fragment; and from V-97020: UW 28676, Lp4 fragment. Questionably, from V-90029: UW 27111, Rp4 fragment; from V-90039: UW 27093, Lp4 fragment, and UW 27097, Lp4 fragment; from V-90043: UW 27102, Lp4 fragment; from V-90060: UW 27079, Rp4 fragment; from V-90082: UW 27084, Lp4 fragment, UW 27118, Rp4 fragment, UW 31460, Lp4 fragment; from V-93021: UW 27081, Lp4; and from V-96010: UW 27082, Lp4 fragment.

*Baiotomeus lamberti*—From V-90029: UW 27047, Lp4, UW 27048, Rp4, UW 27054, Lp4, UW 27071, Lp4, UW 27155, RP4, UW 28119, RP4 fragment, UW 27185, LM1, UW 27186, RM1 fragment, UW 27722, LM1 fragment, and UW 31707, RM1; from V-90039: UW 27133, LM1; from V-90060: UW 28848, LM1 fragment; and from V-90082: UW 28135, RP4, UW 28112, LM2, and UW 28132, RM2. Questionably, from V-90029: UW 27119, Rp4, UW 27865, RP4, UW 31080, RP4 fragment, and UW 31686, LP4 fragment; from V-90093: UW 28662, LM1 fragment.

*Baiotomeus* sp.—From V-91007: UW 27116, Lp4 fragment. Questionably, from V-90057: UW 27107, Lp4 fragment; and from V-90082: UW 27099, Rp4 fragment, and UW 31464, Lp4 fragment.

?*Liotomus sinclairi*—From V-90029: UW 27173, RP4, and UW 31869, LP4 fragment; From V-90039: UW 28627, LP4 fragment; from V-90082: UW 27064, Rp4, UW 28125, RP4, and UW 31429, LP4 fragment.

*Catopsalis calgariensis*—From V-90068: UW 28928, broken Lm2.

*Catopsalis fissidens?*—From V-90107: UW 28880, Rm1 fragment.

*Fractinus palmorem*—From V-90043: UW 27063, Lp4; from V-96010: UW 28389, Lp4 fragment.

*Acmeodon secans*—From V-90029: UW 28062, RM1; and from V-90057: UW 28730, RM1 fragment.

*Gelastops joni*—From V-90029: UW 28078, Rm3, and UW 28296, Lmx trigonid; from V-90032: UW 28486, Rm2; from V-90060: UW 28293, Rmx trigonid; and from V-90082: UW 31226, Rm2.

*Gelastops* sp. cf. *G. parvus*—From V-91007: UW 28885, m2 trigonid fragment.

*Paleotomus carbonensis*—From V-90029: UW 31133, Rmx trigonid; from V-90063: UW 28439, Rm3 trigonid; and from V-91007: UW 27819, RM2 fragment.

*Paleotomus* sp. cf. *P. carbonensis*—From V-90029: UW 27996, LMx fragment; and from V-90071: UW 28480, LMx fragment.

*Paleotomus milleri*—From V-90082: UW 31455, Rm2 trigonid; and from V-96010: UW 28955, Lm1.

cf. *Pararyctes*—From V-90032: UW 28639, Rm1 or 2.

*Aphronorus orieli*—From V-90029: UW 28383, Rp4; UW 28014, Rm1; UW 28050, Lm1; UW 28077, Rm1; UW 28056, Rm2; UW 28247, left dentary fragment with m2; UW 27826, Lm2; UW 31030, Rm2; UW 28320, Lmx trigonid; UW 27739, Lmx talonid; UW 27981, RM1; UW 27994, RM1; UW 28039, RM2; and UW 28052, LM2; from V-90046: UW 28643, Lm2; from V-96010: UW 28598, Rp4; and from V-96035: UW 28550, Lm1. Questionably, from V-90029: UW 28009, Lm3.

*Aphronorus ratatoski*—From V-90068: UW 28933, Rp4.

