Chapter 6

Stratigraphy and Taphonomy of Grizzly Buttes, Bridger Formation, and the Middle Eocene of Wyoming

JOHN P. ALEXANDER and BENJAMIN J. BURGER

1. Introduction 165
2. Geology 170
   2.1. Palaeoclimate 171
   2.2. Lithology 172
3. Taphonomy 176
   3.1. Crocodilian Predation 179
   3.2. Mammal Predation 180
   3.3. Raptor Predation 181
   3.4. Intrusion 185
4. Notharctid Primates 186
   References 192

1. Introduction

For over a century the Bridger Formation of southwestern Wyoming has yielded fossils of many important middle Eocene vertebrate taxa. This formation is of particular interest to the study of ancient primates because their remains are plentiful. In fact, the first fossil primates described from the Western Hemisphere, *Omomys* carteri and *Notharctus tenebrosus* were found here (Leidy, 1869, 1870). Arguably, the premier fossil collecting locale within the Green River Basin is an area known as Grizzly Buttes (Figure 1). Although

---

JOHN P. ALEXANDER and BENJAMIN J. BURGER • Division of Paleontology, American Museum of Natural History, New York, New York 10024-5192.

Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats, edited by Gregg F. Gunnell, Kluwer Academic/Plenum Publishers, New York, 2001.

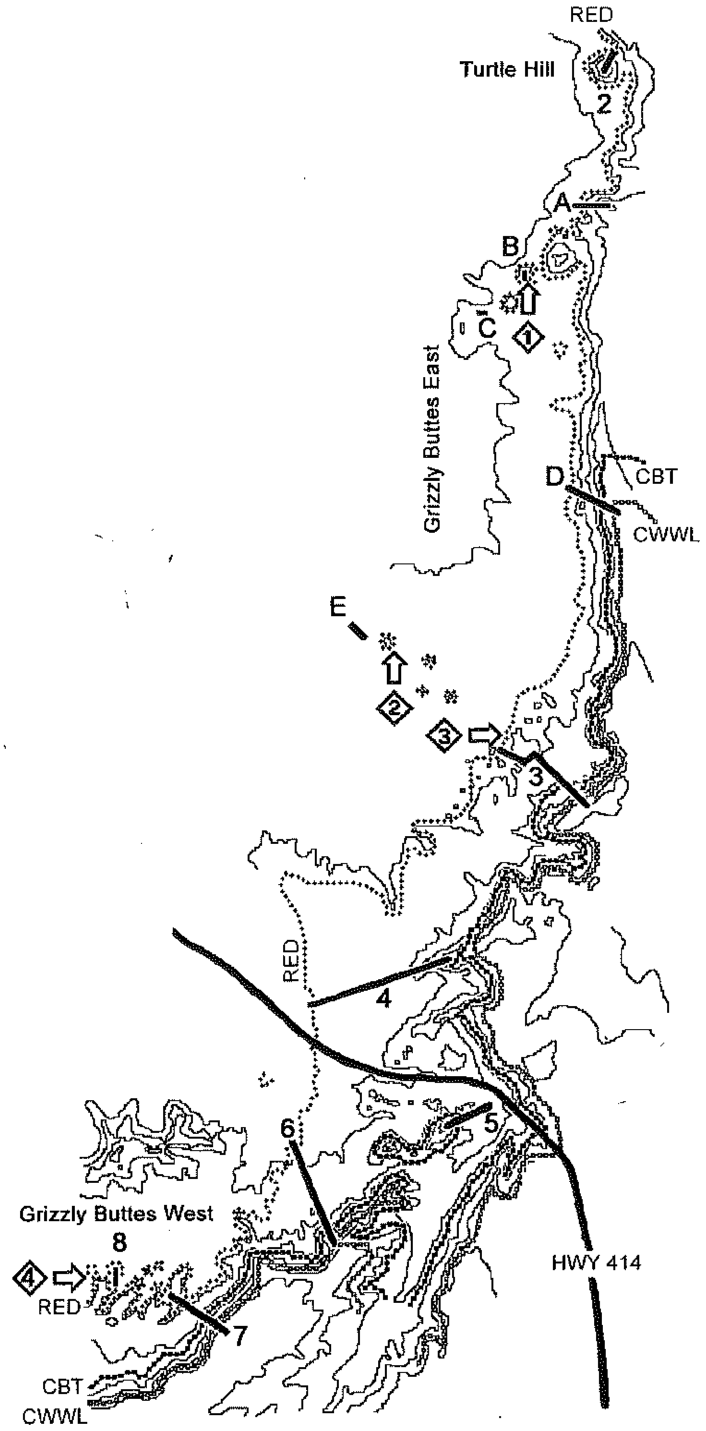

FIGURE 1. Map of Grizzly Buttes, southern Green River Basin, Uinta Co. Wyoming. Diamond symbols indicate principal fossil bearing areas which have produced articulated skeletons. ⟨1⟩ "Cosmodrome", ⟨2⟩ "Windy City", ⟨3⟩: "Forbidden City", ⟨4⟩ "Donner Pantry". Letters A-D and numbers 1–8 indicate position of sections in Figure 2 and Figure 3. RED: Grizzly Buttes Red Bed, CBT: Church Butte Tuff , CWWL: Cottonwood White Layer. HWY 414: Wyoming State Highway 414 = old "Burnt Fork Road". Section 4 = approximately 1 km.

the place name has disappeared from official maps and the local lexicon (West, 1990), it is well established in the paleontological literature. The area has a rich history. Both O. C. Marsh and E. D. Cope collected from these outcrops in the 1870's extending their professional rivalry to the description of Bridgerian mammals (Wheeler, 1961). The area is figured by H. F. Osborn (1910) as the "famous" locality of Grizzly Buttes.

Standing within the Blacks Fork Member of the Bridger Formation, the Grizzly Buttes are a set of low hills eroding out of dissected cliff exposures extending in an arc to the southeast of the towns of Lyman and Mountain View, Wyoming. Field parties from many institutions probably collected here between 1870 and 1900, but it was Walter Granger of the American Museum of Natural History (AMNH) who first documented Grizzly Buttes as a distinct area in his unpublished field report on the expedition of 1903. He identified Grizzly Buttes East as the exposures running 7 km along the eastern side of Smith's Fork of the Green River and Grizzly Buttes West as the outlying hills and walls now known as Crooked Canyon which run 6 km westward to the mouth of Little Dry Creek. The dividing line between the two is Wyoming State Highway 414, known to Granger as the "Henry's Fork road". Granger stated "It is, in fact, probably the richest spot (in fossil remains) in the entire Bridger bad lands".

The sheer volume of vertebrate fossils collected by the Granger expeditions lead to a body of scholarship in which many type specimens were named. These works include several major monographs (Hay, 1908; Matthew, 1909; Gregory, 1920) and numerous papers describing specimens decades after their original discovery (Simpson, 1931). As these earlier collections refer to stratigraphic or aerial distinctions of no greater resolution than "upper" or "lower" beds or Grizzly Buttes "East" or "West", emphasis will be placed on more recent collections. Since 1983, field parties from the AMNH have returned to Grizzly Buttes and recovered many vertebrate skeletons (Alexander, 1992; Wallace, 1994). Among these specimens are well preserved skulls, jaws and skeletons of notharctid and omomyid primates, creodonts, carnivores, rodents, palaeanodonts, perissodactyls and artiodactyls.

Remarkably, the stratigraphic relationships within Grizzly Buttes has never been closely examined. Walter Granger, in his field notes of 1903, noted that attempts to identify local marker beds and to map the stratigraphy of this area were abandoned after a few days due to the complexity of the problem. This deficiency has presently been addressed. Utilizing standard survey methods the first detailed geologic cross sections of Grizzly Buttes (Figures 2–3) were produced for this study in 1996 and 1997. The stratigraphic position of AMNH fossil producing localities are indicated by number on these columns (Table 1). Important beds are described and informally named. The depositional history of each fossiliferous layer is inferred based on field observations of mineralogy, weathering, repose, texture and clast size.

Dr. Emmett Evanoff of the University of Colorado at Boulder has conducted geologic fieldwork in the basin since 1991. He has refined Matthew's stratigraphic system of 1909 by identifying important new stratigraphic marker units

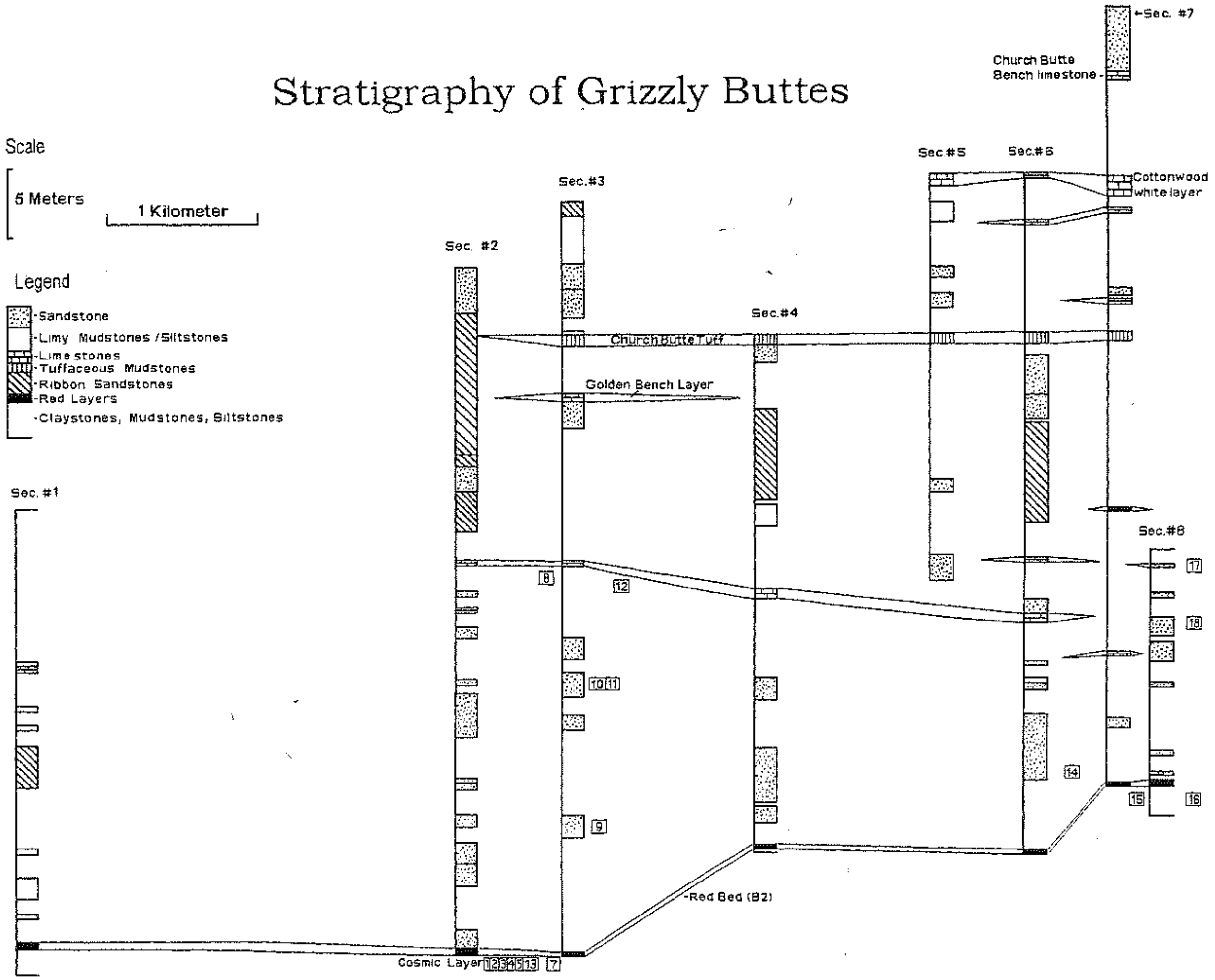

FIGURE 2. Stratigraphic sections, Grizzly Buttes (see text for further discussion).

