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Ph.D. degree in Geological Sciences

Major professor

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AN ANALYSIS OF THE HERPETOFAUNA AND PALEOENVIRONMENT OF THE WASATCH AND BRIDGER FORMATIONS (MIDDLE EOCENE), AT SOUTH PASS, WYOMING

VOLUME 1

By

Rachael J. Walker

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Geology

1999

ABSTRACT

AN ANALYSIS OF THE HERPETOFAUNA AND PALEOENVIRONMENT OF THE WASATCH AND BRIDGER FORMATIONS (MIDDLE EOCENE), AT SOUTH PASS, WYOMING

By

Rachael J. Walker

The middle Eocene Wasatch and Bridger formations of the Green River Basin of Wyoming have yielded abundant remains of fossil amphibians, lizards, amphisbaenians, and snakes.

Latest Wasatch (Wa7) and earliest Bridgerian (Br0) basin margin assemblages have been recovered from near South Pass on the northeastern margin of the basin and from the Desertion Point-Little Muddy section on the western margin. Early Bridgerian (Br1) basin center faunas are represented by collections from Desertion Point-Little Muddy and Big Island. The Bridger Basin contains basin center assemblages ranging in age from Br1 through Br3 (middle to late Bridgerian).

Lostcabinian (Wa7) and Gardnerbuttean (Br0) assemblages were poorly known before recent collections at South Pass. These levels contain the lizards Glyptosaurus sylvestris, Machaerosaurus torrejonensis, Saniwa ensidens, Palaeoxantusia sp., Xestops vagans, Parasauromalus olseni, Restes rugosus,

glyptosaurine "indet A", an amphisbaenid; and the snakes Dunnophis microechinis, Boavus occidentalis, Calamagras primus, Coniophis sp., a rhinophrynid, and a salamander. "Bridgerian A" (Br1) assemblages containthe lizards Glyptosaurus sylvestris, Xestops vagans, Parasauromalus olseni, Saniwa ensidens, an amphisbaenid; and the snakes Boavus occidentalis, and Coniophis sp., and record the earliest appearances of the lizards Paraglyptosaurus hillsi, Palaeoxantusia fera, and Tinosaurus stenodon. Taxa recovered from the "Bridgerian B" and "Bridgerian C" (Br2 and lower Br3) include all lizards found in older levels and the earliest appearances of Palaeoxantusia borealis, Tinosaurus pristinus, Eodiploglossus borealis, and Apodosauriscus minutus.

The diversification of this lizard assemblage through time is a reflection of climatic warming which occurred during the late Wasatchian through middle Bridgerian but also may be influenced by the smaller sample size of principally basin margin assemblages for Wa7 and Br0.

The fossil assemblages and sedimentary stratigraphy at South Pass indicate the presence of an alluvial fan produced by reverse movement on the Continental and Wind River faults. This basin margin environment provided diverse habitats which in turn supported a wide variety of amphibian, lizard, amphisbaenid, and snake species.

To my parents, Martin and Elizabeth Walker,

and to Dr Keith Cox.

ACKNOWLEDGMENTS

Many people deserve thanks for their part in this thesis. Firstly, I wish to thank Dr. J. Alan Holman, for his help and for having confidence in me. I also wish to thank Dr. William S. Bartels for his immeasurable help in the field and for his patience in editing. I would also like to thank the rest of my committee, Dr. Grahame. J. Larson, Dr. Ralph E. Taggart, and Dr. Kay Holecamp for their advice and guidance.

This study is part of the university of Michigan/Albion College investigation of the Green River Basin of Wyoming. Thank you to Dr. Gregg F. Gunnell and Dr. William S. Bartels for allowing me to be part of this project, and for their guidance and friendship in the field. Thank you also to Drs. Con Childress, Beth Strasser, and George Junne for their work collecting many of the specimens used in this study. Thank you to Dr. Mike Gottfried for advice and editing of my disertation, and to Dr. Bill Cambray, and Paula Hildebrandt for helping me in many areas related to both my work and life at Michigan State University.

This project was supported by the Paleontological Society, the National Science Foundation, the National Geographic Society, the Carnegie-Mellon Fund (Albion College), and Michigan State University.

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SPECIMEN ABBREVIATIONS

UM - University of Michigan specimens.

WPM - Wisconsin Public Museum specimens.

LOCALITY ABBREVIATIONS

BB - Bridger Basin

BI - Big Island-Blue Rim

BRW - Bridger West Collection

SP - South Pass

PR - Pinnacle Rocks

LA - Little America

Foster Reservoir - (UM103927)

Q - (UM103690)

INSTITUTIONAL ABBREVIATIONS

AMNH = American Museum of Natural History, New York

ANSP = Academy of Natural Sciences, Philadelphia

CM = Carnegie Museum, Pittsburg

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge

MSU & MSUH = Michigan State University, Vertebrate Paleontology Collection, East Lansing

NMNS = National Museum of Canada

PU = Princeton University Museum

SMNH = Saskatchewan Museum of Natural History, Regina

UA = University of Alberta, Department of Geology, Edmonton

UCMP = University of California, Museum of Paleontology, Berkeley

UM = University of Michigan, Ann Arbor

USNM = Museum of Natural History, Smithsonian Institution, Washington (D.C.)

WPM = Wisconsin Public Museum, Milwaukee

YPM & PMNH = Peabody Museum of Natural History, Yale University, New Haven

INTRODUCTION

The middle Eocene Wasatch and Bridger formations of Wyoming have yielded abundant remains of fossil amphibians, turtles, lizards, snakes, crocodilians and mammals for over one hundred years. The mammals and large reptiles have been well studied by several workers (Gazin, 1952; 1976; Gunnell and Bartels, 1994), but the amphibians and smaller reptiles have been largely overlooked. Over the years, thousands of specimens of the herpetofauna have been obtained by quarrying, surface collection, and wet and dry screening, but until now, few were identified or described, and none put in a precise stratigraphic context. These groups are the only significant part of the fauna not yet analyzed and are the subject of this project.

In 1989 G. F. Gunnell (University of Michigan) began an extensive field research project in the Green River Basin to investigate the area's early Bridgerian vertebrate faunas. In 1994 localities at South Pass were first sampled as part of this current project (Plate 1). The occurrence of these deposits, in an area less well studied than the classic Bridger sections to the southwest, provided opportunities for faunal comparison between contemporaneous deposits of the basin center and basin margin areas, and between deposits of the different temporal units.

This study describes the stratigraphy, sedimentology, and the amphibian and squamate faunas of the South Pass area from the Wa7 (Lostcabinian), Br0 (Gardnerbuttean), and Br1 (Bridgerian A), in order to compare these with the better known areas to the southwest. These include the R. M. West Collection from Br2 (Bridgerian B) and the lower Br3 (Bridgerian C) in the Bridger Basin area, and the University of Michigan collection from Br1 and Br2. The stratigraphic relations between the areas of South Pass, Big Island, and the Bridger Basin are given in Figure 1. The stratigraphy and position of fossil bearing localities in the Bridger Basin are given in Figure 2. The study concludes with an examination of the paleoclimate and microhabitats of the area, and the evolutionary, zoogeographic, and ecological differences between the faunas, both horizontally within temporal zones, and vertically through the section.

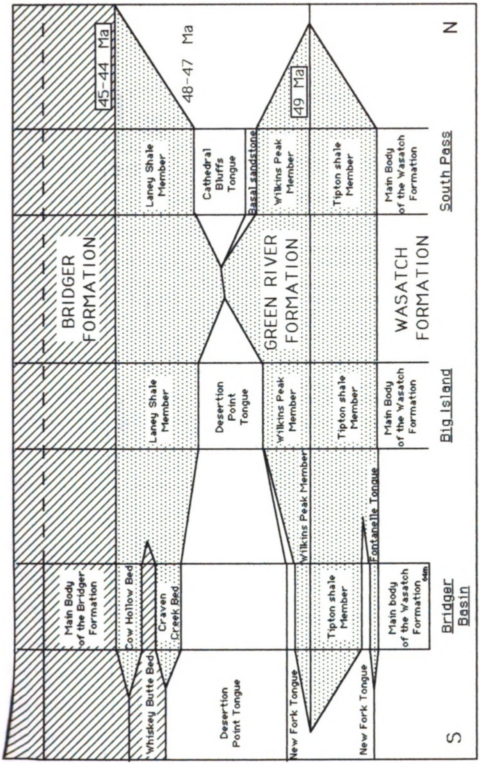

Figure 1. Generalized stratigraphic section for the Green River Basin

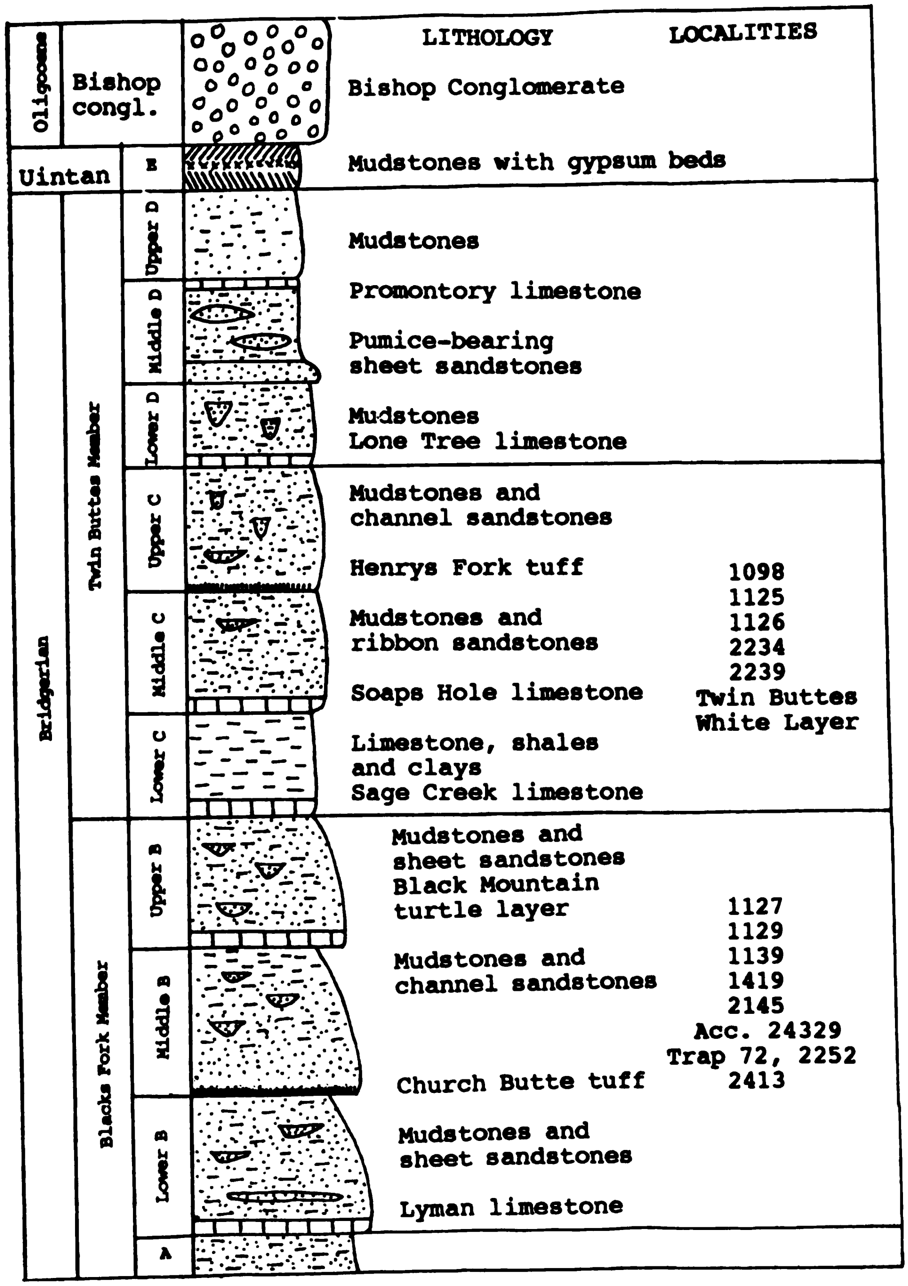

Figure 2. Stratigraphic column of the Bridger Formation in the southern Green River Basin, from Evanoff et. al. (1998).

LOCATION AND DESCRIPTION

The Green River Basin covers southwestern Wyoming. It has been defined as a structural basin, first by Engelmann (1858), and also as an area encompassing the Tertiary rocks of the area (Sears and Bradley, 1924; Osborn, 1929). Love (1961) proposed that the former be the accepted definition, and that is used here.

The principle area of this study is the South Pass region in the northern Green River Basin, about 16 km south of Atlantic City which was first extensively studied by Nace (1939), and by Zeller and Stephens (1969). The area lies at the boundary between the Green River and Great Divide basins, and has been referred to by some as the Red Desert Basin, although Love (1961) proposed that this name be abandoned.

Additional collections have been made in three areas in the Green River Basin. The Big Island area is in the center of the basin and is represented by the Br1. To the west of this is the Desertion Point-Little Muddy area which was extensively studied by Zonneveld (1994). This area includes Wa7 and Br0 localites from the basin margin and Br1 and Br2 localities from more central areas. To the south, the Bridger Basin has been collected by R. M. West, and studied recently by Evanoff et. al. (1998). Collections from all four areas have been used in the systematic paleontology section of this study. The positions of these areas are shown on Figure 3.

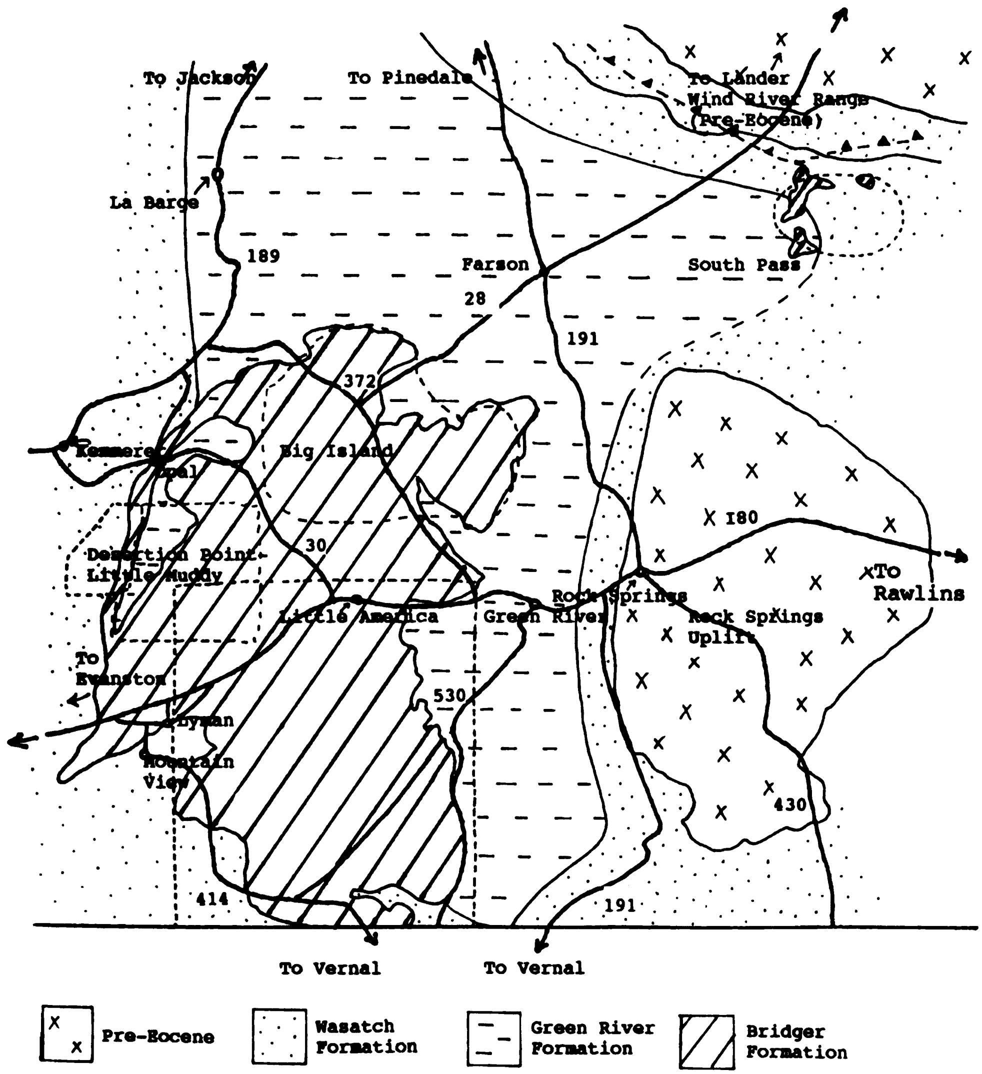

Figure 3. Map of the Green River Basin showing areas studied and lithological units.

MATERIALS AND METHODS

The fossils included in this study were collected by the University of Michigan-Albion College field parties during the summers of 1989 through 1998. All specimens reside at the University of Michigan Museum of Paleontology. Most were recovered by quarrying and surface collection, although dry and wet screening methods were also used.

The small herpetofaunal taxa were identified by comparison with existing collections, and from descriptions in the literature. The majority of the samples collected are cranial and vertebral elements, many of which are in good condition and can be identified to the generic or specific level. Modern skeletons from the Michigan State University Museum were also used for comparative study where specimens had Recent analogs.

Next, following the methods of Gingerich (1989), Gunnell et.al. (1992), and Gunnell (1994), the faunal variation was examined vertically and horizontally within the Wasatch and Bridger formations, from both lacustrine and alluvial deposits. Following this, the taphonomic grade of the assemblages was assessed with respect to breakage, abrasion, completeness, elements preserved, and general condition of the specimens, in an attempt to reconstruct the paleoenvironment and depositional characteristics of the area. In this excersize, the Wasatch and Bridger deposits of

South Pass were compared laterally, from the basin margin to those of the classic sections from the basin center. Then the Br2 deposits from the entire area were compared, vertically, through the stratigraphic column, with the more poorly drained, wetter units of the Br1 and Br3. Following this, the paleoenvironmental reconstructions based on the herpetofauna could be compared with those based on the mammal assemblages previously published by Gunnell and Bartels (1994). It is difficult to fine tune the paleoenvironment reconstruction based on amphibian and reptile species alone, because modern day analogs of early Tertiary species are not common. However, some analogues of the Bridger taxa are known to be very restricted today on the basis of climate or habitus, and may indicate the ecology and environment of that time. Although the taxa present in these deposits are often very different from their modern relatives, there are morphological analogs in modern faunas that occupy the same niches (Bartels, 1983).

I then compared my data from the South Pass area with that from the better known localities in the center of the basin, in an attempt to quantify the faunal and paleoecological similarities between zones Wa7, Br0 and Br1 in the South Pass area, and zones Wa7, Br0, Br1, Br2, and Br3 to the southwest.

PREVIOUS INVESTIGATIONS

A large amount of field research has been conducted in the Green River Basin since fossils were first discovered there in the 1850s (West, 1976; 1990). Hayden (1869; 1873) named, defined, and described the Wasatch, Green River and Bridger formations. Further work on facies and tongues of the Wasatch Formation was done by Schultz (1920), Nace (1939), Oriel (1961; 1962), Bradley (1964), Culbertson (1965), Roehler (1965; 1991; 1992a; and 1992b), Zeller and Stephens (1969), West (1969), and Sullivan (1980). The iron enrichment of the red beds was discussed by Braunagel and Stanley (1977) and paleosol formation by Rettalack (1983a; 1983b), Bown and Kraus (1987), Kraus (1987), Kraus and Bown (1993).

The Green River Formation and paleolimnology of Lake Gosiute have been studied extensively by Bradley (1959 and 1964), Bradley and Eugster (1969) and Boyer (1982) with further work done on the formation's facies, depositional environments and inter-relationships by Roehler (1965), Eugster and Surdam (1973), Surdam and Wolfbauer (1975), Lundell and Surdam (1975), Desborough (1978), Surdam and Stanley (1979; 1980), Sullivan (1980), and Roehler (1992a; 1992b).

The stratigraphic relationships in the Bridger Formation have been discussed by Matthew (1909), Osborn (1929), Koenig (1960), Oriel (1961), Bradley (1964), West (1969), McGrew and

Sullivan (1970), Gunnell and Bartels (1994), and Evanoff et. al. (1998). Descriptions of the facies have been given by Koenig (1960), Bradley (1964), Roehler (1973b), and Sullivan (1980).

Most paleontological studies have focused on the fishes of the Green River Formation and the mammals and large reptiles of the middle beds of the Bridger Formation. Work has been done on Eocene lizards by Gilmore (1928), Hecht (1956; 1959), McGrew and Sullivan (1970), Meszoely (1970), Sullivan (1979; 1986), Meszoely, Estes and Haubold (1978), Schatzinger (1980), Estes (1983), Estes and Hutchison (1980), Gauthier (1982), and West (1990). Eocene snakes have been studied by Gilmore (1938), Holman (1977; 1979), and Rage (1984). The amphibians of the Eocene have been studied by Auffenberg and Goin (1959), Hecht (1959), Estes (1965; 1969; 1981), Meszoely (1966; 1967), Naylor (1978; 1981), Henrici (1991), and Sanchiz (1998). The paleoenvironment of the area has been discussed by MacGinitie (1969), Roehler (1993), Zonneveld (1994), and Gunnell and Bartels (1994; in prep).

LITHOSTRATIGRAPHY

The Eocene sedimentary rocks of the Green River Basin are of two general origins, alluvial and lacustrine (Bradley, 1964). The mountainous source areas bounding the basin vary in lithic composition which is reflected in the nature of the alluvial Tertiary rocks derived from them. To the west, the Overthrust Belt is comprised of Paleozoic and Mesozoic marine sedimentary rocks, the Wind River Mountains to the northeast are comprised of Precambrian igneous and metamorphic rocks (West 1969), the Uinta Mountains source consists of primarily Mississippian limestones (Crews and Ethridge, 1993) and sandstones and metaquartzites (Sullivan, 1980).

The Wasatch and Bridger formations were laid down between 57.5 Ma and 48 Ma when the Laramide Orogeny caused rapid uplift, resulting in the deposition of thick, fluvial sediments in intervening basins. These formations interdigitate, with either a distinct or gradual contact, with the Green River Formation which comprises a huge lens of fine-grained, generally calcareous sedimentary rock of lacustrine origin (Bradley, 1964). The outcrop pattern of these formations is shown in Figure 3. The stratigraphic relationship between the members and tongues of the Wasatch, Green River, and Bridger formations is shown in Figure 1.

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Wasatch Formation

The Wasatch Formation was named by Hayden (1869) for exposures in Echo and Weber canyons, Utah. Hayden (1869) defined the formation as variegated red sandstones and conglomerates, and distinguished it from the thinly laminated chalky shales of the Green River Formation that, he noted, had a distinctive banding. However, the great variety of rock types comprising the Wasatch make a definition difficult, and Oriel (1961) pointed out that many rocks in this area do not fit into either of these categories, being neither red, nor exhibiting the distinctive banding. He also rejected a system used by some that defined the two formations based on their fluvial or lacustrine origins.

The Wasatch Formation in the study area is predominantly made up of mudstones, siltstones, and shales, with some sandstones and conglomerates. The most striking feature of the outcrops is their red and green variegation (Bradley, 1964). The coloration is due to the redistribution and differential concentration and hydration or dehydration of ferric iron compounds in different parts of the profile, in a dry environment where oxidation could occur (Bown and Kraus, 1987). These red beds occur in couplets with green beds which together represent a single period of deposition during flooding. The red beds resulted from syndepositional chemical and hydrological conditions in the alluvial sediments which were favorable for the formation of hematite in the clay-rich mud rock, and the removal of iron oxides from the silt-rich mud rock. The mechanism proposed was a combination of original depositional variation in the iron concentrations associated with textural differences in the floodplain deposits, and early post-depositional depletion of iron in the non-red layers with vertical migration of that iron to the red beds (Braunagel and Stanley 1977).

Oriel (1962) and Bradley (1964) applied the term "Main Body of the Wasatch Formation" to those beds underlying the Green River Formation. Oriel (1962) divided the Wasatch into five units, from oldest to youngest; the Chappo Member, the La Barge Member, which makes up the Main Body of the Wasatch Formation, the Middle Tongue (New Fork and Cathedral Bluffs tongues), Upper Tongue (renamed the Desertion Point Tongue; Sullivan, 1980), and an unnamed conglomerate which interfingers with the Green River Formation. A younger tongue, the Niland, was subsequently described by Bradley (1964), Culbertson (1965) and Roehler (1965).

Roehler (1965) recognized three main lithofacies within the Wasatch Formation. The red-bed fluviatile facies is the most common and makes up most of the Main Body of the Wasatch. It is made up of brightly colored detrital rocks with some interbedded limestones and marls. These deposits show abrupt variations and gradations in lithology and color. The coarser clastic siltstones and sandstones are typically less brightly colored and occur in thin, but extensive, sheetlike bodies. Lenticular sandstones and conglomerates are also present (Sullivan, 1980).

The red-bed facies grades mountainwards into the "pediment facies" (Sullivan, 1980) which consists of red and gray-green fanglomerate deposits with interbedded sandstones. These are conglomerate successions related to tectonic movement (Tracey et al. 1961) and contain sub-angular to rounded clasts derived from the Wind River Range (Sullivan, 1980).

The non-red fluviatile-paludal facies locally replaces the red-bed facies. It is characterized by gray and green mudstones and sandstones locally rich in carbonaceous shales and subbituminous coal deposits. These non-red deposits were laid down during more humid periods when Lake Gosiute expanded to fill a greater area within the basin (Sullivan, 1980).

The Main Body of the Wasatch Formation

The areal extent of the Main Body of the Wasatch is shown in Figure 4. The formation consists predominantly of green, red, and purple banded mudstone interbedded with claystone and marlstone, and is early Eocene in age (Sullivan, 1980). Sandstone and conglomerate beds occur low in the section and at the basin margins (Oriel, 1962; Oriel and Tracey, 1970). It was divided by Oriel (1962) into the Chappo Member, which is Clarkforkian in age, and the

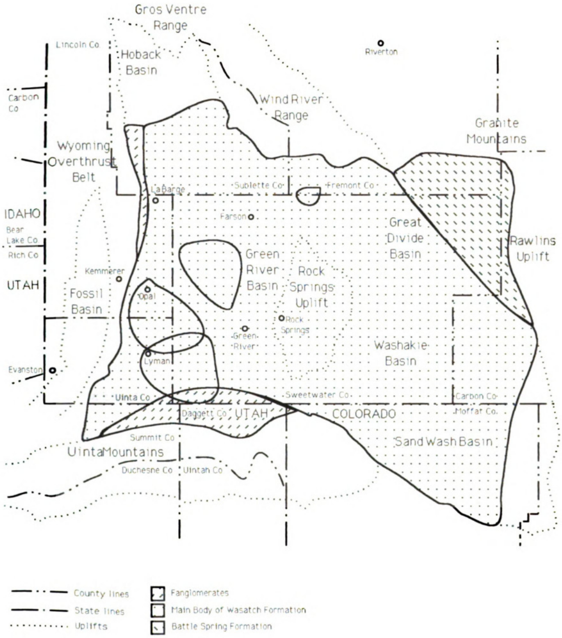

Figure 4. Areal extent of the Main Body of the Wasatch and Battle Spring formations

overlying La Barge Member which is Lostcabinian in age (Zonneveld, 1994). At the basin margins, both consist of variegated red, purple, orange, tan and gray mudstone, with interbedded sandstone and conglomerate, and are separated from one another by an angular unconformity (Oriel, 1962; Roehler, 1993). In the center of the basin the sediments are of the same lithology, but are gray and green due to being more water saturated (Roehler, 1993). The unit has an irregular thickness which increases towards the basin margins. Towards the basin center it thins and grades into the Niland, Alkali Creek, Cathedral Bluffs, and Desertion Point tongues of the Wasatch Formation (Roehler, 1992b).

The Cathedral Bluffs Tongue

The Cathedral Bluffs Tongue of the Wasatch Formation was first described and named the Cathedral Bluffs Bed by Schultz (1920). Sears and Bradley (1924) renamed the deposits the Cathedral Bluffs Tongue of the Wasatch Formation. It is exposed to the north of the Rock Springs Uplift in the Green River Basin, where it interfingers with the Wilkins Peak Member in the center of the basin (Bradley, 1964), and to the north with the Tipton Shale, Laney, and Godiva members (Roehler, 1992b) of the Green River Formation. The Cathedral Bluffs Tongue is Lostcabinian in age, and overlies the New Fork Tongue of the Wasatch Formation (Sullivan, 1980). It consists of a wedge of alluvial sediments predominantly made up of gray mudrocks banded with red, purple, and orange layers. Near the basin margin sandstones and conglomerates occur (Bradley, 1964; Roehler, 1992b).

The Desertion Point Tongue

The Desertion Point Tongue was named by Sullivan (1980) as equivalent to the Upper Tongue of the Wasatch Formation of Oriel (1961). It is Gardnerbuttean in age (Zonneveld, 1994). The unit consists of a red-bed fluviatile clastic unit cropping out along the western margin of the Green River Basin. The bed thins, and the red coloration diminishes towards the basin center. Towards the south the bed becomes thicker and coarser nearer the source in the Uinta Mountains. This tongue was deposited contemporaneously with the Cathedral Bluffs Tongue of the north and central basin (Sullivan 1980). The areal extent of the Cathedral Bluffs and Desertion Point tongues are shown in Figure 5.

The New Fork Tongue of the Wasatch Formation was first described by Donovan (1950) and then redefined by Oriel (1961). It is Lostcabinian in age, and crops out along the western margin of the Green River Basin and is contemporaneous with the Cathedral Bluffs Tongue (Sullivan, 1980). It consists of a thick wedge of alluvial sediments comprised of gray and light green sandy mudstone banded with red and purple. Greenish-gray sandstones occur as irregular beds and lenses (Bradley, 1964; Lawrence, 1965; Sullivan,

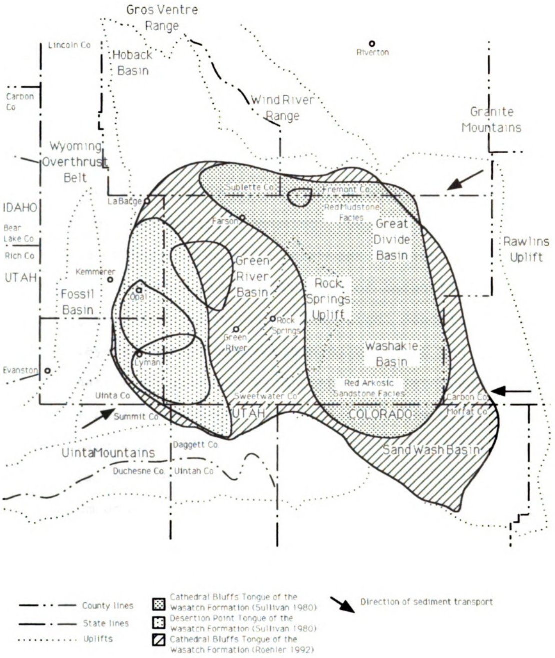

Figure 5. Areal extent of the Cathedral Bluffs and Desertion Point tongues of the Wasatch Formation according to Sullivan (1980) and Roehler (1992).

1980). It interfingers with the Tipton Shale and Wilkins Peak members of the Green River Formation (Lawrence, 1965).

Green River Formation

The Green River Formation was named by Hayden (1869) for the exposures of early to middle Eocene beds along the Green River west of Rock Springs, Wyoming. They consist of light-gray, brown or buff dolomitic marlstones, shales, oolitic limestones, mudstones and litharenites of lacustrine origin containing salt-crystal molds, bedded algal deposits, and volcanic layers. Throughout the basin, units of the Green River Formation intertongue with both the Wasatch and Bridger formations representing the continual change in areal extent of Lake Gosiute throughout the late early and early middle Eocene (Bradley, 1964).

Surdam and Wolfbauer (1975) and Surdam and Stanley (1979) recognized three major lithofacies; the carbonate facies, the laminated carbonate facies or oil shale facies, and the evaporite or trona facies. The carbonate facies consists of thinly bedded calcareous and dolomitic mudstone with stromatolitic and oolitic limestone, marlstone, siltstone, and oil shale. Desiccation features are common but fossils are rarely found. It commonly grades laterally into the laminated carbonate or oil shale facies. The oil shale is made up of alternating layers of dark, kerogen-rich and lighter, kerogen-poor carbonates. The evaporite facies consis

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consists of bedded trona deposits associated with oil shale and dolomitic mudstone. Thin clastic beds of sandstone and mudstone may be developed locally (Sullivan, 1980).