*Aphronorus* sp. cf. *A. ratatoski*—From V-90029: UW 31131, Rp4; UW 27942, Rm1; UW 27984, Rm1; UW 31130, Lm2 trigonid; UW 31135, Lm2 trigonid; UW 28027, Lmx trigonid; and UW 28043, Rm3; from V-90047: UW 28453, Rm2; from V-90060: UW 28862, Lm1 trigonid, and UW 28775, LM1; from V-90064: UW 27797, Rm2; from V-90082: UW 31235, Rm2; UW 31447, Lm2 trigonid; UW 31227, LM1; and UW 31228, LM1; from V-90112: UW 28761, Rp4, and UW 28764, RM1; and from V-91007: UW 28886, Lm1.

?*Aphronorus*—From V-90029: UW 28069, Rp4.

*Coriphagus* sp. cf. *C. encinensis*—From V-90082: UW 28560, LM1, and UW 31229, LM1; and from V-91007: UW 27820 Mx fragment.

*Pantolambda cavirictis*—From V-90057: UW 27036, LM3.

Pantolambdidae gen. indet.—From V-90112: UW 28768, Mx fragment; and from V-93024: UW 28878, tooth fragment.

*Litomylus dissentaneus*—From V-90029: UW 28308, incomplete dentary with p4, m2–m3; UW 28054, Lm1; UW 28055, Lm1; UW 27956, Lm2; UW 28002, Rm2; UW 28067, Lm3; UW 27961, RM1; UW 28051, LM1 fragment; UW 27190, RM2; UW 27977, RM2; and UW 28301, RM2 fragment; from V-90039: UW 28626, LM1 fragment; from V-90057: UW 28733, RM1 fragment; from V-90063: UW 28401, RM1 fragment; from V-90064: UW 28512, Rm2, and UW 28513, Lm2; from V-90071: UW 28697, Rm3; and from V-96020: UW 28540, Rm2. Questionably, from V-90029: UW 31058, RM2; from V-90032: UW 31000, RMx fragment; from V-90082: UW 31249, RM2; from V-91007: UW 28902, RM2 fragment.

*Litomylus* sp.—From V91007: UW 28891, LM2 fragment.

?*Litomylus*—From V-90029: UW 28363, RMx fragment.

*Haplaletes disceptatrix*—From V-90029: UW 27949, RM2; and from V-90082: UW 31233, fractured RM2.

*Promioclauenus acolytus*—From V-90029: UW 27935, Lm2; UW 27954, Lm2; UW 27964, Rm2; UW 27990, Lm2; UW 28330, Lm2; UW 28018, Lm3; UW 27751, Rmx trigonid; UW 28297, Lmx; UW 31128, Rmx trigonid; UW 31570, Lmx trigonid; UW 31572, broken Rmx; UW 31607, Lmx trigonid; UW 21188, LM1; UW 27948, RM1; UW 27988, RM1; UW 28031, LM1; UW 27937, RM2; and UW 27962, LM2; from V-90033: UW 28535, RMx fragment; from V-90047: UW 28455, Rm1; from V-90060: UW 28291, Lm1, and UW 28290, Rm3; from V-90064: UW 28263, RM1 fragment, and UW 28814, LMx fragment; from V-90071: UW 28698, RM2; from V-90082: UW 31241, LM2; from V-90091: UW 31026, RM1; from V-90112: UW 28797, RM1; from V-91007: UW 27815, Rmx trigonid; and from V-96010: UW 28594, LMx fragment. Questionably, from V-90029: UW 27997, LM1; UW 28010, RM1; UW 27750, LM2 fragment; UW 27972, RM3; and UW 27975, LM3; from V-90047: UW 28757, Lmx; from V-90064: UW 28516, Rm3; and from V-90082: UW 31237, RMx.

?*Promioclauenus*—From V-90029: UW 27976, LMx.

*Litaletes disjunctus*—From V-90029: UW 27995, LM1, and UW 31569, Rmx trigonid; from V-90039: UW 28575, Rmx trigonid; and from V-90071: UW 28469, Rm3.

*Protoselene* sp. cf. *P. opisthacus*—From V-90029: UW 28045, broken Rm1 or 2 and UW 31573, broken Lmx trigonid; and from V-90044: UW 28640, Rmx trigonid.