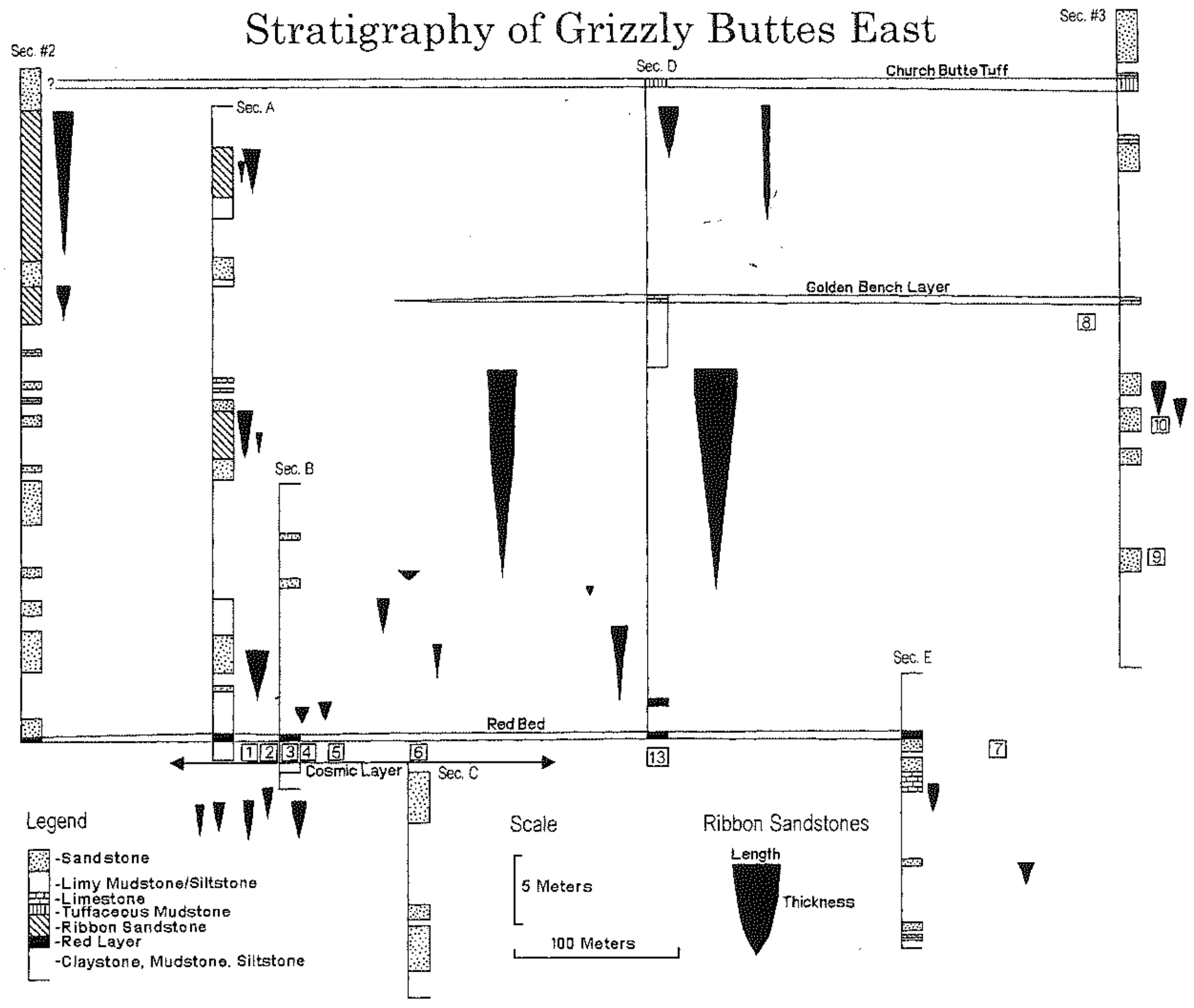

FIGURE 3. Stratigraphic sections, Grizzly Buttes East (see text for further discussion).

Table 1. Grizzly Buttes localities [#] appearing in Figures 2 and 3

Horizon 1: "Cosmic Layer" or "Red Bed" Localities, 47.3 m below Church Butte Tuff

[1] Amphitheatre, Gallery 1-3, Hanging Gallery, Painted Turtle, Pink Floyd, Powerline Hill, Trionyx Hill
[2] Conquistador Hill
[3] Butch Hill
[4] Cosmic Hill
[5] Wrong Hill
[6] Thule Butte
[7] Windy City: Barbs Butte, Dawn of Man, Franks Ridge, Leahanne's Lintel, Stock Yard
[13] Hernia Hill
[15] Corner Hill, Donner Pantry, Outer Wall, Donner Wall
[16] Spanish Saddle
[17] Golden Crown, Gator Bowl

Horizon 2: Crooked Canyon Localities, 33.6 m below Church Butte Tuff

[14] Crooked Crotch, Crooked Crotch North, Wasp Waste, Horseshoe Corner

Horizon 3: Forbidden City/Woodburne Localities, 26.4 m below Church Butte Tuff

[8] East Berlin, Forbidden City North, Serpent Mound, Tiergarten
[9] Great Wall, Northgate
[10] Hermes Hill
[11] Inner Sanctum
[12] Asian Gate, Simba Gate

such as the "Church Butte tuff" and the "Golden" limestone (Evanoff *et al.*, 1998). We follow his system.

2. Geology

The Bridger Formation consists of 650 m of mostly horizontal fluvial and lacustrine beds deposited in the Green River Basin, an asymmetrical Laramide downwarp, with roughly a north-south axis from the Wind River Range to the Uinta Mountains (Evanoff and Ivy, 1992). Its sedimentary sources are airborne and fluvially transported pyroclastics from the Absaroka volcanic field 300 km to the north (Bradley, 1964; Smedes and Prostka, 1972). Smectite, a clay mineral derived from altered volcanic glass, is common in the mudstones. It causes the rock to swell when wet, weathering outcrops into crumbly "popcorn" surfaces.

Most museum Bridger collections are correlated utilizing W. D. Matthew's (1909) stratigraphic divisions A through E. Bridger A and B are grouped into the Black's Fork Member (Wood, 1934). With a maximum thickness of 137 m (Evanoff and Ivy, 1992), the Bridger B interval is subdivided into units B1 through B5 (Matthew, 1909). It is delineated from the Bridger A below by a thick ostracodal limestone and from the Bridger C above by the Sage Creek white layer, a thick bed of resistant limestone. Grizzly Buttes includes the uppermost B1 beds and much of the B2 interval and falls within the Br-2 biostratigraphic zone (Gunnell and Bartels, 1994). Bridger Formation localities and biostratigraphy are well documented (McGrew and Sullivan, 1970; Gazin, 1976; West, 1976).

Mauger (1977) provided potassium-argon radiometric age determinations on biotite from the Big Island Tuff within the Wilkins Peak Member of the Green River Formation which is laterally correlative with the lower Bridger Formation. Recalibrated dates of 50.4 +/ 1.1 and 50.1 +/ 1.2 MA appear in Krishtalka *et al.* (1987). At about 50 MA, the Bridger B interval falls within the first million years of the Bridgerian Land Mammal Age (Krishtalka *et al.*, 1987).

2.1. Palaeoclimate

Toward the east, the Lower Bridger Formation interdigitates with the Laney Shale Member of the Green River Formation which was laid down in ancient Lake Gosiute. Flora from the Laney Member indicate a warmer climate during the middle Eocene than at present, with an average temperature of 19° C (MacGinitie, 1969). The global thermal maximum for the entire Cenozoic reached its zenith during the earliest middle Eocene (Savin, 1977; Savin and Douglas, 1984). The Grizzly Buttes local fauna flourished during a period of global warming possibly due a carbon dioxide greenhouse effect (Rea *et al.*, 1989).

The arboreal nature of primates makes their variety and abundance good indicators of the degree of forest density and diversity that existed at Grizzly Buttes. The diversity of North American primate genera is never again as great as it is during the time period which brackets the deposition of the Blacks Fork Member (Stucky, 1992). Gunnell and Bartels (1994) produced a cenogram which ranked body weights of the mammalian species found at Grizzly Buttes. The body mass distribution of the Grizzly Buttes fauna compares favorably with that observed in modern closed forest communities in tropical Africa which experience warm, moist conditions. An annual rainfall of 71 cm has been estimated for the early Bridgerian. This rainfall would have peaked in the late spring and early summer (MacGinitie, 1969). The Blacksforkian environment at Grizzly Buttes may have been somewhat wetter than the preceding Gardnerbuttean during which the Laney Shale was deposited (Gunnell and Bartels, 1994).

The paleolatitude of the Green River Basin during the Bridgerian was 5° to 8° south of its modern latitude of 41° north (Roehler, 1993). At this time "paratropical" floras reached as far as 60° north latitude. A paratropical flora is defined as subtropical vegetation augmented by a diversity of deciduous broad-leafed trees and shrubs (Wing, 1987). This includes the juxtaposition of palms and ferns with oak, elm, maple and beech (Brown, 1929, 1934). That such a forest grew at Grizzly Buttes is based on circumstantial evidence from correlated Green River Formation deposits. Pollen from the Green River Formation includes that of conifers such as pine, spruce and fir indicating environmental zonation on the mountains surrounding the basin of at least 2000m elevation (McGrew and Casilliano, 1970). The fossil wood found at Grizzly Buttes is of poor quality and pollen has yet to be recovered.

2.2. Lithology

2.2.1. Sandstones

The base of Grizzly Buttes lies 60m below the Church Butte tuff. Above this base the sedimentary sequence of fluvial and lacustrine beds are incised by channel sandstones. Twenty seven ribbon sandstone channels were identified in Grizzly Buttes East (Figure 3). Grain sizes range from very fine sand (4.0 phi) to volcanoclastic pebbles (4.0 phi) which give many of the channels a blue to reddish color.

The Moxa Arch is a nearby monocline to the northwest, quiescent since the early Eocene (Royse, 1993). This arch caused slight thickness and facies changes, and discontinuities in limestone distributions (Murphey, 1995). Crossbedding and troughs in ribbon sandstones indicate a strong southwest paleocurrent flow at Grizzly Buttes with an azimuth of 230° to 240°. This indicates that drainage at Grizzly Buttes was affected by the Moxa Arch to the northwest.

The channels show no abnormal geometry and suggest relatively stable meandering rivers. Some of the smaller channels indicate larger ranges of flow direction from northwest to southeast. One unusual discovery within this sequence are the only hemispheroid stromatolites (cyanobacteria) known within a Bridger Formation channel.

Vertebrate elements were occasionally entrained as bed load in stream channels. *Baena* and *Echmatemys* turtle shells are often found as lag within these paleochannels. In two separate instances, the skulls of the brontothere *Palaeosyops* cf. *paludosus* (AMNH 129396) and the crocodile *Crocodylus affinus* (AMNH 25557), were found lying directly on dense beds of *Plesielliptio*, a freshwater mussel that requires clear, flowing water (Hanley, 1974).

2.2.2. Cosmic Layer

The most important fossiliferous bed at Grizzly Buttes is the "cosmic" layer (Alexander, 1992b), which was previously identified as a volcanic ash in error (Alexander, 1994b). The base of this locally traceable layer lies 47.3m below the Church Butte tuff. The cosmic layer is interpreted to be the result of high sedimentation due to a series of flooding events along the wooded shoreline by a persistent lake to the south. This is evidenced by a lack of euhedral biotite crystals, a sharp lower contact, uniform thickness, and the presence of fossilized wood.

Although sand channels of later age truncate the cosmic layer on Turtle Hill and Wrong Hill, no allochthonous channel sandstones are formed within the cosmic layer. Rapid deposition of the cosmic layer is further indicated by the excellent preservation of many vertebrate skeletons. The inundation of the forest floor by at least temporary standing water is indicated by the presence of the snail *Biomphalaria* which lives today in shallow freshwater environments in tropical South America (Thompson, 1984).

The sediment was sufficiently silty and structureless to support the burrowing habits of amphisbaenian (limbless) lizards when the forest floor was dry. A skeleton of the rhineurid *Spathorhynchus fossorum* (AMNH 25556) was found within cosmic layer Unit 3 on Cosmic Hill which includes elements not previously described by Berman (1973).

The cosmic layer has four subunits. Unit 1 is a hard silver siltstone 0.7 m thick with calcareous pillows. It forms a prominent bench which caps Thule Butte (Figure 2, Section 4). Fossils include vertebrates, wood, and *Biomphalaria*. Unit 2 is only found in the area around Butch Hill referred to as the "Cosmodrome". It consists of a 0.9 m thick hard gray siltstone which breaks down readily in water. Cosmic Quarry at the base of Butch Hill in Unit 2 has yielded the skeleton of one female (AMNH 129382) and articulated remains of two additional *Notharctus tenebrosus* individuals (Alexander, 1992, 1994) and a lizard, cf. *Saniwa* (AMNH 29992). A partial skull, mandible and associated postcranial elements of a juvenile *N. tenebrosus* (AMNH 129384) were found approximately 20 m west of Cosmic Quarry.

Unit 3 varies lithologically from north to south. On Turtle Hill (Figure 2, Section 3) the layer is a brown to red mudstone 0.45 m thick with geothite crystals. In the most fossiliferous area it consists of an olive green to silver pillow forming limy siltstone. In 1988 the most complete skeleton of *N. tenebrosus* yet described (AMNH 127167) was found in Unit 3.