The Green River Formation can be divided into members on the basis of varying lateral extent, lithology and intertonguing relationships with the Wasatch and Bridger formations. Those units cropping out in the study areas are the Wilkins Peak Member and the Laney Shale Member which can, in some areas, be separated into the lower Craven Creek Bed and the upper Cow Hollow Bed (Sullivan, 1980).

The Tipton Shale Member

The Tipton Shale Member of the Green River Formation were first described and named by Schultz (1920). It is of Lostcabinian age (Sullivan, 1980). The Tipton Tongue crops out to the north of the Rock Springs Uplift where is interfingers with the Wasatch Formation. Along the eastern margin of the Green River Basin, contemporaneous units are named the Tipton Shale Member because it is not separated from the main body of the Green River Formation by Wasatch units (Culbertson, 1965). The Tipton Tongue is made up of tan to grayish-brown oil shale, limy sandstone, mudstone, sandstone, and algal limestone (Bradley, 1964). The lower part of the unit is named the Scheggs Bed (Roehler, 1991), and was deposited during the first major expansion of Lake Gosiute (Roehler, 1992b; Roehler, 1993). This unit is predominantly drab brown in color. The overlying Rife Bed (Roehler, 1991) is a drab gray color, and its first appearance marks the closing off of drainages leaving the Green River Basin, a major climate change, and an abrupt change in the waters of Lake Gosiute from fresh to saline (Roehler, 1993).

The Wilkins Peak Member

The Wilkins Peak Member of the Green River Formation crops out in the Green River Basin and represents a period of repeated transgressions and regressions of Lake Gosiute (Roehler, 1992b; Roehler, 1993). It is Gardnerbuttean in age (Zonneveld, 1994). Its areal extent is shown in Figure 6. The member consists of sandy, dolomitic marlstone and marly shale with abundant saline minerals and is contemporaneous with the Catherdral Bluffs and Desertion Point tongues of the Wasatch Formation (Bradley, 1964). The relationship between these units is shown in Figure 7. Marginal mud flats and playas developed during lowstands (Roehler, 1993). The Wilkins Peak Member is divided into lower, middle, and upper units that represent different paleogeographies and salinities of Lake Gosiute (Sullivan, 1980; Roehler, 1992b).

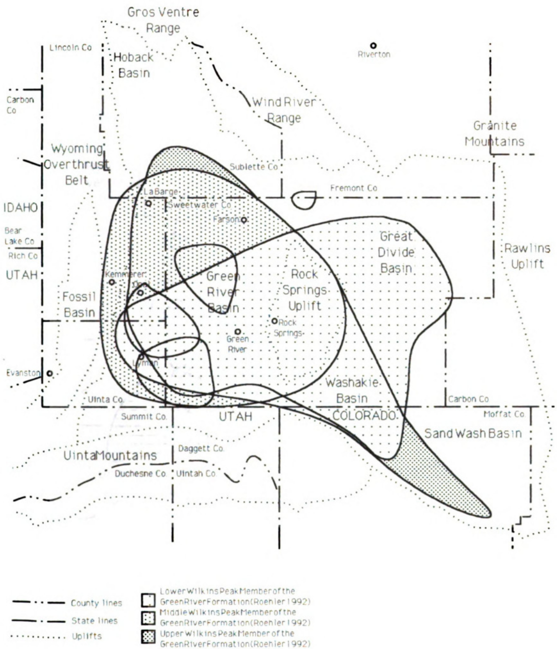

Figure 6. Areal extent of the lower, middle, and upper units of the Wilkins Peak Member of the Green River Formation.

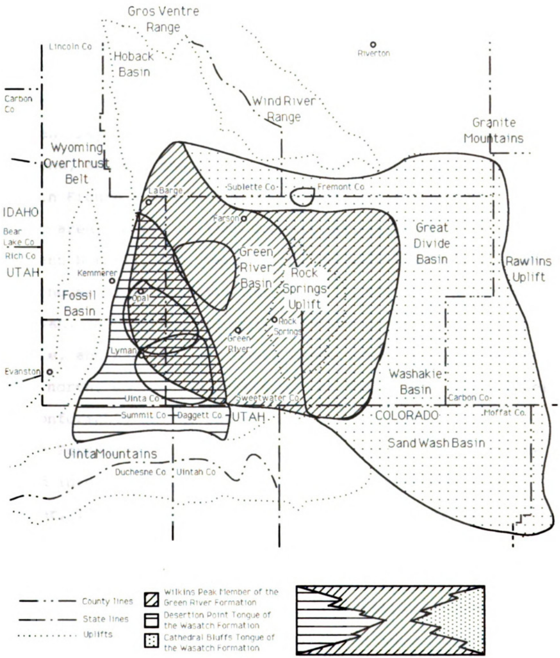

Figure 7. Areal extent and intertonguing of the Wilkins Peak Member of the Green River Formation, and the Desertion Point and Cathedral Bluffs tongues of the Wasatch Formation.

The Laney Shale Member

The Laney Shale Member of the Green River Formation was first named and described by Schultz (1920) and crops out along the eastern margin of the Green River Basin as resistant layers of tuffaceous sandstone, marlstone, muddy sandstone, and oil shale. Its areal extent and facies are shown in Figure 8 and Figure 9. The unit represents the maximum areal extent of Lake Gosiute during the Bridger A (Br1) and B (Br2), and overlies the Cathedral Bluffs and New Fork tongues of the Wasatch Formation in the north and west (Sullivan, 1980). Here the unit consists of shale and mudstone, and has little organic matter. The Laney thins out to the north, so that in some areas at South Pass the Bridger lies conformably on the Cathedral Bluffs Tongue of the Wasatch Formation (Bradley, 1964). The Laney Shale Member is divided into the LaClede, Sand Butte, and Hartt Cabin beds (Roehler, 1992a). The LaClede Bed was deposited as Lake Gosiute expanded and the lake water changed from saline to fresh as an outlet for the lake developed. The LaClede Bed marks the longest period of sustained lacustrine deposition of Lake Gosiute (Roehler, 1992b). The overlying Sand Butte Bed was layed down during a period of increased volcanic activity and climatic cooling. As a result, Lake Gosiute retreated southward, with periodic expansions northward and eastward. The top of the Laney Shale Member, the Hartt Cabin Bed was layed down during the final contraction of Lake

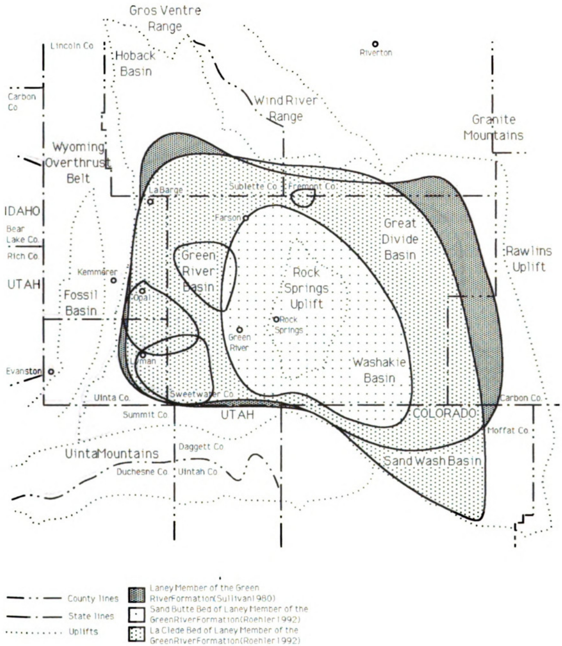

Figure 8. Areal extent of the Laney Shale Member of the Green River Formation according to Sullivan (1980), and the Sand Butte and LaClede beds of the Laney Shale Member according to Roehler (1992).

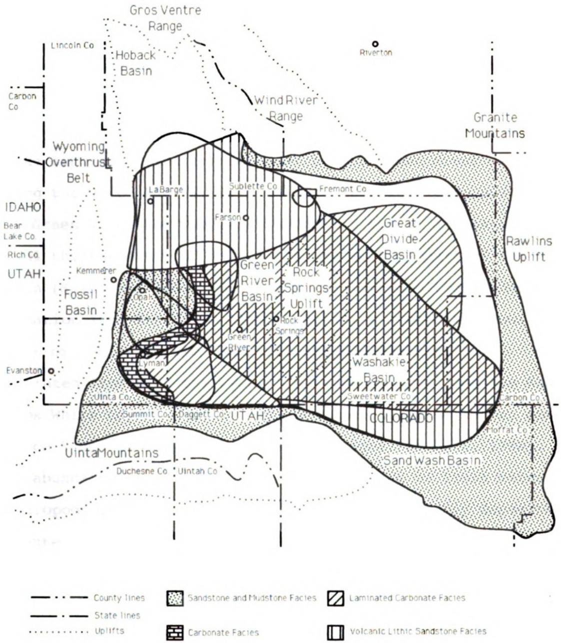

Figure 9. Areal extent of the facies of the Laney Shale Member of the Green River Formation

Gosiute during the late middle Eocene (Roehler, 1993).

Bridger Formation

The Bridger Formation was named by Hayden (1873) for the rocks exposed in the central part of the Green River Basin along the Union Pacific Railroad. It occupies large areas of the Green River and Washakie basins and has an estimated total thickness of 650 m in the south central part of the basin (Sullivan, 1980). Matthew (1909) divided the Bridger Formation into Bridger A through E, using nine calcareous tuffs or 'white layers' as stratigraphic markers. A is separated from B by the Lyman Limestone, B from C by the Sage Creek White Layer, C from D by the Lonetree White Layer, and D from E by the "upper limestones" (Evanoff et. al., 1998). The abundance of carbonates and the presence of fresh water gastropods indicate that these layers were probably deposited in extensive, but shallow, lakes (Bradley, 1964).

Wood (1934) grouped the Bridger A and B naming the unit the Blacks Fork Member, and grouped the Bridger C and D naming that unit the Twin Buttes Member. The Sage Creek White Layer separates these members and consists of two beds, a white, hard, platy marlstone and a light-brown, hard, platy marlstone. It is extensive in the southern Green River Basin but loses its white coloration to the east. Evanoff et. al. (1998) described and measured stratigraphic sections from the Bridger Basin where the material used in this study was collected. They re-examined the marker beds used by Matthew (1909) and proposed the name Turtle Bluff Member for the Bridger E.

Since its original definition Koenig (1960) has included strata from northeastern Utah and northwestern Colorado in the Bridger, and divided the formation into lower, middle, and upper based on lithologic variation. The areal extent of the lower, middle, and upper Bridger are shown in Figure 10 and Figure 11. Roehler (1973) re-established the term Washakie Formation for those beds in the Washakie Basin which are of approximately the same age, but differ in color, detailed lithology and stratigraphic relationships from the rocks of the Bridger Formation.

The Bridger Formation is predominantly made up of shallow lake, lake margin and fluvial deposits and represents a moist, closed forest environment which developed on the margins of Lake Gosiute and thus generally lacks the red beds seen in the Wasatch Formation (Roehler, 1992a). It resembles the Wasatch Formation except in having fewer red beds and more volcanic ash (Sullivan, 1980). The formation intertongues with, and overlies, the Green River Formation but for the most part the position of the base of the Bridger is uncertain as it grades downwards and laterally into this lacustrine unit. The Bridger is at its thickest in the southern Green River Basin, near Twin Buttes, where it reaches 750 m; at South Pass the formation is only about 155 m. The oldest beds are exposed around the margins of the

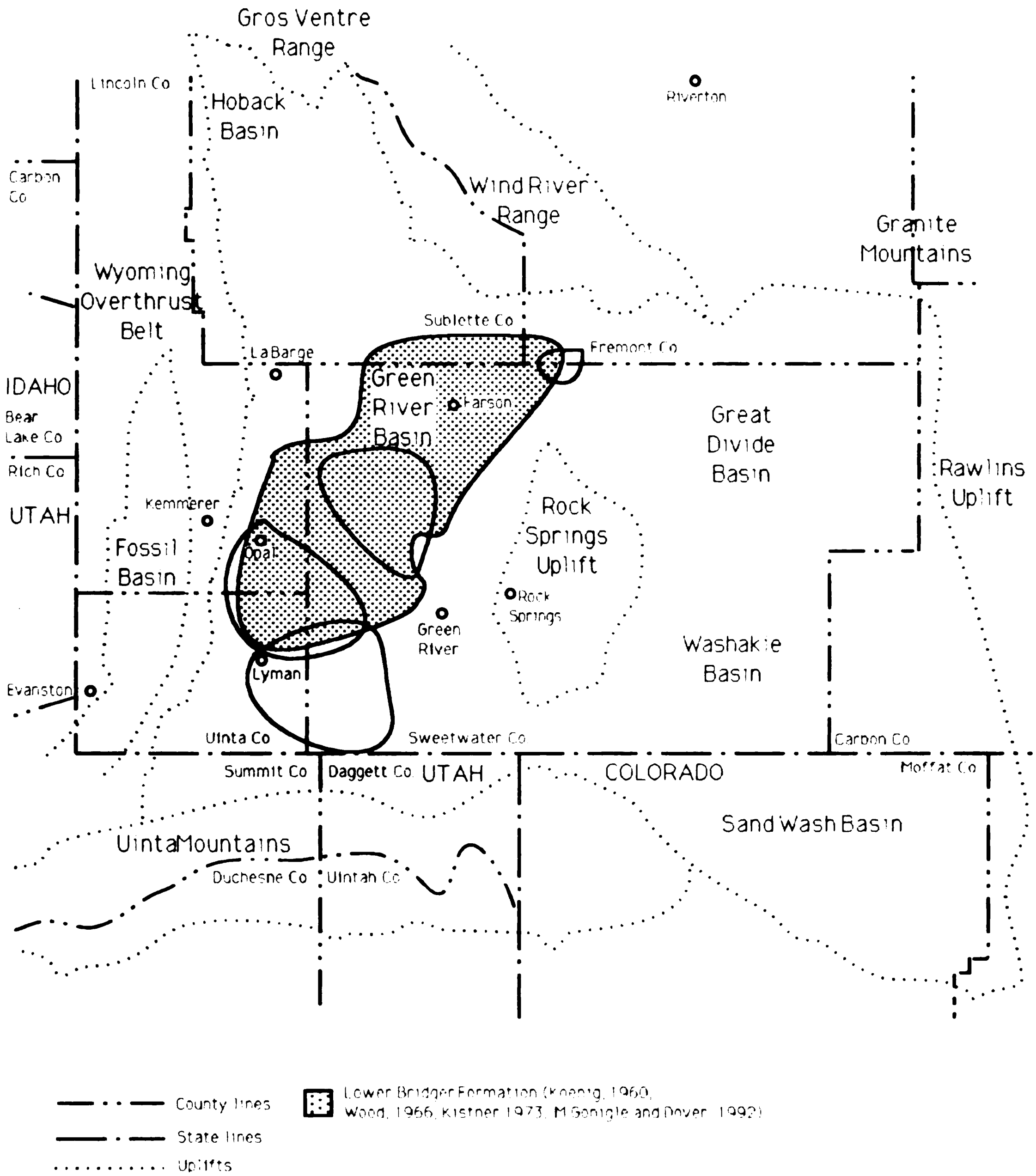

Figure 10. Areal extent of the lower Bridger Formation

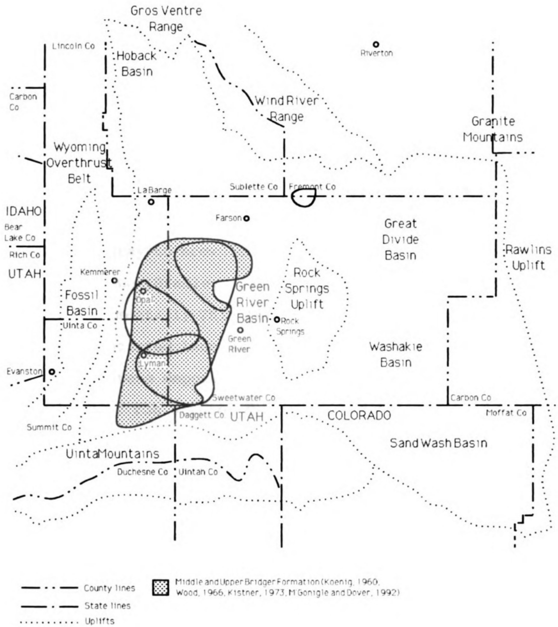

Figure 11. Areal extent of the middle and upper Bridger Formation

formation's outcrop with successively younger beds exposed in a series of terraces in the southern part of the basin. In the north, these younger beds were either never deposited, or were subsequently removed (Koenig, 1960).

The Bridger consists of sandy tuffaceous mudstone ranging in color from light gray to dark green to grayish brown, though local pink and dull red banding occurs. Interbedded with the mudstones are beds and lenses of crossbedded gray to brownish-gray medium-grained tuffaceous muddy sandstone (Bradley, 1964). Koenig (1960) described six types of sediment: 1) Thin fresh-water tuffaceous limestone, marl and associated lacustrine sandstone and shale. 2) Channel sandstone deposits. 3) Flood plain deposits, making up the bulk of the Bridger Formation. 4) Deltaic and lacustrine sandstones and siltstones. 5) Lignitic and coaly deposits and 6) volcanic material. Near uplifts, the Bridger becomes coarse grained and locally conglomeratic. The conglomerates to the south contain clasts of Mississippian limestone (Crews and Ethridge, 1993), quartzites and metaquartzites (Sullivan, 1980) from the Uinta Mountains. To the north, clasts of hornblende schist and granite were derived from the Wind River Mountains (Stiedtmann et. al., 1983). Volcanic ash beds are common and most beds of the Bridger are tuffaceous with some clastic content. Thin limestone and marlstone layers form conspicuous benches while carbonaceous sandstones, shales, and clays are rare (Bradley 1964). Koenig (1960) proposed a volcanic source for virtually all the Bridger Formation sediments, except the calcareous layers, due to the absence of recognizable detrital material and the remarkable similarity in mineral composition exhibited by the Bridger deposits.

The ash layers were most likely derived from the Absaroka Range to the north, and are made up of andesitic and rhyolitic tuffs occuring in irregular beds and lenses that exhibit cross bedding and lenticularity suggesting reworking by streams. Postdepositional alteration sometimes gives these rocks a vivid coloration, particularly bluish-gray and deep green. However, typically they weather to a pale greenish-gray color. The large areal extent and lack of reworking of the ash deposits suggests that the ash falls choked the drainage channels and caused the overloaded streams to meander widely until former stream gradients were re-established. Some deposits, however, show more reworking and a greater admixture of clastic material (Bradley, 1964).

The Whiskey Butte Bed

The Whiskey Butte Bed was named by Sullivan (1980) for the lower Bridger sediments from the western margin of the Green River Basin previously termed the Lower Bridger (McGrew and Sullivan, 1970; Kistner, 1973). It is a fluviatile unit at the base of the Bridger that merges with the Laney Shale Member of the Green River Formation to the south. The unit is comprised of light gray or green siltstone, mudstone, and claystone, with coarser beds becoming increasingly important higher in the section. Volcanics from the Absaroka Range provide much of the sediment that has subsequently been reworked by streams and highly weathered (Sullivan, 1980). Thin marlstones and limestones occur that originated along the margins of a playa lake (Wolfbauer and Surdam, 1974). Fine to coarse grained, poorly sorted, volcanic lithic sandstones occur as sheetlike bodies interbedded with conglomerates (Sullivan, 1980). The Whiskey Butte Bed represents a regression of Lake Gosiute, and corresponds to the Bridger A of Matthew (1909), and an age of Br1 (Gunnell and Bartels, 1994).

The Main Body of the Bridger Formation

At South Pass, the Main Body of the Bridger Formation overlies the Laney Shale Member of the Green River Formation, and consists of gray and green mudstone, sandstones, and algal limestones. This unit is also Br1 in age (Bartels, pers. com.).

In the Bridger Basin, the limestone and marlstone layers make up conspicuous and extensive white layers used to identify faunal boundaries. In an area between Opal and Hampton, Wyoming, McGrew and Sullivan (1970) lettered the white layers of the Bridger A as A through G, and the units they separate were numbered I through VIII. In this area the Bridger A is underlain in part by the Upper Tongue of the

Green River Formation, the Craven Creek Bed (Sullivan, 1980), and by the Upper Tongue of the Wasatch Formation, the Desertion Point Tongue (Oriel, 1961). It is overlain by the Bridger B. The unit can be separated into upper and lower units by a 50-foot-thick lacustrine bed which is probably a tongue of the Laney Shale Member of the Green River Formation (McGrew and Sullivan, 1970).

FOSSIL VERTEBRATE LOCALITIES

Localities at South Pass

SP1 (Br1)

Predominantly red-brown siltstone, sandstone and conglomerate. The conglomerate is clast supported and consists of sub-angular, boulder-sized quartz, metamorphic and igneous rocks from the Wind River Mountains to the north. The bed exhibits a rapid decrease in grain size upwards at the boundary with the overlying sandstone. It lacks sorting, stratification, or channel filling features. It is non-stratified, has non-erosive bases, and lacks grading. It has yielded no fossils, and no imbrication, or other fabrics, were seen. The sandstone is red-brown, coarse grained, massive, and contains sub-angular quartz, feldspar, mafics, and rock fragments. Although for the most part unfossiliferous, many vertebrate remains were found associated with one very well consolidated mudstone and sandstone layer near the center of the locality. SP1 is on the northwestern side of Continental Fault across from all other localities, thus its position in the section is unclear.

SP2 (Br0)

A sequence of variegated siltstones and mudstones.

SP3 (Br0)

A sequence of variegated siltstones and mudstones.

SP4 (Br0)

Predominantly green siltstones and sandstones with some red beds towards the base of the section. The upper green beds were unfossiliferous, while the red beds yielded few vertebrate remains.

SP5 (Br0)

A sequence of green, red, and purple siltstones and sandstones.

SP6 (Br0)

Situated in the area known as Honeycomb Buttes to the southeast of the local badlands. The locality consists of spectacularly colored siltstones and sandstones. The well developed paleosols are green, red, and purple and very fossiliferous. Towards the top of the section, turtle and crocodile remains were found, while lower down more terrestrial vertebrates were found associated with the red and purple layers. For the most part the green layers were unfossiliferous, while the darker layers yielded some associated specimens in good condition.

SP7 (Br0)

Alternating green and red beds with occasional orange horizons. These were predominantly siltstones between 10 cm and 2 m thick, dipping very slightly to the east. The most productive layers were the dark red beds near the top of the section.

SP8 (Br0)

Red and green siltstone and sandstone layers, again dipping slightly to the east. The most productive layers were again the dark red beds, but at SP8 the layers were those low in the section. This locality was very productive, perhaps due to the large number of flat areas of washout from the badlands where most fossils were found.

SP9 (Br0)

Adjacent to SP8 to the west, and exhibiting much the same lithology. Again, the lower red beds were the most productive while the higher beds yielded crocodile and turtle remains.

SP10 (Br0)

A sequence of roughly horizontal green, red, and purple weathering layers. The beds ranged from poorly sorted green, red, and brown sandstones to moderately sorted dark green siltstones. All layers were unfossiliferous except the lowest fine grained, red siltstone at the north end of the locality, which yielded some bone fragments and one marsupial tooth.

SP11 (Br0)

A series of green and red, unfossiliferous siltstones and sandstones.

SP12 (Br0)

A sequence of variegated siltstones and mudstones.

SP13 (Br0)

A sequence of variegated siltstones and mudstones.

SP14 (Br0)

A sequence of variegated siltstones and mudstones.

SP15 (Br0)

A sequence of variegated siltstones and mudstones.

SP16 (Br0)

Green, red, and brown siltstones and sandstones containing isolated pockets of fossiliferous rock. The most productive layers were the red beds, while some layers produced only turtle and crocodile remains. One such bed contained a 1.5 m thick layer of nothing but crocodile fragments, while others produced turtle and crocodile remains. These taxa also appeared in abundance in the layers where more terrestrial remains were found.

SP17 (Br0)

Adjacent to SP16 to the north, and also consists of green, red, and brown siltstones and sandstones. The crocodile and turtle rich layers are also present here, while the red beds produce the most specimens of terrestrial reptiles and mammals.

SP18 (Br0)

To the west of both SP16 and SP17, this locality exhibits the same lithologies. Again, the turtle and crocodile rich layers are found as well as the layers rich with more terrestrial vertebrate remains.

SP19 (Br0)

Predominantly red beds with some green and brown layers. The lithologies range from siltstone to sandstone and are largely unfossiliferous. Those fossils found were poorly preserved.

SP20 (Br0)

Just to the north of SP19, and seperated from it by red sand flats. SP20 had the same lithologies present as at SP19 and was similarly lacking in vertebrate remains.

SP21 (Br0)

Adjacent to SP20, along the western edge of the North Fork of Bear Creek drainage. SP21 yielded few fossils. The area consisted of green and red siltstones and sandstones.

SP22 (Br0)

Green, red, and brown mudstones, siltstones, and sandstones. The brown, fine siltstone and mudstone layers were the most fossiliferous, yielding some teeth. Other layers mostly contained crocodile and turtle remains, some of which were very complete.

SP23 (Br0)

A sequence of green, red, and brown mudstones, siltstones, and sandstones. Again, the most productive layers were the brown, fine grained siltstones and mudstones. These were very productive, yielding 26 catalogued specimens in one afternoon.

SP24 (Br0)

To the north of SP6 and consists of the same brightly colored green, red, and purple siltstones and sandstones. However, it was not as rich in vertebrate material, which again was found predominantly in the red and purple layers.

SP25 (Br0)

Predominantly red siltstones and sandstones with some green layers. Fossils mainly came out of the red beds, high in the section.

SP26 (Br0)

The locality is a large drainage flanked by green and red siltstones and sandstones. This locality was very fossiliferous, with most remains being found in pockets in siltstone layers or on green siltstone flats. Further north into the valley, fossils finds diminished as we reached the top of the section.

SP27 (Br0)

To the north of locality SP18. It consists of green and red siltstone and sandstone. Vertebrate remains were mainly found in isolated pockets within the red beds.

SP28 (Br0)

North of Continental Peak, the locality consists mainly of green siltstones and sandstones, with few thin red beds. Occasional, thin conglomerates with subrounded pebbles of quatrz, metamorphic and igneous rocks from the Wind River Mountains occur. Some mammal remains were found in the finer grained beds, but the most common fossils were lizards weathering out of the green "popcorn" layers of siltstone, and accumulating at the base of the cliffs. Much of the area was covered with well rounded cobbles of metamorphic and igneous rocks, presumably washed in from the Wind River Mountains by glacial rivers during the Pleistocene.

SP29 (Br0)

A sequence of green and red siltstones and sandstones. Largely unfossiliferous, though with some small concentrations of fragmentary vertebrate remains.

SP30 (Br0)

A sequence of variegated siltstones and mudstones.

SP31 (Br0)

Forming part of the eastern side of the North Fork of Bear Creek, the sediments at SP31 are green and red siltstone and sandstone. Few fossils were found.

SP32 (Br0)

A sequence of variegated siltstones and mudstones.

SP33 (Br0)

A sequence of variegated siltstones and mudstones.

SP34 (Br0)

A sequence of variegated siltstones and mudstones.

SP35 (Br0)

A sequence of variegated siltstones and mudstones.

SP36 (Br0)

This locality occurs towards the head of the North Fork of Bear Creek, and consists of green and red-orange siltstone and sandstone. Here, the fossiliferous zones were small green pockets within the red-orange layers. These appeared to be produced by diagenetic alteration of the red-orange layers, perhaps associated with the fossil material's presence as the pockets were sporadic and generally occurred near the top of beds.

SP37 (Br0)

To the northwest of SP36, also consisting of green and red-orange siltstones and sandstone. Again, fossils were found in green pockets in the red-orange layers.

SP38 (Br0)

To the west of SP36, this is a large locality of green and red-orange siltstones and sandstones. Small vertebrate remains were again associated with the small green pockets, while larger remains came out of the red-orange layers. There are three distinct horizons containing massive amounts of crocodile and turtle remains. These occur near the base of the section, approximately at the middle of the section, and also near the top. Only turtle and crocodile fragments are found here, some of which are complete. The layers are laterally continuous and cover an area of about a mile in an east-west direction, and extend northward up the drainages at the edge of the locality.

SP39 (Br0)

This locality is higher in the section and north of SP38. The locality consists of green and orange-red siltstone and sandstone.

SP40 (Br0)

A sequence of variegated siltstones and mudstones.

SP41 (Br0)

South of SP38 and consisting of a series of green and red siltstones and sandstones.

SP42 (Br0)

A sequence of variegated siltstones and mudstones.

SP43 (Br0)

A sequence of variegated siltstones and mudstones.

SP44 (Br0)

A sequence of variegated siltstones and mudstones.

SP45 (Br0)

A sequence of variegated siltstones and mudstones.

SP46 (Br0)

This locality is described in detail in the stratigraphy section.

SP47 (Br0)

The locality consists of red beds at the base of a northeast trending bluff. Some fossils were found at the base of the bluffs.

SP48 (Br0)

This locality is above SP47 and consists of gray beds above the red sequence of SP47. Fossils were recovered from the lowest resistant ledge.

SP49 (Br0)

Consists of a series of red beds at the base of a southeast facing bluff. There are more orange and purple layers than were seen at SP47. Fossils were found in the gray beds near the base of the section.

SP50 (Br0)

A series of gray beds above SP47.

SP51 (Br0)

A series of low, north facing exposures of siltstones and mudstones.

SP52 (Br0)

Consists of a group of east facing exposures consisting of siltstones and mudstones.

SP53 (Br0)

The locality comprises a ridge of siltstones and mudstones.

SP54 (Br0)

Consists of siltstones and mudstones forming a group of low hills along the drainage of Bear Creek.

SP55 (Br0)

Consists of a series of low beds at the head of the valley northeast of SP26.

SP56 (Br0)

Consists of a sequence of siltstones and mudstones.

SP57 (Br0)

Just east of SP56, in a southeast opening valley. Bright orange, fossiliferous siltstones occur as series of low exposures.

SP58 (Br0)

Consists of a small, white, sandy exposure which yielded few fossils

SP59 (Br0)

Made up of two isolated hills which are poorly exposed.

SP60 (Br0)

Consists of a series of variegated siltstones and mudstones forming a south facing bluff.

SP61 (Br0)

A series of siltstones and mudstones making up a west facing exposure.

SP62 (Br0)

Forms the flanks of the valley where SP61 is found. It consists of a sequence of siltstones and mudstones.

SP63 (Br0)

Consists of siltstones and mudstones forming isolated hills in the valley just north of SP26.

SP64 (Br0)

Consists of a series of siltstones and mudstones making up a low, south facing exposure north of SP63

SP65 (BrO)

Due south of SP63, lying along the southern flank of the same valley. It consists of siltstones and mudstones forming a series of low exposures around a prominent north pointing bluff.

SP66 (BrO)

Due west of SP46 and consists of predominantly gray-green siltstones and mudstones making up exposures along the base of a series of bluffs.

SP67 (BrO)

Southwest of SP46 and consists of predominantly gray-green siltstones and sandstones making up a group of low hills and exposures.

SP68 (BrO)

Consists of siltstones and mudstones making up a series of north facing exposures along a ridge in the center of a valley.

SP69 (BrO)

Consists of siltstones and mudstones forming a ridge.

SP70 (BrO)

Makes up a prominent ridge west of SP65. It consists of siltstones and mudstones forming a north facing exposure.

SP71 (Br0)

Is made up of a series of exposures above SP5. It consists of siltstones and mudstones forming a large, east facing bluff.

SP72 (Br0)

North of SP61 and consists of siltstones and mudstones forming a series of low exposures around the base of the valley.

SP73 (Br0)

Consists of siltstones and mudstones forming a series of south facing low exposures.

SP74 (Wa7)

Consists of a series of low exposures of siltstones and sandstones at the base of a north-south trending ridge. The fossiliferous horizon is a yellowish channel lag sandstone.

SP75 (Wa7)

Made up of a small exposure at the base of a yellowish channel lag sandstone.

SP76 (Br0)

Not very fossiliferous. It consists of siltstones and mudstones forming a series of low exposures in a narrow valley.

SP77 (Br0)

North of SP76, and consists of siltstones and mudstones forming an east-west trending ridge running across the same narrow valley.

SP78 (Br0)

This locality is described in detail in the stratigraphy section.

SP79 (Br0)

This locality is described in detail in the stratigraphy section.

SP80 (Br0)

Situated between SP6 and SP57 in a small south facing valley. It consists of a sequence of siltstones and mudstones.