*Anisonchus sectorius*—From V-90060: UW 28288, Rm2; from V-90064: UW 28273, right dentary fragment with m1 and broken m2 and m3; UW 27795, Rm2; and UW 28826, LM3; and from V-90071: UW 28696, RMx fragment.

*Periptychus carinidens*—From V-90029: UW 28258, Lp2; UW 31121, px fragment; UW 28242, Lm2; UW 28246, R?P2; and UW 28307, RP4; from V-90047: UW 28742, mx fragment; from V-90050: UW 28554, RP2; from V-90056: UW 28341, px; from V-90064: UW 27801, Rm3; from V-92047: UW 31392, left maxillary fragment with P2–M3; and from V-96010: UW 28727, px. Questionably, from V-90030: UW

28340, px fragment; from V-90048: UW 28335, px; from V-90052: UW 28738, P3?; from V-90061: UW 28657, tooth fragment; from V-90062: UW 28866, tooth fragment, and UW 28872, tooth fragment; from V-93024: UW 31485 Px? fragment; and from V-96010: UW 28943, Px fragment.

*Periptychus* sp.—From V-90029: UW 30046, px fragment; from V-90047: UW 28747, tooth fragment, and UW 28752, tooth fragment; from V-90056: UW 28545, m?x fragment, and UW 28342, px fragment; from V-90057: UW 28731, Mx fragment; and from V-93021: UW 28707, tooth fragment. Questionably, from V-90029: UW 28762, tooth fragment, and UW 28974, tooth fragment; from V-90062: UW 28873, Px fragment; from V-90070: UW 28507, tooth fragment; and from V-90089: UW 24334, tooth fragment.

*Ectocion collinus*—From V-90029: UW 27971, Lp4, and UW 28245, LP4; from V-90031: UW 28541, Lmx; from V-90045: UW 23095, LM1 fragment; from V-90082: UW 28569, LP3; from V-90084: UW 28347, Rmx; and from V-90108: UW 28695, Rmx. Questionably, from V-90029: UW 28322, Rmx fragment; from V-90047: UW 28739, LM3 fragment; and from V-96010: UW 28949, P4.

*Phenacodus* sp.—From V-90063: UW 28334, RM1 or 2; and from V-90119: UW 28687, Rp4.

*Tetraclaenodon puercensis*—From V-90029: UW 31567, Mx fragment, and UW 31804, RM1; from V-90039: UW 31813, M3 fragment; from V-90041: UW 28337, Lm2 trigonid from; from V-90042: UW 28345, Lm2 trigonid; from V-90043: UW 28583, Rp4; UW 28584, Lm3; and UW 31806, LP4; from V-90046: UW 28641, m1 trigonid; from V-90047: UW 28741, Lm1 trigonid, and UW 28743, Lm1 fragment; from V-90048: UW 28645, Mx fragment; from V-90049: UW 28278, m2 trigonid; from V-90055: UW 31805, Lm2; from V-90060: UW 31807, LM1, UW 28843, M2, and UW 31816, LM1–3; from V-90062: UW 28867, P4; from V-90068: UW 31809, RP3, and UW 31814, LM2; from V-90082: UW 31238, Rm2 fragment; from V-90083: UW 31483, Rm2, and UW 28538, Lm3; from V-90101: UW 31802, Lm3; from V-90112: UW 28796, Lm3 trigonid; UW 31801, Rm3; UW 31803, Rm3; and UW 31815, RM2; from V-90115: UW 28689, Rm2; from V-92047: UW 28559, Rp4; from V-93021: UW 28702, Lm1, and UW 28703, Lm3; from V-93022: UW 31812, LM2 fragment; and from V-96010: UW 28590, Rm1 trigonid; UW 28769, m2 trigonid; UW 28948, Rm2 talonid; UW 31808, RM1; and UW 28976, M2 fragment. Questionably, from V-90029: UW 31810, LM1 fragment; from V-90032: UW 31019, LM2 fragment; from V-90070: UW 28502, M3 fragment; from V-90112: UW 31811, RM1 fragment; and from V-96010: UW 28947, LP3.

Phenacodontidae gen. indet.—From V-90044: UW 28282, mx trigonid; and from V-90108: UW 28981, Rmx.

*Myrmecoboides montanensis*—From V-90029: UW 28017, Rmx.