In 1996, one of only four known skeletons of the rare palaeanodont *Metacheiromys marshi* (AMNH 131777) was found in Unit 3 on Butch Hill. The first of these four skeletons, is the type of the *M. osborni* (AMNH 11549) a junior synonym of *M. marshi* (Schoch, 1984). AMNH 11549 was found in "lower beds" at Grizzly Buttes East in 1903 (Osborn, 1904), probably in the immediate vicinity of the 1996 specimen. AMNH 131777 was found by chance when the overburden was removed from an isolated skull and mandible of an unusually robust example of *Thinocyon* cf. *T. velox* (AMNH 131831). In 1993, an articulated skeleton of *Thinocyon velox* was also found in this unit, about 60 m east of the *Metacheiromys* site. In 1997, an apparent nest of the eggs of an as yet unidentified turtle was found a meter from this skeleton.

Skeletons of *Notharctus*, proviverrine creodonts, and the rare serrated-toothed ziphodont crocodile *Pristichampsus vorax* (AMNH 29993) have been found at "Windy City", a site 5 km to the southwest (Figure 1). Here Unit 3 is olive green but less limy. It correlates to a relatively thick limestone measured on Round Top Hill (Figure 2, Section 6). There is a facies change toward the southwest, indicative of low energy lake deposition.

Unit 4 of the cosmic layer is an olive-gray, very fine grained sandstone (3.5–4.0 phi). It forms calcareous pillows and a prominent bench. At Butch Hill it is 1.4 m thick. The cosmic layer is continuous to the southwest, passing through "Horrible Hill" (MPM Locality 2416) (West, 1979) and other hills which flank Crooked Canyon. It reappears along the opposite wall of Crooked Canyon where erosion has exposed the top of the bedding plane at the "Donner Pantry" and "Spanish Saddle" localities. This horizontal table covers a sixteenth of a section or about 100,000 square meters. This exposure is equivalent to a two meter ribbon of vertical cross section of the cosmic layer following the contour of the landscape for 500 kilometers. "Donner Pantry" has more exposure of the cosmic layer than the rest of Grizzly Buttes combined. Surface collection at this locality has produced a diverse assemblage of fossil mammals including skeletons of *Notharctus, Smilodectes, Thinocyon, Orohippus,* and *Antiacodon*, and a complete skull and mandible of *Hyrachyus*.

The cosmic layer has undergone compressive plastic flow, causing elements to drift out of anatomical position during the process of fossilization. Fragments with sharp, but ancient contacts are often found displaced by many centimeters. This has led to the discovery of articulated skeletons when only isolated elements are in evidence on the surface. Recent expeditions have been successful despite intensive collection in this area for more than a century. Many well preserved specimens attributed to Grizzly Buttes now residing in museum collections may have been obtained from these lacustrine strata. Indeed, matrix adhering to a specimen of *Mesonyx obtusidens* (AMNH 19203) collected by George Olsen from "lower beds" at Grizzly Buttes East in 1922 appears to have come from the cosmic layer.

The new notharctid sample forms a reference set of individuals from a narrow stratigraphic horizon against which the collections of Hayden, Carter, Marsh, Cope and Granger (which have only crude stratigraphic and aerial resolution) can be compared. It also permits the study of morphological variation among penecontemporaneous individuals. The cosmic layer has demonstrated the local lithosympatry of *N. tenebrosus* and *N. pugnax* (Alexander, 1994b).

2.2.3. Red Bed

Grizzly Buttes has more bench forming siltstones and abundant channel sandstones than is typical for the rest of the Bridger Formation. There are relatively fewer smectitic layers at Grizzly Buttes, making those present more noticeable, and therefore good stratigraphic markers. Lying conformably upon the cosmic layer is a highly smectitic dark brown mudstone that is dramatically exposed throughout the area. At various locations in the southern Green River Basin large amounts of goethite give this bed a red to port wine stain color. This "Red Bed" marks the transition between Bridger the B1 and B2 levels of Matthew (1909).

The Red Bed is interpreted to be transitional to a more terrestrial environment that is drier or better drained as it represents a period of incipient soil development. It thickens from 0.6 m elsewhere to 1.7 m near Butch Hill. It contains localized claystone clasts and ranges from clay to very fine grained sand (10.0 3.5 phi). The Red Bed is abundantly fossiliferous. Complete shells of the turtles *Echmatemys*, *Baena*, *Baptemys*, and *Arctotrionyx* are commonly found within the Red Bed, lying directly on the contact with the cosmic layer. Dentitions of *Notharctus* and *Hyopsodus* also are common.

2.2.4. Above Red Bed

Higher in the section is an upper smectitic layer. Fossils such as a skull of the alligator *Allognathosuchus* (AMNH 25566), abundant crocodile scutes, and remains of soft shelled turtles (Trionychidae), document a wetter, marshier environment. It is similar in exposed color to the Red Bed layer. It ranges in lithology from a clay clastic conglomerate to a clay free mudstone. On Turtle Hill (Figure 2, Section 1), it contains well rounded, multicolored claystone clasts, of pebble size (2.0 to 4.0 phi). Geothite crystals are common on the surface. To the south of Butch Hill, the unit is represented by a breccia of highly angular, brown claystone clasts, with mudstone matrix, indicating occasional desiccation. Above the upper smectitic layer the presence of channel sandstones indicates a drier or better drained environment.

At the "Forbidden City" locality there occurs a set of siltstone beds lithologically similar to the cosmic layer, but 20 m higher. R. M. West and M. O. Woodburne collected in the western half of this area in 1970 and named it the "Woodburne Locality" (MPM Locality 2415), (West, 1979). Well preserved articulated skeletons are found where ever this lithology is encountered. These include two skeletons each of *Smilodectes gracilis* (AMNH 131762, 131763) and *Notharctus tenebrosus* (AMNH 131764, 131945), and the first known skull of *Omomys carteri* (AMNH 130000). Fish bones and the bivalve *Plesielliptio* are common, indicating a more clear water environment. Fossilized wood also occurs.

2.2.5. Snow White Layer

The "snow white" layer is a thick highly smectitic tan mudstone which stands out against darker units in the area of "Forbidden City". Geothite is present, but does not stain the bed red. Toward the north, the layer is truncated by channels and structureless brown sandstones. The "snow white" layer represents a wetter or less well drained environment. Thickening of this bed toward the south indicates the expansion of the lake from that direction. An as yet, undescribed partial articulated bird skeleton was recently found in this layer.

2.2.6. Golden Layer

The "golden limestone" is the thinnest (0.4 m) of those few limestones that occur in the Bridger B. It weathers to a distinct yellow color. It outcrops below the Cottonwood White Layer just south of "Butch Hill", and can be traced 10 km southwest into Crooked Canyon in Grizzly Buttes West where it caps a hill known as "Golden Crown".

2.2.7. Church Butte Tuff

Channels in the beds between the golden limestone and the Church Butte tuff again represent a drier or better drained environment. The Church Butte tuff is named for Church Buttes 20 km to the north. It is one of only a few lithified tuffs that occur within the Bridger Formation. The layer is extremely flaky, dark brown to dark gray and easily recognized from a distance. It serves as the datum of stratigraphic correlation between measured sections in Grizzly Buttes because it represents a single eruptive event, (as yet undated). It is restricted to the south, and is exposed relatively high on the outcrops. The presence of large euhedral crystals of biotite and hornblende and abundant Ca plagioclase feldspars indicate absence of reworking and fluvial transport. Radiometric dating of this layer will be extremely helpful in reconstructing the stratigraphy and paleontology of the formation.

3. Taphonomy

The productive lacustrine layers at Grizzly Buttes have several unusual taphonomic characteristics. They represent discrete depositional lake shore flooding events so that there is isochroneity of the specimens incorporated within them. They are more abundantly fossiliferous than adjacent units. The faunal list of Grizzly Buttes has been tabulated for both the "old" AMNH collection, made in the early 1900's and the "new" collection made in the 1990's (Table 2). The percentage breakdown of the most significant orders of the fauna appears as a pie chart (Figure 4). Thirteen mammalian orders are represented in these collections. Several mammal orders are presumed to be present at Grizzly Buttes, but are not present in the AMNH sample. Their absence can readily be explained by either their original rarity in the fauna such as tillodonts or their minute size and difficulty of recovery as is the case for marsupials. Several orders have never been reported from Bridger B beds but appear in both younger and older faunas, and are assumed to be present elsewhere in the Intermontane West during this interval. These include the orders Dinocerata (Wheeler, 1961), Dermoptera and Multituberculata (McKenna, 1990; Stucky, 1992).

Hyopsodus accounts for fully one third of the entire fauna. The aggregate percentage of all primate species accounts for just under 20% of the fauna and places second to *Hyopsodus*. Perissodactyls and rodents represent 17% and 12% of the fauna respectively. Each of the other orders represent from 6% to less than 1% of the fauna. *Hyopsodus* falls at the small end of mass distribution for Grizzly Buttes while the perissodactyls fall in the mid to upper range of body mass (Gunnell and Bartels, 1994).

Several factors are at work which affect what ultimately finds its way into the collection. One of these is collection bias. Large animals leave behind large and obvious bones in the fossil record that are more readily noticed in the field than minute elements from small animals. (Behrensmeyer and Hill, 1980).

Table 2. Faunal List for Grizzly Buttes specimens in AMNH collection.

- PISCES
  - Lepisosteiformes
    - Lepisosteidae
      - *Lepisosteus* sp.
  - Amiiformes
    - Amiidae
      - *Amia* sp.
  - Teleostei
    - Teleostei indet.
      - Ictaluridae indet.
- AMPHIBIA
  - Urodela indet.
- REPTILIA
  - Testudines
    - Baenidae
      - *Baena arenosa*
    - Trionychidae
      - *Amyda* sp.
    - Emydidae
      - *Echmatemys* sp
    - Dermatemydidae
      - *Baptemys* sp.
  - Lacertilia
    - Anguidae
      - cf. *Proglyptosaurus*
      - *Saniwa* sp.
  - Amphisbaena
    - Rhineuridae
      - *Spathorhynchus fossorum*
  - Crocodilia
    - Crocodylidae
      - *Crocodylus affinus*
    - Pristichampsidae
      - *Pristichampsus vorax*
    - Alligatoridae
      - *Allognathosuchus* sp.
- AVES
  - Neognatha
    - sp. indet.
- MAMMALIA
  - Mammalia indet.
  - Pantolesta
    - Pantolestidae
      - Pantolestidae indet.
      - *Pantolestes* cf. *natans*
      - *Pantolestes longicaudus*
      - *Pantolestes* sp.
  - Insectivora
    - Insectivora indet.
  - Erinaceoidae
    - Talpidae
      - Talpidae indet.
      - *Scenopagus edenensis*
    - Nyctitheriidae
      - Nyctitheriidae indet.
      - *Marsholestes dasypelix*
      - *Nyctitherium serotinum*
  - Primates
    - Microsyopidae
      - *Microsyops elegans*
      - *Microsyops* sp.
    - Notharctidae
      - Notharctidae indet.
      - *Notharctus* sp.
      - *Notharctus tenebrosus*
      - *Notharctus pugnax*
      - *Smilodectes gracilis*
    - Omomyidae
      - *Omomys carteri*
      - *Omomys* sp.
      - *Anaptomorphus* sp.
      - *Uintanius ameghini*
  - Creodonta
    - Creodonta indet.
    - Hyaenodontidae
      - Hyaenodontidae indet.
      - *Limnocyon verus*
      - *Limnocyon* sp.
      - *Machaeroides aeothen*
      - Proviverrinae indet.
      - *Proviverra grangeri*
      - *Proviverra minor*
      - *Proviverra pungens*
      - *Proviverra rapax*
      - *Proviverra* sp.
      - *Thinocyon mustelinus*
      - *Thinocyon velox*
      - *Thinocyon* sp.
      - *Tritemnodon agilis*
    - Oxyaenidae
      - *Patriofelis ulta*
  - Carnivora
    - Carnivora indet.
    - Miacidae
      - Miacidae indet.
      - Miacinae indet.
      - *Miacis parvivorus*
      - *Miacis* sp.
      - *Oödectes herpestoides*
      - *Oödectes proximus*
      - *Uintacyon antiquus*
      - *Uintacyon vorax*
      - *Uintacyon* sp.
      - *Vulpavus completus*
      - *Vulpavus ovatus*
      - *Vulpavus palustris*

(continued)

Table 2 (Continued)

- *Vulpavus profectus*
- *Vulpavus* sp.
- Viverravidae
  - Viverravidae indet.
  - *Viverravus* sp.
  - *Viverravus gracilis*
  - *Viverravus sicarius*
- Pholidota
  - Metacheiromyidae
    - *Metacheiromys marshi*
    - *Metacheiromys dasypus*
  - Epoicotheriidae
    - Epoicotheriidae indet.
- Condylarthra
  - Hyopsodontidae
    - *Hyopsodus minusculus*
    - *Hyopsodus paulus*
    - *Hyopsodus* sp.
- Tillodontia
  - Esthonychidae
    - *Trogosus* sp.
- Artiodactyla
  - Homacodontidae
    - *Antiacodon pygmaeus*
    - *Helohyus plicodon*
- Acreodi
  - Mesonychidae
    - *Mesonyx obtusidens*
- Perissodactyla
  - Perissodactyla indet.
  - Equidae
    - *Orohippus pumilus*
    - *Orohippus* sp.
  - Brontotheriidae
    - Brontotheriidae indet.
    - *Limnohyops matthewi*
    - *Limnohyops monoconus*
    - *Limnohyops priscus*
    - *Palaeosyops major*
    - *Palaeosyops paludosus*
    - *Palaeosyops* sp.
  - Helaletidae
    - *Helaletes intermedius*
    - *Helaletes nanus*
    - *Helaletes* sp.
    - *Hyrachyus eximius*
    - *Hyrachyus modestus*
- Rodentia
  - Rodentia indet.
  - Paramyidae
    - *Leptotomus grandis*
    - *Leptotomus parvus*
    - *Leptotomus sp.*
    - *Paramys delicatior*
    - *Paramys delicatus*
    - *Pseudotomus robustus*
    - *Paramys* sp.
    - *Reithroparamys delicatissimus*
    - *Taxymys* sp.
    - *Thisbemys plicatus*
  - Sciuravidae
    - Sciuravidae indet.
    - *Sciuravus nitidus*
    - *Sciuravus* sp.