SP81 (Br0)

Consists of a series of siltstones and mudstones making up a group of high exposures above SP41.

SP82 (Br0)

Consists of a sequence of siltstones and mudstones.

SP83 (Br0)

Made up of a sequence of siltstones and mudstones.

SP84 (Br0)

Consists of a series of siltstones and mudstones forming the wall of a south facing "amphitheater" east of SP64 and northwest of SP42.

SP85 (Br0)

Lies along the east side of the North Fork of Bear Creek valley. It consists of a series of siltstones and mudstones forming a group of low exposures.

SP86 (Br0)

A low, isolated butte made up of gray-green siltstones and mudstones. Only lizard osteoderms were recovered.

SP87 (Br0)

Consists of an isolated butte made up of siltstones and sandstones that were relatively unfossiliferous.

SP88 (Br0)

Made up of a series of siltstones and mudstones forming the walls of a long, south facing valley to the east of SP87. A small number of isolated teeth were recovered.

SP89 (Br0)

Consists of the upper green beds at SP79 that were generally unfossiliferous. In discussions of SP79, only the "Flats" area belong to SP89.

SP90 (Br0)

Consists of a series of siltstones and mudstones on the east side of Continental Peak.

SP91 (Br0)

Made up of a series of siltstones and mudstones making up Five Fingers Butte.

SP92 (Br0)

Consists of a series of gray siltstones and mudstones on either side of the North Fork of Bear Creek.

SP93 (Br0)

Consists of a series of variegated siltstones and mudstones just above the Tipton Tongue of the Green River Formation, which contains abundant stromatolites.

SP94 (Br0)

Consists of a sequence of siltstones and mudstones making up a series of low exposures on the west side of Continental Peak.

SP95 (Br0)

Made up of a series of siltstones and mudstones forming a group of low, west facing exposures on the west side of Continental Peak above SP90.

SP96 (Br0)

Consists of a series of siltstones and mudstones above SP95 at Continental Peak.

SP97 (Br0)

Made up of a series of siltstones and mudstones above SP96 at Continental Peak.

SP98 (Br0)

Consists of a series of gray siltstones and mudstones forming a low exposure southwest of SP78 in a broad valley along Red Creek.

SP99 (Br0)

Consists of a series of mottled paleosols forming a southeast facing exposure.

SP100 (Br0)

Consists of a sequence of siltstones and mudstones forming an isolated butte and south facing exposure in the drainage of the North Fork of Bear Creek.

SP101 (Br1)

Made up of a series of deposits on the northwest side of Continental Peak.

SP102 (Brl)

Made up of a series of exposures on the northwest side of Continental Peak below SP101.

SP103 (Br0)

In a deeply incised valley north of SP87, and consisting of a series of siltstones and mudstones.

SP104 (Brl)

Consists of a series of exposures on the northeast side of Continental Peak.

SP105 (Br0)

Consists of a sequence of siltstones and mudstones forming an east-west trending ridge and isolated north-south trending ridge south of SP5.

SP106 (Br0)

Consists of a series of deposits near the base of the northern side of Continental Peak.

SP107 (Br0)

Made up of a series of deposits west of SP52.

SP108 (Br0)

Consists of a series of deposits west of SP107

SP109 (Br0)

Consists of a series of gray-green siltstones and mudstones forming a low exposure in a small drainage.

SP110 (Br0)

Made up of a red and green mottled bed near the base of two east facing valleys in the northeast part of the North Fork of Bear Creek.

SP111 (Br0)

A series of deposits on the west side of Continental Peak just below the summit.

SP112 (Br0)

A series of deposits on the west side of Continental Peak just below the summit.

SP113 (Br0)

Consists of a sequence of siltstones and mudstones forming a series of south facing exposures and an isolated butte northwest of SP5.

SP114 (Br1)

Consists of a sequence of deposits on the northeast side of Continental Peak.

SP115 (Br0)

Made up of a sequence of siltstones and mudstones.

SP116 (Br0)

Consists of a sequence of siltstones and mudstones.

SP117 (Br1)

Consists of a sequence of deposits at the base of the east side of Continental Peak.

SP118 (Br1)

Consists of a sequence of deposits at Continental Peak.

Localities at Big Island

BI15 (Br1)

BI20 (Br1)

BI26 (Br1)

BI38 (Br1)

BI40 (Br1)

Localities at Desertion Point-Little Muddy

BB7 (Br1)

BB56 (Br2)

BB83 (Br2)

BB91 (Br2)

Localities at Bridger Basin

1419 (Br2)

1098 (Br3)

1125 (Br3)

1126 (Br3)

1127 (Br2)

1129 (Br2)

1139 (Br2)

2145 (Br2)

2234

2239 (Br3)

2406 (Br3)

2413

2827 (Br3)

Accumulation 24329 (Br2)

Trap 72, 2522 (Br2)

Twin Buttes White Layer

FAUNAL LIST

Kingdom Animalia

Phylum Chordata

Class Amphibia

Infraclass Lissamphibia

Order Caudata

Suborder Cryptobranchoidea

Family Cryptobranchidae

Cryptobranchus saskatchewanensis

Suborder Proteoidea

Family Proteidae

Necturus krausei

Suborder Ambystomatoidea

Family Scapherpetontidae

Scapherpeton tectum

Piceoerpeton willwoodense

Superorder Salentia

Order Anura

Suborder Mesobatrachia

Superfamily Pipoidea

Family Rhinophrynidae

Rhinophrynidae indeterminate

Class Reptilia

Order Squamata

Suborder Lacertilia

Infraorder Iguania

Family Iguanidae

Parasauromalus olseni

Family Agamidae

Tinosaurus stenodon

Tinosaurus pristinus

Infraorder Scincomorpha

Superfamily Cordyloidea

Family Xantusiidae

Palaeoxantusia fera

Palaeoxantusia borealis

Infraorder Anguimorpha

Superfamily Anguioidea

Family Xenosauridae

Subfamily Xenosaurinae

Restes rugosus

Family Anguidae

Subfamily Anguinae

Machaerosaurus torrejonensis

Subfamily Anniellinae

Apodosauriscus minutus

Subfamily Glyptosaurinae

Tribe Melanosaurini

Xestops vagans

Tribe Glyptosaurini

Glyptosaurus sylvestris

Paraglyptosaurus hillsi

Glyptosaurine "indet A"

Subfamily Diploglossinae

Eodiploglossus borealis

Superfamily Varanoidea

Family Varanidae

Saniwa ensidens

Order Amphisbaenia

Amphisbaenia indeterminate

Order Serpentes

Suborder Alethinophidia

Superfamily Anilioidea

Family Aniliidae

Coniophis indeterminate

Superfamily Booidea

Family Boidae

Subfamily Boinae

Boavus occidentalis

Subfamily Erycinae

Calamagras primus

Ogmophis indeterminate

Subfamily Tropidopheinae

Dunnophis microechinis

SYSTEMATIC PALEONTOLOGY

The following is a description and discussion of the fossils found within the South Pass thesis area (1994-1998), the Big Island-Blue Rim area (University of Michigan expeditions prior to 1994), and the southern Green River Basin (Bridger Basin collections made by R. M. West prior to 1990 and University of Michigan from 1989 to 1993). All taxa are described using examples, and genera and species are given diagnoses from the literature, where noted, and from my own observations. Described specimens are all catalogued University of Michigan (UM) specimens. Localities are given where the information was available. Measurements were made using dial calipers calibrated to 0.1 mm. The intention is to give a detailed description of taxa described elsewhere in less detail, to amend previous diagnoses where necessary, and to document the changing composition of the vertebrate community found in the Green River Basin, and specifically the South Pass area, during the middle Eocene.

The classification of the Caudata follows Estes (1981), the classification of the Anura follows Sanchiz (1998). The classification of the Lacertilia follows Estes (1983) and Sullivan (1986 and 1989). The classification of the Serpentes follows Rage (1984). The classification of the Lacertilia, particularly the Glyptosaurini, has undergone extensive revisions which are shown in Table 5 and Table 6 (page 232 and page 233). Other sources are referenced in the diagnosis, description, or discussion of individual taxa.

Class Amphibia Linnaeus, 1758

Infraclass Lissamphibia *sensu* Gadow, 1901

Order Caudata Oppel, 1811.

Suborder Cryptobranchoidea Dunn, 1926.

The cryptobranchoids include the small, Asian Hynobiidae and the large, North American Cryptobranchidae. Both groups differ from other salamanders in the retention of primitive states; the angular bone is separate, the nasals are in contact medially, an egg sac surrounds the ovum, they have external fertilization, and microchromosomes are present (Estes 1981). Dunn (1926) identified two shared derived characters; the first ceratobranchial and first epibranchial are fused, and the puboischiotibialis and pubotibialis muscles are fused.

Family Cryptobranchidae Cope, 1889.

This is a group of large salamanders and hellbenders, differing from the Hynobiidae in their incomplete metamorphosis. They lack eyelids, have a row of larval teeth paralleling the maxillary row, and lack a lacrimal and septomaxilla. There are two genera, Cryptobranchus and Andrias (Estes 1981).

Cryptobranchus Leuckart, 1821.

Type species -- Cryptobranchus alleganiensis Daudin, 1802.

Referred species -- Cryptobranchus guildayi Holman, 1977; Cryptobranchus saskatchewanensis Naylor, 1981.

Diagnosis -- This group consists of North American cryptobranchids differing from Andrias in being much smaller, in having an open gill slit, an ossified hyoid arch, second visceral arch and third visceral arch, frontals that form part of the margin of the naris, the nasals excluded from the pars facialis, a long narrow prefrontal, a greater separation between the maxilla and pterygoid, and an angle of 15 to 20 degrees between the neural spine and the centrum (Meszoely, 1966).

Age and Distribution -- Paleocene; Canada, early Eocene; Wyoming, USA, Pleistocene; Maryland, to Recent; North America.

Cryptobranchus saskatchewanensis Naylor, 1981.

Figures 12 and 13

Type specimen -- UA 14858

Type locality -- Late Paleocene, Ravenscrag Formation, southern Saskatchewan, Canada.

Previously referred specimens -- UA 14852, UA 14853 and UA 14856 (same specimen), UA 14854, UA 14855, UA 14857, UA 14859, UA 14860, UA 14861, UA 14862, UA 14863, UA 14864, UA 14866, UA 14867, UA 14869, UA 14870, UA 14871, UA 14873, UA 14874, UA 14875, UA 14897, UA 14898, and UA 14914; late Paleocene, Ravenscrag Formation, southern Saskatchewan, Canada . UM 71316; early Eocene, Willwood Formation, Wyoming.

Diagnosis -- The dental shelf below the tooth row is wide, and the dental gutter is shallow. The symphysis is approximately tripartate, with slight labial wrinkling (Naylor, 1981). *C. saskatchewanensis* differs from *C. alleganiensis* in having a deeper flange on the dentary ventral to the dental gutter, and in being of larger size; from *Andrias* in having a narrower flange in the dentary (Estes, 1981), in having a shallow medial groove in the dentary that leads to, or near, the symphysis, and the height of the pars dentalis being equal to that of the non-toothed ramus (Naylor, 1981).

Age and Distribution -- Late Paleocene; Saskatchewan, Canada, early Eocene; Wyoming, USA.

Referred specimens -- UM 105219, UM 105220, UM 105221, UM 105144, UM 105222, UM 105145, UM 105223, UM 105224, UM 105225, UM 105226, UM 105227, UM 105228, and UM 105229.

These specimens are referred to _Cryptobranchus saskatchewanensis_ on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Left maxilla. UM 105144 (Figure 12). Locality; 1129

This specimen consists of the anterior portion (2.4 mm) of a left maxilla bearing eight broken teeth. The teeth are small, closely spaced, slightly anteroposteriorly compressed, have missing tips, and pits at the center of their bases.

In lingual view, the pars palatina is at right angles to the pars dentalis, and is missing dorsally. The dental gutter is wide and shallow. Dorsal to the pars palatina, the pars facialis is vertical. A small longitudinal groove lies along the lingual side of the pars palatina. In labial view the external surface of the pars palatina is slightly pitted and bears two oval foramina. The anterior-most foramen lies mid-way down the external surface, the posterior one is dorsal to this. The anterior edge of the maxilla is irregular where the suture with the premaxilla occurs. In anterior view, this suture surface is pitted and grooved.

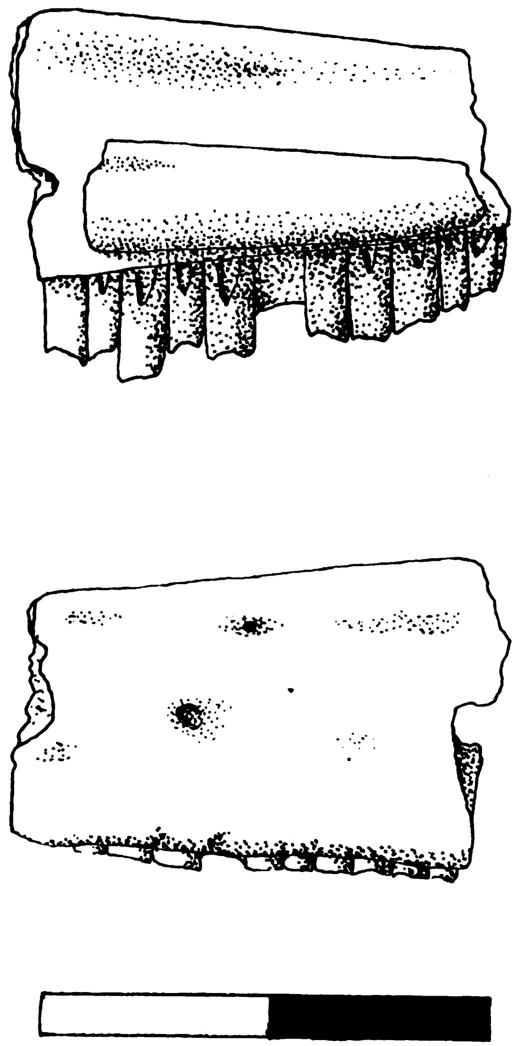

Figure 12. Cryptobranchus saskatchewanensis. UM 105144. Left maxilla, lingual and labial views. Scale bar is 2mm.

Left dentary. UM 105145 (Figure 13). Locality; 2239

This specimen is a portion (3.7 mm) of an anterior dentary with the symphysis missing. There are seven teeth, all of which are small, closely spaced, anteroposteriorly compressed, and broken below the crown. In lingual view, the subdental shelf is wide and deep, and tapers anteriorly. The dental gutter is wide and deep. A ventral flange lies ventral to the shallow, open Meckelian groove. In labial view, the external surface is slightly pitted. Mid-way down this surface is an area of small, oval foramina.

Discussion -- The type represents the earliest known cryptobranchid (Naylor, 1981). The specimens referred here to *C. saskatchewanensis* all have a combination of the following characters; many numerous teeth with anteroposteriorly compressed bases, teeth positioned so that their lingual edges lie posterior to their labial edges, a dentary with a distinct, wide, shallow gutter which bears irregularly spaced foramina, a deep pars dentalis, foramina in the external surface of the pars facialis, the pars palatina is at right angles to the pars dentalis, and the premaxilla-maxilla articulation is irregularly ridged, grooved, and pitted (Naylor, 1981). While none of these characteristics are considered diagnostic, specimens referred here closely resemble the specimens described by Naylor (1981).

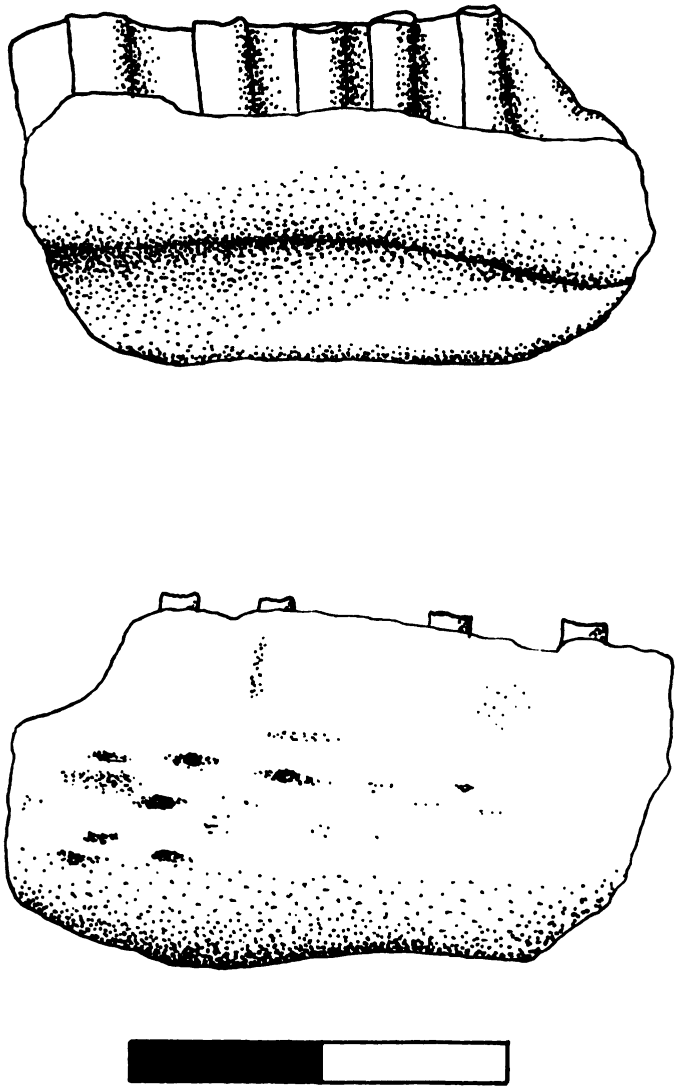

Figure 13. <u>Cryptobranchus</u> <u>saskatchewanensis</u>. Left dentary, lingual and labial views. Scale bar is 2 mm. UM 105145.

Suborder Proteoidea (Noble, 1931) emended Edwards, 1976.

This group includes the Proteida (Noble, 1931) and the Batrachosauroididae (Estes, 1969; Edwards, 1976). Estes (1981) included both groups on the basis of two characters. The first is the common presence of a columellar process of the squamosal, but Hecht and Edwards (1976) noted the presence of a columellar process in Ambystoma mexicanum, thus bringing this character into doubt. The second is heterotopic ossifications in the ligamentum squamoso-columellare, a shared derived character (Estes, 1975; Hecht and Edwards, 1976).

Family Proteidae Hogg, 1838.

This is a group of elongate, paedomorphic, perennibranchiate salamanders with the following shared derived characters; the parasphenoid nearly reaches the occipital condyle, the presence of two gill slits, the absence of ypsiloid cartilage, and a chromosome number, n=19 (Edwards, 1976). They are found in the late Paleocene to Holocene of North America, the middle Miocene to Holocene of Europe, and the Miocene of Kazakhstan (Estes, 1981).

Necturus Rafinesque, 1818.

Type species -- Necturus maculosus Rafinesque, 1818.

Referred species -- Necturus sp. Holman, 1962; Necturus krausei Naylor, 1978.

Diagnosis -- This is a group of salamanders with four toes on each foot, moderate elongation, 17 to 19 presacrals, and no maxilla. The posterior processes of the frontals are widely separated on the midline, the opisthotic is separate, and the neural spines unicipital. They have bicipital, divergent rib-bearers and functional eyes (Estes 1981).

Age and Distribution -- Paleocene; Canada, Pleistocene; Florida, to Recent; North America.

Necturus krausei Naylor, 1978.

Figure 14

Type specimen -- UA 14310

Type locality -- Late Paleocene, Estevan Coalfield, Upper Ravenscrag Formation, southern Saskatchewan, Canada.

Previously referred specimens -- UA 14311, UA 14312, UA 14313, UA 14314, and UA 14315; late Paleocene, Estevan

Coalfield, Upper Ravenscrag Formation, southern Saskatchewan, Canada.

Diagnosis -- *N. krausei* differs from the other species of *Necturus* in having more elongate neural spines, well-developed hollow dorsal rib-bearers, more anteroposteriorly-elongate posterior zygapophyses (Estes, 1981), and more elongate hyperpophyses (Naylor, 1978).

Age and Distribution -- Late Paleocene; Saskatchewan, Canada, Pleistocene; Florida, USA, Holocene; Eastern USA.

Referred specimens -- UM 105230, UM 105231, UM 105232, UM 105233, UM 105234, UM 105235, UM 105236, and UM 105146.

These specimens are referred to *Necturus krausei* on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Vertebra. UM 105146 (Fig. 14). Locality; 1129

This specimen is an almost complete trunk vertebra. Its dimensions are; length between the pre- and postzygapophyses: 4.5 mm, width of the anterior cotyle: 1.5 mm, height of the anterior cotyle: 1.1 mm. In anterior view, the cotyle is

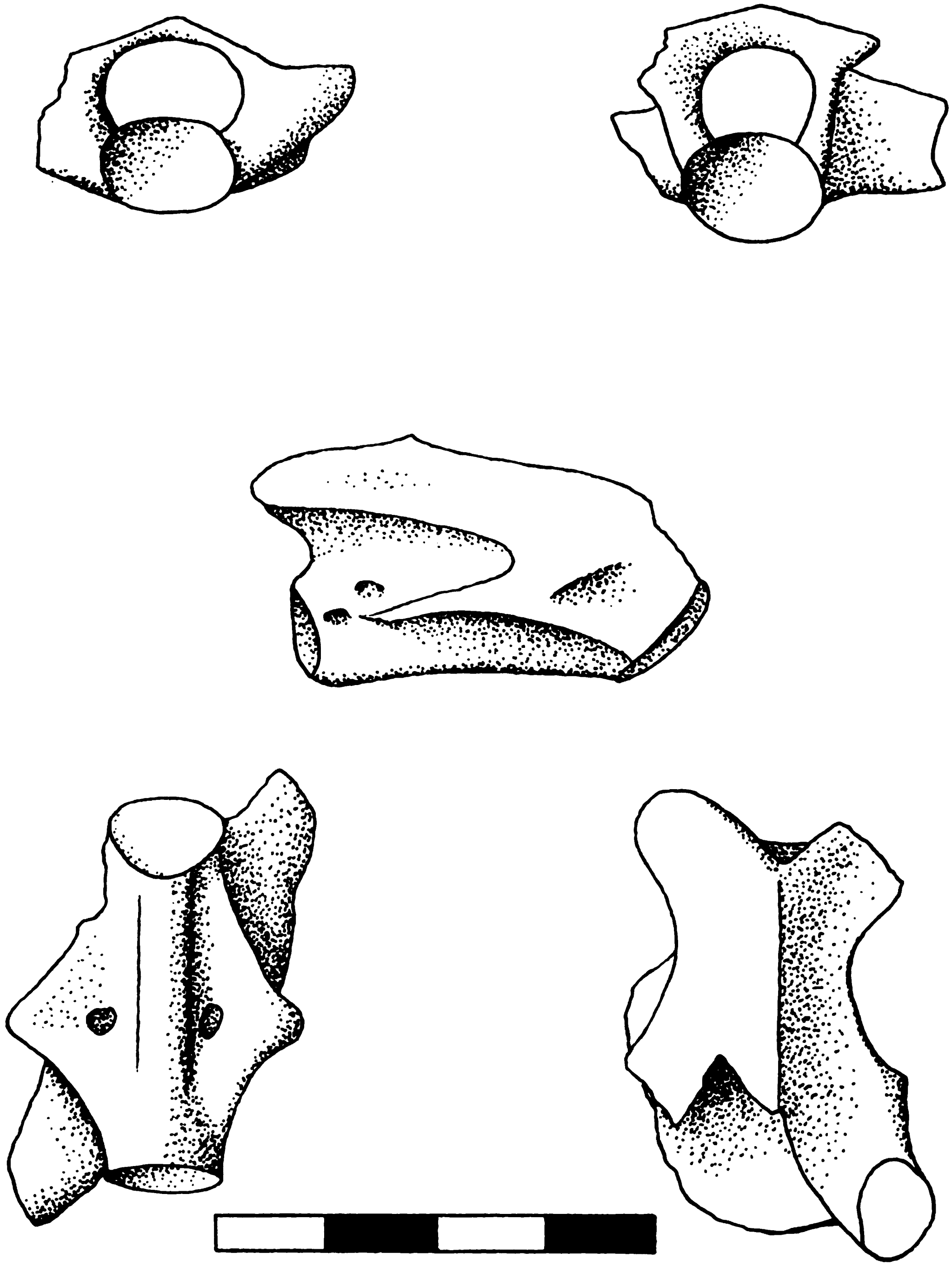

Figure 14. Necturus krausei. UM 105146. Trunk vertebra, anterior, posterior, lateral, dorsal, and ventral views. Scale bar is 4 mm.

dorsoventrally compressed with a slightly flattened dorsal edge. The one remaining prezygapophysis emerges from the lateral edge of the cotyle and projects dorsolaterally. Its articulation surface points laterally and slightly dorsally. In posterior view, the cotyle is also oval with a flattened dorsal edge. The neural canal is tripartate and high. The postzygapophysial articulation points slightly dorsally.

In ventral view, the centrum bears a blunt hemal keel and wide, flat ventral laminae which are broken before the point where the rib-bearers would have diverged. They are pierced by two large, subcentral foramina. The cotyles are slightly laterally expanded with respect to the width of the centrum. In dorsal view, the prezygapophyses would have been more divergent than the postzygapophyses. The lateral edges of the neural arch are concave. The neural spine is distinct and sharp. The prezygapophysial facet is oval, and projects anterolaterally at an angle of 30 degrees from the neural spine. In lateral view, the anterior cotyle points anteroventrally, the posterior cotyle, posteroventrally. The neural arch is low. The neural spine is low and increases in height posteriorly. The rib-bearers are missing.

Discussion -- The type and previously referred specimens represent the earliest record of the Proteidae (Naylor, 1978). The vertebrae referred here have a combination of the diagnostic characters, and characters given in the description of *N. krausei* by Naylor (1978); a low neural spine increasing in height posteriorly, well developed ventral laminae, and dorsally flattened cotyles; and Estes (1981); delicate, elongate, and amphicoelous vertebrae, subcircular cotyles, the presence of basapophyses, and bicipital rib-bearers.

Suborder Ambystomatoidea Noble, 1931.

This group includes the Dicamptodontidae, Amystomatidae, and Scapherpetontidae, all of which have caudosacral and caudal vertebrae with intervertebral exits for the spinal nerves. They have a fused angular and prearticular, elongated premaxillary spines, and anterior basapophyseal trunk musculature (Estes, 1981).

Family Scapherpetontidae Auffenberg and Goin, 1959.

This is a group of large, extinct salamanders. They have long and slender neural spines, a subcentral keel, nasals, a blunt dorsal process on the premaxilla, a reduced pars facialis on the maxilla, and a separate prearticular and articular. The vomer has an anterior row of teeth parallel with the maxillary and premaxillary teeth (Estes, 1981). Edwards (1976) placed this group within the Dicamptodontidae on the basis of the presence of spinal nerve foramina in the caudal vertebrae and their absence in the precaudal series.

Here, they are retained in their own family on the basis of the shared derived characters given by Estes (1981).

Scapherpeton Cope, 1876

Type species -- Scapherpeton tectum Cope, 1876

Referred species -- None.

Diagnosis -- This group has amphicoelous vertebrae which lack basapophyses. The skull is paedomorphic, but the maxilla is present (Estes, 1981). They have non-pedicellate teeth (Estes, 1976).

Age and Distribution -- Upper Cretaceous (Campanian) to Paleocene (Tiffanian) USA and Canada.

Scapherpeton tectum Cope, 1876

Figure 15

(Synonyms -- Scapherpeton laticolle, Scapherpeton excisum, Scapherpeton favosum, Hemitrypus jordanianus, Hedronchus sternbergi Cope, 1876)

Type specimen -- AMNH 5682

Type locality -- Upper Cretaceous, Judith River Formation, Montana, USA.

Previously referred specimens -- PU 20583 and PU 19500; late Paleocene, Fort Union Formation, Shaff Quarry, Park County, Wyoming, USA, MCZ 3673; late Cretaceous, Hell Creek Formation, McCone County, Montana, USA.

Diagnosis -- *S. tectum* differs from *Lisserpeton* in having cotylar ossification, in having less rounded cotyles, more robust ossification, small fossae on either side of the subcentral keel, a poorly-developed zygapophysial ridge, more numerous, smaller teeth, and a parietal lacking a deep, well-defined fossa for muscle attachment (Estes, 1965). The atlantes of *L. bairdi* and *Scapherpeton* are very similar, but a combination of the shorter centrum, lack of a deeply conical posterior cotyle, and the relatively short and pointed intercotylar process which is constricted at the base in *S. tectum* separate them, although overlap may occur in one or more of these characters (Estes, 1965).

Age and Distribution -- Upper Cretaceous (Campanian) to Paleocene (Tiffanian) USA and Canada.

Referred specimens -- UM 105237, UM 105238, UM 105147, UM 105239, UM 105240, UM 105241, UM 105242, UM 105243, and UM 105244.

These specimens are referred to _Scapherpeton_ _tectum_ on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Vertebra. UM 105147 (Figure 15). Locality; 2827

This specimen is an almost complete sacro-caudal or caudal vertebra. Its dimensions are; height: 4.4 mm, width at the postzygapophyses: 2.9 mm, length between the prezygapophyses and postzygapophyses: 6.1 mm, length of the centrum: 5.2 mm, width of the anterior cotyle: 3.1 mm, height of the anterior cotyle: 2.6 mm, width of the posterior cotyle: 3.5 mm, height of the posterior cotyle: 2.6 mm, greatest width of the neural canal: 1.3 mm, height of the neural canal: 0.7 mm.

In anterior view, the cotyle is subrounded and ossified. The prezygapophyses emerge from the dorsolateral edge of the cotyles and project dorsolaterally. The facets point at 45 degrees dorsolaterally. In posterior view, the cotyle is subrounded, and the neural foramen lies dorsally. The neural canal is low and wide. The postzygapophyses point at 45 degrees dorsolaterally. In ventral view, the centrum has no keel. There is a very small subcentral foramen on one side of the midline. Winglike ventral laminae project from the centrum, which are broken at their tips.

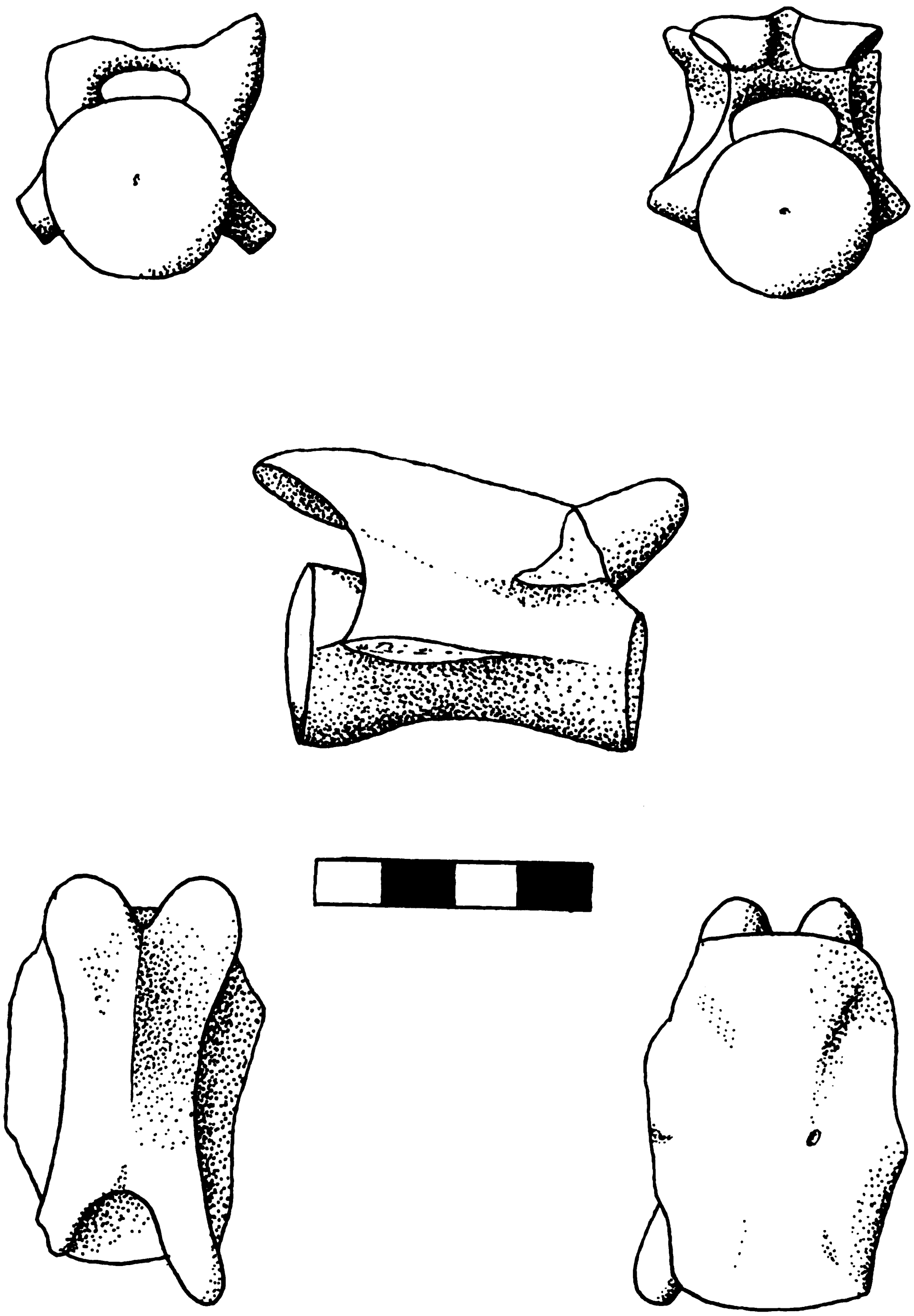

Figure 15. Scapherpeton tectum. Vertebra, anterior, posterior, lateral, dorsal, ventral views. Scale bar is 4 mm.