*Prodiacodon puercensis*—From V-90029: UW 28024, Rm2; from V-90060: UW 28292, Rm2, and UW 28781, LMx fragment. Questionably, from V-90029: UW 16031, RM3 fragment.

*Prodiacodon concordiarcensis*—From V-90029: UW 28257, Rp4, UW 16034, Rm2? trigonid, UW 28007, Rmx, UW 28023, Rmx, UW 27746, Rm3, and UW 27944, Lm3; from V-90032: UW 28497, Rp4; from V-90039: UW 28236, Rmx; and from V-90082: UW 31294, Lmx fragment. Questionably, from V-90029: UW 28063, P3?, and UW 28325, LMx fragment; and from V-90082: UW 31326, LMx fragment, and UW 31329, RM3 fragment.

?*Prodiacodon*—From V-90029: UW 27760, Rmx fragment; and from V-96010: UW 28726, Rp4 trigonid.

*Claenodon ferox*—From V-90029: UW 28251, Lmx talonid, and UW 28243, RM 1 or 2 fragment; from V-90039: UW 28719, LM3; from V-90062: UW 31818, right dentary fragment with roots of m1–2, and crown of m3; from V-90064: UW 27792, RM3; and from V-96011: UW 28728, M 1 or 2 fragment.

*Mimotricentes subtrigonus*—From V-90029: UW 27189, Rm1, UW 28327, Lmx talonid, UW 28385, Lmx talonid, and UW 28013, LM3 fragment; from V-90032: UW 28484, LM3; from V-90047: UW 28740, Lm2 trigonid; from V-90060: UW 28779, RM3 fragment, and UW 28283, Lm2 talonid; from V-90063: UW 28409, LM1; from V-90121: UW 28729, Lm2; and from V-96010: UW 28960, RM3. Questionably, from V-90060: UW 28285, Lm1 talonid.

*Chriacus pelvidens*—From V-90029: UW 27966, Lm3, UW 28328, Rm3, UW 28071, RM2, and UW 31819, Rmx fragment; from V-90039: UW 28623, LM2 fragment; from V-90060: UW 28286, Lm3, and UW 28783,



LM1 fragment; from V-90063: UW 28444, R?M2 fragment; and from V-90112: UW 28760, RM2 fragment. Questionably, from V-90089: UW 24335, Rmx trigonid.

*Chriacus orthogonius*—From V-93021: UW 28701, Rm2.

?*Chriacus*—From V-90029: UW 27757, LM1 fragment; from V-96010: UW 28600, RM1 fragment.

*Thryptacodon* sp. cf. *T. demari*—From V-90029: UW 21787, Rm1.

*Navajovius kohlhaasae*—From V-90029: UW 27965, Lm2, UW 31051, RM1 fragment, and UW 27747, LM3; and from V-90064: UW 27806, Rm2. Questionably, from V-90029: UW 27720, Lmx talonid; and from V-90039: UW 28634, Rmx talonid, and UW 28635, Rmx talonid.

*Pronothodectes* sp. cf. *P. jepi*—From V-90029: UW 28065, LM1 fragment, and UW 31612, Lm3 talonid; and from V-90039: UW 28234, LP3?.

*Nannodectes intermedius*—From V-90029: UW 27968, Lm1, UW 27827, Rm2, UW 16032, partial left dentary with i1, p3–4, and m2–3, and alveoli for c and p2, and roots of m1, UW 28248, partial left dentary with m2–3, UW 28020, RM1, UW 27832, RM1–2, UW 27986, RM3, and UW 31859, partial left maxilla with p4–m2; from V-90032: UW 28084, left maxilla with P2–4 and M1–3; from V-90055: UW 28555, RP4. Questionably, from V-90029: UW 27837, Lm1, UW 27831, Lm2, UW 27833, Rm2, UW 27980, Rm2, UW 31611, Rm3 talonid fragment, and UW 28250, partial left dentary with p3–4 and m1.

*Nannodectes simpsoni*—From V-90063: UW 28391, LP4. Questionably, from V-90063: UW 28393, Lmx fragment, UW 28413, Lmx trigonid, and UW 28404, LM3.