Collection methods other than surface prospecting are needed to recover the less visible microfauna. These include wet and dry screening of sediment (Hibbard, 1949; McKenna, 1962), and picking or sieving tiny fossils which have been deposited by ants on their hills (Delson, 1971; Robinson, 1994). Neither method was used at Grizzly Buttes by Granger in the early 1900's, but both have been employed in recent collecting. Analysis of hundreds of tiny teeth found on the "1K Anthill" site near Cosmic Hill remains to be finished. It has already produced rare milk teeth of *Hyopsodus*, notharctid primates, and cf. *Omomys*. The 1K Anthill sample is not included in Table 2.

Arboreal notharctid primates represent only 13% of all cataloged mammal fossils within the AMNH Grizzly Buttes collection (Figure 4), yet they are the family most often found as articulated skeletons. They are so well preserved that such delicate elements as sesamoids, hyoids and auditory ossicles are frequently found in articulation. In contrast, the far more common taxon *Hyopsodus paulus* which represents 34% of this collection has only been found as fragmentary dentitions within these beds. The short-limbed *Hyopsodus* was certainly more terrestrial than the notharctids, but it has been interpreted as both fossorial (Gazin, 1968) and semiarboreal in habits (Matthew, 1928). It may have been more analogous to modern hyraxes than lagomorphs as a small bodied generalist herbivore.

Matthew (1909) observed that *Thinocyon* is the most abundant of Bridger "carnivora" in the AMNH collection. It represents about 1% of the collection. This pattern has been sustained in the recent collection. Skeletons of this possibly arboreal, mink-like taxon are found as commonly as those of the notharctid primates. Fossorial forms such as the paleanodont *Metacheiromys* and the rhinuerid *Spathorhynchus* have been found as well preserved skeletons. Aquatic vertebrates, particularly reptiles, are abundant throughout the cosmic layer. Turtle shells fragments often litter the landscape. Elements of the baenid turtle *Baena arenosa* are the most common vertebrate remains found at Grizzly Buttes. Complete shells of this taxon are frequently encountered. Many examples have been described (Hay, 1908; Gaffney, 1972). Remains of aquatic mammal genus *Pantolestes* are also found. Delicate items such as reptile eggs are also occasionally preserved.

There appears to be a taphonomic bias in the cosmic layer toward the preservation of arboreal, fossorial, and aquatic forms as complete skeletons, selectively altering the fossil assemblage between the moment of death of individual organisms and the actual remains found.

3.1. Crocodilian Predation

The *Pristichampsus vorax* skeleton (AMNH 29993) found at "Windy City" is remarkable for a number of reasons. It is unusually complete, including the skull, jaws, and front and hind limb material not previously described that will address longstanding questions about its locomotor behavior (Langston, 1975). It is also very rare toward the center of the Green River Basin, yet apparently abundant around the basin margins (Gunnell and Bartels, 1997). Although the type specimen of *Crocodylus vorax* (YPM 249), later synonymized as *Pristichampsus vorax* (Langston, 1975), comes from elsewhere in the Bridger Basin (Troxell, 1925), the lost holotype of "*Crocodylus ziphodon*" (Marsh, 1871), whose description conforms to that of *P. vorax*, was found by a Yale party at Grizzly Buttes in 1870 (Langston, 1975).

Upon preparation of this skeleton, it was discovered that a nearly complete left hind-himb of the perissodactyl *Helaletes* sp. was lodged entirely within its ribcage. The mammalian material includes parts of the pelvis, several lower lumbar vertebrae, the femur, tibia, calcaneum and a number of pedal elements. Several of these elements exhibit parallel grooves and scratches which match the spacing of the serrations on the teeth of the *Pristichampsus.* Similar scratches are also incised on a partial skull of *Hyopsodus paulus* (AMNH 129391) found elsewhere at Grizzly Buttes.

This circumstance is entirely consistent with the predatory and feeding habits of modern crocodilians. They are known to snatch prey at the water's edge with their jaws, drown their victims, and tear them apart by twisting motions of their bodies. This process is described in detail in the apparent bisection of a specimen of the adapid primate *Europolemur koenigswaldi* by an Eocene crocodile at Messel, Germany (Franzen and Frey, 1993). The *Helaletes* remains found within the Grizzly Buttes *Pristichampsus* appear to be this reptile's last meal.

Amazingly, this same situation was encountered by Troxell (1925) in his description of the type specimen of "*Crocodylus*" *vorax* (YPM 249) from the Bridger Formation. Thoracic vertebrae of a mammal, perhaps the perissodactyl *Hyrachyus* sp. were found in such close proximity with the skull that Troxell suspected that "the crocodilian was feeding on a small rhinoceros or titanothere a short time before both were buried, hence the name *vorax*" (Troxell, 1925: figure 22). Such examples as these may offer a possible explanation for the unusual body size distribution of articulated mammal remains encountered at Grizzly Buttes. In the absence of stream action sorting body parts, predator feeding behavior is a possible mechanism for explaining the discovery of well preserved, and articulated portions of mammalian bodies.

Common terrestrial mammals of medium to large body size such as the perissodactyls *Helaletes*, *Hyrachyus* and *Palaeosyops* are not commonly found as complete skeletons, but rather as articulated body "portions". For example, a complete left pes of *Palaeosyops* (AMNH 129392) truncated at mid-tibia and a remarkably complete and articulated skull and mandible of *Hyrachyus* (AMNH KF 97-6) have been found in isolation.

3.2. Mammal Predation

An entirely different taphonomic process may have been at work to explain the frequency of occurrence of the arboreal mammals. There may be a size bias at work selectively under representing smaller arboreal forms such as *Omomys* and *Microsyops* and favoring the notharctids *Notharctus* and *Smilodectes.* Several of the new notharctid individuals show evidence of predation, exhibiting multiple puncture wounds. These remains are found in a condition that is simply too complete to have been significantly impacted by the feeding habits of mammalian predators and scavengers which tend to reduce prey remains to fragments (Behrensmeyer and Hill, 1980; Andrews, 1990). Heavily chewed bones are not often found at Grizzly Buttes. Concomitantly, the remains of large bodied Bridgerian mammalian predators are relatively rare at Grizzly Buttes, accounting for roughly 1% of the AMNH collections. The coyote-sized hyaenodontid *Tritemnodon agilis* and the wolf-sized mesonychid *Mesonyx obtusidens* are represented by only three and seven

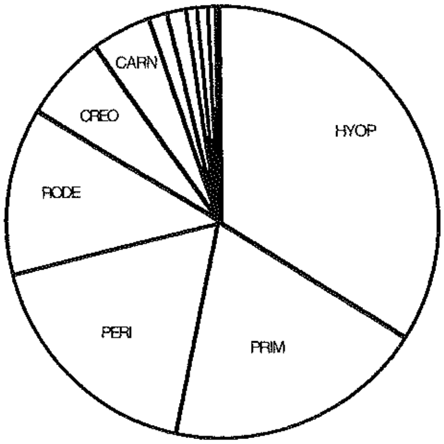

FIGURE 4. Rank order and percentage breakdown of mammalian orders: HYOP—*Hyopsodus sp.*, "Condylarthra" (34.3%); PRIM—Primates (19.5%); PERI—Perissodactyla (17.7%); RODE—Rodentia (12.6%); CREO—Creodonta (6.6%); CARN—Carnivora, Miacoidea (4.3%); Not shown—Pantolesta (1.6%), Artiodactyla (1.4%), "Insectivora" (0.8%), Palaeanodonta (0.7%), Acreodi (0.7%), and Tillodontia (0.2%). The AMNH Grizzly Buttes mammal collection consists of 451 identified specimens collected during the 1991–1996 field seasons and 494 cataloged specimens collected by Walter Granger and others between 1903 and 1906. N = 945. Several hundred additional specimens have been found during the 1997–1999 field seasons.

specimens respectively. Only a single dentition of the panther-sized oxyaenid *Patriofelis ulta* appears in the AMNH Grizzly Buttes collection. The rarity of climax predators in the sample is a logical reflection of their relative rarity in a normal trophic pyramid (Behrensmeyer and Hill, 1980).

3.3. Raptor Predation

It is more likely that the distribution of smaller mammal remains is a result of predation by raptorial birds. The *Omomys* Quarry found 70 m above the base of Bridger C predominantly contains the remains of the primate *Omomys*. It also includes remains of birds including owls (Strigiformes) (Murphey, 1990). This unique accumulation has been interpreted as the fossilized remains of owl pellets, (Murphey *et al.*, 1998). Owl pellets are regurgitated packets of undigested bones and hair of prey consumed by owls (Andrews, 1990). The omomyids *Tetonius* and *Shoshonius* can be inferred to be nocturnal in habit because their enlarged orbits approach the condition of *Tarsius* (Beard and Krishtalka, 1991; Beard and MacPhee, 1994). A nocturnal adaptation would have made *Omomys* particularly susceptible to owl predation (Murphey *et al.*, 1998). Several features of the *Omomys carteri* skull from "Forbidden City" (AMNH 130000) suggest that it too may represent remains from within an owl pellet. These include the preservation of delicate elements such as the premaxillae and nasals, a calcarious veneer adhering to some of its surfaces, and a dentary that is cemented to the palate out of anatomical position (Alexander and MacPhee, 1999a, 1999b).

The most obvious evidence of predation in the primate sample is seen in a male *N. tenebrosus* (AMNH 127167). This specimen bears at least three puncture wounds. A deep puncture occurs on the posterior margin of the left supraorbital process (Figure 5B, arrow). The wound is roughly triangular in cross section with rounded sides 4.0 mm, 3.5 mm and 3.5 mm in length. The edges of the hole are smoothly rounded and bend inward, a condition consistent with the penetration of fresh bone by a tooth or claw. A prominent compressive fracture is found in the identical position on the right supraorbital process. It is roughly circular and 3.0 mm in diameter. It indicates a tooth or claw that pressed about 1.0 mm into fresh bone, but did not puncture the skull. A third "unnatural" hole is found on the right maxilla 6.0 mm inferior to the lacrimal duct. It is oval in cross section and measures 2.0 mm by 1.5 mm. The initial interpretation of these marks on the skull of AMNH 127167 was that this individual's head had been gripped in the maw of a mammalian predator, perhaps the miacoid carnivore *Vulpavus* sp. (Alexander, 1992). The punctures resemble wounds on a partial skull of a juvenile *Australopithecus robustus* found in cave breccia deposits at Swartkrans in South Africa. Two circular holes in the hominid skull were probably the result of the penetration of the lower canines of a leopard, *Panthera pardus*, into each parietal. The upper canines would have penetrated the missing orbits. This damage would have occurred when the individual was dragged up into a tree by a leopard (Brain, 1974).

In addition, there are also apparent wounds on an isolated but complete *N. tenebrosus* mandible AMNH 131765 found only a few hundred meters from AMNH 127167. This specimen is interpreted by canine root diameter to be a female. The left dentary is compressed at m3 indicating a great force was applied to the specimen when the bone was still fresh and unmineralized. The specimen bears a contusion on the buccal boarder of the right dentary which has a complementary puncture just superior to the mandibular foramen on the medial aspect (Figure 5F, right arrow). This puncture trends anteriorly indicating a deep penetration from posterior to the jaw.