In dorsal view, the neural arch is narrow and elongate. It bears a short, distinct neural spine. The lateral edges of the neural arch are concave. The prezygapophyses are more divergent than the postzygapophyses, which have a long, narrow indentation between them. In lateral view, the ventral surface of the centrum is concave. The neural arch is high and the zygapophysial ridges weak. The postzygapophyses project further posteriorly than the cotyle, the prezygapophyses have their tips missing.

Discussion -- Auffenberg and Goin (1959) assigned the four species from Cope (1876) to *S. tectum*, and erected the family Scapherpetontidae. Estes (1964) assigned *Hemitrypus jordanianus* and *Hedronchus sternbergi* to *S. tectum*. The specimens from the University of Michigan represent the latest occurence of *S. tectum*.

Piceoerpeton Meszoely, 1967.

Type species -- *Piceoerpeton willwoodense* Meszoely, 1967.

Referred species -- None.

Diagnosis -- This is a group of large scapherpetontids from the late Paleocene of Saskatchewan, Montana, and Wyoming, and the early Eocene, of Wyoming and Ellesmere. They lack an intercotylar process, as do the Batrachosauroididae, but Piceoerpeton is deeply amphicoelous. They are large, and have circular cotyles, a centrum that is short relative to the diameter of the cotyles, a rounded ventral centrum surface with no keel or processes, and a large lateral fossa anterior to the base of the transverse process (Meszoely, 1967). They differ from other scapherpetontids and cryptobranchids in having a low pars facialis on the maxilla (Estes, 1980), trunk vertebrae with a robust and dorsally flattened leading edge to the neural spine, and in having a relatively much larger fossa anterior to the base of the transverse processes (Meszoely, 1967); from Scapherpeton and Lisserpeton in having more robust ossification, much more robust limbs, a rudimentary odontoid process, more rounded and less depressed anterior atlantal cotyles, interdigitating premaxillary and maxillary sutures, and a massive mandibular symphysis; from Scapherpeton in having rounded cotyles lacking calcified tissue, dorsal rib-bearers originating from the dorsolateral margin of the neural arch, and medially expanded pars palatina on the premaxilla (Estes, 1969; Naylor and Krause, 1981); and from Lisserpeton in lacking an intercotylar process (Estes, 1980).

Age and Distribution -- Late Paleocene; Montana, and Wyoming, USA, Saskatchewan and Alberta, Canada, early Eocene; Wyoming, USA and Ellesmere, Canada.

Piceoerpeton willwoodense Meszoely, 1967.

Figure 16

(*Synonym* -- *Piceoerpeton willwoodensis* Meszoely, 1967)

Type specimen -- PU 18021

Type locality -- Early Eocene, Willwood Formation, Park County, Wyoming, USA.

Previously referred specimens -- PU 16946; middle Paleocene, Highway Blowout, Tongue River Formation, Montana, USA, PU 17838a-c; early Eocene, Fossil Hollow, Polecat Bench Formation, Wyoming, USA, PU 20662, PU 20666, PU 20788, PU 20855, PU 21241a-d, UM 64569, UM 72613, UM 73660, UM 74066, and UM 74067; early Eocene, Cedar Point Quarry, Polecat Bench Formation, Wyoming, USA, UM 68429; early Eocene, Willwood Formation, Wyoming, USA, NMNS 32390, NMNS 32391, NMNS 32392, NMNS 32393, NMNS 32404, and NMNS 32405, early Eocene, Eureka Sound Formation, Ellesmere Island, Canadian Arctic Archipelago, UA 14306; Canyon Ski Quarry, Paskapoo Formation, Alberta, Canada, UA 14307, UA 14800, UA 14801, UA 14802, UA 14803, UA 14804, UA 14805, UA 14806, UA 14807, UA 14808, UA 14816, UA 14817, UA 14818, UA 14819, UA 14820, UA 14821, UA 14822, UA 14823, UA 14824, UA 14825, UA 14826, UA 148227, UA 148228, UA 14829, UA 14830, UA 14831, UA 14832, UA 14833, UA 14834, UA 14835, UA 14836,

UA 14838, UA 14839, UA 14840, UA 14841, UA 14842, UA 14843, UA 14844, UA 14845, UA 14846, UA 14847, UA 14865, UA 14872, UA 14899, UA 14900, UA 14903, and UA 14911; early Eocene, Roche Percee sites, Ravenscrag Formation, Saskatchewan, Canada.

Diagnosis -- The cotyles are dorsoventrally flattened, irregular ovals, and are deeply concave in comparison to most other salamanders (Naylor and Krause, 1981). *P. willwoodense* differs from *Batrachosauroides gotoi* in lacking opisthocoelous vertebrae, and in having the dorsal arm of the rib-bearers originate at the flattened roof of the neural arch (Estes, 1969). The dentary is massive, the Meckelian groove is narrow, and the sulcus dentalis is weak. There is a medial groove in the dentary for the coronoid (Estes and Hutchison, 1980).

Age and Distribution -- Late Paleocene; Montana, and Wyoming, USA, Saskatchewan and Alberta, Canada, early Eocene; Wyoming, USA and Ellesmere, Canada.

Referred specimens -- UM 105245, UM 105246, UM 105247, UM 105248, UM 105249, UM 105250, UM 105251, UM 105252, UM 105253, UM 105254, UM 105255, UM 105256, and UM 105148.

These specimens are referred to <u>Piceoerpeton willwoodense</u> on the basis of the possession of one or more of the above diagnostic characteristics.

<u>Description</u> --

Left dentary, coronoid and prearticular. UM 105148 (Figure 16). Locality; 1139

This specimen consists of an almost complete dentary, and partial coronoid and prearticular. The specimen is 6.3 mm long and 3.8 mm deep. It bears twelve teeth all broken below the crown. They are small, narrow, closely spaced, and slightly anteroposteriorly compressed. In lingual view, the dentary tapers anteriorly, and bears a narrow Meckelian groove. The coronoid and prearticular lie dorsal to the dentary. The coronoid is dorsal to the prearticular, and is sub-triangular and missing posteriorly. Its dorsal suture with the dentary, and ventral suture with the prearticular are approximately horizontal. The anterior end of the coronoid tapers to a point where the dentary, coronoid and prearticular meet. The prearticular is subtriangular and missing posteriorly. It fills in the posterior portion of the Meckelian groove. Its dorsal suture with the coronoid is approximately horizontal, its ventral edge slopes ventroposteriorly from its contact with the dentary. The bone tapers to a point where the three bones meet. Where it meets

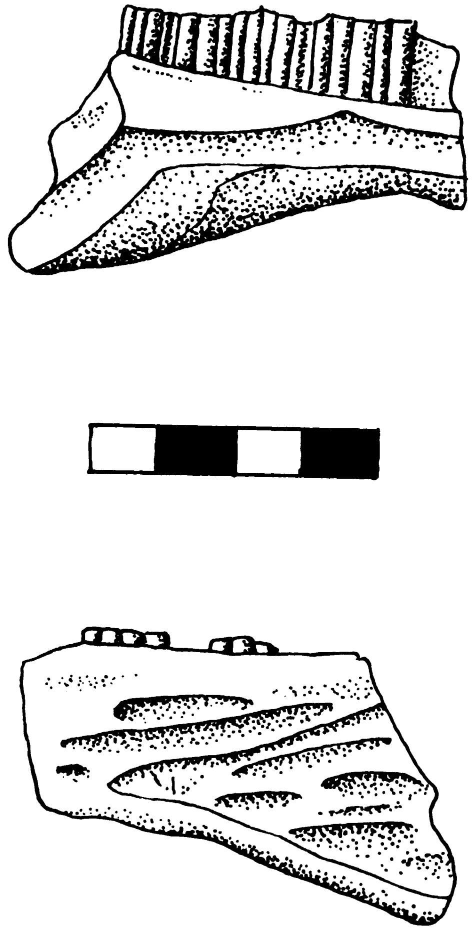

Figure 16. Piceoerpeton willwoodense. UM 105148. Left dentary, coronoid and prearticular. Scale bar is 4 mm.

the coronoid, both bones are lingually expanded.

In labial view, only the dentary is exposed. It has a sculpture pattern of deep grooves and sharp ridges except along its dorsal and ventral edge where it is smooth. In dorsal view, the labial surface is straight, and the lingual surface slightly concave.

Discussion -- The specimens agree with the characteristics given by Estes and Hutchison (1980); a massive dentary, a narrow Meckelian groove, a weak sulcus dentalis, and a medial groove for the coronoid, when that bone is not present.

Caudata indet

Reffered specimens -- UM 105257, UM 105258, UM 105259, UM 105260, UM 105261, UM 105262, UM 105263, UM 105264, UM 105265, UM 105266, UM 105267, UM 105268, UM 105269, UM 105270, UM 105271, UM 105272, UM 105273, UM 105274, UM 102361 (in part), UM 104364, UM 104710, UM 102835 (in part), and UM 103785 (in part).

Description -- These specimens are referred to the caudata on the basis of their elongate, amphicoelous vertebrae.

Superorder Salentia Laurenti, 1768

Order Anura Rafinesque, 1815

Suborder Mesobatrachia Laurent, 1979

Superfamily Pipoidea Fitzinger, 1843

The Pipoidea generally have eight opisthocoelous presacral vertebrae and lack parasphenoid alae (Trueb and Cannatella, 1982). They have moderately dilated sacral diapophyses, and the scapula is overlain by the clavical (Duellman, 1975). They have a suite of unique larval features (Trueb and Cannatella, 1982)

Family Rhinophrynidae Gunter, 1859 "1858"

This is a group of fossil and extant frogs ranging from the late Paleocene to Recent (Henrici, 1991). The only living genus and species is *Rhinophrynus dorsalis*, a burrowing, anteating frog, which lives on the coast of southern Texas to Costa Rica (Holman, 1972). They have opisthocoelous or amphicoelous, biconcave vertebrae (Kluge, 1966; Estes, 1975), and sacral vertebrae with a notch in the posterior arch (Estes, 1975) and expanded diapophyses (Henrici, 1991). The atlas has a posterior central cavity and a vertically oriented condylar facet (Hecht, 1959). The humerus is short and robust, with a large ventral crest, small medial epicondyle, raised olecranon scar flanked by shallow channels, a strongly angulated shaft, and a ridge running from the medial condyle to the prominant ventral crest (Estes, 1975).

Rhinophrynidae indet.

Figure 17

<u>Referred specimens</u> -- UM 105275, UM 105276, UM 105277, UM 105278, UM 105279, UM 105280, UM 105281, UM 105282, UM 105283, UM 105284, UM 105285, UM 105286, UM 103570, UM 103559, UM 103350, UM 102923, UM 102739, UM 103480, UM 103007, UM 102729, and UM 103317.

These specimens are referred to Rhinophrynidae indet. on the basis of the possession of one or more of the above familial, diagnostic characteristics for the humerus.

<u>Description</u> --

Distal right humerus. UM 103559 (Figure 17). Locality; SP23

This specimen is a partial humerus, 7.7 mm long. The maximum width at the distal end is 4.2 mm, the maximum diameter of the shaft is 6.2 mm. The shaft is robust and expanded dorsoventrally, with a prominent ridge running from the medial epicondyle to the ventral crest which is high and distinct. This gives the shaft a tear shaped cross-section.

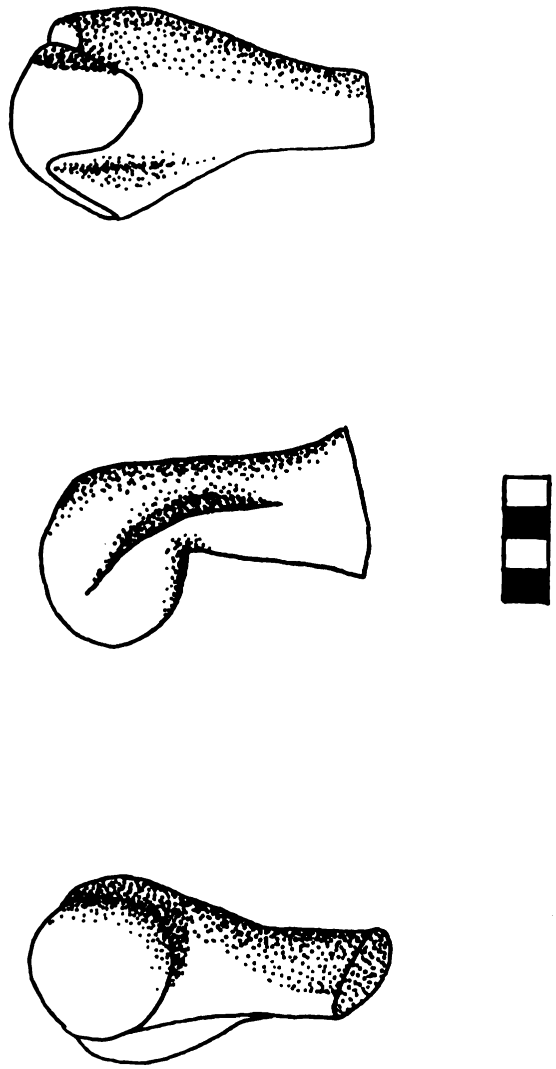

Figure 17. Rhinophrynidae indet. UM 103559. Distal right humerus. Scale bar is 4 mm.

The humeral ball is sub-round, being slightly compressed anteroposteriorly and proximal to this is a shallow ventral fossa cubiti. The lateral epicondyle is small compared with the humeral ball, the medial epicondyle is slightly smaller. In dorsal view, there is a raised olecranon scar flanked by two shallow channels lying between the scar and the lateral and medial epicondyles. In anterior view, the shaft rapidly expands dorsoventrally proximal to the humeral ball.

Discussion -- There are three fossil species of Rhinophynidae, Eorhinophrynus septentrionalis from the late Paleocene to middle Eocene of North and Central America (Hecht, 1959; Estes, 1975), Rhinophrynus candensis from the early Oligocene of Saskatchewan, Canada, and Rhinophrynus dorsalis from the very late Pleistocene of Mexico to Recent (Holman, 1975). It is likely that the University of Michigan specimens are referrable to Eorhinophrynus sp. due to their age and distribution, but they are too fragmentary to make a generic diagnosis.

Amphibia indet.

Referred specimems -- UM 105287, UM 105288, UM 105289, UM 105290, UM 105291, UM 105292, UM 105293, UM 105294, UM 105295, UM 105296, UM 105297, UM 105298, UM 105299, UM 105300, UM 105301, UM 105302, UM 105303, UM 105304, UM 105305, UM 105306, UM 105307, UM 105308, UM 105309,

UM 105310, UM 105311, UM 105312, UM 105313, UM 105314,
UM 105315, UM 105316, UM 105317, UM 105318, UM 105319,
UM 105320, UM 105321, UM 105322, UM 105323, UM 105324,
UM 105325, UM 105326, UM 105327, UM 105328, UM 105329,
UM 105330, UM 105331, UM 105332, UM 105333, UM 105334,
UM 105335, UM 105336, UM 105337, UM 105338, UM 105339,
UM 105340, UM 105341, UM 105342, UM 105343, UM 105344,
UM 105345, UM 105346, UM 105347, UM 105348, UM 105349,
UM 105350, UM 105351, UM 105352, UM 105353, UM 105354,
UM 105355, UM 105356, UM 105357, UM 105358, UM 105359,
UM 105360, UM 105361, UM 105362, UM 105363, UM 105364,
UM 105365, UM 105366, UM 105367, UM 105368, UM 105369,
UM 105370, UM 105371, UM 105372, UM 105373, UM 105374,
UM 105375, UM 105376, UM 105377, UM 105378, UM 105379,
UM 105380, UM 105381, UM 105382, UM 105383, UM 105384,
UM 105385, UM 105386, UM 105387, UM 105388, UM 105389,
UM 105390, UM 105391, UM 105392, UM 105393, UM 105394,
UM 105395, UM 105396, UM 105397, UM 105398, UM 105399,
UM 105400, UM 105401, UM 105402, UM 105403, UM 105404,
UM 105405, UM 105406, UM 105407, UM 105408, UM 105409,
UM 105410, UM 105411, UM 105412, UM 105413, UM 105414,
UM 105415, UM 105416, UM 105417, UM 105418, UM 105419,
UM 105420, UM 105421, UM 105422, UM 105423, UM 105424,
UM 105425, UM 105426, UM 105427, UM 105428, UM 105429,
UM 103785 (in part), UM 102361 (in part), UM 102835 (in part), UM 103364, UM 103439, UM 103785, UM 100398, UM 102855, UM 102704, UM 102771 and UM 103252.

Description -- The dentaries are very fragmentary and are assigned to the amphibia on the basis of their very small, very tightly packed, pedicellate teeth. The vertebrae are assigned on the basis of their amphicoelous centra. UM 105388 is a partial distal right humerus, and is similar to all other humeri in the collection. It is 4.1 mm long, has a maximum width at the distal end of 1.5 mm, and the shaft has a diameter of 0.7 mm. The shaft is slender and has a subcircular cross-section. The radial condyle is subround in ventral view. There is a prominent, oval ulnar condyle and a deep ventral fossa cubiti. There is no indication of ventral, lateral, or distal crests. The olecranon scar is oval and pronounced.

Class Reptilia Laurenti, 1768

Order Squamata Oppel, 1811

Suborder Lacertilia Owen, 1842

The Lacertilia comprise all lizards except the primitive, Mesozoic Eolacertilia, which include the paliguanids, kuehneosaurids and fulenids. The Lacertilia are more derived, particularly with respect to their modified temporal region, including the complete separation of the squamosal and paroccipital by the supratemporal, and the reduction of the dorsal squamosal process (Estes, 1983). The vertebrae are both amphicoelous and procoelous, though the primitive amphicoelous condition was probably secondarily derived (Estes 1983).

Infraorder Iguania Cuvier, 1807

The Iguania include the extant families Iguanidae, Agamidae, and Chamaeleonidae and the extinct families Euposauridae and Arretosauridae, and has been hypothesized to be the sister group of the Scleroglossa (the non-iguanian squamata) by Frost and Etheridge (1989). The Iguanidae is presently composed of the anoloids, the basiliscines, the crotaphytines, the iguanines, the morunasaurs, the oplurines, the sceloporines, and the tropidurines. Their earliest fossil record is from the Upper Cretaceous, but since scleroglossan squamates are well diversified in the Upper Jurassic, it is assumed that the iguanians were present in the Jurassic (Frost and Etheridge 1989).

Iguania is not definable by shared derived characteristics except for the position of the parietal foramen on the fronto-parietal suture and the fused frontals. However, both these conditions do appear in other lizard groups. All iguanians have a dorsal process on the squamosal (also seen in Teiidae), which is probably the primitive state (Estes 1983).

Family Iguanidae Gray, 1827

This is generally the most primitive lacertilian group. These taxa have marginal teeth which are usually homodont and either simple, triconodont or polycuspate. The vertebral number is 21-27, usually 24. A zygosphene and zygantrum may be present or absent, the caudal centra may be with or without autotomy septa.

Parasauromalus Gilmore, 1928.

Type species -- *Parasauromalus olseni* Gilmore, 1928.

Referred species -- None.

Diagnosis -- The generic diagnosis is taken from Gilmore (1928) and Estes (1983), and is unemended. The members of this taxon are Eocene iguanids having a robust mandible, compared with the other iguanians, with the Meckelian sulcus closed but not fused to the large splenial (Estes, 1983). They were first described by Gilmore (1928) on the basis of their distinctive dentary and closely-spaced, pleurodont, weakly flared teeth bearing striations at right angles to the cutting edge. The main cusp is large, blunt and spoon-shaped with the tip directed lingually. Minute lateral cusps are present on the posterior teeth, separated from the main cusp by shallow vertical grooves. These lateral cusps distinguish the genus from other iguanids. The tooth shaft is long and straight with about one third of the tooth above the parapet of the jaw. Their bases are excavated in their centers, suggesting iguanid affinities. The teeth closely resemble those of the living genus Sauromalus ater. The skull and jaw are relatively specialized in having the borders of the dentary closed but not fused anterior to the splenial, strong canthal crests, and expanded supratemporal fenestrae.

Age and Distribution -- Early to middle Eocene; Wyoming, late Eocene; California, USA.

Parasauromalus olseni Gilmore, 1928.

Figures 18, 19, 20, and 21

Type specimen -- AMNH 1620, partial right dentary with associated splenial.

Type locality -- Early Eocene, Wind River Formation, Fremont County, Wyoming.

Previously referred specimens -- PU 13457; early Eocene, Wind River Formation, Lost Cabin, Wyoming. PU 17654; early Eocene, Willwood Formation, Arminto, Wyoming. TPM 3947; early Eocene, Willwood Formation (Lysian), Bighorn Basin, Wyoming. USNM 1805; middle Eocene, Bridger Formation, Wyoming. UCMP; middle and late Eocene, Santiago, Friars and Mission Valley formations, San Diego County, California.

Diagnosis -- The teeth are closely spaced. The tooth crowns are blunt and tricuspid, bearing distinct accessory cusps. These are separated from the main cusp by two shallow, but distinct, grooves running down the anterior and posterior edges of the lingual surface of the crown. Fine striations occur on the crowns of some specimens that run at right angles to the cutting edge, over both the lingual and labial surface. A carina runs along the tip of the crown, which points slightly lingually. The closed, but unfused, Meckelian groove lies near the ventral edge of the dentary, and is covered by the splenial. This bone is flat, and bears two foramina. The lingual shelf is thick in lingual view, and thins posteriorly. There are five small mental foramina on the external surface of the dentary.

Age and Distribution -- Early to middle Eocene, Wyoming, late Eocene, California.

Referred specimens -- UM 105430, UM 105431, UM 105432, UM 105433, UM 105434, UM 105435, UM 105436, UM 105437, UM 105438, UM 105439, UM 105440, UM 105103, UM 105441, UM 105442, UM 105443, UM 105444, UM 105445, UM 105446, UM 105447, UM 105448, UM 105449, UM 105450, UM 105451, UM 105452, UM 105453, UM 105454, UM 105455, UM 105456, UM 105457, UM 105458, UM 105459, UM 105460, UM 105461, UM 105462, UM 105463, UM 105464, UM 105465, UM 105466, UM 105467, UM 105468, UM 105469, UM 105470, UM 105471, UM 105472, UM 105473, UM 105474, UM 105475, UM 105476, UM 105477, UM 105478, UM 105479, UM 105480, UM 105481, UM 105482, UM 105483, UM 105484, UM 105485, UM 105486, UM 105487, UM 105488, UM 105489, UM 105490, UM 105491, UM 105492, UM 105104, UM 105493, UM 105494, UM 105495, UM 105496, UM 105497, UM 105498, UM 105499, UM 105500, UM 105501, UM 105502, UM 105503, UM 105504, UM 105505, UM 105506, UM 105507, UM 105508, UM 105509, UM 105510, UM 105511, UM 105512, UM 105513, UM 105514, UM 105515, UM 105516, UM 105517, UM 105518, UM 105519, UM 105520, UM 105521, UM 105522, UM 105523, UM 105524, UM 105525, UM 105526, UM 105527, UM 105528, UM 105529, UM 105530, UM 105531, UM 105532, UM 105533, UM 105534, UM 105535, UM 105536, UM 105537, UM 105538, UM 105539, UM 105540, UM 105541, UM 105542, UM 105543, UM 105544, UM 105545,

UM 105546, UM 105547, UM 105548, UM 105549, UM 105550,
UM 105551, UM 105552, UM 105553, UM 105554, UM 105555,
UM 105556, UM 105557, UM 105558, UM 105559, UM 105560,
UM 105561, UM 105562, UM 105563, UM 105564, UM 105565,
UM 105566, UM 105567, UM 105568, UM 105569, UM 105570,
UM 105571, UM 105572, UM 105573, UM 105574, UM 105575,
UM 105576, UM 105577, UM 105578, UM 105579, UM 105580,
UM 105581, UM 105582, UM 105583, UM 105584, UM 105585,
UM 105586, UM 105587, UM 105588, UM 105589, UM 105590,
UM 105591, UM 105592, UM 105593, UM 105594, UM 105595,
UM 105596, UM 105597, UM 105598, UM 105599, UM 105600,
UM 105601, UM 105602, UM 105603, UM 105604, UM 105605,
UM 105606, UM 105607, UM 105608, UM 105609, UM 105610,
UM 105611, UM 105612, UM 105613, UM 101419, UM 100811,
UM 100785, UM 100535, UM 101425, UM 103369, UM 100702,
UM 101293, UM 100982, UM 101430, UM 103496, UM 101423,
UM 103302, UM 98745, UM 102461, UM 102767, UM 98746,
UM 100989, UM 103292, UM 100432, UM 100644, UM 98747,
UM 98795, UM 98748, UM 100768, UM 102835 (in part),
UM 104694, UM 104729, WPM 83, WPM 88, and WMP 197.

These specimens are referred to Parasauromalus olseni on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- There are two basic tooth types in the University of Michigan collection. These two groups were initially designated "*Parasauromalus olseni*" and "*Parasauromalus* new species" (see discussion).

UM 105430, UM 105432, UM 105439, UM 105440, UM 105103, UM 105444, UM 105446, UM 105447, UM 105453, UM 105455, UM 105456, UM 105457, UM 105458, UM 105459, UM 105472, UM 105473, UM 105474, UM 105480, UM 105482, UM 105484, UM 105485, UM 105486, UM 105487, UM 105490, UM 105104, UM 105493, UM 105496, UM 105497, UM 105499, UM 105500, UM 105501, UM 105502, UM 105504, UM 105506, UM 105507, UM 105508, UM 105511, UM 105513, UM 105514, UM 105520, UM 105523, UM 105532, UM 105533, UM 105538, UM 105546, UM 105548, UM 105574, UM 105575, UM 105576, UM 105577, UM 105578, UM 105579, UM 105580, UM 105581, UM 105582, UM 105583, UM 105584, UM 105585, UM 105586, UM 105587, UM 105588, UM 105589, UM 105590, UM 105591, UM 105592, UM 105593, UM 105594, UM 105597, UM 105598, UM 105599, UM 105600, UM 105601, UM 105602, WPM 83, WPM 88, and WPM 197 belong to "*Parasauromalus olseni*". This tooth type is most like Gilmore's original description (1928). They are closely-spaced, pleurodont, and weakly flared. They bear striations at right angles to the cutting edge on the lingual and labial sides of the crown. The main cusp is large, blunt, and spoon-shaped with the tip directed lingually. Minute lateral cusps are present on the posterior teeth, separated from the main cusp by shallow vertical grooves. Essentially, all the above specimens have the same morphology as the description by

Gilmore (1928), but only UM 105473 exhibits spoon shaped crowns with the tips pointing inwards, and most have sharp points. The groove between the main and lateral cusps is shallow but distinct, while the striations on the crown are fine and occur on both sides of the tooth. Some specimens are identical to Gilmore's description except that they have no striations (UM 105444 and UM 105457) which is most likely due to variation or, in some cases, wear (UM 105457). UM 105485 has larger lateral cusps than the type plus fewer, but more distinct, striations on the main cusp. UM 105472 exhibits a small knob at the tip of its crown and has a distinct slit running up its shaft, which is probably post-mortem.
UM 105474 has teeth that are inclined, probably posteriorly.

UM 105431, UM 105433, UM 105434, UM 105435, UM 105436, UM 105437, UM 105438, UM 105441, UM 105442, UM 105443, UM 105445, UM 105448, UM 105449, UM 105450, UM 105451, UM 105452, UM 105454, UM 105460, UM 105461, UM 105462, UM 105463, UM 105464, UM 105465, UM 105466, UM 105468, UM 105469, UM 105470, UM 105471, UM 105475, UM 105476, UM 105477, UM 105478, UM 105481, UM 105483, UM 105488, UM 105489, UM 105491, UM 105492, UM 105104, UM 105494, UM 105495, UM 105498, UM 105503, UM 105510, UM 105512, UM 105515, UM 105516, UM 105517, UM 105518, UM 105519, UM 105521, UM 105522, UM 105524, UM 105525, UM 105526, UM 105527, UM 105528, UM 105529, UM 105530, UM 105531, UM 105535, UM 105536, UM 105537, UM 105539, UM 105540,

UM 105541, UM 105542, UM 105543, UM 105544, UM 105545, UM 105547, UM 105549, UM 105550, UM 105551, belong to "Parasauromalus new species". Again these specimens are similar to the description of Gilmore (1928), in that they are blunt and possess lateral cusps similar to the type, but few show striations (e.g. UM 105437, UM 105441, UM 105452, and UM 105463). UM 105492 fits this type except its teeth have exaggerated lateral cusps. The teeth of UM 105476 are worn, but resemble this type except for their bulbous bases which are excavated in the center.

Several specimens (UM 105467, UM 105479, UM 105505, and UM 105548) do not fit into either group. UM 105482 has one tooth pointing at a severe angle labially. UM 105456 has several teeth in the maxilla similar to both groups, while other specimens seem to be of an intermediate type with respect to shape and the presence or absence of striations (e.g. UM 105479 and UM 105505).

Right dentary. UM 105103 (Figure 18). Locality; Accumulation 24329

The specimen consists of the posterior portion (5.3 mm) of the right dentary with anterior and some posterior parts missing. It has three complete and three broken teeth. They are closely spaced with no gap between the teeth. The most anterior three teeth are partial roots. They are

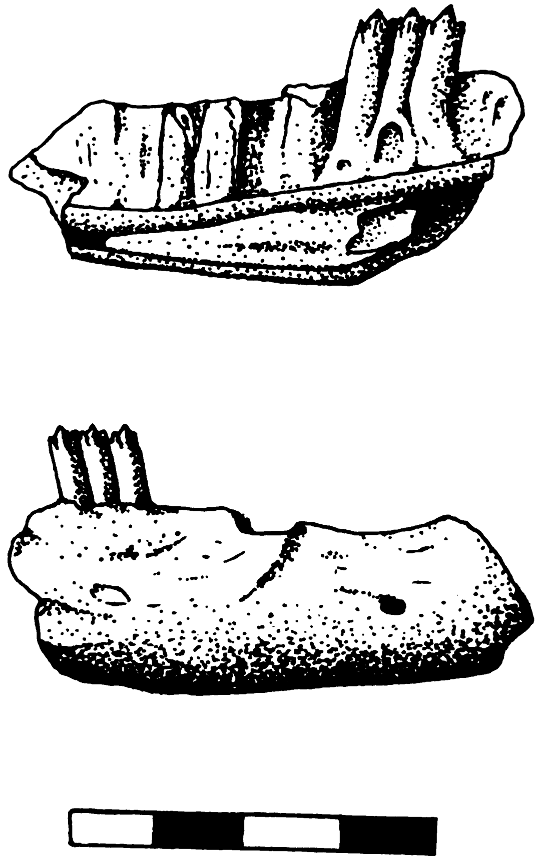

Figure 18. Parasauromalus olseni. UM 105103. Right dentary, lingual and labial views. Scale bar is 4mm.

anteroposteriorly compressed, with oval cross-sections. The roots of the next three teeth are anteroposteriorly compressed, with an oval cross-section, and are parallel-sided in lingual view. Their bases are eroded. The crowns are tricuspid, bearing distinct accessory cusps separated from the main cusp by a groove running down the crown. Striations occur at right angles to the cutting edge over the lingual surface of the crown. The tips point slightly lingually.