*Nannodectes?*—From V-90029: UW 28373, Rmx talonid, UW 27786, LM1 fragment, and UW 27771, LM2? fragment; from V-90063: UW 28421, Rm3 talonid; and from V-96020: UW 28686, Rmx trigonid.

*Plesiadapis praecursor*—From V-90029: UW 27835, Lm1, UW 27836, Lm1, and UW 27992, LP4 fragment. Questionably, from V-90029: UW 28366, Lmx talonid; from V-90039: UW 28629, Lm1 trigonid; and from V-96007: UW 28463, LM3.

*Plesiadapis rex*—From V-90063: UW 28405, Lm1, UW 28438, Rm2, and UW 28442, RMx fragment; from V-96037: UW 28677, Rm2. Questionably, from V-90054: UW 28271, LMx fragment.

*Plesiadapis?*—From V-90029: UW 27766, Lmx talonid; from V-90039: UW 28234, LP3?.

*Chiromyoides?*—From V-90063: UW 28165, Rm3.

*Palaechthon alticuspis*—From V-90029: UW 27192, RM3; from V-90047: UW 28756, Rm1? trigonid; from V-90064: UW 28529, LMx fragment; from V-90082: UW 31317, Lmx trigonid, and UW 31332, Rm2 trigonid; from V-91007: UW 28925, Lm2 trigonid. Questionably, from V-90029: UW 31584, partial right dentary with damaged m2 and roots of m3; from V-90032: UW 31023, LMx fragment; from V-90060: UW 28847, Rmx talonid, UW 28852, Rmx talonid, and UW 31171, Rm1? trigonid; from V-90064: UW 28531, RMx fragment; and from V-90082: UW 31251, Lm2, and UW 31256, Rm2 trigonid.

*Palaechthon nacimenti*—From V-90029: UW 27193, Lm1, UW 27194, Rm1, and UW 27777, broken Lm2; from V-90039: UW 28229, LM3; from V-90060: UW 28619, Lm2, and UW 31153, Lm1 trigonid; from V-90063: UW 28448, LMx fragment; from V-90064: UW 28813, Lm3 talonid; from V-90082: UW 31296, Lm1 trigonid, and UW 31285, Lm3 talonid; from V-90112: UW 28758, LM2 fragment; from V-96010: UW 28669, LM2 fragment, and UW 28596, LM2 fragment. Questionably, from V-90029: UW 31613, Rm3 talonid.

*Palenochtha minor*—From V-90029: UW 27752, RM1; from V-90032: UW 28482, RM1; from V-90060: UW 31178, Rmx talonid, and UW 31200, Lm1; and from V-90082: UW 31328, Lm1. Questionably, from V-90060: UW 31155, RMx fragment, and UW 31174, RMx fragment.

*Plesiolestes problematicus*—From V-90029: UW 31068, Lm3; from V-90060: UW 28708, Rm1, and UW 28713, Lm3; and from V-90082: UW 31310, Rm3 talonid. Questionably, from V-90032: UW 31025, Lp4 fragment; and from V-90060: UW 31164, RMx fragment.



*Plesiolestes sirokyi*—From V-90029: UW 31901, Rm1; and from V-96007: UW 28462, Lm2. Questionably, from V-90029: UW 28370, Rm1 talonid.

*Picrodus silberlingi*—From V-90029: UW 28614, partial left maxilla with P4–M1, UW 31454, partial right dentary with p4–m1, and UW 31586, Lm1 talonid; and from V-90039: UW 28235, Rm2.

*Paromomys depressidens*—From V-90029: UW 27195, RM1 or 2; and from V-90082: UW 31286, LMx fragment. Questionably, from V-90064: UW 28520, LMx fragment.

*Eudaemonema cuspidata*—From V-90060: UW 28777, RM3.

*Elphidotarsius* sp.—From V-90082: UW 31259, Rm1.

cf. *Protictis*—From V-90029: UW 28008, RM2, and UW 28053, RM2; from V-90121: UW 28680, LM1; from V-91007: UW 27810, broken LM1.

*Litocherus lacunatus*—From V-90060: UW 31145, Rm2; and from V-90064: UW 27798, Rm2–3 from V-90064.