The wounds on AMNH 127167 and AMNH 131765 are consistent with the hunting and feeding patterns of raptorial birds (Rettig, 1978; Kerbis, 1997). A skull of a cebus monkey, *Cebus apella* from the Neil Rettig collection of the Field Museum (FMNH) shows damage similar to that found on AMNH 127167. This *Cebus* skull was collected from beneath the nesting site of a breeding pair of harpy eagles (*Harpia harpyjia*) at Moria Creek, Guyana in 1991. Out of the cebid remains found in this study (MNA = 30), only three cebid skulls were recovered (J. Kerbis, personal communication). One of these uncataloged skulls displays deep puncture wounds to the lacrimal region of both orbits, presumably inflicted by the talons of the harpy eagle.

A University of Michigan collection of mammalian remains found beneath nests of the crowned eagle *Stephanoaetus cornatus* from the Kibale Forest in

Uganda was examined in the course of this study (Mitani and Sanders, in prep.). Remains included hyraxes, small bovids, and several species of catarrhine monkey. All are documented as food remains of crowned eagles. One skull of the red colobus monkey, *Colobus badius* (field number 110), displays one talon puncture wound to each orbit and one to the left zygomatic. Of greatest interest is a talon wound low on the left frontal posterior to the postorbital constriction. The margins of this 6.0 mm circular puncture are bent inward indicating an entry wound into fresh bone. It is accompanied by a complimentary exit wound found on the inferior surface of the left sphenoid. This is established on the basis of the displacement of a 3.0 mm oval patch of bone still hinged on the margin of the hole. The entry and exit wounds are not in direct line with each other, but are rather, consistent with the passage of a recurved talon along an arcuate trajectory.

The maxillary wound on AMNH 127167 resembles the exit wound on Kibale 110. This lead to a reexamination of a damaged region within the right lacrimal of AMNH 127167 that is roughly 6.0 mm in diameter. These marks are now interpreted as a recurved talon wound which entered the right orbit and exited the right maxilla. This evidence strongly suggests that AMNH 127167 was the victim of a predatory bird, probably a diurnal eagle, based on body size and presumed diurnal habits of *Notharctus*.

That this specimen is generally complete indicates that the corpse may have been dropped before it could be fed upon. Such instances have been observed with modern eagles (Struhsaker and Leakey, 1990). The observed feeding behavior of eagles such as the Harpy Eagle *Harpia harpyjia* can also explain the relative completeness of primate remains. Adult Harpy Eagles which are efficient feeders, tend to damage and break apart the skulls of monkeys and tree sloths during feeding, while nesting young eagles which are relatively inefficient feeders, will leave complete vertebral columns with the skull and limbs sometimes attached. Sometimes they are held together with skin (Rettig, 1978). Such a carcass might enter the fossil record without clear indication of having been consumed by a predator.

Several multi-year studies of prey remains found in association with nesting pairs of crowned hawk eagles in the Kibale Forest of southwestern Uganda have produced compelling evidence of a taphonomic process at work on arboreal primates and terrestrial mammals such as hyraxes and smaller antelopes. Arboreal primates (monkeys) constitute the predominant prey species at well over 80% of the remains, (Brown, 1982; Skorupa, 1988; Struhsaker and Leakey, 1990). These large eagles (3.4–4.1 kg) selected prey according to species, age and sex. Among the larger red colobus monkeys *Colobus badius*, young juveniles and infants were selected. Among smaller bodied monkey species, adult males were selected. "Eagle prey selectivity by species generally supports the hypothesis that polyspecific associations among monkeys are effective deterrents against predation", (Struhsaker and Leakey, 1990). Eagle prey selectivity has a major impact on the populations and sex ratios of a number of monkey species (Struhsaker and Leakey, 1990). Although the predator/prey ratio for the Kibale eagles is much higher than that of the resident felids, their annual take of prey is lower (Struhsaker and Leakey, 1990).

Body size is a major consideration in prey selection among eagles, but it isn't absolute. Eagles are capable of killing species much larger than themselves such as the bushbuck (*Tragelaphus scriptus*). At 30 kg, young bushbucks can exceed six times the weight of an adult Crowned Eagle. If an eagle is incapable of bringing a victim back to its nest whole, it will dismember it and carry away selected pieces such as limbs, leaving the axial skeleton behind, (Brown, 1971; Daneel, 1979; Jarvis *et al.*, 1980; Gargett, 1990).

A similar study of crowned eagles was conducted in Cape Province, South Africa (Jarvis *et al.*, 1980). Here, the eagles live in forest patches surrounded by open grassland where the rock hyrax (*Procavia* capensis) is common and becomes the most common prey species (42%), followed by blue duiker (*Cephalophus monticola*, 16%), juvenile bushbucks (*Tragelaphus scriptus*, 12%), and vervet monkeys (*Cercopithecus pygerythrus*, 8%). In Kenya, where rock hyraxes are abundant, they are the preferred prey of crowned eagles (Brown, 1976).

Another study involving black eagles, *Aquila verreauxii*, was conducted in Matobo National Park, Zimbabwe, a savanna area with numerous rock koppies (Barry and Barry, 1996). Here, the rock hyrax, *Procavia capensis*, and the yellow-tailed hyrax, *Heterohyrax brucei*, constitute over 90% of the prey species. *Procavia* (4.53 kg), is as large or larger than *Aquila verreauxii* making them a more difficult to kill (Gargett, 1990). *Heterohyrax* (3.25 kg) was preyed on more heavily than *Procavia.* This may be due to its smaller size or its more diurnal habits which would have made it more susceptible to predation (Barry and Barry, 1996). Because of their greater weight, *Procavia* are often consumed at the kill site or decapitated (Gargett, 1990). Fewer skulls and jaws of *Procavia* were found at eagle nesting sites than those of *Heterohyrax.*

Such a taphonomic process would have a major effect on the fossil record in a fauna where eagles were once at work. This could explain why some species at Grizzly Buttes are commonly found as jaws or skull fragments and others as skeletons. There is a suite of taxa in the Grizzly Buttes fauna with body sizes comparable to these African taxa (Gunnell and Bartels, 1994). The ungulates *Hyopsodus paulus* (0.22 kg), *Antiacodon pygmaeus* (1.67 kg), *Orohippus pumilus* (7.33 kg), *Helaletes nanus* (15.52 kg), and the primates *Notharctus tenebrosus* (3.43 kg) and *Smilodectes gracilis* (1.88 kg) would have been likely targets for any contemporary eagles. The small body size of *Hyopsodus* may have resulted in the more complete dismemberment and destruction of its remains because predators may have been more apt to consume it whole than other prey mammals. This phenomenon might explain the paucity of its postcranial elements in the fossil record.

The fossil remains of large raptors like the owl *Protostrix saurodosis* have been described from the Bridger Formation (Wetmore, 1933). It is reasonable to believe that raptorial birds like hawks or eagles were present in the paratropical forest of Grizzly Buttes. Eagles specializing in primate predation are found in many tropical environments today. These include the Harpy Eagle of South America, the Crowned Eagle of Africa and the Philippine Eagle. Izor (1985) observed that monkeys were the only arboreal mammals that Harpy Eagles selected disproportionately to their availability. Although these are opportunistic predators, arboreal primates may be the optimal prey for their hunting behaviors (Skorupa, 1989). The large bird which may have inflicted the contusions observed on AMNH 127167 remains as yet unknown. In light of the data available for modern primate hunting birds, the apparent ratio of species of *Notharctus* and *Smilodectes* at Grizzly Buttes may more reflect the feeding habits of such birds than their actual numbers when living. These taxa are equally common at other Bridger B samples such as Church Buttes, but are not as frequently encountered as skeletons.

3.4. Intrusion

Intrusive burrowing of *Spathorhynchus* is one of several forms of bioturbation. *Metacheiromys* was certainly a burrowing animal, filling a niche comparable to the pangolin or the armadillo (Simpson, 1931). Although the *M. osborni* skeleton (AMNH 131777) is complete, the elements were found completely disarticulated in a dense concentration less than 50 cm across. This situation is consistent with the animal having died within a subterranean burrow which filled with water, resulting in the maceration of the corpse and the jumbling of the remains. There was however, no obvious intrusive contact surrounding the skeleton observed during excavation.

The fossilized nesting burrows of insects are a common feature at Grizzly Buttes. These resemble modern nest cells of the order Apoidea. These fossilized "bee cells" are roughly the size and shape of olive pits. Fossil cells often preserve the distinctive spiral closure of sealed cells and the caved in lid of chambers from which grown bees emerged. They result from the sedimentary filling or crystallization of egg chambers excavated by non-hiving bees. Modern bee species dig these chambers as shallow as 5 cm and as deep as 3 m beneath the surface (Rozen, 1984a; 1984b; 1993). Bees often seal these chambers with waxy substances and deposit a ball of ingested pollen upon which an egg is laid. The pollen ball is food for the growing bee larva. It may be possible to extract fossil pollen from unhatched bee cells. There is a direct relationship between the size of a bee cell and the insect that pupates within it. Differences in the size and form of these fossilized cells suggests that a number of bee species lived at Grizzly Buttes. This variety is also an indicator of the richness and complexity of the flowering plants and trees that the adult bees would have pollinated. When a young bee emerges from a cell, it cuts off the top with its mandibles, and fills in the empty chamber with sediment as it works its way to the surface.

Such empty cells are uncommon at Grizzly Buttes. Unopened cells in which the larva died without emerging are abundant. These are identifiable because they are complete and contain geode-like crystals rather than sediment. These gregarious bees will often dig egg chambers in large concentrations (Rozen, 1984a; 1984b; 1993). Several such concentrations have been found at Grizzly Buttes. One site, in sediments laterally equivalent to the cosmic layer, contains hundreds of bee cells within a single 10 cm horizon. Such a concentration indicates that the horizon was above the water table at the time of the intrusion. One explanation for the general failure of the cells to hatch is the possibility that the water table rose after the eggs had been laid. This is consistent with the interpretation of the cosmic layer and other beds having been formed by lake shore inundation.

4. Notharctid Primates

Although elements tend to be complete, many Bridger specimens have suffered severe plastic deformation. Gregory (1920) failed to account for this when describing the type skull of *Notharctus osborni* (AMNH 11466) (Granger and Gregory, 1917). This specimen was determined to be a junior synonym of *N. tenebrosus* by Robinson (1957). This resulted in an unnaturally long and narrow reconstruction based on a spurious resemblance to *Lemur catta* (Gregory, 1920). Gazin (1958) recognized that the profile of *Smilodectes gracilis* (USNM 21815) had been dorsoventrally distorted. He corrected for this in a dashed line reconstruction (Gazin, 1958, Pl. 2: figure 3). This correction was ignored in later reconstructions, such as those found in Simons (1964). These errors have been perpetuated for decades. Reconstructions of male and female *N. tenebrosus* and *S. gracilis* developed and illustrated by J. Alexander attempt to rectify this situation (Figures 6–7). The rostrae of *Notharctus* and *Smilodectes* are more reduced than generally believed (Figure 6).

Notharctus tenebrosus and *Notharctus pugnax* are frequently found together in the same layer at Grizzly Buttes (Alexander, 1994b). Of 114 notharctid specimens in the AMNH Grizzly Buttes collection, 77 have been attributed to the genus *Notharctus*. *N. tenebrosus* (n = 59), the smaller of the two species of *Notharctus* is numerically the most common species. *N. pugnax* (n = 10), the large bodied species, is the least common. The ratio between *N. tenebrosus* and *N. pugnax* is approximately 6 : 1. Eight specimens in the sample were attributable only to *Notharctus* sp.

According to arguments made by Shoshani (1992), the numerical prevalence of a ratio of 5 : 1 or greater of one taxon (species A) over another closely related taxon (species B) that shares the same habitat such as a diverse forest suitable for euryphagous species can be used to predict that species A is phylogenetically more primitive, and more of an environmental generalist than species B. Shoshani used the case of five species pairs syntopically and sympatrically sharing the same habitats, in particular the hyraxes *Heterohyrax brucei* and *Procavia capensis*. The case of *Notharctus tenebrosus* and *N. pugnax* is problematic as the later species appears to be gnathically less derived than the former. Perhaps *N. pugnax* may have been more specialized in its diet. The ratio of *Notharctus tenebrosus* to *Smilodectes gracilis* however, fits perfectly into the Shoshani paradigm. The smallest bodied notharctid at Grizzly Buttes *S. gracilis* (n = 12) is less common than *N. tenebrosus. S. gracilis* is the most derived of all known notharctid species, demonstrating a number of autapomorphies of the skull and dentition (Alexander, 1993; Rose *et al.*, 1999). Although *N. tenebrosus* with its completely fused dentaries is more derived than other species of *Notharctus* (Beecher, 1983; Alexander, 1993), it is far more similar to all other known notharctids, and may be interpreted as more of an ecological generalist than *Smilodectes*. Larger samples are needed to make these inferences statistically meaningful.