The dentary in lingual view has a thin lingual shelf which thins and slopes dorsally to the posterior. The ventral edge of the dentary is convex. Between this and the lingual shelf is the splenial which covers the Meckelian groove. It is smooth and flat except where broken posteriorly. Where the bone is broken, two indentations suggest the position of two foramina. In labial view, the dentary is cracked and pitted, which is probably post-mortem. There is one mental foramen anteriorly. It is sub-circular and lies slightly closer to the dorsal edge of the dentary than to the ventral edge. In dorsal view, the lingual shelf is narrow, and narrows posteriorly.

Left dentary. UM 98795 (Figure 19). Locality; BB 83

The specimen consists of the posterior portion (4 mm) of the left dentary bearing seven complete teeth. The teeth are closely spaced, with slight gaps between them. The most anterior tooth has an anteroposteriorly compressed root, with

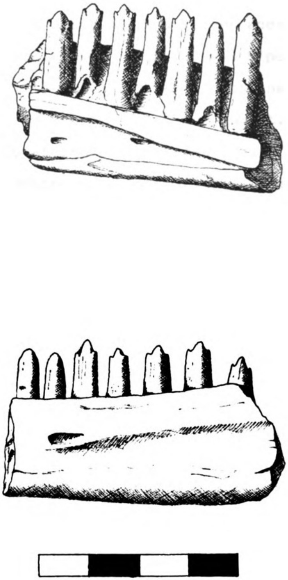

Figure 19. Parasauromalus olseni. UM 98795. Left dentary, lingual and labial views. Scale bar is 4 mm.

an oval cross-section, and is parallel-sided in lingual view. The crown tapers to a point and has slight accessory cusps. A carina runs along the tip of the crown which points slightly lingually. The next tooth is similar except the tip is worn. The third tooth is relatively broad and robust. The base of the root is anteroposteriorly compressed, but just ventral to the crown it is expanded anteroposteriorly. The crown has pronounced accessory cusps and a carina running across the tip from which striations run at right angles down the lingual face. The fourth tooth is small, with an anteroposteriorly compressed root. The crown tapers to a point, and has slight accessory cusps. The fifth tooth is similar to the third, as is the sixth except that it is more slender and the base is eroded. The seventh tooth is also like the third except it is shorter and recurved posteriorly.

In lingual view, the dentary has a thin lingual shelf that thins posteriorly. The ventral edge of the bone is convex. Between the lingual shelf and ventral edge is the splenial filling in the Meckelian groove. It is flat, with two foramina, one ventral to the fourth tooth, one ventral to the sixth tooth. Both are oval and distinct. In labial view, the dentary is smooth. There is one mental foramen anteriorly which lies closer to the dorsal edge of the dentary than to the ventral edge. It is tear shaped, pointing posteriorly, and distinct. In dorsal view, the lingual shelf is narrow and narrows posteriorly.

Left dentary. UM 100982 (Figure 20). Locality; 1419

The specimen consists of the anterior portion (8.8 mm) of the left dentary. It has one complete tooth and seven broken teeth. The most anterior four teeth are partial roots with most of the tooth missing. The next two teeth are more complete. The roots are anteroposteriorly compressed with an oval cross-section. The seventh tooth is complete, slender, and parallel-sided in lingual view. It is anteroposteriorly compressed, with an oval cross-section. The crown tapers to a point which is inclined lingually, and bears very slight accessory cusps. A carina runs along the tip from which striations run at right angles down the lingual surface of the crown. The eighth tooth is similar to the seventh except that the tip is missing and the crown worn.

The lingual shelf is thick in lingual view, and thins posteriorly. The Meckelian groove is positioned near the ventral edge of the dentary. The anterior portion of the dentary is expanded dorsally and lingually at the symphysis. In dorsal view, the exterior edge of the dentary is convex, the interior concave. The lingual shelf is narrow except at the anterior tip where it is lingually expanded. The mental foramina are exposed on the exterior surface. In labial view, the dentary tapers to a point anteriorly. It is smooth, except for five small mental foramina. All are anterior of the seventh tooth and lie closer to the dorsal edge of the dentary than to the ventral edge. The most anterior foramen

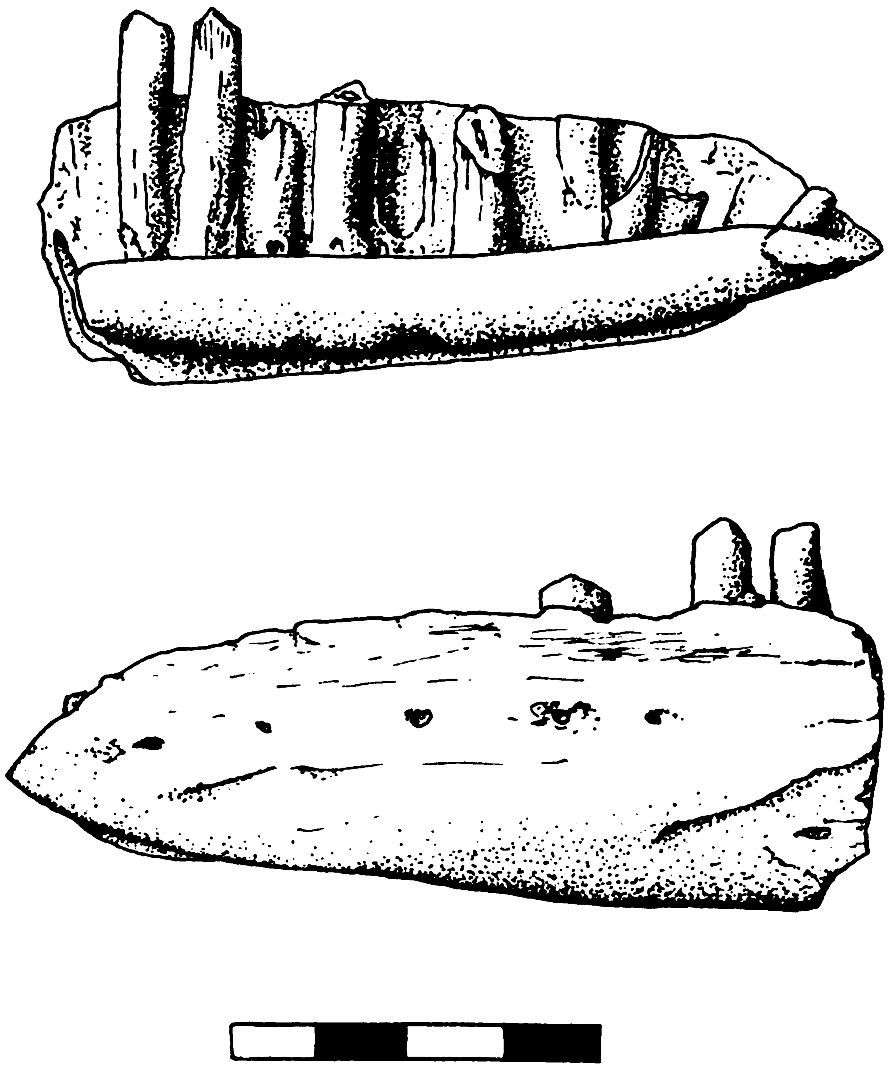

Figure 20. Parasauromalus olseni. UM 100982. Right dentary, lingual and labial views. Scale bar is 4 mm.

is oval, the others circular. The ventral edge of the dentary is straight except where the Meckelian groove is exposed at the anterior tip. In ventral view, the Meckelian groove lies in the center of the ventral surface posteriorly, and on the labial side anteriorly. It tapers and ends just before the anterior end of the dentary, ventral to the expanded symphyseal area.

Maxilla. UM 105104 (Figure 21). Locality; 1129

This specimen consists of a portion (6.6 mm) of the maxilla, with anterior and posterior parts missing. From its morphology it is most likely the right posterior part of the maxilla. It bears nine complete teeth and one broken tooth which are closely spaced with no gap between them. The first tooth is anteroposteriorly compressed and parallel-sided in lingual view. The crown has distinct accessory cusps, separated from the central cusp by grooves. All three cusps are pointed and bear carinae from which striations radiate at right angles. The second tooth is similar except that it points posteriorly, the third points anteriorly. The fourth, fifth and sixth teeth have faint striations and the groove between cusps is less distinct. The seventh tooth is relatively short and bears very slight accessory cusps. The eighth tooth is also short. It has an expanded base and a tapering crown like the others. The ninth tooth points posteriorly and has very slight accessory cusps. The tenth

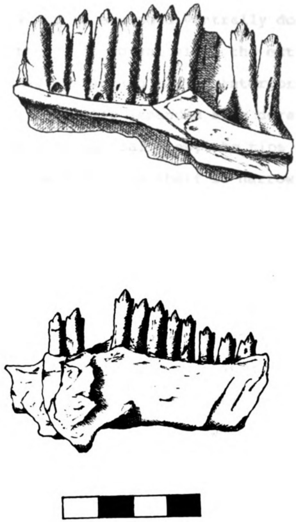

Figure 21. Parasauromalus olseni. UM 105104. Maxilla, lingual and labial views. Scale bar is 4mm.

tooth is a partial root.

In lingual view, the maxillary shelf is straight, thin, and horizontal posteriorly. Anteriorly, the shelf is thin and straight but turns dorsally and is expanded ventrally dorsal to the seventh and eighth teeth. In dorsal view, the external surface of the maxillary shelf is straight. The interior surface is straight up to a lingually expanded area dorsal of the seventh and eighth teeth. In ventral view, the tips of the teeth point lingually. The maxillary shelf is narrow, except posterior to the tenth tooth where it is labially expanded.

Discussion -- Estes (1983) states that P. olseni has striated tooth crowns, and teeth that project about 35% above the parapet of the jaw. Both striated and unstriated teeth are found in this collection. Since most teeth are very well-preserved the lack of striations is not due to wear, therefore I initially separated the specimens into two species; "Parasauromalus olseni" and "Parasauromalus new species". I also measured the percent of projection above the parapet of the jaw of fifteen specimens from each group (Table 1 and Table 2). This showed that not only did the range of percentage overlap between the two groups, but that the figure given by Estes for P. olseni (35% projection above the jaw parapet) was inaccurate. In addition, the dentaries and maxillae of the two groups do not show any distinguishing characteristics, and the tooth morphology of some specimens are intermediate between the two groups. The differences are, therefore, probably due to variation, and I have included all specimens in P. olseni, which may have striated or unstriated teeth.

Results from Table 1 and Table 2:

	"Parasauromalus olseni"	"Parasauromalus n. sp."
Mean:	41.33%	44.44%
Standard deviation:	7.83	7.84
Range:	32.7	31.4

Table 1. Measurements of "*Parasauromalus olseni*".

Specimen	total tooth length	height above jaw parapet	percent above jaw parapet
UM 105440	2.2 mm	0.8 mm	36%
UM 105444	1.6 mm	0.6 mm	37.5%
UM 105447	2 mm	0.9 mm	45%
UM 105455	1.5 mm	0.7 mm	46.6%
UM 105457	1.8 mm	0.8 mm	44.4%
UM 105458	2 mm	1.2 mm	60%
UM 105459	1.7 mm	1 mm	58.8%
UM 105472	1.5 mm	0.8 mm	53.3%
UM 105473	1.5 mm	0.6 mm	40%
UM 105474	1.4 mm	0.7 mm	50%
UM 105480	1.8 mm	0.8 mm	44.4%
UM 105482	1.5 mm	0.5 mm	33.3%
UM 105484	1.6 mm	0.7 mm	43.8%
UM 105485	1.7 mm	0.7 mm	41.2%
UM 105487	1.5 mm	0.6 mm	40%
UM 105604	1.3 mm	0.4 mm	30.8%
UM 105605	1.3 mm	0.4 mm	30.8%
UM 105607	1.2 mm	0.4 mm	33.3%
UM 105609	1.3 mm	0.4 mm	30.8%
UM 105585	1.5 mm	0.6 mm	40%
UM 105586	1 mm	0.4 mm	40%

Table 1 (cont'd)

Specimen	total tooth length	height above jaw parapet	percent above jaw parapet
UM 105588	1.6 mm	0.6 mm	37.5%
UM 105592	2.2 mm	0.6 mm	27.3%
UM 105593	1.9 mm	0.8 mm	42%
UM 105595	1.6 mm	0.7 mm	43.8%
UM 105597	1.8 mm	0.7 mm	38.8%
UM 105598	1.6 mm	0.8 mm	50%
G130	1.8 mm	0.8 mm	44.4%
G132	2.3 mm	0.9 mm	39%
G135	2.9 mm	1.3 mm	44.8%

Table 2. Measurements of "Parasauromalus new species".

Specimen	total tooth length	height above jaw parapet	percent above jaw parapet
UM 105441	1.6 mm	0.8 mm	50%
UM 105442	0.8 mm	0.4 mm	50%
UM 105443	1.2 mm	0.6 mm	50%
UM 105445	1.8 mm	0.8 mm	44.4%
UM 105448	1.2 mm	0.5 mm	41.6%
UM 105452	1.8 mm	0.7 mm	38.8%
UM 105460	1.9 mm	0.7 mm	36.8%
UM 105461	1.3 mm	0.5 mm	38.5%
UM 105462	1.4 mm	0.7 mm	50%
UM 105463	1.2 mm	07 mm	58.3%
UM 105464	1.2 mm	0.6 mm	50%
UM 105465	1.2 mm	0.5 mm	41.6%
UM 105469	1.3 mm	0.6 mm	46%
UM 105470	1.6 mm	0.6 mm	37.5%
UM 105471	1.4 mm	0.5 mm	35.7%
UM 105515	1.7 mm	0.6 mm	35.3%
UM 105516	2.2 mm	1.3 mm	59.1%
UM 105521	1.3 mm	0.6 mm	46.2%
UM 105522	1.7 mm	0.8 mm	47.1%
UM 105528	1.7 mm	0.8 mm	47.1%
UM 105531	1.2 mm	0.6 mm	50%

Table 2 (cont'd)

Specimen	total tooth length	height above jaw parapet	percent above jaw parapet
UM 105535	1.8 mm	0.6 mm	33.3%
UM 105536	1.4 mm	0.7 mm	50%
UM 105537	1.4 mm	0.7 mm	53.8%
UM 105539	1.4 mm	0.6 mm	42.9%
UM 105540	2.1 mm	1.1 mm	52.4%
UM 105542	1.4 mm	0.7 mm	50%
UM 105544	1.4 mm	0.5 mm	35.7%
UM 105551	1.8 mm	0.5 mm	27.7%
UM 105553	1.5 mm	0.5 mm	33.3%

Parasauromalus indet.

Referred specimens -- UM 105614, UM 105615, UM 105616, UM 105617, UM 105618, UM 105619, UM 105620, UM 105621, UM 105622, UM 105623, UM 105624, UM 105625, UM 105626, UM 105627, UM 105628, UM 105629, UM 105630, UM 105631, UM 105632, UM 105633, UM 105634, UM 105635, UM 105636, UM 105637, UM 105638, UM 105639, UM 105640, UM 105641, UM 105642, UM 105643, UM 105644, UM 105645, UM 105646, UM 105647, UM 105648, UM 105649, UM 105650, UM 105651, UM 105652, UM 105653, UM 105654, UM 105655, UM 105656, UM 105657, UM 105658, UM 105659, UM 105660, UM 105661, UM 105662, and UM 105664.

These specimens are referred to *Parasauromalus* indet. on the basis of the possession of one or more of the following diagnostic characteristics; the Meckelian groove is closed but not fused to the splenial, the lingual shelf is thick in lingual view and thins posteriorly, there is a groove (the dental gutter) between the bases of the teeth and the lingual shelf, and there are up to five small mental foramina on the external surface of the dentary.

Description -- These specimens are tentatively referred to *Parasauromalus* indet. due to similarities in the morphology of the dentaries and maxillae, the Meckelian groove, and the lingual shelf. All are edentulous, or bear worn and broken teeth.

Discussion -- These specimens are assigned to *Parasauromalus* indet. due to the characters given above. They are probably *P. olseni*, since this is the only species found in the assemblage, but without the presence of teeth and the posterior portion of the dentary they cannot be assigned to this species with any certainty. A second species is not indicated. Although the anguids have a similar Meckelian groove anteriorly, the sub-dental platform is inclined and there is no groove between this feature and the lingual shelf, making it possible to distinguish between anguid indet. and *Parasauromalus* indet.

Iguanidae indet.

Figure 22

Referred specimens -- UM 105665, UM 105666, UM 105667, UM 105668, UM 105669, UM 105670, UM 105671, UM 105672, UM 105673, UM 105674, UM 105105, UM 105677, UM 105678, UM 105679, UM 105680, UM 105681, UM 105682, UM 105683, UM 105684, UM 105685, UM 105686, UM 105687, UM 105688, UM 105689, UM 105690, UM 105691, UM 105692, UM 105693, UM 105694, UM 105695, UM 105696, UM 105697, UM 105698, UM 105699, UM 105700, UM 105701, UM 105702, UM 105703,

UM 105704, UM 105705, UM 105675, UM 105676, UM 101482 (in part), and UM 103038 (in part).

Description --

Vertebra. UM 105105 (Figure 22) Locality; 2413

This specimen is an almost complete thoracic vertebra. Its dimensions are; height: 2 mm, width at the prezygapophyses: 2 mm, width at the postzygapophyses: 1.5 mm, length between the pre- and postzygapophyses: 2.5 mm, width of the condyle: 0.5 mm, width of the cotyle: 0.5 mm, length of the neural spine: 1.5 mm, length of the neural arch along the midline: 3.1 mm, length of centrum: 2mm. The condyle and anterior edge of the neural arch are missing.

In anterior view, the cotyle is dorsoventrally compressed. The neural canal is hemicircular, and slightly tripartate. The prezygapophyses point dorsolaterally at about 30 degrees from the horizontal, and do not project far laterally. The diapophyses are pointed and project ventrolaterally at about 30 degrees from the horizontal. The diapophyses and prezygapophyses are connected by concave areas of bone lateral to the cotyle, each pierced by a paracotylar foramen. There is a weak zygosphene. The neural arch is broad, and moderately high. The neural spine is thin and moderately high. In posterior view, two hypapophyses, ventral to the centrum are exposed. Dorsally, there is a weak

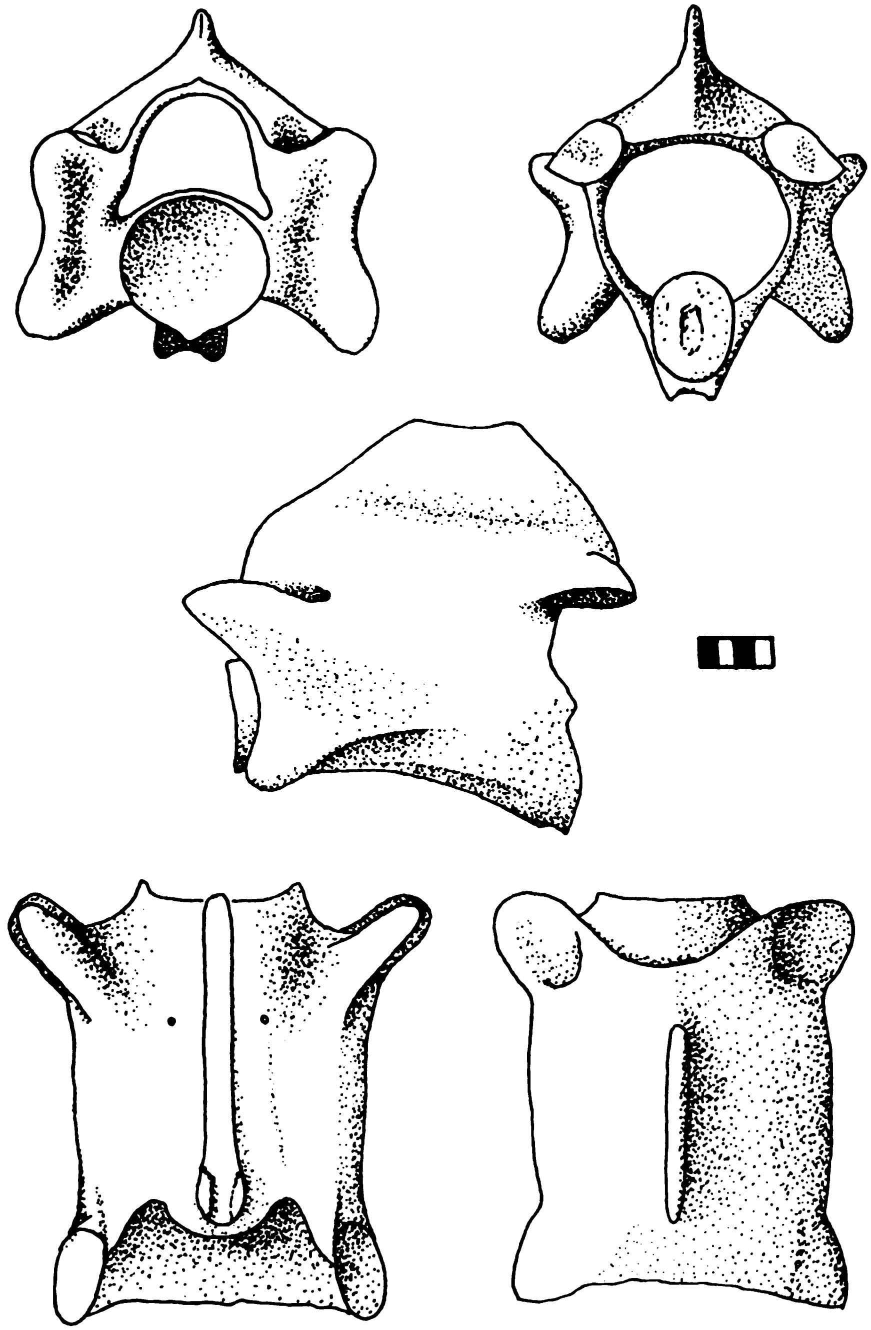

Figure 22. Iguanidae indet. UM 105105. Thoracic vertebra, anterior, posterior, lateral, ventral, and dorsal views. Scale bar is 4 mm.

zygantrum. The postzygapophyses point dorsolaterally at about 30 degrees from the horizontal, and do not project far laterally.

In dorsal view, the prezygapophyses project further laterally than the postzygapophyses. The prezygapophysial facets are oval. The sides, and posterior margin of the neural arch are very slightly concave. In ventral view, the centrum lacks a hemal keel. It has two, small subcentral foramina on either side of the midline. The postzygapophysial facets are oval. In lateral view, the ventral surface of the centrum is concave. The diapophyses project further ventrally than the ventral margin of the centrum. There is a very weak zygapophysial ridge. The neural spine increases in height posteriorly.

Discussion -- Four lizard families (the Iguanidae, Teiidae, Cordylidae and Lacertidae) have facets similar to the zygosphene-zygantrum complex, however, they differ from snakes in the following ways; the zygosphene does not overhang the prezygapophyses, there may be more than a 90 degree angle between the zygosphene and prezygapophysial facets, the zygosphene and prezgapophyses are not necessarily separated by a non-articular area, the anterodorsal lip of the centrum is deeply notched (Hoffstetter and Gasc 1969). The Cordylidae and Lacertidae do not have fossil records in North America. Teiids are found in North America only in the Cretaceous, Miocene, Pliocene, Pleistocene, and Holocene, though it is likely they could be found in the Eocene, however, their vertebrae are more robust and square in dorsal view than the University of Michigan specimens.

Family Agamidae Gray, 1827

This is an old world family of Africa, Asia, and Australia, that spread to northern Asia, Europe, and North America during peak Eocene tropicality (Estes 1983). It is included in the Acrodonta, a group made up of the Agamidae and Chamaeleonidae, and supported by a number of unique features (Frost and Etheridge 1989).

The agamids share derived characters with the chamaeleonids; acrodont, permanent teeth and a reduced Meckelian groove, which suggest a relationship between the two groups, but the skull and temporal region suggest a relationship with the Iguanidae (Moody 1980). In agamids the premaxilla is fused and the postfrontal is absent. The vertebral centra usually have a sagittal ridge ventrally. There are no autapomorphies for the group (Estes 1983).

Tinosaurus Marsh, 1872.

Type species -- *Tinosaurus stenodon* Marsh, 1872.

Referred species -- *Tinosaurus pristinus* Leidy 1872; *Tinosaurus* cf. *T. stenodon*, *Tinosaurus asiaticus* Gilmore

1943; Tinosaurus sp. Hecht and Hofstetter 1962; Tinosaurus lushihensis Dong 1965 and Tinosaurus doumuensis Hou 1974.

Diagnosis -- The generic diagnosis is taken from Gilmore (1928) and Estes (1983), and is unemended. Tinosaurus represents a group of poorly known agamids that were widely distributed in the northern hemisphere during the Eocene. They are identified on the basis of tooth morphology and stratigraphic occurrence (Estes 1983). The teeth fall into two categories, those along the posterior portion of the dentary and those on the premaxilla and corresponding positions on the dentary. The former are typically small, triangular and tricuspid posteriorly, with denticles and tooth size reducing anteriorly. The anterior teeth are unicuspid and are relatively tall, conical, and sharply pointed. The external side of the ramus exhibits vertical grooves between the teeth, due to wear by the opposing upper teeth (Gilmore, 1928). The teeth are acrodont to sub-acrodont. They are firmly ankylosed to a short and slightly inclined surface on the internal side of the jaw but are not fully acrodont as in Sphenodon. The Meckelian groove is open, large, and well-defined (Gilmore 1928).

Age and Distribution -- Paleocene; People's Republic of China, middle Eocene; Wyoming, USA, late Eocene; People's Republic of China and Mongolian People's Republic.

Tinosaurus stenodon Marsh, 1872.

Figures 23 and 24

(Synonyms -- Tinosaurus lepidus Marsh 1872; Thinosaurus lepidus Nopcsa 1908)

Type specimen -- YPM 615.

Type locality -- Sublette County, Wyoming; Bridger Formation; Middle Eocene.

Diagnosis -- The dentary has a large, open Meckelian groove running close to the ventral edge of the dentary on the lingual side. On the labial side there are up to five large, evenly spaced mental foramina. The labial surface is smooth and convex in cross-section. The dentaries meet at the symphysis with an angle of about 60 degrees, in dorsal view. The teeth are triangular and anteroposteriorly compressed with blunt cutting edges. Some are recurved, agreeing with Marsh (1872) who described the teeth of T. stenodon as pointed and curved backwards. The grooves between the teeth on the labial surface of the dentary are short and shallow.

Previously referred specimens -- YPM 615; Sublette County, Wyoming; Bridger Formation; middle Eocene.

Age and Distribution -- Middle Eocene, Wyoming.

Referred specimens -- UM 105706, UM 105707, UM 105708, UM 105709, UM 105710, UM 105711, UM 105712, UM 105713, UM 105714, UM 105715, UM 105716, UM 105717, UM 105718, UM 105719, UM 105720, UM 105721, UM 105722, UM 105723, UM 105724, UM 105725, UM 105726, UM 105727, UM 105728, UM 105106, UM 105729, UM 105730, UM 105731, UM 105732, UM 105733, UM 105734, UM 105735, UM 105107, and UM 105736.

These specimens are referred to *Tinosaurus stenodon* on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- The majority of the specimens consist of teeth attached to fragmentary bone. Where possible I have described the dentary, maxilla or premaxilla. The teeth are generally well-preserved, though some are worn.

The posterior teeth typically have low crowns, and are acrodont, triangular and tricuspid posteriorly, with denticles and tooth size anteriorly reduced. The anterior teeth are relatively large, unicuspid, and sharply pointed. The external surface of the ramus generally exhibits vertical grooves between the teeth, and in some cases these are very pronounced (UM 105716). Between one-fourth and two-thirds of the tooth projects above the jaw line. Though some are broken and/or worn, enough of some of the teeth are present to make a diagnosis. The Meckelian groove is open.

UM 105706, UM 105707, UM 105708, UM 105709, and UM 105710 lack lateral cusps and are probably teeth from the anterior part of the jaw. They generally resemble equilateral triangles. UM 105711, UM 105712, UM 105713, UM 105714, UM 105715, UM 105716, UM 105717, UM 105718, UM 105719, UM 105720, UM 105721, UM 105722, UM 105723, UM 105725, UM 105726, UM 105728, UM 105106, UM 105729, UM 105731, UM 105732, UM 105733, UM 105734, UM 105735, UM 105107, and UM 105736 exhibit lateral cusps so they could be from either the anterior or posterior part of the dentary. Lateral cusps vary in width and height, most likely due to intraspecific variation, though in some cases this could be caused by wear. All teeth are rough equilateral triangles. UM 105720 is asymmetrical, having only one lateral cusp. Marsh (1872) described the anterior teeth of _T_. _stenodon_ as occasionally having one lateral cusp on the front edge of the tooth. Some teeth exhibit additional grooves on their crowns. UM 105719 is bulbous at the bases of its teeth, seen most easily in lateral view. In some specimens there was enough associated bone to describe.

Right dentary. UM 105106 (Figure 23). Locality; 1139

The specimen consists of the anterior portion (10.3 mm) of the right dentary. It has three complete and six broken teeth. The most anterior tooth is complete. It is conical, unicuspid, and sharply pointed. Posterior to this are two

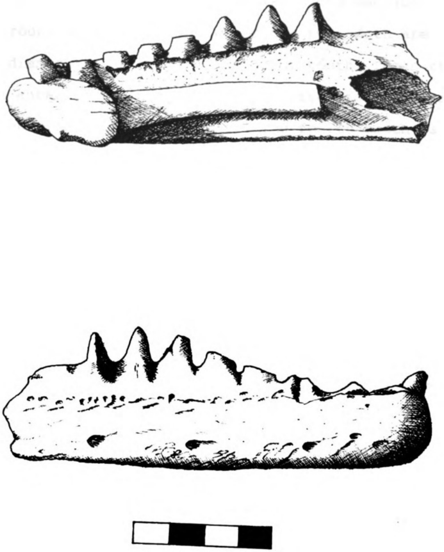

Figure 23. <u>Tinosaurus</u> <u>stenodon</u>. UM 105106. Right dentary, lingual and labial views. Scale bar is 4mm.

broken teeth. The first has a triangular cross section, the second is round and is the smaller of the two. Both are larger in diameter than the most anterior tooth. These teeth are of the anterior tooth type. The posterior teeth are all laterally compressed and triangular. The fourth tooth is the smallest in the tooth row. All subsequent teeth increase in size posteriorly and this and the next four teeth are unicuspid and broken at the tip. The sixth tooth is the first to show accessory cusps, which form butresses at the base of the crown and are not separated from the main cusp by a groove. All teeth posterior to this exhibit the same lateral cusp arrangement.

In lingual view, the dentary can be divided into two parts; a straight main body of the ramus bearing the posterior teeth, and an expanded area at the symphysis bearing the anterior teeth. The ramus consists of the rounded dentary, divided longitudinally by the deep, large, open Meckelian groove running its entire length. The Meckelian groove ends just below the posterior end of the symphysis. Ventral to the tooth row an area of bone appears characteristically weathered away and 'spongy'. It undercuts the posterior teeth and a groove runs between this area and the main body of the dentary. The anterior end of the jaw curves inwards to form a large, ovoid area where the two dentaries meet. The jaws meet at an angle of about 60 degrees. In dorsal view, this area is roughly triangular. The ramus is straight except where it curves lingually at its anteriormost end. The most posterior teeth are positioned on the lingual side, the more anterior teeth on the labial side, with a gradual transition between the two groups of teeth. In dorsal view, it can be seen that the teeth are not inclined to the lingual or labial side, unlike T. pristinus.

In labial view, slight grooves cut by the maxillary teeth (extending 0.5 mm below the point where the teeth meet) occur between the posterior teeth. The entire external surface of the dentary has a distinct, horizontal row of small pits starting at the base of the fourth tooth and continuing to the posterior of the specimen. Ventrally these are several small, narrow grooves running obliquely and there are five mental foramina. Four are large, and roughly equally spaced (from between 1.5 mm and 2.5 mm apart), while one is very small, slightly more dorsal than the others, and lies between the two most anterior foramina.