The ratio of one Grizzly Buttes species to another that is actually found in the assemblage is of course subject to taphonomic processes. Since the cosmic layer constitutes a *lagerstätten* deposit it is not subject to the sort of fluvial processes which sort bones in quarry samples according to size (Shotwell, 1958). This is further aided by the fact that the notharctids are of similar body size (Shoshani, 1992).

The new notharctid material permits a brief comparison of the gross skeletal morphology and individual variation of these taxa. *Smilodectes* has a proportionately larger lower body than *Notharctus*, so the identification of lower limb elements is problematic. The overlap in size of *N. tenebrosus* and *S. gracilis* postcranials has probably led to their general confusion. The taxonomic identification of all lower Bridger Formation notharctid postcranials not associated with dentitions may require reevaluation. Several of the new skeletons have well preserved hands and feet. AMNH 127167 has the most complete manus (Figure 5D) of any Eocene primate found in North America (Hamrick and Alexander, 1996). The *Notharctus* skeletons (AMNH 131764, 131772) and *Smilodectes* skeletons (AMNH 131762, 131763) preserve partial extremities.

The postcranials of female *N. tenebrosus* are considerably shorter in length and more gracile than those of males. For example, the fibula of AMNH 131764 (a male) is 111.5 mm long with a mid shaft diameter of 4.5 mm and shows developed muscle scars, while the comparable dimensions of the female AMNH 129382 are 93.5 mm and 3.5 mm respectively. The juvenile *N. tenebrosus* skeleton (AMNH 131772) has most epiphyses unfused and yet has a completely adult dentition indicating a prolonged period of postcranial development for this species. AMNH 131772 is identified as a female on the basis of the root diameter of the adult canine root (Alexander, 1994a). This specimen also has partially articulated feet (note hallux, Figure 5E) aiding the attribution of isolated juvenile postcranial material to this species. Remains of developmentally younger individuals of *N. tenebrosus* have also been found. AMNH 131830 from "Butch Hill" consists of a mandible fragment with dp4 and m1 in the crypt, associated unerupted M1 and M2 and an associated tibia without epiphyses. AMNH 129384 is the most important of these juvenile specimens. It consists of a nearly complete mandible with dp3–4, m1–2 and m3 in the crypt, and a partial skull with a clearly separated metopic suture between the frontals. A maxillary fragment which includes DP1–4 is present, as well as several as yet unprepared postcranial elements. By far the developmentally youngest individual is AMNH 131959, a partial pelvis and lower back of an

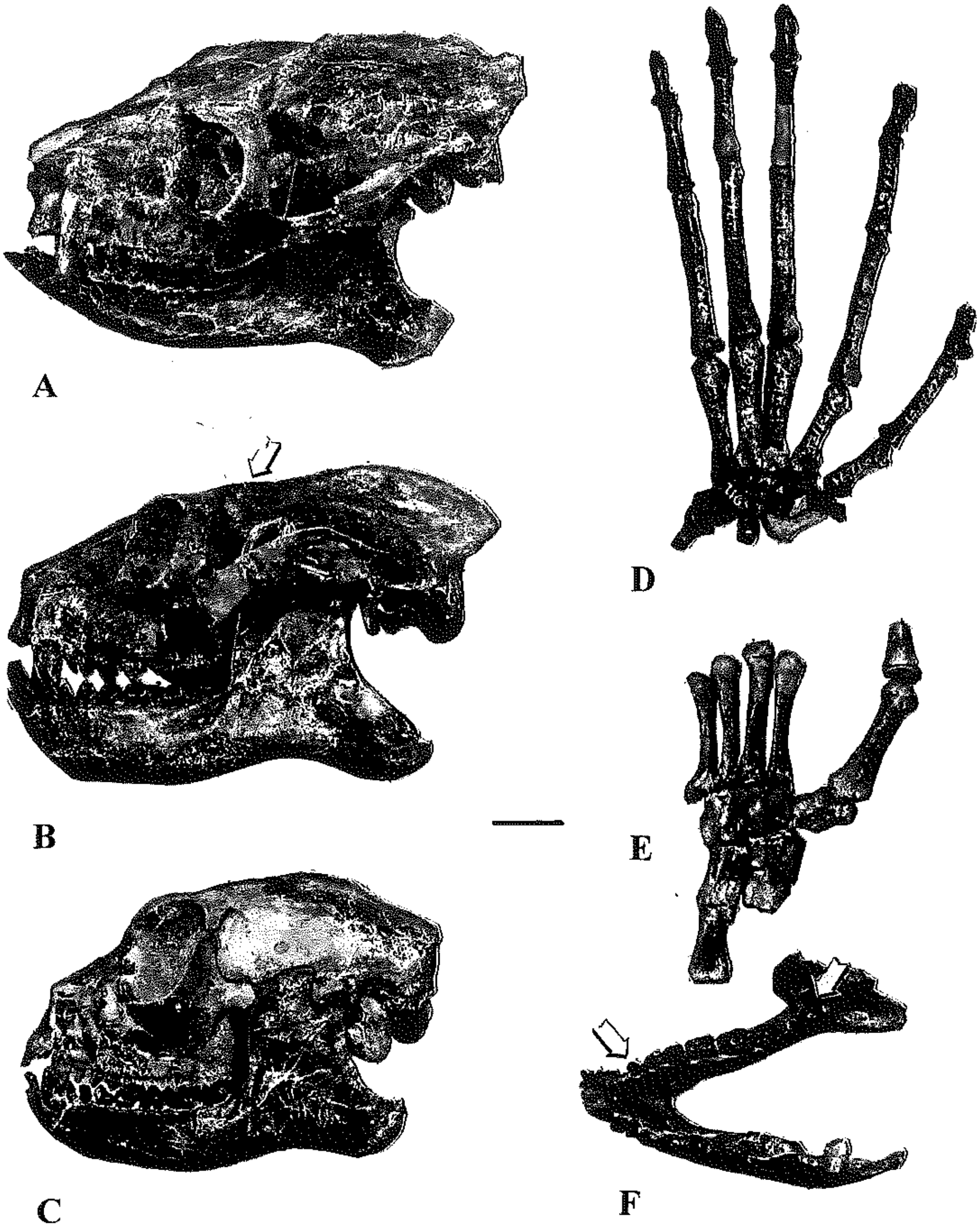

FIGURE 5. Representative notharctid specimens from Grizzly Buttes, Wyoming. A, AMNH 131764, *Notharctus tenebrosus* skull (male, image reversed); B, AMNH 127167, *Notharctus tenebrosus* skull (male); C, AMNH 131762, *Smilodectes gracilis* skull; D, AMNH 127167, *Notharctus tenebrosus* left manus; E, AMNH 131772, *Notharctus tenebrosus* partial right pes (juvenile, image reversed); F, AMNH 131765, *Notharctus tenebrosus* mandible female. Scale bar = 10.0 mm.

unidentified infant of a notharctid. The right ilium and ischium appear to have been separated by a cartilaginous pad suggesting that this individual was a non-ambulatory neonate. Isolated deciduous teeth of notharctids of uncertain attribution have also been found through screen washing.

The sagittal crest of male *N. tenebrosus* (AMNH 131764) terminates posteriorly in a distinctive button-shaped prominence at the apex of the lambdoidal crest anchoring strong temporalis, masseter and trapezius muscles (Figure 5A). This region is missing on AMNH 127167. A muted expression of the sexually dimorphic cranial features seen in *N. tenebrosus* occurs in *S. gracilis* (Alexander, 1994a). USNM 21815 and AMNH 131762 are probably males exhibiting larger canines, greater bizygomatic breadth and better defined temporal lines than USNM 17994 and AMNH 131763 which are probably females. Gazin (1958) observed that the auditory bullae of *S. gracilis* are larger than those of *N. tenebrosus*: that of AMNH 131762 (Figure 5C) (1.0 cm) is twice as voluminous as that of AMNH 131764 (Figure 5B) (0.5 cm). Contrary to Beecher (1983), in the new Grizzly Buttes sample, the mandibular symphysis of both *N. tenebrosus* and *N. pugnax* is always fused, often with the suture completely obliterated. There is a median symphyseal groove on the labial surface, similar to that of *N. pugnax* (Beecher, 1983), that splits halfway down the symphysis into two diverging scars for attachment of the mentalis musculature (Figure 7A). Considerable confusion has existed about the taxonomic status of *N. tenebrosus* and *N. pugnax* (Robinson, 1957). The new synchronous sample has helped to distinguish the two species (Alexander, 1994b). It confirms the type description of *N. pugnax* (Granger and Gregory, 1917), later statistically justified by Gingerich (1979).

A pair of thyrohyals were recovered with the skeleton of a female *N. tenebrosus*, AMNH 129132. Each of these thyrohyals is approximately four times as massive as a thyrohyal found with the hyoid apparatus of a late juvenile *Adapis parisiensis* (NMB QW 1). This element was recently discovered during preparation of the skull of NMB QW 1 (Alexander, 1996). This skull was mentioned by Stehlin (1912), but not figured. A stylohyal and epihyal were also found articulated to the basicranium of *S. gracilis* (AMNH 131762). Hyoids may open a completely new line of evidence for the interpretation of early primate phylogeny (Alexander, 1996), as they differ remarkably among living prosimians and the primitive condition for the apparatus is unknown. The large medially recurved mandibular angles of both *N. tenebrosus* and *S. gracilis* provide for an extensive area of attachment for the superficial masseter and medial pterygoid muscles and may have supported a large hyolaryngeal apparatus, perhaps permitting more resonant vocalization. The mandibular angle accounts for 14% of dentary length in *N. tenebrosus* (AMNH 127167) and 15% in *S. gracilis* (AMNH 131762) (Figure 5C). The mandibular angle of *Pelycodus jarrovii* (AMNH 55514) (Froehlich *et al.*, 1995) extends only 3.0 mm beyond the posterior border of the ascending ramus. Unfortunately the dentary of AMNH 55514 is not complete, preventing a percentage comparison with the other taxa.

Dental abnormalities have been observed in the new AMNH sample indicating a wide range of individual variation within a contemporaneous population. Rosenberger *et al.* (1985) noted that YPM 12956, a male *N. tenebrosus* dentition also from the Bridger B2 level, had lost the crown of its left P1/ and that replacement bone had covered the root in its crypt. A similar condition is seen in AMNH 131764, an adult male. The tip of a second tooth protruding at this locus suggests that the P/2 had failed to replace the dP/2 whose unresorbed root is still in place. In the adult female AMNH 131765 (Figure 5F, left arrow), the right P/1 is completely absent with no evidence of a root or alveolus. The left P/1 in this specimen is hypertrophied and similar in size to the left P/2. The question of the occlusion of upper and lower incisors in notharctids raised by Rosenberger *et al.* (1985) can be addressed in AMNH 131762 (*Smilodectes*) (Figure 5C). The in situ I1/ shows considerable attritional wear on the apical surface, obliterating the mesial prong of the I1/ noted by Greenfield (1995). Prior to this wear stage, it probably would not have been in contact with I/2. As wear progressed on I1/, it first engaged the I/1 and then both the I/1 and the I/2. Rosenberger *et al.* (1985) correctly surmised that the I2/ of *Smilodectes* is so small that it probably did not occlude with I/2 at any stage of wear.

S. gracilis possesses several diagnostic features not previously observed by Gregory (1920) or Gazin (1958) that distinguish it from all other notharctids. The domed frontal bones observed by Gazin (1958) override the nasal root, giving the nasal origin a squared off appearance (Figures 6–7C, D). There is a small foramen 1.0 mm below each orbital rim where the zygomatic ascends to form the postorbital bar (Figure 5C). In *Notharctus* this feature varies from a semicircular notch in AMNH 127167 (Figure 5B) to absent in AMNH 131764 (Figure 5A).

In *Smilodectes* a thin groove runs horizontally on the lateral surface of each dentary (Figure 5C, Figure 6C-D). It varies in length from 3.0 mm in AMNH 131774 to 13.0 mm in AMNH 131763 and can vary between the left and right sides of a single individual; in AMNH 131774 it is occurs only on the left dentary. It is a superficial channel for a blood vessel which runs posteriorly from the mandibular foramen ventral to the first molar. This character is sufficiently diagnostic to permit specific identification of edentulous jaw fragments.

ACKNOWLEDGMENTS. The authors wish to acknowledge the invaluable assistance of the following individuals.