Maxilla. UM 105107 (Figure 24). Locality; 1125

The specimen consists of a portion (5.7 mm) of a left maxilla and bears three teeth. The most anterior tooth is triangular, pointed, blade-like in ventral view, and curved to point posteriorly. It is taller and thinner than the others, has a bulbous base, is sharply laterally compressed, and has a slight accessory cusp on one side. The middle tooth is the same shape as the first but exhibits a slightly bulbous base. One lateral cusp is distinct, the other less

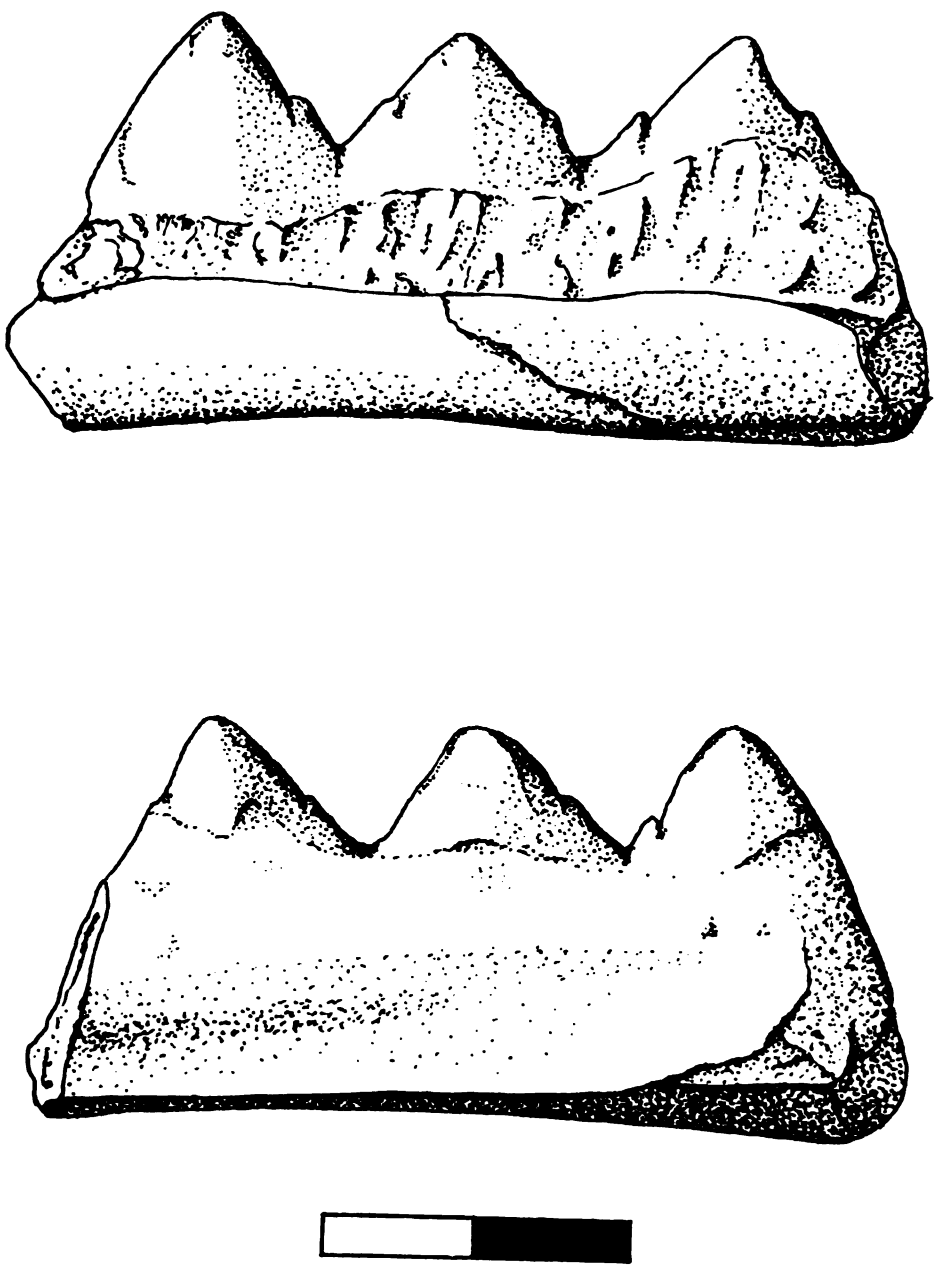

Figure 24. Tinosaurus stenodon. UM 105107. Maxilla, lingual and labial views. Scale bar is 4 mm.

so. The most posterior tooth has distinct accessory cusps on both the anterior and posterior sides. It is broken at the base and has a slightly irregular cutting edge.

In lingual view, the teeth are attached to a lingually expanded maxillary shelf. In labial view, the external surface is flat and is very worn and eroded. In dorsal view, the maxillary shelf is broad and flat with longitudinal ridges running along its length. In occlusal view, the teeth appear upright and narrow, and lie in a straight line.

Tinosaurus pristinus Leidy, 1872.

Figures 25 and 26

Type specimen -- ANSP 9134.

Type locality -- Bridger Formation, Wyoming; middle Eocene.

Diagnosis -- Tinosaurus pristinus has more conical teeth than other species of the genus, as well as smaller lateral cusps and a wide and conspicuous horizontal, perforated groove running below the teeth on the lingual side of the jaw (Gilmore 1928). The dentary has up to four small, unevenly spaced mental foramina. In cross-section, the external surface of the dentary has two distinct straight edges meeting at an obtuse angle half-way down the dentary. The Meckelian groove is located on the midline of the ramus, running along its lingual side. The jaws meet at an angle of about 40 degrees. The teeth are more conical that in T. stenodon and have bulbous bases. Their cutting edges are acutely blade-like. The grooves cut between the teeth are longer and deeper.

Previously referred specimens -- None

Age and Distribution -- Middle Eocene, Wyoming.

Referred specimens -- UM 105737, UM 105738, UM 105739, UM 105740, UM 105741, UM 105742, UM 105743, UM 105744, UM 105745, UM 105746, UM 105747, UM 105748, UM 105749, UM 105750, UM 105751, UM 105752, UM 105753, UM 105754, UM 105108, UM 105755, UM 105756, UM 105757, UM 105758, UM 105759, UM 105760, UM 105761, UM 105762, UM 105763, UM 105764, UM 105765, UM 105766, UM 105767, UM 105768, UM 105769, UM 105770, UM 105771, UM 105772, UM 105773, UM 105774, UM 105775, UM 105776, UM 105777, UM 105109, UM 105778, UM 105779, UM 105780, UM 105781, UM 105782, UM 105783, UM 105784, and UM 105785.

These specimens are referred to Tinosaurus pristinus on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- UM 105772 and UM 105776 are typical in having conical, closely spaced teeth, with small lateral cusps. Most specimens have teeth bearing a simple cutting edge, but those of UM 105744 are slightly compressed to form blade-like edges. The teeth of UM 105739 and UM 105740 have a shorter base than the others, though are otherwise similar. UM 105771 possibly shows striations on the tips of the crowns, but this may be due to poor preservation. The teeth of UM 105109 and UM 105778 are recurved, with the latter specimen having badly broken teeth and lacking lateral cusps, but possessing the outer groove between the teeth that is characteristic of the genus. Lingually, UM 1057744 and UM 105784 show a horizontal groove running between both cutting edges of the tooth, just below the lateral cusps. UM 105763, UM 105764, and UM 105777 exhibit two vertical grooves on the lingual surface on both anterior and posterior ends of each tooth. They begin at the cutting edge, on either side of the tip of the crown, and run between the lateral cusps, ending just below the base of these cusps. UM 105757 has, on the lingual side, both the horizontal groove described above and a lengthening of the groove between the lateral cusps which continues to the base of the tooth.

Left dentary. UM 105108 (Figure 25). Locality; 2827

This specimen consists of the anterior portion (13.5 mm) of the left dentary with the anterior tip missing. It contains five complete and five broken teeth. The most anterior tooth appears to be the only one of the anterior type, being oval in cross section. Most of this tooth is broken so its shape is indeterminable. The second tooth is similarly broken and smaller than the first. It is laterally compressed with no accessory cusps. Successive teeth increase in size posteriorly. The third tooth has one posterior lateral cusp, the fourth is large, but broken in such a way as to obscure the possible presence of accessory cusps. The fifth tooth is complete, laterally compressed and triangular. It has two accessory cusps divided from the main cusp by a shallow groove. The next two teeth are broken at their tips and have two, small, ill-defined cusps forming butresses at the base of their crowns. The eighth tooth has well-defined accessory cusps, while the ninth has well-defined lateral cusps. Although laterally compressed to a degree, the teeth are more conical than those of Tinosaurus stenodon and have bulbous bases.

In lingual view, the dentary is less eroded and pitted than in specimens of T. stenodon though this may be a post-mortem feature. The Meckelian groove is centrally located in the main body of the ramus. In labial view there is little pitting on the exterior surface of the dentary, though the

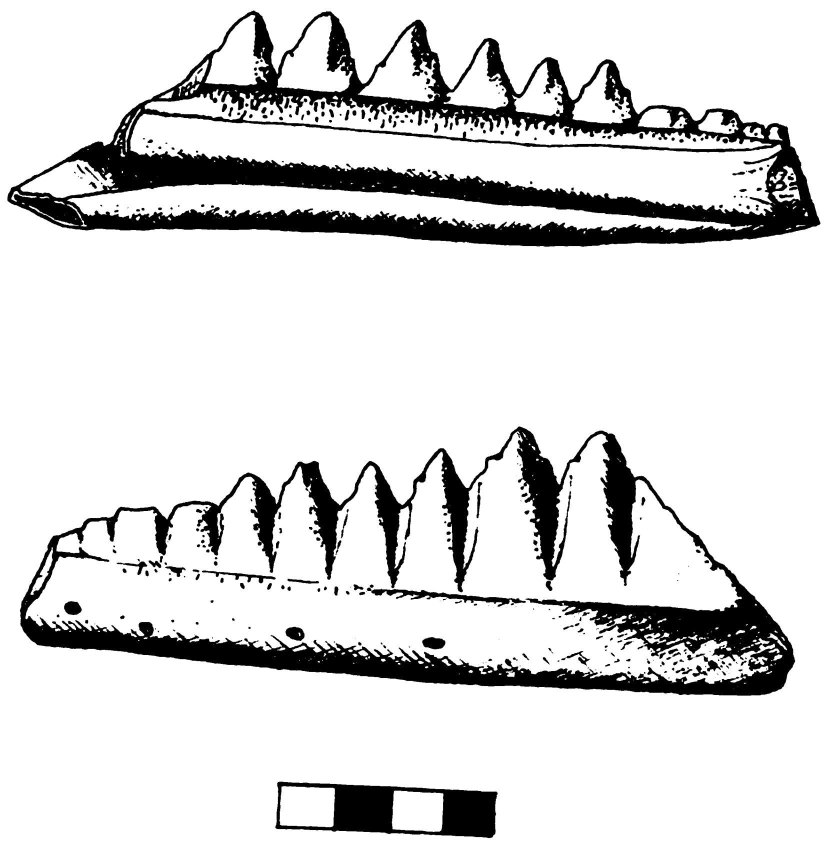

Figure 25. Tinosaurus pristinus. UM 105108. Left dentary, lingual and labial views. Scale bar is 4 mm.

horizontal line is still present. There are four small mental foramina. They are circular to ovoid, unevenly spaced and lie in a line below the midline of the dentary. In cross-section, *T. stenodon* has a smooth convex, exterior outline, while *T. pristinus* has two distinct straight areas meeting at an obtuse angle half way down the dentary. The tips of the posteriormost teeth appear slightly bulbous and the groove between the teeth is deeper and longer (up to 1.48 mm below the point where the teeth meet).

In dorsal view, some of the anterior end of the dentary has been broken away, but a portion of the symphysis remains. It has a similar shape to that found in *T. stenodon* except that the jaws would have met at an angle of about 40 degrees. Again, the more posterior teeth are on the lingual side of the jaw, the more anterior towards the lingual side. The jaw is slightly inclined so that in dorsal view the teeth point lingually, unlike the condition in *T. stenodon*.

Maxilla. UM 105109 (Figure 26). Locality; Twin Buttes White Layer

This specimen is a left maxilla with both anterior and posterior ends missing. It contains three teeth, all of which are recurved and point posteriorly. The most anterior tooth has a distinct anterior accessory cusp and an indistinct posterior one. It is triangular, pointed, has a bulbous base, and is very conical. The next tooth is the same shape except

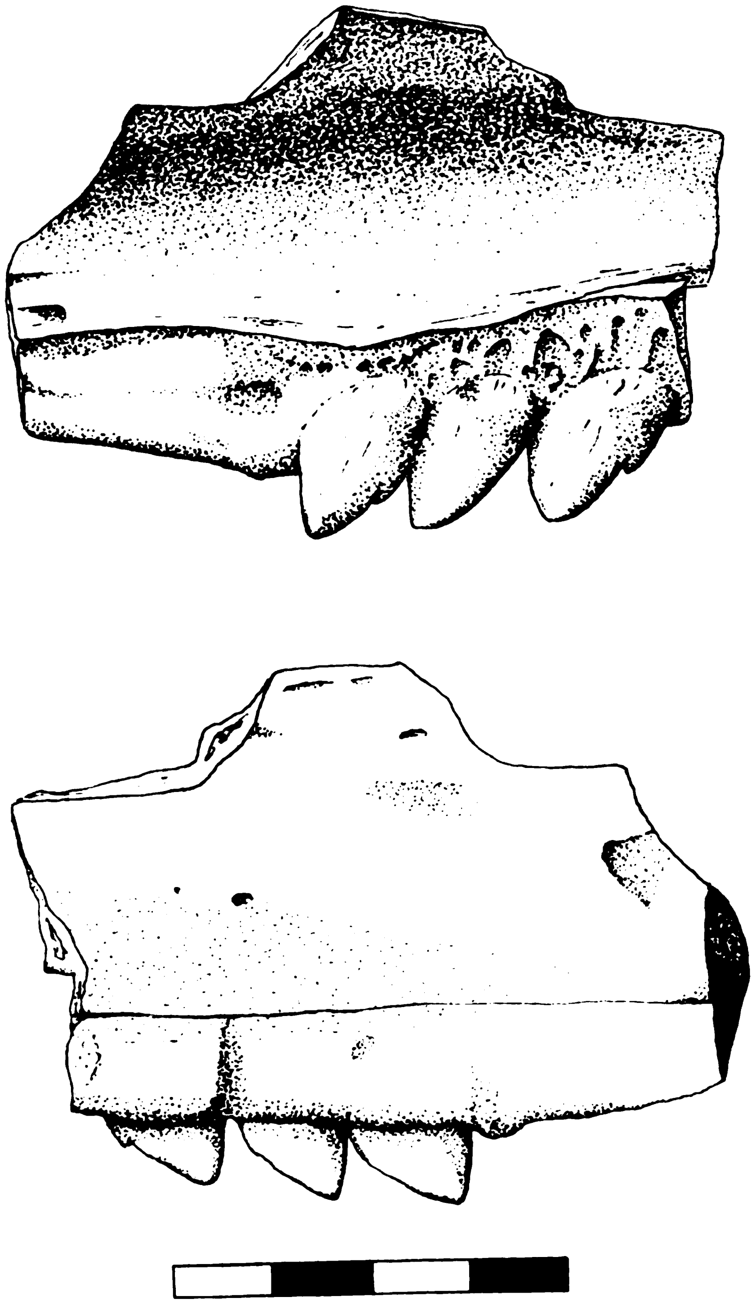

Figure 26. Tinosaurus pristinus. UM 105109. Maxilla, lingual and labial views. Scale bar is 4 mm.

it has no accessory cusps. The most posterior tooth is similar to the middle tooth.

In lingual view, the maxilla is thin dorsally, expanding lingually at the tooth row to form a maxillary shelf to which the teeth attach. The shelf thins posterior to the last tooth. In labial view, the maxilla has a smooth external surface except for grooves cut between each tooth, presumably by the opposing dentary teeth. The grooves are deep near the tooth, becoming more shallow dorsally, and are roughly triangular in shape. The ventral profile, where the teeth meet the maxilla, is straight except for these indentations. In ventral view, the external margin of the maxilla is straight. The bone tapers posterior to the most posterior tooth to form a blade-like projection. The teeth are upright. In cross-section, the ventral part of the maxilla is flat, the dorsal part convex.

Discussion -- Estes (1983) stated that the teeth of *T. stenodon* are less closely spaced than in other species of the genus. He defined this as the "space occupied by three teeth" (Estes, 1983 pp54). This is really a measurement of the diameter of the teeth, since they are near-symmetrical triangles that meet at their bases. However, this is still useful in determining a possible difference between *T. stenodon* and *T. pristinus*. The distance between the tips of two teeth can be measured to give the diameter of the teeth, and, in order to account for the variation in size between specimens, the height of the two teeth can be measured and averaged (Figure 27). The averaged height divided by the width will give the relative diameter, the higher number equating to smaller diameter, or less closely spaced teeth as given by Estes (1983). After measuring the referred specimens I found they do not fit the general rule given by Estes (1983). Despite this, there are enough diagnostic characters for _T_. _stenodon_ and _T_. _pristinus_ given above, to justify the two species.

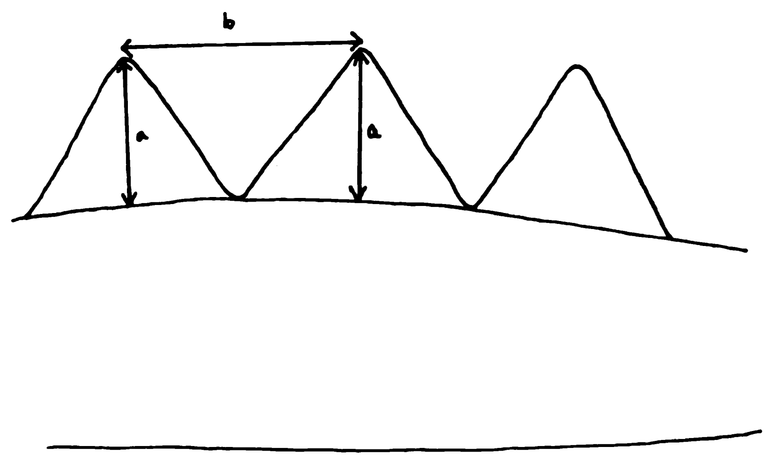

Figure 27. Measurements taken to compare Tinosaurus teeth. a: tooth height (taken for two teeth and averaged). b: distance between two teeth.

Table 3. Measurements of the teeth of Tinosaurus stenodon.

Specimen	Height (average height of two teeth)	Width (distance between tooth tips)	Height ÷ width
UM 105706	1.6 mm	1.7 mm	0.9
UM 105710	1.6 mm	1.6 mm	1
UM 105712	1.9 mm	1.7 mm	1.1
UM 105718	0.9 mm	1 mm	0.9
UM 105721	1 mm	0.9 mm	1.1
UM 105722	1.4 mm	1.2 mm	1.2
UM 105723	1.6 mm	1.4 mm	1.1
UM 105726	0.8 mm	0.9 mm	0.9
UM 105106	1 mm	1 mm	1
UM 105107	1.2 mm	1.6 mm	0.8

Table 4. Measurements of the teeth of _Tinosaurus pristinus_.

Specimen	Height (average height of two teeth)	Width (distance between tooth tips)	Height ÷ width
UM 105738	0.9 mm	1.3 mm	0.7
UM 105739	1.1 mm	1.4 mm	0.8
UM 105741	1.2 mm	1.5 mm	0.8
UM 105743	1.2 mm	1.3 mm	0.9
UM 105744	1.6 mm	1.9 mm	0.8
UM 105745	1.5 mm	1.3 mm	1.2
UM 105746	1.5 mm	1.9 mm	0.8
UM 105754	1.5 mm	1.1 mm	1.4
UM 105108	1.5 mm	1.4 mm	1.1
UM 105766	2 mm	1.7 mm	1.2

Tinosaurus indet.

Figures 28 and 29

Referred specimen -- UM 105786, UM 105787, UM 105788, UM 105117, UM 105789, UM 105790, UM 105791, UM 105792, UM 105793, UM 105794, UM 105118, and UM 105795.

These specimens are referred to *Tinosaurus* indet. on the basis of the possession of one or more of the following diagnostic characteristics; the dentaries have an open Meckelian groove, simple anterior teeth, and triangular posterior teeth, they have sub-acrodont dentition.

Description --

Dentary. UM 105117 (Figure 28). Locality; 1139

This specimen consists of a portion (6.5 mm) of a left anterior dentary. It contains five broken teeth. The two anteriormost teeth are partial roots. They are anteroposteriorly compressed, and have an oval cross-section. The third tooth is conical, and has its tip missing. The fourth and fifth teeth consist of the base of two teeth ankylosed to the dentary. They are laterally compressed.

The dentary has a thick lingual shelf and an open Meckelian groove at the lingual edge of the ventral surface. The anterior tip of the dentary is expanded lingually to form

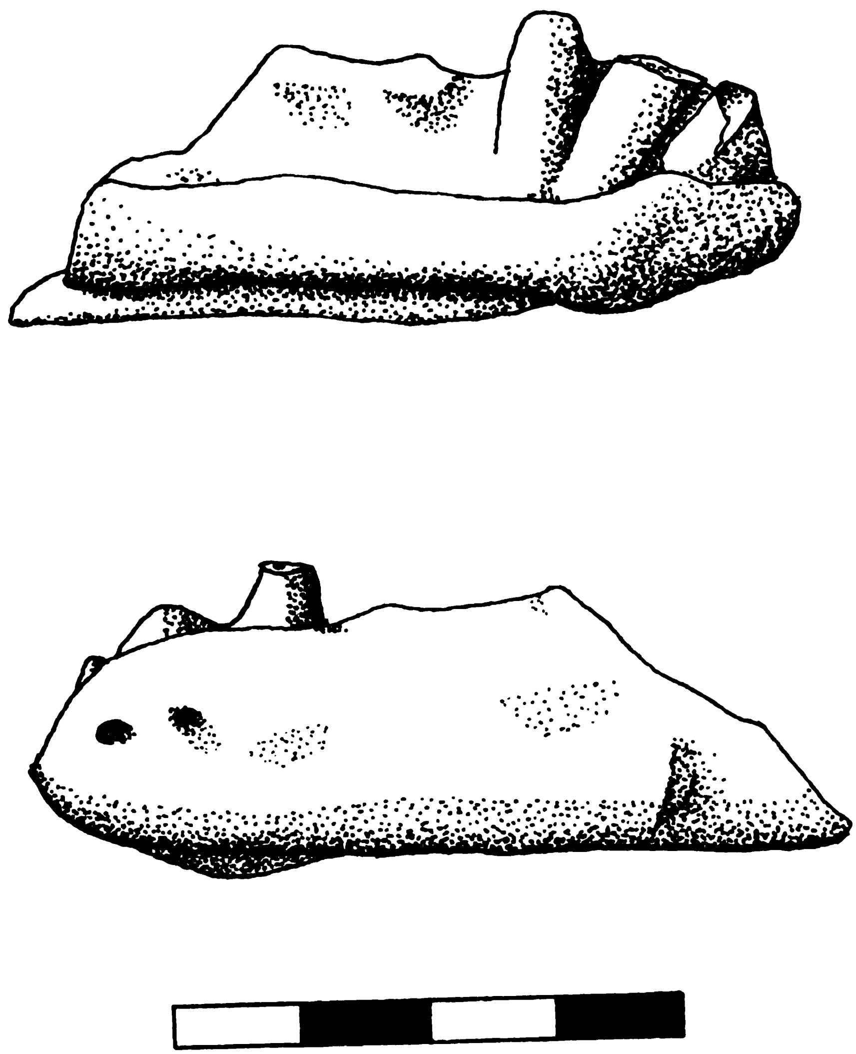

Figure 28. Tinosaurus indet. UM 105117. Left dentary, lingual and labial views. Scale bar is 4 mm.

a triangular area in dorsal view. There are two distinct, ovoid mental foramina ventral to the first and second teeth, lying midway down the dentary.

Premaxilla. UM 105118 (Figure 29). Locality; 1139

This specimen consists of an almost complete premaxilla, 3.7 mm wide and 5.5 mm long. It contains three conical teeth, with simple tapering points. The central tooth is the smallest. The teeth lie on a sub-dental platform that is flat except for a ventral, conical projection on its lingual edge. Posterior to the platform is the posterior projection of the premaxilla. Along its ventral surface is a central ridge running anteroposteriorly. On either side are four foramina. The anterior pair are small and ovoid, the posterior pair large and ovoid. Part of the posterior end of the premaxilla is missing. In dorsal view, the external surface is concave, semicircular anteriorly, and punctured by two foramina near the lateral edge, dorsal to the two outer teeth. The posterior projection is parallel-sided laterally, and has an irregular surface, probably produced by post-mortem processes.

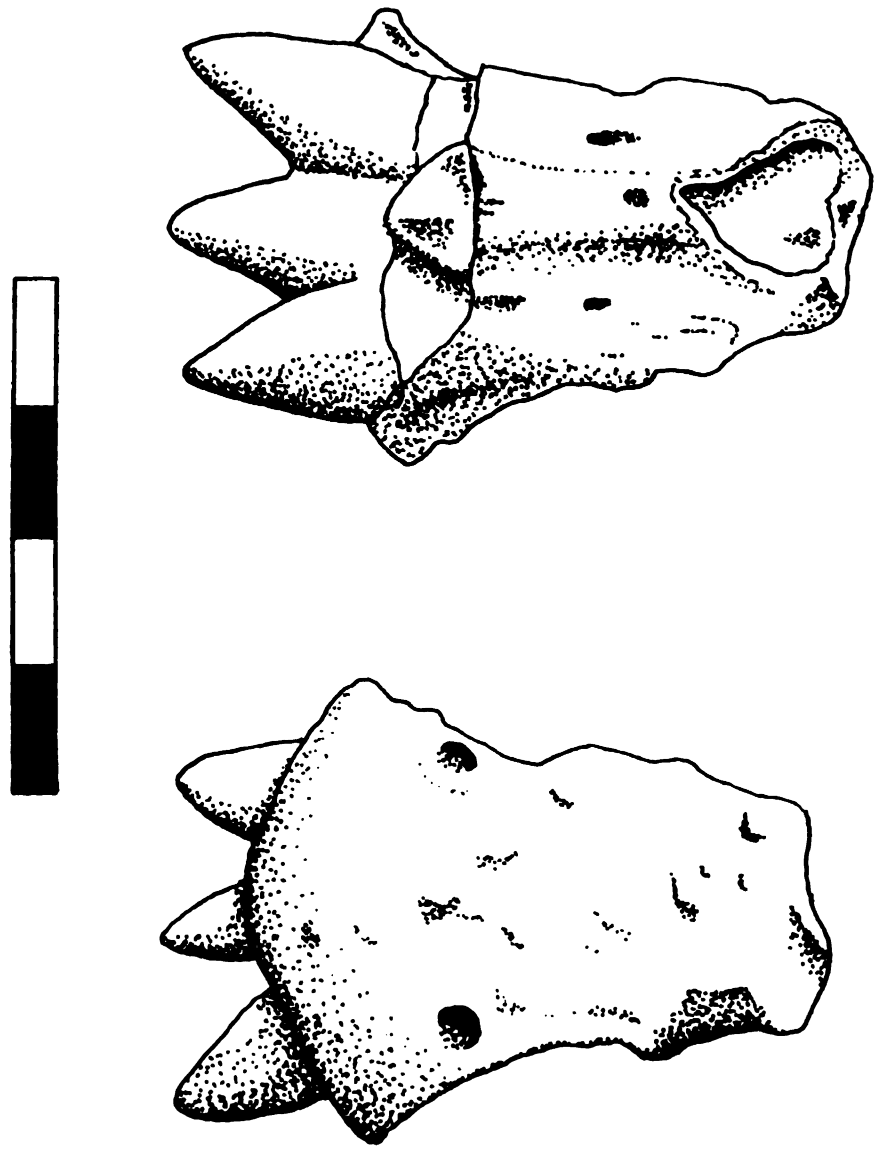

Figure 29. Tinosaurus indet. UM 105118. Premaxilla, lingual and labial views. Scale bar is 4 mm.

Discussion -- These specimens are referred to Tinosaurus indet. as they have the characteristics given in the diagnosis, but their teeth are worn or missing making a specific identification impossible. The premaxillary teeth are similar to the anterior teeth of the dentary. However, premaxillary teeth of different taxa are often similar, therefore UM 105794, UM 105118, and UM 105795 are tentatively referred to Tinosaurus indet. A third species is not indicated.

Infraorder Scincomorpha Camp, 1923

Superfamily Cordyloidea Fitzinger, 1826

Family Xantusiidae Baird, 1859

The Xantusiidae share the following character states; the skull is broad and depressed, the upper temporal fenestra is closed by the union of the squamosal, postfrontal-postorbital and parietal are fused, the cheek teeth are conical, triconodont or tritubercular, the palate is toothless, and the vertebrae non-synovial (Estes, 1983). Historically the family has been classified with the scincomorphs. Gauthier (1980) agreed with this classification on the basis of the parietal lappets overlapping the frontals, the regular pattern of enlarged head osteoderms, and the presence of cephalic osteoderms. Estes (1983) classified the Xantusiidae and hypothesized that the scincomorphs are most closely related to the cordylids. The Xantusiidae were relatively common in the Paleocene and Eocene of Wyoming and Montana.

Palaeoxantusia Hecht, 1956

Type species -- Palaeoxantusia fera Hecht, 1956.

Referred species -- Palaeoxantusia borealis Holman, 1972; Palaeoxantusia allisoni, Palaeoxantusia kyrentos Schatzinger, 1980.

Diagnosis -- The generic diagnosis is taken from Hecht (1956), Schatzinger (1980), and Estes (1983), and is unemended. *Palaeoxantusia* is a moderately large, robust xantusiid with a distinct spleniodentary depression, and a distinct groove along the posterolateral margin of the spleniodentary for the adductor mandibulae externus superficialis (Hecht, 1956). Schatzinger (1980) added that the spleniodentary depression is variable and the teeth bear well-developed lateral cusps. *Palaeoxantusia* differs from *Xantusia* in having relatively larger teeth in a more robust dentary, a distinct spleniodentary depression, and a groove for the adductor mandibulae externus superficialis (Hecht, 1956); from *Klauberina* in lacking strong cuspation of the teeth and in being smaller with a lower tooth count; from *Cricosaura* in having a lower tooth number and greater body size.

The dentary is robust and fused with the splenial. Two spleniodentary foramina are present. The larger of these lies just posterior to the last tooth, the smaller and less distinct just posterior to it. A third foramen occurs on the medial surface near the mandibular symphysis. Teeth are excavated at their bases indicating a non-anguinomorph pattern of tooth replacement (Estes, 1983). Although Estes (1983) believed it was not possible to define the genus adequately I believe there are significant shared characteristics, given above, with which to define *Palaeoxantusia*.

Age and distribution -- Middle Paleocene; Montana, middle Eocene; Wyoming and late Eocene; California, USA, Saskatchewan, Canada.

Palaeoxantusia fera Hecht, 1956.

Figures 30, 31, 32, and 33

Type specimen -- AMNH 3815.

Type locality -- Sublette County, Wyoming; Bridger Formation; Middle Eocene.

Diagnosis -- The generic diagnosis is emended from Holman (1972). In dorsal view, the lingual shelf thickens anteriorly. The dental gutter is shallow. The anterior sulcus dentalis has a width equal to the width of the posterior tooth. The coronoid rises sharply in lingual view though it does not project far posteriorly. Its dorsal edge is concave and the bone thin and bladelike in dorsal view. The coronoid incision is shallow, having indistinct borders. On the exterior surface of the dentary are five or less regularly spaced mental foraminae. Where the dentary meets the teeth there is no gap. In dorsal view, the posterior teeth are lingually positioned and the anterior teeth are more labial. The change is gradual and very slight. The teeth have two distinct striations on the crown forming a cutting edge which develops into small accessory cusps in some specimens. There is a small bulbous central cusp as in P. borealis, but no striations on the crown. It differs from P. borealis in having less prominent sulci dentali, lingual facets, and labial adductor fossae. There are five mental foramina.

Previously referred specimens -- AMNH 38121, PU 16775, and PU 16776; Carter County; Montana; Tongue River Formation; middle Paleocene. AMNH specimens; Carbon County, Wyoming; Fort Union Formation; middle Paleocene.

Age and distribution -- Middle Paleocene, Montana; middle Eocene, Wyoming.

Referred specimens -- UM 105113, UM 105796, UM 105797, UM 105798, UM 105799, UM 105800, UM 105801, UM 105802, UM 105803, UM 105804, UM 105805, UM 105806, UM 105807, UM 105808, UM 105809, UM 105810, UM 105811, UM 105812, UM 105813, UM 105814, UM 105815, UM 105816, UM 105817, UM 105818, UM 105819, UM 105820, UM 105821, UM 105822, UM 105823, UM 105824, UM 105825, UM 105826, UM 105827, UM 105828, UM 105110, UM 105829, UM 105830, UM 105831, UM 105832, UM 105833, UM 105834, UM 105835, UM 105836, UM 105837, UM 105838, UM 105839, UM 105840, UM 105841, UM 105842, UM 105112, UM 105843, UM 105844, UM 105845, UM 105846, UM 105111, UM 105847, UM 105848, UM 105849, UM 105850, UM 105851, UM 105852, UM 105853, UM 101472, and UM 102025.