Dr. Emmett Evanoff (UCM), Dr. Peter Robinson (UCM), Paul C. Murphey (UCM), Dr, Eugene S. Gaffney (AMNH) and Dr. Robert M. West for making unpublished stratigraphic and locality information of the Bridger Area available for this study. Dr. Laurie Bryant (BLM) for permitting access to Federal lands. Dr. Julian Kerbis (FMNH) and Dr. William Sanders (UMMP) for access to modern primate collections. Dr. Gregg F. Gunnell for review of this manuscript and body mass estimates of Bridger fauna. Dr. Jerome G. Rozen Jr. (AMNH) for advice on bee cells. Dr. Jeheskel Shoshani (CIS) for discussion of numerical prediction of environmental specialization. Dr. Dawne Adams

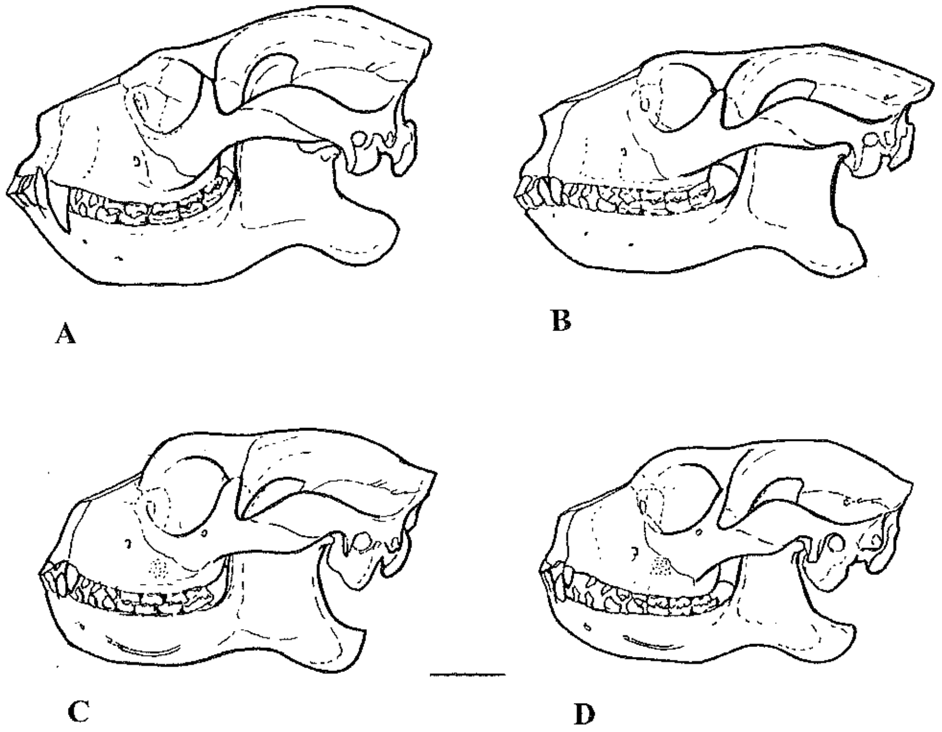

FIGURE 6. Reconstructions of skulls of Bridgerian notharctids in left lateral view. A, male *N. tenebrosus* based on AMNH 127167 and AMNH 131764; B, female *N. tenebrosus* based on AMNH 11466, AMNH 129382, and AMNH 131765; C, male *S. gracilis* based on USNM 17994 and AMNH 131762; D, female *S. gracilis* based on USNM 21815 and AMNH 131763. Scale bar = 10.0 mm.

(Baylor University), Thomas M. Alexander, Peter Ambrose (NPS), Rachel C. Benton (NPS), Dr. Richard Cifelli (OMNH), Dr. Susan Ford (SIU), Dr. Daniel Gebo (NIU), Dr. Marc Godinot (MNHN) Dr. Robert Martin (AIMUZ), Dr. Carl A. Morck, and Dr. Andrew Nelson (UWO) for logistical and financial support of field work. Dr. Robert L. Anemone (SUNY Geneseo), John Bennett (UCM), Patrick Buchmann, Sebastian Fernandez, Kenneth Filchak, Lee Ann Jolly, Linda Levitch, Patrick Light, Leahanne Sarlo, Matthew Turnow and David Wilcotts for assistance in the field. Dr. Eric Delson (CUNY), Dr. Terry Harrison (NYU), Lorraine Meeker (AMNH), Dr. Maureen O'Leary (SUNY Stony Brook) and Chester Tarka (AMNH) for assistance in the preparation of this manuscript. Research reported herein was conducted under BLM permits 209WYPA94, 231WY94 and 306WY94.

Acronyms used in text: AIMUZ—Anthr. Inst. Mus. Urchel, Zurich; AMNH—American Museum of Natural History; BLM—Bureau of Land Management; CUNY—City University of New York; FMNH—Field Museum of Natural History; MPM—Milwaukee Public Museum; MNHN—Museum National d'Historie Naturelle, Paris; NIU—Northern Illinois University; NPS—

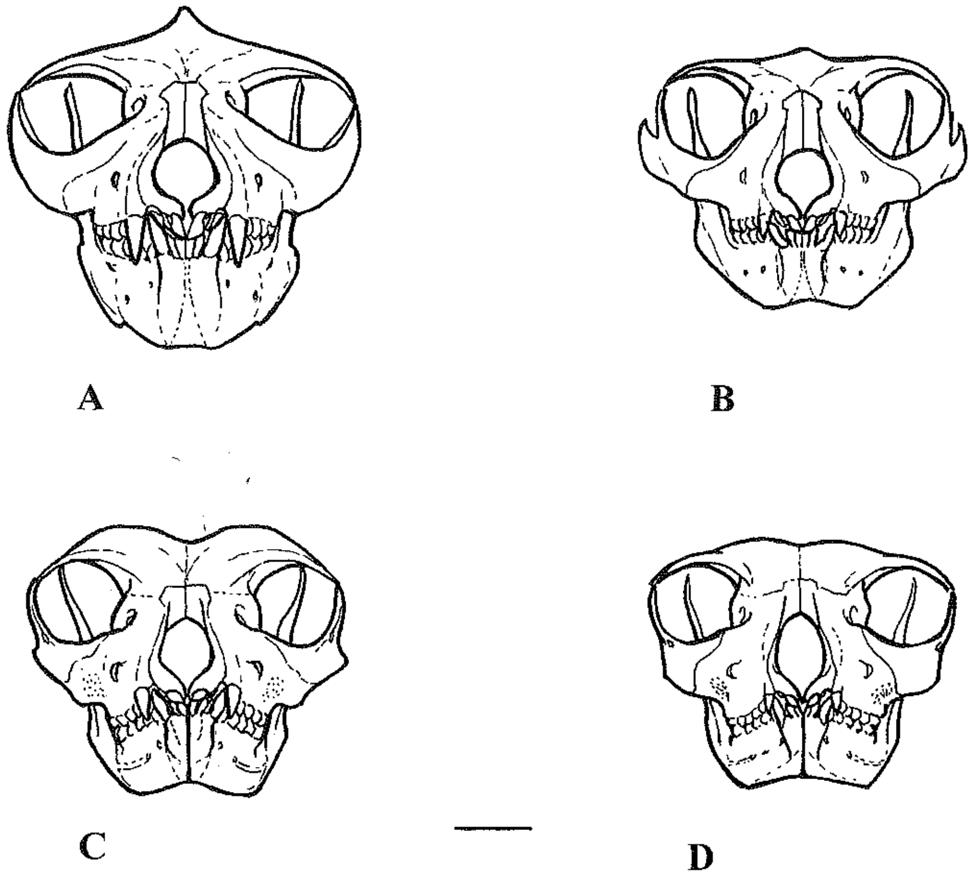

FIGURE 7. Reconstructions of skulls of Bridgerian notharctids in frontal view. Labels as in Figure 1. Scale bar = 10.0 mm.

National Park Service; NYU—New York University; OMNH—Oklahoma Museum of Natural History; SUNY—State University of New York; SIU—Southern Illinois University; UCM—University of Colorado, Boulder; UMMP—University of Michigan Museum of Paleontology; USNM—U.S. National Museum (Smithsonian Institution); UWO—University of Western Ontario; YPM—Yale Peabody Museum.

References

Alexander, J. P., 1992, Alas poor *Notharctus*, *Natural History* **101(8)**:54–59.

Alexander, J. P., 1993, *The splanchnocranial anatomy of the Eocene primate* Notharctus, M. A. Thesis, Hunter College, City University of New York.

Alexander, J. P., 1994a, Evidence for sexual dimorphism in the primate family Notharctidae, *Folia Primatol.* **63**:59–62.

Alexander, J. P., 1994b, Sympatry of two species of *Notharctus* in the Bridger Basin, Wyoming, *Jour. Vert. Paleont.* **14**(supplement to 3):14A.

Alexander, J. P., 1996, Elements of the hyoid apparatus of several Eocene adapiform primates, *Jour. Vert. Paleont.* **16**(supplement to 3):19A.

Alexander, J. P., and MacPhee, R. D. E., 1999a, Skull of *Omomys carteri*, an Eocene omomyid Primate, *American Journal of Physical Anthropology* Supplement 28, p. 83.

Alexander, J. P., and MacPhee, R. D. E., 1999b, Skull morphology of *Omomys carteri*, *Jour. Vert. Paleont.* **19**(supplement to 3):29A.

Andrews, P., 1990, *Owls, Caves and Fossils*, University of Chicago Press, Chicago.

Barry, R. E., and Barry, L. M., 1996, Species composition and age structure of remains of hyraxes (Hyracoidea: Procaviidae) at nests of black eagles, *Jour. Mammal.* **77(3)**:702–707.

Beard, K. C., and Krishtalka, L., 1991, First skull of the early Eocene primate *Shoshonius cooperi* and the anthropoid-tarsier dichotomy, *Nature* **349**:64–67.

Beard, K. C., and MacPhee, R. D. E., 1994, Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea, in: *Anthropoid Origins* (J. G. Fleagle, and R. F. Kay, eds.), Plenum Press, New York, pp. 55–97.

Beecher, R. M., 1983, Evolution of the mandibular symphysis in Notharctinae (Adapidae, Primates), *Intl. Jour. Primatol.* **4**:99–112.

Behrensmeyer, A. M., and Hill, A., 1980, *Fossils in the Making*, University of Chicago Press, Chicago.

Berman, D. S., 1973, *Spathorhynchus fossorum*, a Middle Eocene Amphisbaenian (Reptilia) from Wyoming, *Copeia* **4**:704–721.

Bradley, W. H., 1964, Geology of the Green River Formation and associated Eocene rocks in southwestern Wyoming and adjacent parts of Colorado and Utah, *U.S. Geol. Surv. Prof. Paper* **496A**:1–86.

Brain, C. K., 1974, A hominid skull's revealing holes, *Natural History* **83(10)**:44–45.

Brown, L. H., 1971, The relationship of the Crowned Eagle *Stephanoaetus cornatus* and some of its prey animals, *Ibis* **113**:240–243.

Brown, L. H., 1976, *Eagles of the World*, Purnell: Cape Town.

Brown, L. H., 1982, The prey of the Crowned Eagle *Stephanoaetus cornatus* in Central Kenya, *Scopus* **6**:91–94.

Brown, R. W., 1929, Additions to the flora of the Green River Formation, *U. S. Geol. Surv. Prof. Pap.* **154**:279–299.

Brown, R. W., 1934, The recognizable species of the Green River Flora, *U. S. Geol. Surv. Prof. Pap.* **185C**:45–77.

Daneel, A. B. C., 1979, Prey size and hunting methods of the Crowned Eagle, *Ostrich* **50**:120–121.

Delson, E., 1971, Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming, *Bull. Amer. Mus. Nat. Hist.* **146**:307–364.

Evanoff, E., Brand, L., and Murphey, P., 1998, Bridger Formation (middle Eocene) of southwest Wyoming: widespread marker units and subdivisions of Bridger B through D, *Dakoterra* **5**:115–122.

Evanoff, E., and Ivy, L., 1992, Roadlog Manila, Utah to Fort Bridger, Wyoming, along Utah 43 and Wyoming 414, in: *Field Guide to geologic excursions in Utah and adjacent areas of Nevada, Idaho, and Wyoming* (J. R. Wilson, ed.), Utah Geol. Surv. Misc. Pub. **923**:368–373.

Flynn, J. J., 1986, Correlation and geochronology of middle Eocene strata from the western United States, *Palaeogeogr., Palaeoclimat., Palaeoecol.* **55**:335–406.

Franzen, J. L., and Frey, E., 1993, *Europolemur* completed, *Kaupia* **3**:113–130.

Froehlich, J., Alexander, J. P., and Froehlich, D., 1995, *Pelycodus* premolars and other new specimens from the San Jose Formation of New Mexico, *Jour. Vert. Paleont.* **15**(supplement to 3):30A.

Gaffney, E. S., 1972, The systematics of the North American family Baenidae (Reptilia, Cryptodira), *Bull. Amer. Mus. Nat. Hist.*, **147**:243–319.

Gargett, V., 1990, *The Black Eagle*, Acorn Books, Randburg, South Africa.

Gazin, C. L., 1958, A review of the Middle and Upper Eocene primates of North America, *Smithson. Misc. Coll.* **136**:1–112.

Gazin, C. L., 1968, A study of the Eocene condylarthran mammal *Hyopsodus*, *Smithson. Misc. Coll.* **153**:1–90.

Gazin, C. L., 1976, Mammalian faunal zones of the Bridger Middle Eocene, *Smithson. Contribs. Paleobiol.* **26**:1–25.

Gingerich, P. D., 1979, Phylogeny of Middle Eocene Adapidae (Mammalia, Primates) in North America: *Smilodectes* and *Notharctus*, *Jour. Paleont.* **53**:153–163.

Granger, W., and Gregory, W. K., 1917, A revision of the Eocene primates of the genus *Notharctus*, *Bull. Amer. Mus. Nat. Hist.*, **37**:841–859.

Greenfield, L. O., 1995, The anterior dentition of adapids and anthropoid origins, *Folia Primatol.* **65**:59–84.

Gregory, W. K., 1920, On the structure and relations of *Notharctus*, an American Eocene primate, *Mem. Amer. Mus. Nat. Hist.* **3**:1–243.

Gunnell, G. F., and Bartels, W. S., 1994, Early Bridgerian (middle Eocene) vertebrate paleontology and paleoecology of the southern Green River Basin, Wyoming, Contrib. *Geol., Univ. Wyo.* **30**:57–70.

Gunnell, G. F., and Bartels, W. S., 1997, Basin margin mammalian assemblages from the Wasatch Formation (Bridgerian) of the northeastern Green River Basin, Wyoming: anachronistic taxa and the origin of new genera, *Jour. Vert. Paleont.* **17**(supplement to 3):51A.

Hamrick, M. W., and Alexander, J. P., 1996, The hand skeleton of *Notharctus tenebrosus* (Primates, Notharctidae) and its significance for the origin of the primate hand, *Amer. Mus. Novitates* **3182**:1–20.

Hanley, J. H., 1974, *Systematics, paleoecology and biostratigraphy of nonmarine Mollusca from the Green River and Wasatch Formations (Eocene), southwestern Wyoming and northwestern Colorado*, Ph.D. Thesis, University of Wyoming, Laramie.

Hay, O. P., 1908, The fossil turtles of North America, *Carnegie Inst. Wash. Publ.* **75**:1–568.

Hibbard, C. W., 1949, Techniques of collecting microvertebrate fossils, *Contrib. Mus. Paleont. Univ. Mich.* **8**:7–19.

Izor, R. J., 1985, Sloths and other mammalian prey of the Harpy Eagle, in: *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas* (G. G. Montgomery, ed.) Smithsonian Institution Press, Washington, D.C., pp. 343–346.

Jarvis, M. J. F., Currie, M. H., and Palmer, N. G., 1980, Food of crowned eagles in the Cape Province, South Africa, *Ostrich* **51**:215–218.

Kerbis, J. C., 1997, Taphonomy of tropical forest environments: monkey eating eagles as agents of bone accumulation, *Jour. Vert. Paleont.* **17**(supplement to 3):56A–57A.

Krishtalka, L., West, R. M., Black, C. C., Dawson, M. R., Flynn, J. J., Turnbull, W. D., Stucky, R. K., McKenna, M. C., Bown, T. M., Golz, D. J., and Lillegraven, J. A., 1987, Eocene (Wasatchian through Duchesnean) Biochronology of North America, in: *Cenozoic Mammals of North America Geochronology and Biostratigraphy* (M. O. Woodburne, ed.), University of California Press, Berkeley, pp. 77–117.

Langston, W., Jr., 1975, Ziphodont Crocodiles: *Pritichampsus vorax* (Troxell), new combination, from the Eocene of North America, *Fieldiana Geology* **33**:291–314.

Leidy, J., 1869, Notice of some extinct vertebrates from Wyoming and Dakota, *Proc. Acad. Nat. Sci. Phila.* **21**:63–67.

Leidy, J., 1870, Descriptions of *Palaeosyops paludosus*, *Microsus cuspidatus* and *Notharctus tenebrosus*, *Proc. Acad. Nat. Sci. Phila.* **22**:113–114.

MacGinitie, H. D., 1969, The Eocene Green River Flora of northwestern Colorado and northeastern Utah, *Univ. Calif. Pub. Geol. Sci.* **83**:1–140.

Marsh, O. C., 1871, Notice of some fossil mammals from the Tertiary formation, *Amer. Jour. Sci.* **2**:35–44, 120–127.

Matthew, W. D., 1909, The Carnivora and Insectivora of the Bridger Basin, middle Eocene, *Mem. Amer. Mus. Nat. Hist.* **9**:289–567.

Matthew, W. D., 1928, The evolution of mammals in the Eocene, *Proc. Zool. Soc. London* **1927**:947–985.

Mauger, R. L., 1977, K-Ar ages of biotites from tuffs in Eocene rocks of the Green River, Washakie, and Uinta basins, Utah, Wyoming, and Colorado, *Univ. Wyo. Contrib. Geol.* **15**:17–41.

McGrew, P. O., and Casilliano, M., 1970, Geological history of Fossil Butte National Monument and Fossil Basin, *National Park Service Occasional Papers* 3.

McGrew, P. O., and Sullivan, R., 1970, The stratigraphy and paleontology of Bridger A, *Contrib. Geol. Univ. Wyo.* **9**:66–85.

McKenna, M. C., 1962, Collecting small fossils by washing and screen, *Curator* **3**:221–235.

McKenna, M. C., 1990, Plagiomenids (Mammalia: ?Dermoptera) from the Oligocene of Oregon, Montana, and South Dakota, and middle Eocene of northwestern Wyoming, in: *Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior, North America* (T. M. Bown, and K. D. Rose, eds.), Geol. Soc. Amer. Spec. Pap. **243**:211–234.

Murphey, P. C., 1990, Depositional setting and fauna of the *Omomys* Quarry, a possible owl site in the Bridger Formation (Middle Eocene) of Southwestern Wyoming, *Jour. Vert. Paleont.* **16**(supplement to 3):55A.

Murphey, P. C., 1995, *Paleontology, distribution and history of a middle Eocene lacustrine deposit in the Bridger Formation, southwestern Wyoming*, Master's Thesis, University of Colorado, Boulder.

Murphey, P. C., Torick, L., Bray, E., Chandler, R., and Evanoff, E., 1998, Taphonomy and paleoecology of the Omomys Quarry, an unusual fossil accumulation from the Bridger Formation, Wyoming, *Jour. Vert. Paleont.* **18**(supplement to 3):65A.

Osborn, H. F., 1904, An armadillo from the Middle Eocene (Bridger) of North America, *Bull. Amer. Mus. Nat. Hist.* **20**:163–165.

Osborn, H. F., 1910, *The Age of Mammals in Europe, Asia, and North America*, Macmillan, New York.

Rea, D. K., Zachos, J. C., Owen, R. M., and Gingerich, P. D., 1989, Global change at the Paleocene-Eocene boundary: climatic and evolutionary consequences of tectonic events, *Palaeogeogr., Palaeoclimat., Palaeoecol.* **79**:117–128.

Rettig, N. L., 1978, Breeding behavior of the harpy eagle *Harpia harpyjia*, *The Auk* **95**: 629–643.

Robinson, P., 1957, The species of *Notharctus* from the Middle Eocene, *Postilla* **28**:1–27.

Robinson, P., 1994, *Myrmekomomys*, a new genus of Micromomyine (Mammalia, ?Microsyopidae) from the lower Eocene rocks of the Powder River Basin, Wyoming, *Contribs. Geol. Univ. Wyo.* **30**:85–90.

Roehler, H. W., 1993, Eocene climates, depositional environments, and geography, Greater Green River Basin, Wyoming, Utah and Colorado, *U. S. Geol. Surv. Prof. Paper* **1506F**:1–74.

Rose, K. D., MacPhee, R. D. E., and Alexander, J. P., 1999, Skull of early Eocene *Cantius abditus* (Primates: Adapiformes) and its phylogenetic implications, with a reevaluation of "*Hesperolemur*" *actius*, *American Journal of Physical Anthropology* **109**:523–539.

Rosenberger, A. L., Strasser, E., and Delson, E., 1985, Anterior dentition of *Notharctus* and the adapid-anthropoid hypothesis, *Folia Primatol.* **44**:15–39.

Royse, F. R., Jr., 1993, An overview of the geologic structure of the thrust belt in Wyoming, northern Utah, and eastern Idaho, in: *Geology of Wyoming*, Memoir no. 5, The Geological Survey of Wyoming, pp. 272–311.

Rozen, J. G., Jr., 1984a, Nesting biology of Diphaglossine bees (Hymenoptera, Colletidae), *Amer. Mus. Novitates* **2786**:1–33.

Rozen, J. G., Jr., 1984b, Comparative nesting biology of the bee tribe Exomalopsini (Apoidea, Anthophoridae), *Amer. Mus. Novitates* **2798**:1–37.

Rozen, J. G., Jr., 1993, Nesting biologies and immature stages of the Rophitine bees (Halictidae) with notes on the cleptoparasite *Biastes* (Anthophoridae) (Hymenoptera: Apoidea), *Amer. Mus. Novitates* **3066**:1–28.

Savin, S. M., 1977, The history of the Earth's surface temperature during the past 100 million years, *Ann. Rev. Earth Planet. Sci.* **5**:319–355.

Savin, S. M., and Douglas, R. G., 1984, Sea level, climate, and the Central American land bridge, in: *The Great American Biotic Interchange* (F. G. Steli, and S. D. Webb, eds.), Plenum, New York, pp. 303–324.

Schoch, R. M., 1984, Revision of *Metacheiromys* Wortman, 1903 and a review of the Palaeanodonta, *Postilla* **192**:1–17.

Shoshani, J., 1992, Ecology and taxonomy: a new approach, using *Heterohyrax* vs *Procavia* as a case study, *Israel Jour. Zool.* **38**:399–416.

Shotwell, J. A., 1958, Intercommunity relationships in Hemphillian (mid-Pliocene) mammals, *Ecology* **39**:271–282.

Simons, E. L., 1964, The early relatives of man, *Sci. Amer.* **7**:1–14.

Simpson, G. G., 1931, *Metacheiromys* and the Edentata, *Bull. Amer. Mus. Nat. Hist.* **55**:295–381.

Skorupa, J. P., 1989, Crowned Eagles *Strephanoaetus coronatus* in rainforest: observations on breeding chronology and diet at a nest in Uganda, *Ibis* **131**:294–298.

Smedes, H. W., and Prostka, H. J., 1972, Stratigraphic framework of the Absaroka Volcanic Super group in the Yellowstone National Park region, *U.S. Geol. Surv. Prof. Paper* **729C**:1–33.

Stehlin, H. G., 1912, Die Saugetiere des Schweizerischen Eocaens. Critischer Catalog der Materialen. Part 7, *Abh. der Schweiz. Pal. Ges.* **38**:1165–1298.

Stucky, R. K., 1992, Mammalian faunas in North America of Bridgerian to Early Arikareean "Ages" (Eocene and Oligocene), in: *Eocene-Oligocene Climatic and Biotic Evolution* (D. R. Prothero, and W. A. Berggren, eds.), Princeton University Press, Princeton, pp. 464–493.

Struhsaker, T. T., and Leakey, M., 1990, Prey selectivity by crowned hawkeagles on monkeys in the Kibale Forest, Uganda, *Behav. Ecol. Sociobiol.* **26**:435–443.

Thompson, F., 1984, *Freshwater snails of Florida, a manual for identification*, University of Florida Press, Gainesville.

Troxell, E. L., 1925, The Bridger Crocodiles, *Amer. Jour. Sci.* **9**:29–72.

Wallace, J., 1994, *The American Museum of Natural History's Book of Dinosaurs and other Ancient Creatures*, Simon and Shuster, New York.

West, R. M., 1976, Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming. Part 1. History of field work and geological setting, *Contribs. Biol. Geol., Milwaukee Publ. Mus.* **7**:1–12.

West, R. M., 1979, Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming. Part 3. Notes on *Hyopsodus*, *Contribs. Biol. Geol., Milwaukee Publ. Mus.* **25**:1–52.

West, R. M., 1990, Vertebrate Paleontology of the Green River Basin, Wyoming, 1840–1910, *Earth Sciences History* **9**:45–56.

Wetmore, A., 1933, The status of *Minerva antiqua*, *Aquila ferox*, and *Aquila lydekkeri* as fossil birds, *Amer. Mus. Novitates* **680**:1–4.

Wheeler, W. H., 1961, Revision of the Uintatheres, *Bull. Peabody Mus. Nat. Hist.* **14**:1–93.

Wing, S. L., 1987, Eocene and Oligocene floras and vegetation of the Rocky Mountains, *Ann. Missouri Bot. Garden* **74**:176–212.

Wood, H. E., 1934, Revision of the Hyrachyidae, *Bull. Amer. Mus. Nat. Hist.* **67**:181–295.