These specimens are referred to <u>Palaeoxantusia</u> <u>fera</u> on the basis of the possession of one or more of the above diagnostic characteristics.

<u>Description</u> -- Most teeth of both the dentary and maxilla are concave, with the tips of the crowns pointing lingually. They have very faint striations. Lingually, on either side of the crown, there are two striations parallel to the edge of the crown and, in most cases, a small, bulbous cusp in the center. The teeth are generally straight in lingual view, and have parallel sides. Some have a vertical groove running up the center of the tooth shaft, in some enlarging near the base of the tooth to form a small, ovoid indentation, especially well displayed in UM 105113. The bases are excavated at their center indicating a non-anguinomorph tooth replacement pattern. Approximately the top one-third of the tooth projects above the jaw parapet and in most specimens the anteriormost teeth of the dentary are inclined anteriorly. At the center of the base of most teeth is an indentation, which is often larger on alternate teeth.

The variation in tooth morphology may be a result of the different position of the teeth in the jaw. For example, UM 105827 represents the posterior part of the mandible and these teeth show very slight lateral cusps with more obvious striations at the crown edges, while UM 105828 is probably from a more anterior part of the ramus and has no lateral cusps and less obvious striae.

UM 105113 is the only specimen that is an almost complete dentary. It contains ten teeth, and is lacking only the very anterior end. Thus, this specimen does not have the characteristic lingually expanded symphysis.

All lower jaw specimens have a closed Meckelian groove and a straight dentary that exhibits regularly spaced mental foraminae in a line approximately half-way up the bone's labial surface. There are five or less foraminae in all specimens, except in UM 105113 which has five in a horizontal row and one on the anterior tip close to the ventral surface. In all other respects this specimen resembles *P. fera*. Ventral to the coronoid process, in labial view (in UM 105821, UM 105826, UM 105110, and UM 105836), there is a small indistinct depression indicating the position of the adductor mandibulae externus superficialis (Hecht, 1956). In dorsal view, the tooth row is straight and the anterior tip of the dentary does not appear to curve lingually to meet its counterpart. There are two sulci dentali where the posterior part of the dentary is preserved. The larger of the two is exhibited by UM 105827 and UM 105836. Both are preserved in UM 105113, UM 105821, UM 105826 and possibly UM 105110. Posterior to the last tooth is a high coronoid process of the dentary exhibiting a deep lingual coronoid incision, preserved in UM 105827, UM 105836 and possibly in UM 105826.

Most of the maxillae are badly broken but do show a straight-sided external surface exhibiting a line of regularly spaced foramina similar to those on the dentary.

Spleniodentary. UM 105110 (Figure 30). Locality; 1126

This specimen consists of the left posterior portion (4.1 mm) of the spleniodentary with both anterior and posterior ends missing. It contains four complete and three broken teeth. All show the entire root, but two have their crowns missing. They all are rod-like and slender with parallel sides and have a circular cross-section and an expanded area near the base of the root. The two most anterior teeth are broken at the base of the crown but are otherwise complete and exhibit small replacement pits at the center of their bases. The third tooth is complete and has a large replacement pit at the center of its base. Just dorsal to the parapet of the jaw there is a slight constriction forming a neck just before the tip of the crown. The tip has two very small accessory cusps on either side of the main cusp, separated by a slight groove. Although Estes (1983) states that P. fera has striations on the crown lingually, none were found in this specimen (under 100x magnification) despite very good preservation. At the tip of the crown there is a small, bulbous central cusp pointing lingually. The three teeth to the posterior of this tooth are of similar morphology. The seventh tooth has a more expanded base and the crown is less distinct as there is no constriction below it. Typically, the teeth alternate between those with large and small replacement pits at their bases. The teeth vary little in size, and exhibit an almost straight row of tooth

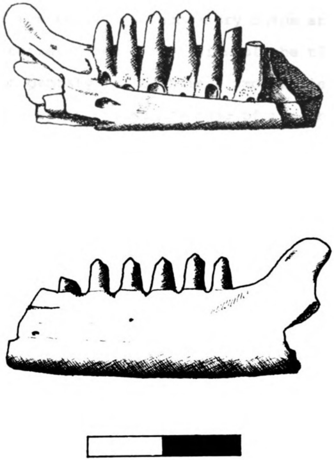

Figure 30. Palaeoxantusia fera. UM 105110. Left dentary, lingual and labial views. Scale bar is 2 mm.

crowns. Therefore, the size of the replacement pit appears unrelated to the size and development of the tooth. On the labial side of the tooth, the accessory cusps are visible only as small butresses on either side of the tip. The transition from dentary to tooth is a smooth one, with the bone seemingly wrapping round the base of the crown with no groove between them.

In lingual view, the jaw has a closed Meckelian groove and a shallow dental gutter. There is no pitting in the dentary bone, except for one large foramen which is positioned directly ventral to the most posterior tooth and is as wide as the width of the tooth's base. It is tear-shaped with a pointed anterior end. The coronoid process of the dentary rises sharply, with a concave dorsal edge, to a point just above the row of tooth tips. The coronoid incision is relatively shallow with an indistinct anterior border and more distinct ventral and posterior borders.

The labial surface of the jaw is smooth with very little pitting. There is one very small, somewhat ventral foramen near the anterior end of the specimen. The dentary profile rises at tooth junctions while there are small indentations between the teeth. The coronoid process is smooth. Ventrally there is a small, semi-circular depression, showing the position of the adductor mandibulae externus superficialis (Hecht, 1956).

In dorsal view, the jaw width increases anteriorly due to the increasing thickness of the lingual shelf. The most posterior tooth occurs slightly lingual to the coronoid process, while anteriorly the teeth are more labial. The coronoid process is thin and bladelike with the anterior end slightly more lingual than the posterior end. Little of the ventral side is visible but it appears to be smooth and evenly rounded.

Dentary. UM 105111 (Figure 31). Locality; 1139

This specimen consists of the left anterior portion (2.8 mm) of the dentary. It contains one complete tooth and seven which have been broken below the crown. The most anterior tooth is broken and is oval in cross-section with its long axis pointing posteriorly. The next tooth is similarly broken and the same shape. The third tooth is broken and also oval in cross-section. More of the root is present, which is rodlike with parallel sides. The fourth tooth is subrounded in cross-section. The root is rodlike with parallel sides and a convex lingual surface. There is a large replacement pit in the center of the base of the root. The fifth tooth looks identical in cross-section. It is the same rodlike shape and has a small replacement pit at its base. The root of the sixth tooth is broken, but it has the same cross-section and shape. The replacement pit is not visible due to the break. The seventh tooth has the same cross-sectional shape for the length of its root, but its lingual side is constricted at the base of the crown giving

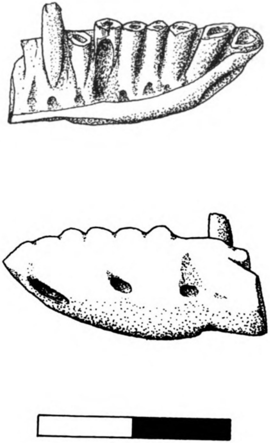

Figure 31. Palaeoxantusia fera. UM 105111. Left dentary, lingual and labial views. Scale bar is 2 mm.

the crown a circular cross-section. The tip is broken but it shows remnants of a longitudinal ridge running across it and then down the edge of the labial surface. There are no striations on the crown. Since most of the replacement pits are missing, it is impossible to see a pattern with respect to size and position in the jaw.

In lingual view, the dentary is smooth with a shallow dental gutter. The dentary's ventral profile is flat until it curves dorsally towards the anterior end. In labial view, the dentary and teeth fit closely together. The dorsal edge of the dentary rises to meet the teeth while between them it is slightly indented. The dentary is smooth except for three large mental foramina. One lies ventrally at the anterior of the dentary under the second and third teeth. It is very large, deep, and ovoid. Posterior to this are two foraminae lying midway down the dentary. The more anterior one is deep, round, and ventral to the fifth tooth, the more posterior one deep, oval, and ventral to the seventh tooth.

In dorsal view, the dentary has a straight labial surface except for the anterior tip which curves lingually. The lingual profile is slightly concave posteriorly, with increased curvature at the anterior end where the dentary is lingually expanded and forms a roughly triangular area. Here, the dental gutter is deep. Lingual to the first two teeth, a dorsal projection overhangs the gutter. All the teeth lie on the lingual edge of the upper dentary and their tips point lingually. The ventral surface is smooth except for an indistinct, shallow, slit-like depression under the expanded anterior end. This depression runs longitudinally along the ventral midline of the dentary. Its posterior border is distinct, while the depression gradually becomes more shallow anteriorly until the area becomes smooth and flat.

Spleniodentary and coronoid. UM 105112 (Figure 32). Locality; 1139

This specimen consists of the left posterior portion of the spleniodentary and the anterior portion of the coronoid (4.8 mm total length). It contains two complete teeth and five teeth broken below the crown. The most anterior tooth is anteroposteriorly compressed with parallel, flat anterior and posterior sides. It is oval in cross-section and has a large replacement pit at the center of its base. The next two teeth have the same shape but the second has a small replacement pit, the third a large one. The first three teeth are broken below the crown. The fourth tooth is complete. It has an oval cross-section and parallel, flat anterior and posterior sides. There is a slight constriction on the lingual surface just ventral to the crown giving the crown a circular cross-section. At the base of the root there is a small replacement pit. A longitudinal ridge runs across the tip and down either side of the crown to end on the lingual surface of the crown. There are no striations. A small bulbous cusp is present at the center of the tip. The fifth tooth is broken below the

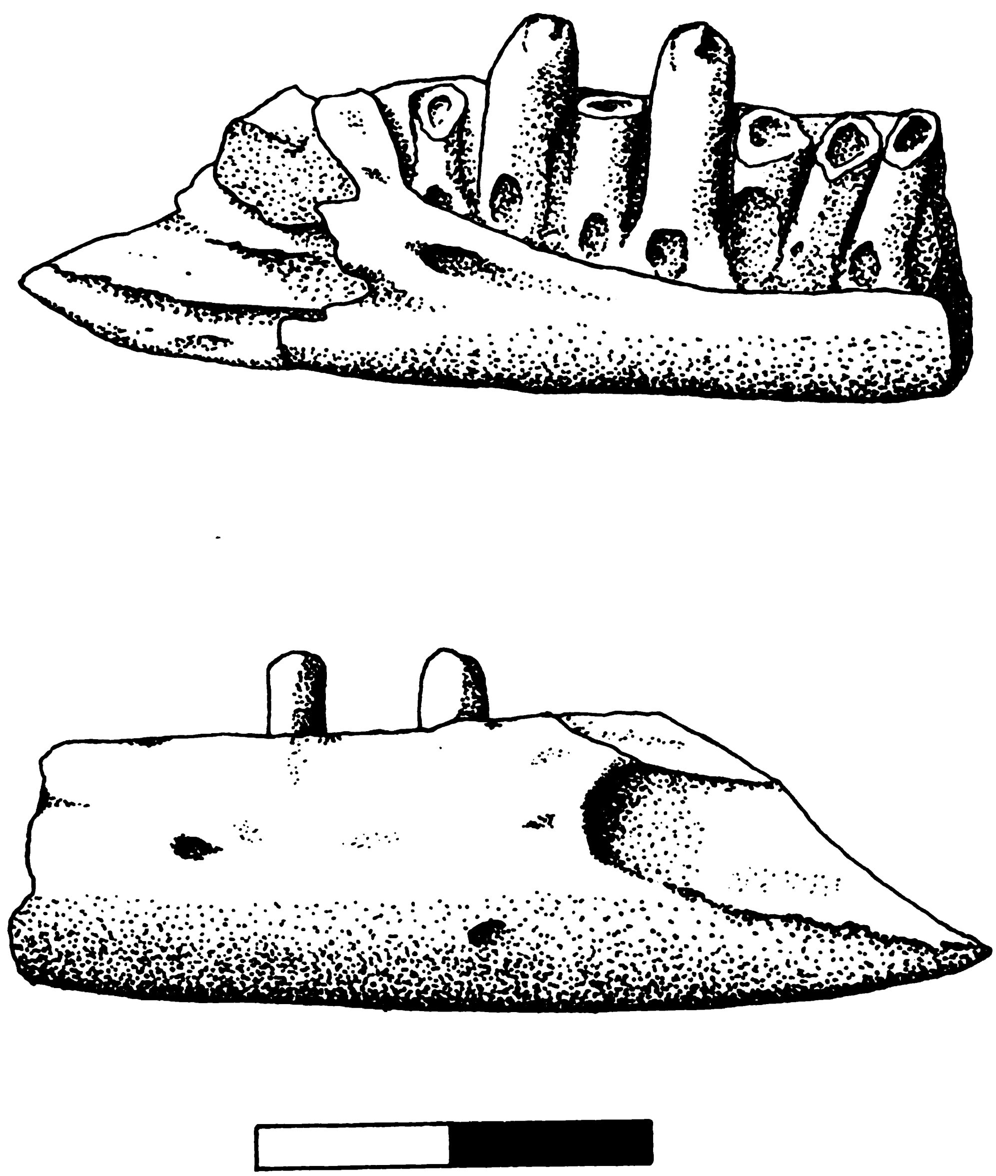

Figure 32. <u>Palaeoxantusia</u> <u>fera</u>. UM 105112. Left dentary, lingual and labial views. Scale bar is 2 mm.

crown and resembles the first three. It has a large replacement pit. The next tooth resembles the fourth except that it has a large replacement pit. The seventh is broken, resembles the first three teeth, and has a small replacement pit. For the most part, the replacement pits alternate from large to small on successive teeth.

In lingual view, the dentary is smooth except for two spleniodentary depressions. The most anterior of the two lies between, and ventral to, the last two teeth. It is the same width as the base of the most posterior tooth. It is ovoid and lies near the dorsal edge of the rounded base of the dentary. The more posterior depression is broken at its midpoint but appears to be oval in shape. It is more ventral than the first, lying on the midline of the rounded dentary. There is a shallow dental gutter which increases in width anteriorly. Most of the coronoid is missing.

In labial view, there is no gap between the dentary and the teeth. There is one tear-shaped, posteriorly positioned mental foramen. There is another slight indentation which may have occurred after death. Posterior to the last tooth there is a depression in the external surface of the coronoid. It is ovoid and slightly concave and indicates the position of the adductor mandibulae externus superficialis (Hecht, 1956). The dentary is slightly pitted, probably due to erosion.

In dorsal view, the teeth appear to point lingually at their tips. The most posterior teeth are positioned on the lingual side of the coronoid, with more anterior teeth becoming successively more labial. This change is gradual and slight. In ventral view, it is possible to see the anterior spleniodentary depression on a small lingual projection of the dentary. The external profile of the dentary is slightly convex. In cross-section the labial surface is also convex.

Spleniodentary. UM 105113 (Figure 33). Locality; 2239

The specimen consists of a portion (6.5 mm) of the spleniodentary, with both the anterior and posterior ends missing. It contains seven complete teeth, two broken below the crown, and one missing tooth. The anterior eight teeth are inclined anteriorly. From the first to the eighth tooth, the angle of inclination decreases until the ninth tooth which is vertical. The most anterior tooth is a partial root, which is sharply inclined anteriorly. At the center of its base is a small replacement pit. The next tooth is round in cross-section and broken below the crown. It has a small replacement pit. The third tooth is complete. The root is anteroposteriorly compressed with anterior and posterior sides flattened. At its base there is a large, central replacement pit. A longitudinal ridge crosses the tip of the crown, then turns ventrally to run along the edge and end on the lingual side of the crown. A small, central, bulbous cusp occurs at the tip. There are no striations. The tip of the fourth tooth is broken but it appears that the crown resembles the tooth anterior to it. The root is circular in

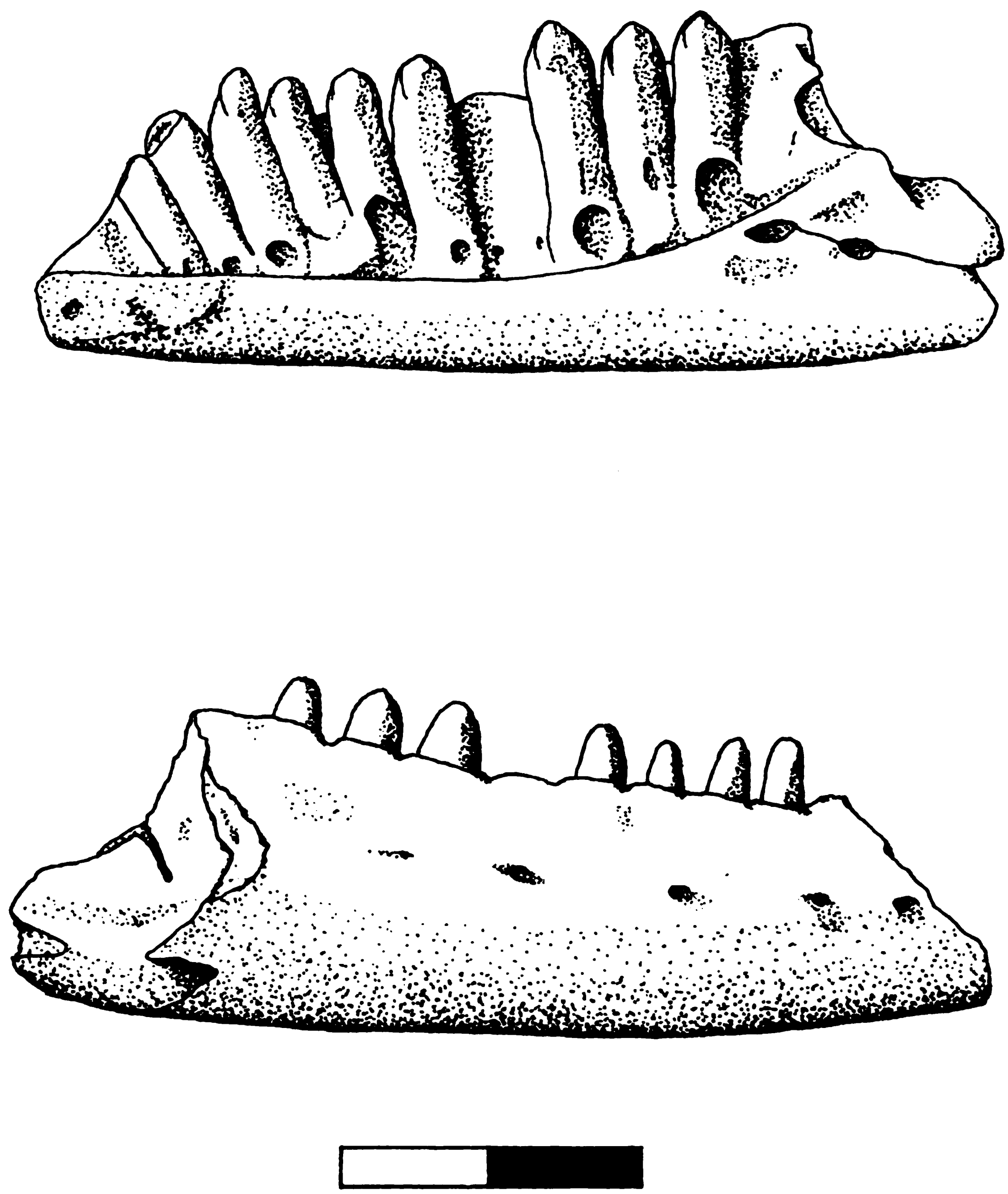

Figure 33. Palaeoxantusia fera. UM 105113. Right dentary, lingual and labial views. Scale bar is 2 mm.

cross-section and has a small replacement pit at the center of its base. A thin layer of bone encircles the base of the tooth. It is high at the edges, low at the center, and has a concave dorsal profile. The fifth tooth is also broken at the tip, but is otherwise identical to the third tooth. Its root is circular in cross-section and contains a large, central replacement pit at its base. The sixth tooth is slightly anteroposteriorly compressed, with flat anterior and posterior sides. Its tip is broken but it appears similar to the preceding ones. Like the fourth tooth, it has a layer of thin bone at its base which contains a small replacement pit. The seventh tooth is missing. The alveoli for this tooth is inclined anterially. The eighth tooth is complete and more conical. There is a slit-like groove just dorsal to the large replacement pit. Its long axis runs up the center of the tooth to about half way up the root. The crown has the same ridge and bulbous central cusps as the others and no striations. The ninth tooth resembles the eighth except that the vertical groove lying dorsal to the small replacement pit is deeper, and it is vertical. The tenth tooth also exhibits this groove but it is very shallow. The entire tooth is curved lingually as opposed to just the crown which is the case for all proceeding teeth. There is a large replacement pit at the center of the base. The crown resembles those described above. The coronoid is partially wrapped around the posterior edge of the tooth.

In lingual view, the dentary is smooth except for two sulci dentali. The more anterior depression lies behind the most posterior tooth and is the same width as the base of this tooth. It is ovoid, and lies towards the dorsal edge of the rounded base of the dentary. The more posterior depression lies more ventrally and on the midline of the rounded dentary. A suture joins the two and runs posteriorly from the posterior depression to the broken end of the specimen. The dental gutter is narrow.

In labial view, the dentary is smooth except for five mental foramina. Those at the anterior end are closer together than those near the posterior, and they are also more ventral. They lie in a line parallel to the dorsal edge of the dentary and are circular to ovoid. There is an additional, very small foramen on the ventral surface near the anterior tip.

In dorsal view, the lingual shelf broadens anteriorly. The most posterior tooth lies lingual to the coronoid process, with the more anterior teeth being slightly labially oriented. The ventral surface is smooth and evenly convex. The external surface of the dentary is smoothly convex, except for the most dorsal part of the external surface which is slightly flattened.

Discussion -- UM 105113 is the only specimen of *Palaeoxantusia fera* that is an almost complete dentary, being broken just posterior to the anterior end. Thus the dentary does not have the characteristic lingually expanded symphysis. The dentary contains ten teeth. By comparison with specimen P84, a posterior right dentary, it is possible to estimate the position of the last tooth. Both specimens exhibit nutritive foramina. Assuming that the most posterior foramen occurs at the same position on the dentary of both specimens it is possible to count back to the most posterior tooth. Similarly, the position of the most anterior sulcus dentalis should correspond. Both these reference points suggest that the most posterior tooth is missing in UM 105113. By comparing the specimen to UM 105111, an anterior left dentary, it is possible to estimate the number of teeth present anterior of the break on UM 105113. The nutritive foramina of P. fera occur in a closely spaced row, except for the most anterior foramen, which is more widely spaced from its neighbor. All five foramina of UM 105113 are closely spaced, thus the break must occur between the anterior two foramina. This suggests that a maximum of four teeth, but possibly only three, are missing. Therefore, UM 105113 has 10 teeth present, one missing tooth within the tooth row, four or possibly three missing anteriorly, and one posteriorly. Thus the number of teeth would have been fifteen, or possibly fourteen. Hecht (1956) gave the tooth number of P. fera as 13-15, while Holman (1972) gave the tooth number for P. borealis as 12-13.

It is impossible to ascertain the position of the first tooth bearing accessory cusps as most specimens are broken at their anterior end or have missing teeth. However, it appears that the first tooth to bear cusps is generally between the sixth and ninth tooth as some positions could be estimated. In UM 105113, the sixth tooth is the first to bear obvious accessory cusps; in UM 105803, the seventh tooth is the most anterior in the jaw and bears cusps; in UM 105809, the eighth tooth bear cusps, the seventh tooth is missing and the sixth lacks cusps; in UM 105812, first on the eighth tooth; in UM 105111, the eighth tooth has accessory cusps, but it is the only tooth present; and in UM 105802, not before the ninth tooth.

<u>Palaeoxantusia</u> <u>borealis</u> Holman, 1972.

Figures 34, 35, and 36

<u>Type specimen</u> -- SMNH 1435.

<u>Type locality</u> -- Hansen Ranch, Saskatchewan, Canada; Calf Creek Local Fauna; Cypress Hills Formation; late Eocene.

<u>Diagnosis</u> -- The specific diagnosis is taken from Holman (1972), and is emended here. The teeth are pleurodont and 12-13 in number with blunt, conical, unicuspid crowns. Some teeth have concave bases that are excavated, indicating a non-anguinomorph type of tooth replacement. Four to five nutrient foramina are present in lateral view. There are four to six irregularly spaced mental foramina on the external

surface of the dentary (Holman, 1972). There is a distinct gap between the dentary and the teeth.

P. borealis differs from P. fera in being smaller, and in having a deeper sulcus dentalis, a more deeply incised lingual notch for the coronoid, external mental foramina that are larger and more irregularly spaced, and a labial adductor fossa that extends more posterially (Holman 1972). Unfortunately the type specimens could not be made available for study.

Previously referred specimens -- SMNH 1436; Hansen Ranch, Saskatchewan; Calf Creek Local Fauna; Cypress Hills Formation; late Eocene.

Age and distribution -- Late Eocene, Saskatchewan.

Referred specimens -- UM 105849, UM 105850, UM 105851, UM 105852, UM 105853, UM 105854, UM 105855, UM 105856, UM 105857, UM 105858, UM 105859, UM 105860, UM 105861, UM 105862, UM 105863, UM 105114, UM 105864, UM 105865, UM 105116, UM 105115, UM 105866, UM 105867, UM 105868, UM 102038, UM 100990, and WPM 81.

These specimens are referred to Palaeoxantusia borealis on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- The teeth are generally straight though some are more bulbous towards the base (UM 105852 and UM 105856). They lack accessory cusps. It is possible that two spleniodentary depressions are seen in UM 105114. The larger one is directly below the most posterior tooth, the smaller one is positioned more posteriorly and ventrally. The larger of the two also appears to be present in UM 105852, UM 105853, UM 105854, and UM 105863, but these specimens are broken at that point.

In ventral view, there is a slit-like groove at the anterior tip of the dentary as seen in UM 105115. Most specimens have five or less mental foramina, typical of P. borealis (Holman 1972) except UM 105115 which has five large foramina in an horizontal row and one at the anterior tip of the dentary close to the ventral surface. In every other respect UM 105115 exhibits the characteristics of P. borealis.

Spleniodentary. UM 105114 (Figure 34). Locality; unknown, Green River Basin

This specimen consists of the left posterior portion (5.7 mm) of the spleniodentary, with both the anterior and posterior ends missing. It has five complete teeth, one broken tooth, and two teeth missing. All but the most posterior tooth are of similar morphology. The most anterior tooth is slightly anteroposteriorly compressed. They have

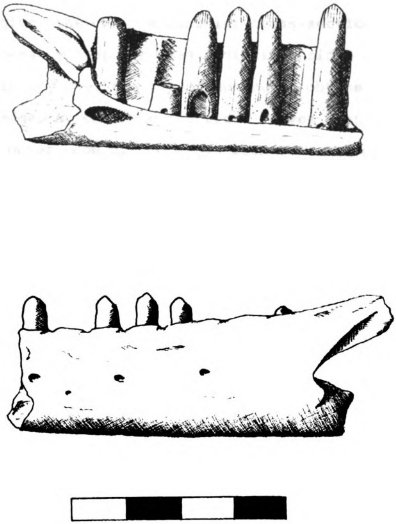

Figure 34. Palaeoxantusia borealis. UM 105114. Left dentary, lingual and labial views. Scale bar is 4 mm.

parallel sides in lingual view, with the posterior and anterior sides flat giving a roughly oval to rectangular cross-section. A lingual constriction dorsal to the jaw parapet gives the crown a circular cross-section. The crown lacks accessory cusps and has a distinct ridge running longitudinally over the tip producing an obtuse, pointed cutting edge. At each end the ridge curves ventrally to run down the outer edge of the crown with the ends converging slightly to end on the lingual surface of the crown. Between these ridges are many, thin striations. The ridge and striations end just dorsal to the parapet of the jaw. At the tip of the crown, in the center, is a bulbous area forming a central cusp from which the striations radiate. The longitudinal ridge passes labial to this, separated from it by a narrow but distinct groove. The bulbous tip points slightly lingually. There are no striations on the labial side of the crown. There is a distinct gap between the tooth and the external surface of the dentary.

The next tooth is missing. The subsequent three teeth are identical to the first except that their bases are slightly expanded. The sixth tooth has only the base of the root present, but appears similar to those previously described. The next tooth is missing. The most posterior tooth is not anteroposteriorly compressed and has no contraction at the base of the crown. It is parallel-sided in lingual view for its entire length and is broader and shorter than the previous teeth. The tip does not appear to have been broken. It lacks the central bulbous cusp and the ridge and striations are less pronounced.

For the most part, the central replacement pits at the tooth bases vary between small and large size in alternate teeth along the tooth row. The last tooth projects only slightly above the parapet of the jaw and has no replacement pit, possibly suggesting that it is only partially grown. In general, the teeth are stouter than those in _Palaeoxantusia fera_ and their tips are blunter and unicuspate.

In lingual view, the dentary consists of the area where teeth attach, and the lingual shelf which thins anteriorly and is less robust than in _P_. _fera_. The dental gutter is deep. The dentary has a closed Meckelian groove and is smooth and unpitted except for a large spleniodentary foramen below the most posterior tooth. It is symmetrical, oval, and wider than the base of the tooth above. Its anterior end lies directly ventral to the anterior side of the last tooth, the posterior end projects slightly posterior of the tooth base. The foramen pierces the dentary exposing the interior of the Meckelian groove. The bone is broken directly posterior to the foramen, however, it is broken in such a way as to suggest the possible presence of a second, more ventral and posterior spleniodentary depression.

The coronoid process of the dentary rises posterior to the last tooth but its dorsal edge is straight. It projects further posteriorly than that of _P_. _fera_, but not as far dorsally above the parapet of the jaw. The lingual coronoid incision is deep, with a strong anterior border running to the tip of the coronoid process, but a very weak posterior border. In labial view, the dentary appears more pitted than P. fera, with four unevenly spaced mental foramina. Three are large, round, evenly spaced, and lie in a horizontal line midway down the dentary. The fourth is smaller and more ventral, lying between the two most anterior foramina. There are slight indentations between the teeth in the dorsal profile of the dentary, but the overall profile is smoother than in P. fera.

In dorsal view, there is no noticeable thickening of the lingual shelf. The coronoid process is wider and more robust than in P. fera. The most posterior tooth is on the lingual side of the coronoid process, almost directly dorsal to the lingual edge of the dentary below. Anterior teeth are positioned more labially. The change is gradual, but more pronounced than in P. fera. The ventral surface appears smooth and evenly rounded. In cross-section, the labial surface is flatter than the heavily convex P. fera.

Dentary. UM 105115 (Figure 35). Locality; 1129

This specimen consists of the right anterior portion (4.4 mm) of the dentary, with the posterior end missing. It contains three complete and five broken teeth. The most anterior five teeth are broken below the crown. Their roots are slightly anteroposteriorly compressed, with the anterior

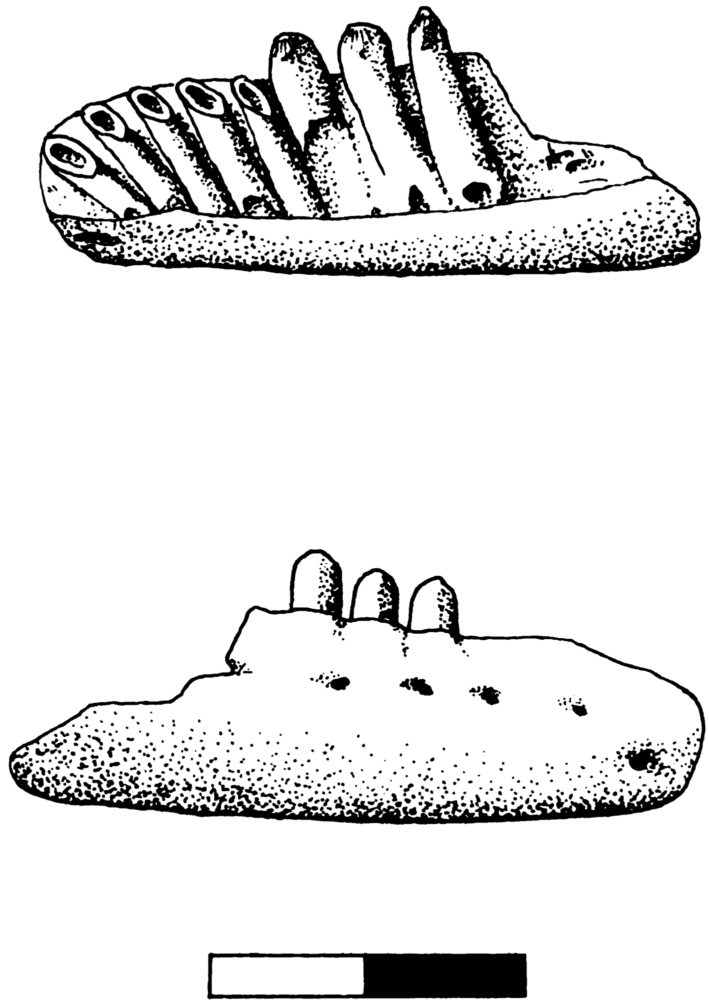

Figure 35. Palaeoxantusia borealis. UM 105115. Right dentary, lingual and labial views. Scale bar is 2 mm.

and posterior sides flattened, giving an oval to rectangular cross-section. All the teeth in the jaw point anterially and have replacement pits at the center of their bases. The sixth tooth has the crown and part of the root present. The most posterior two teeth are complete. The crowns are unicuspate and have a circular cross-section. A longitudinal ridge runs over the tip and then curves ventrally down either side of the crown. As each end of the ridge tapers they turn lingually to end on the lingual surface of the crown. Between them are small, distinct striations radiating from a bulbous, central cusp at the tip. The cutting edge is obtuse and pointed.

In lingual view, the dentary has a closed Meckelian groove, which curves slightly dorsally at the anterior end. The dental gutter is deep. In labial view, the dentary is smooth except for six mental foramina. They are large, symmetrical and circular to oval in cross-section. They are unevenly spaced, with five in a horizontal line slightly dorsal of the mid-point of the dentary. The most anterior foramen is more ventral.

In dorsal view, the tips point slightly lingually. The teeth are positioned in a straight row running down the center line of the jaw. The dentary is straight except for the anterior end which curves slightly lingually. The anterior tip of the dentary is broken and the symphysis is missing, making it impossible to see the extent of expansion at this point. The lingual shelf remains the same width throughout. The ventral surface is smooth. At the anterior tip there is a slit-like depression in the ventral surface running longitudinally along the center line of the dentary.

Maxilla. UM 105116 (Figure 36). Locality; Trap72, 2522

This specimen consists of the left posterior portion (4.73 mm) of the maxilla, with both the anterior and posterior ends missing. It has three teeth, with alveoli for eight more. The most anterior tooth is the largest. It is parallel sided and has a circular cross-section. A longitudinal ridge traverses its tip, turning dorsally to run down the sides and then onto the lingual surface of the crown. On the lingual surface, between the two ends of this ridge there are fine striations radiating from a small, central bulbous cusp. The next tooth is about one-half the size of the first. It is the same shape but its tip has been worn. The most posterior tooth is the smallest. It is of the same shape and is similarly worn. Slightly less than one-half of each tooth projects above the parapet of the maxilla.

In lingual view, the maxilla is thin at the dorsal edge and thickens slightly and irregularly towards the bases of the teeth. Here the teeth attach to a shelf-like projection running the length of the maxilla. It has a straight profile in lingual view. At the seventh tooth from the posterior end the shelf divides into two parts. They diverge slightly and then run parallel to one another. Between them is an indented

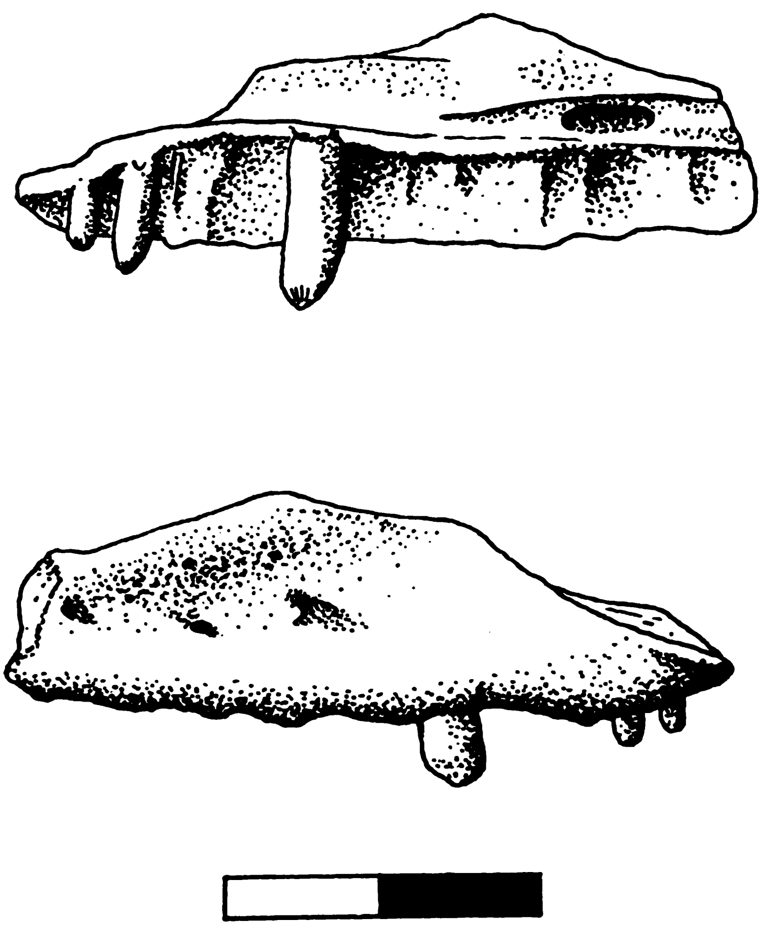

Figure 36. Palaeoxantusia borealis. UM 105116. Maxilla, lingual and labial views. Scale bar is 2 mm.

area containing a large oval depression.

In labial view, the surface of the maxilla is pitted and contains three large vascular foramina. They are circular to oval, deep, and occur at the anterior end of the specimen. There are an addition five small vascular foramina. They too are circular to oval in shape but are more shallow. One lies between the most anterior two large foramina, the others lie more dorsally towards the anterior end of the maxilla. The ventral edge of the maxilla is straight except between the teeth where there are small indentations similar to those on the dentary. There is no gap between the bone and the tooth root. The dorsal profile is concave at the posterior tip, then the edge of the maxilla turns anteriorly and is horizontal until the point where the specimen is broken. This part of the profile runs roughly parallel to the ventral edge of the maxilla, being slightly higher anteriorly.

In cross-section, where the teeth meet the maxilla, the outer surface is slightly convex. Dorsal to this, where the vascular foramina occur, the bone is slightly concave. At its posterior end the maxilla's external surface is flat. In dorsal view, the anterior end of the maxilla appears bladelike, thickening slightly at the maxillary shelf. At the posterior end, the bladelike appearance continues except where it abruptly thickens lingually to form a broad maxillary shelf with a slight longitudinal depression dorsally. In ventral view, the tips of the crowns point lingually, and the area where the teeth meet the maxilla is straight.

Discussion -- The differences seen between P. borealis and P. fera are more significant than those seen between the modern day species Xantusia vigilis and X. henshawi, but less significant than the differences between Xantusia and Klauberina riversiana (Holman, 1972). The lingual shelf in P. borealis does not thicken anteriorly in dorsal view as in P. fera, but thins anteriorly and is less robust. The dental gutter is deep. The anterior sulcus dentalis is wider than the width of the posterior tooth. The coronoid does not rise as sharply as that in P. fera, but extends further posteriorly and has a straight dorsal edge. The coronoid incision is deep with well-defined borders. The teeth are stouter than those in P. fera, and their tips are blunter. They have the same distinct striations as in P. fera, but these do not form slight accessory cusps. Across the tip of the crown is a longitudinal ridge and groove. The crowns have striations radiating from a central bulbous cusp on the lingual surface of the crown. In many specimens, there is a constriction at the base of the crown on the lingual surface. In dorsal view, the posterior teeth are lingual, the anterior teeth more labial, with a more pronounced change than is seen in P. fera. The maxillae contain teeth of the same type, and with the same excavation pattern at their bases, as in the dentary. There are four to six nutritive foramina just dorsal to the tooth row on the external surface.

The Calf Creek specimens described by Holman (1972) possibly represent a new species, separate from P. fera based on these characteristics, but Estes (1983) considered these characteristics to be insignificant. According to Estes (1983), specimens collected in the Bridger Formation of Wyoming, showed considerable overlap between P. fera and P. borealis when they were studied at a later date. However, the specimens collected for this study support the separation of P. fera and P. borealis as described by Holman (1972), since they consistsently exhibit the above suite of diagnostic characteristics. If this is the case, this is the earliest recorded occurrence of P. borealis.

Palaeoxantusia indet.

Figure 37

Referred specimens -- UM 105869, UM 105870, UM 105871, UM 105872, UM 105873, UM 105874, UM 105874, UM 105876, UM 105877, UM 105878, UM 105879, UM 105880, UM 105881, UM 105882, UM 105883, UM 105884, UM 105885, UM 105886, UM 105887, UM 105888, UM 105889, UM 105890, UM 105119, UM 105891, UM 105892, UM 105893, UM 105894, UM 105895, UM 105896, UM 105897, UM 105898, UM 105899, UM 105900, UM 105901, UM 105902, UM 105903, UM 103436 (in part),

UM 103602, UM 103437, UM 104560, UM 104849, WPM 8, and WPM 323.

These specimens are referred to Palaeoxantusia indet. on the basis of the possession of a closed Meckelian groove running the entire length of the dentary, teeth with two distinct striations on the crown, forming a carina, which develop into small accessory cusps in some specimens.

Description --

Dentary. UM 105119 (Figure 37). Locality; 1129

This specimen consists of a portion (5.1 mm) of a left dentary. It contains six broken teeth. The anteriormost tooth is a partial root. It is parallel-sided in lingual view, anteroposteriorly compressed, and has an oval cross-section. The second tooth is a root, broken just ventral to the crown. It is slender, parallel-sided in lingual view, slightly anteroposteriorly compressed, and has an oval cross-section. The next three teeth are partial roots similar to the first. The sixth tooth is similar to the second tooth.

The dentary has a closed Meckelian groove and a thin, distinct lingual shelf. In labial view, there are four regularly spaced mental foramina. The anterior pair are small and round, the posterior pair large and ovoid.

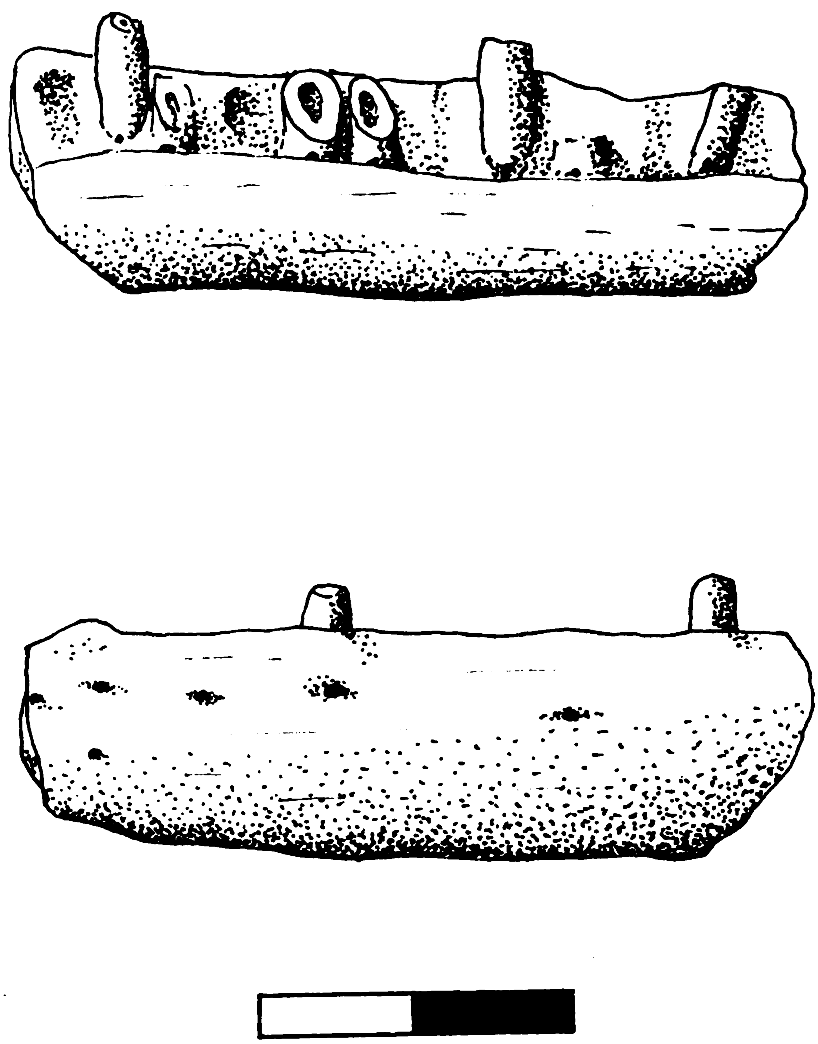

Figure 37. Palaeoxantusia indet. UM 105119. Dentary, lingual and labial views. Scale bar is 2 mm.

Discussion -- These specimens are referred to *Palaeoxantusia* indet. on the basis of the closed Meckelian groove, a unique feature of this genus, and their tooth morphology. However, because the specimens lack the posterior portion of the dentary, where most of the defining characteristics occur, it is impossible to assign them to either *P. fera* or *P. borealis*. However, the combination of characters exhibited by these specimens allows their reference to *Palaeoxantusia* indet. A third species is not indicated.

Infraorder Anguimorpha Fürbringer, 1900

This group contains the sistergroups Anguioidea and Varanoidea. It is characterized by longitudinal rows of enlarged scales on the dorsum, separated by broad areas of granular scutellation. The replacement teeth of the dentary and maxilla tend to originate between older teeth, and then move anteriorly to replace them (Estes, 1983). At maximum adult size, the odontoid, and second and third intercentra, fuse to the axis centrum. There are a large number of presacral vertebrae. The cervical intercentrum is associated with the posteroventral part of the preceding centrum (Gauthier, 1982; Estes, 1983).

Superfamily Anguioidea Fitzinger, 1826

This group contains the Xenosauridae, the Dorsetisauridae and the Anguidae. There are no shared derived characters to define this group, being simply described as more primitive than the varanoids (Estes, 1983).

Family Xenosauridae Cope, 1866

The Xenosauridae is a small, poorly known group of anguimorph lizards with a widespread distribution in the Cretaceous and Tertiary. In this group, tooth succession may be direct or interdental. The cervical hypapophyses are fused, and bear accessory transverse projections on the axis and third cervical. The vertebral column shows only a primitive similarity to anguids (Estes, 1983).

Subfamily Xenosaurinae McDowell and Bogert, 1954

This group has flattened tesserae on the skull roof osteoderms, separated from one another by relatively narrow grooves. The other xenosaurids, Exostinus and Xenosaurus, have subconical skull roof osteoderms that are relatively widely spaced apart.

Restes Gauthier, 1982

Type species -- Restes rugosus (Gilmore 1942).

Referred species -- None.

Diagnosis -- These lizards occur in the late Paleocene and early Eocene of Wyoming. The teeth project relatively far beyond the jaw parapet. Their teeth are blunt, and simple or incipiently bilobed, as in all xenosaurids (Gauthier, 1982). An accessory anterior cusp is present on the posterior dentary and maxillary teeth. They differ from other xenosaurids in having their skull roof osteoderms flattened, and separated by relatively narrow grooves (Estes, 1983). This taxon was originally included in Exostinus (Gilmore,

1928) but has since been placed in the new genus Restes due to the differences in cephalic osteoderms (Gauthier 1982). The frontals are constricted between the orbits yielding an hourglass shape. They are covered with flattened, elongate osteoderms anteriorly, and flattened, sub-rounded osteoderms posteriorly (Gauthier, 1982).

Age and distribution -- Late Paleocene to early Eocene; Wyoming, USA.

Restes rugosus Gilmore, 1942

Figures 38, 39, and 40

(Synonyms -- Exostinus rugosus Gilmore 1942)

Type specimen -- PU 14559.

Type locality -- Park County, Wyoming; Fort Union Formation; late Paleocene.

Diagnosis -- About one-half of the tooth projects above the jaw parapet. The crowns taper to a point, and tend to be bilobate posteriorly. The osteoderms are flattened, subcircular, and slightly raised in their centers. They have an irregular, vermiculate sculpture, consisting of narrow, short grooves in an otherwise flat surface and are separated from one another by grooves. In the most complete maxilla in the collection (UM 105121) they occur in two slightly irregular rows on the bone's external surface. Seven small, regularly spaced, sub-circular foramina lie at the ventral edge of the osteoderms in this specimen.

Previously referred specimens -- PU 14560, PU 14640; from type locality. UCMP 98229, UCMP 100049-100054, and UCMP 119434; Early Eocene, Wasatch Formation, Sweetwater County, Wyoming.

Age and distribution -- Late Paleocene to early Eocene, Wyoming.

Referred specimens -- UM 105904, UM 105120, UM 105905, UM 105906, UM 105907, UM 105908, UM 105909, UM 105910, UM 105911, UM 105912, UM 105122, UM 105913, UM 105914, UM 105915, UM 105121, UM 105916, UM 105917, UM 105918, UM 105919, UM 105920, UM 105921, UM 105922, UM 105923, UM 105924, UM 105925, UM 105926, UM 105927, UM 105928, UM 105929, UM 105930, UM 105931, UM 105932, UM 105933, UM 105934, UM 105935, UM 105936, UM 105937, UM 105938, UM 105939, UM 105940, UM 105941, UM 105942, UM 105943, UM 105944, UM 105945, UM 105946, UM 105947, UM 105948, UM 105949, UM 105950, UM 105951, UM 105952, UM 105953, UM 105954, UM 105955, UM 105956, UM 105957, UM 105958, UM 105959, UM 105960, UM 105961, UM 105962, UM 105963,

UM 105964, UM 105965, UM 105966, UM 104445, UM 104514, WPM 135, and WPM 315.

These specimens are referred to <u>Restes</u> <u>rugosus</u> on the basis of the possession of one or more of the above diagnostic characteristics.

<u>Description</u> --

Dentary. UM 105120 (Figure 38). Locality; Accumulation 24329

This specimen consists of a portion (3.3 mm) of a right dentary. It bears six complete teeth. The anterior most tooth is slightly laterally compressed, with an oval cross-section, and is parallel sided in lingual view. About one half of the tooth projects above the jaw parapet. The crown tapers to a point. The tip is worn, and there are no accessory cusps. The second and third teeth are similar except that their crowns bear carinae extending along the tips and sides of the crowns. The fourth tooth is similar except that the root is missing. The fifth is also the same but the tip of the crown is missing. The sixth tooth is the same except that it is slightly recurved, to point posteriorly. It bears a carina, but the tip of the crown is missing.

In lingual view, the Meckelian groove is fused with a visible join running the length of the dentary where the bone

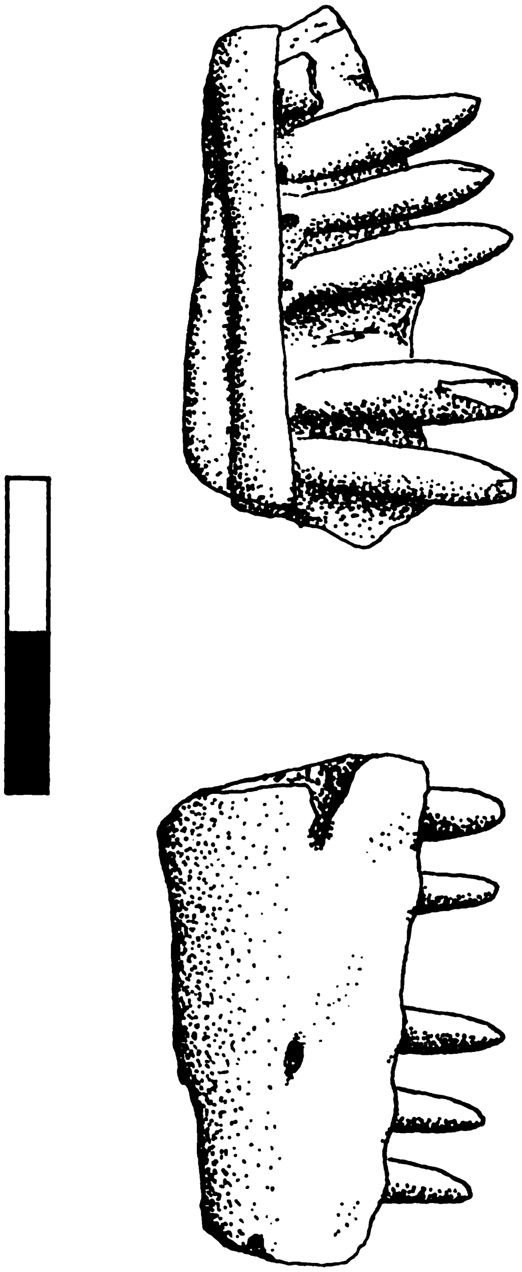

Figure 38. <u>Restes</u> <u>rugosus</u>. UM 105120. Right dentary, lingual and labial views. Scale bar is 2 mm.

has grown together. The lingual shelf is robust and thins posteriorly. The ventral edge of the dentary is cracked, pitted and missing ventrally. In labial view, the dentary is smooth except for some post-mortem cracking ventrally, and two mental foramina. The anterior foramen is circular, the posterior ovoid, and both lie slightly closer to the dorsal edge of the dentary than to the ventral edge. In dorsal view, the lingual shelf is narrow and maintains the same thickness for the entire dentary.

Maxilla. UM 105121 (Figure 39). Locality; 1129

This specimen consists of the anterior portion (4.4 mm) of a left maxilla. It bears seven broken teeth, all partial roots. They are circular in cross-section and parallel sided in lingual view. The maxillary shelf, in lingual view, is thin at its lingual edge. From here is slopes dorsally towards the labial edge. It is smooth and flat with one small, oval foramen. On the labial surface there is a dorsal projection. It is high anteriorly with the dorsal tip pointing lingually. The anterior and posterior sides slope ventrally from the dorsal tip. Anteriorly, the projection forms a low ridge running from the lingual to labial side of the maxillary shelf. Anteriorly, the maxilla tapers to a blunt point, and its dorsal edge is concave.

There are seven osteoderms, which are flattened, subcircular and slightly raised in their centers. They have

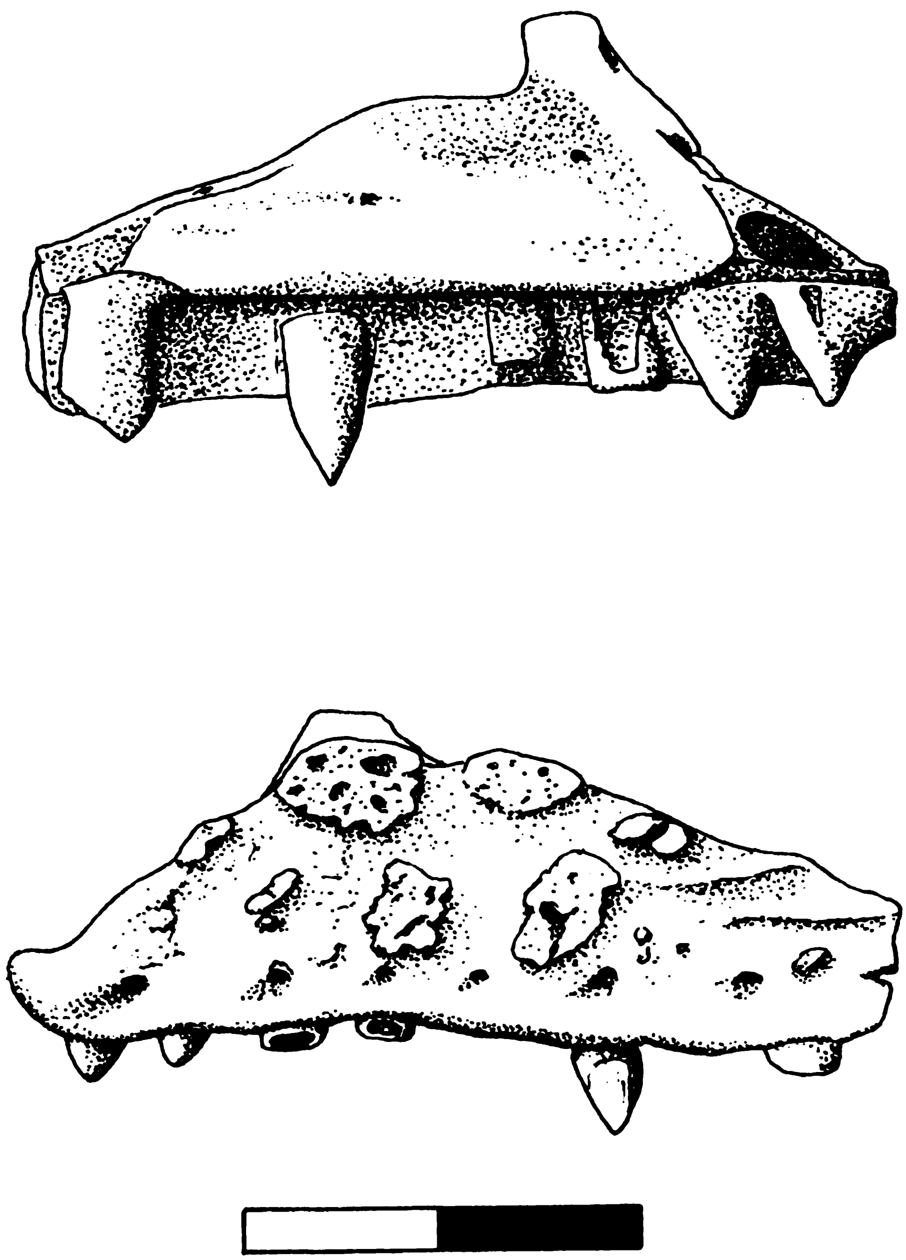

Figure 39. Restes rugosus. UM 105121. Left maxilla, lingual and labial views. Scale bar is 2 mm.

irregular sculpture consisting of narrow, short grooves on an otherwise flat surface. Osteoderms are separated from one another by grooves. They occur in two slightly irregular rows, one dorsal to the other. The most dorsal row consists of three relatively large osteoderms, the most ventral row has five smaller osteoderms. Seven small, regularly spaced, sub-circular foramina lie at the ventral edge of the osteoderms.

Maxilla. UM 105122 (Figure 40). Locality; 1125

This specimen consists of a portion (2.2 mm) of a right posterior maxilla. It bears two complete teeth and one broken one. The most anterior tooth is a partial root. The second tooth is complete. The root is parallel sided in lingual view, and slightly anteroposteriorly compressed at its base. The crown is laterally compressed, and tapers to a point. The root of the third tooth is similar to the first. The crown tapers to a blunt, bilobed tip. One, small accessory cusp is present on the anterior side of the crown, separated from the main cusp by a shallow groove.

The maxillary shelf is flat and horizontal. It is punctured by an ovoid foramen. The labial surface of this maxilla bears only three preserved osteoderms. They are flattened, subcircular with slightly raised centers. They have an irregular vermiculate sculpture and are separated from one another by grooves. They occur in an irregular row.

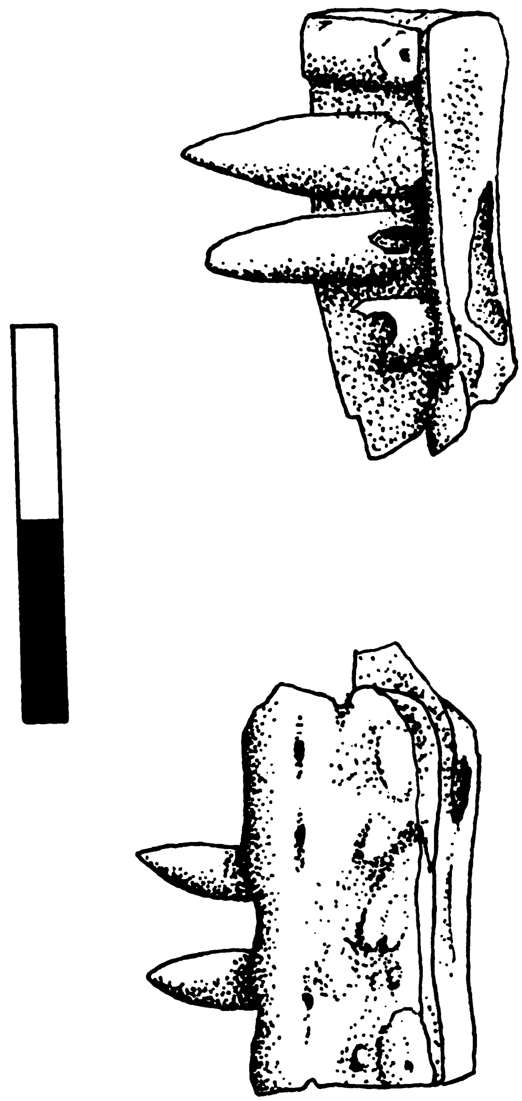

Figure 40. __Restes__ __rugosus__. UM 105122. Right maxilla, lingual and labial views. Scale bar is 2 mm.

Along the ventral edge of the osteoderms is a row of four, ovoid mental foramina. The ventral edge of the maxilla is irregular, being indented between the teeth.

Discussion -- Gauthier (1982) described Restes rugosus in detail. The specimens in this assemblage are assigned to this species on the basis of their close resemblance to Gauthier's specimens, and presence of simple teeth anteriorly and bilobed teeth posteriorly.

Family Anguidae Gray, 1825

The Anguidae first appeared in the Upper Cretaceous, and reached their greatest diversity in the early Tertiary (Gauthier, 1982). They include the Anguinae, the Glyptosaurinae, the Gerrhonotinae and the Diploglossinae (Meszoely, 1970). The family is characterized by having a reduced supratemporal arch and narrowed supratemporal fenestra. The angular process of the dentary is reduced and the surangular occurs well forward of the coronoid. The dentary forms the dorsal and anterior border of the anterior alveolar foramen. The cutting edge of the tooth forms an inward pointing 'V' shape in occlusal view and the crown is often pointed posteriorly producing a recurved, chisel-like tooth. The caudal vertebrae have converging transverse processes. Ventral body osteoderms are present. Rectangular, imbricate scales and osteoderms enclose the body and tail except for the lateral fold and some areas of the limbs and neck. The frontoparietal scales are reduced while the frontal and parietal scales are of larger size. There is an odd number of interparietal scales.

Subfamily Anguinae Gray, 1825

The Anguinae consist of a group of lizards with reduced or absent limbs. The surangular and angular extend far forward of the coronoid. The frontoparietal scales are small, and far from the midline. The presacral vertebrae are flattened ventrally. The second sacral vertebra has lymphapophyses forming transverse processes. The caudal hemal arches are well forward, and fused to the centra (Estes, 1983).

Machaerosaurus Gilmore, 1928

Type species -- *Machaerosaurus* *torrejonensis* Gilmore 1928

Referred species -- ?*Machaerosaurus* *pawneensis* Gilmore 1928

Diagnosis -- The labial surface of the crown is unstriated, the lingual surface is grooved. There are thirteen to fourteen maxillary teeth. Two distinct grooves appear on the posterior maxillary teeth, with the anterior groove being more pronounced than the posterior one. Both extend to the tooth base. The anterior maxillary teeth, and all dentary teeth, bear only one anterior groove, which ends about one-half way down the tooth shaft. The teeth are laterally compressed, slightly recurved, and project about one-half of their height above the parapet of the jaw (Sullivan, 1982).

Age and distribution -- Middle Paleocene, New Mexico, and middle Oligocene, Colorado and Nebraska, USA.

Machaerosaurus torrejonensis Gilmore, 1928

Figures 41, 42, 43, and 44

Type specimen -- AMNH 5184

Type locality -- East Fork Torrejon Arroyo, San Juan County, New Mexico, Torrejonian Formation, Paleocene.

Diagnosis -- The teeth are laterally compressed and recurved. Their crowns taper to a point. They have a round cross-section except for two blade-like ridges running down the anterior and posterior sides of the crown, forming a carina. Striations occur at right angles to the carina running down the lingual surface of the crown. The posterior maxillary teeth have two grooves on the crown's lingual surface.

Previously referred specimens -- AMNH 12034, AMNH 12047, AMNH 12050, AMNH 12051, AMNH 12055, AMNH 12063, AMNH 12066, AMNH 12068, AMNH 12087, AMNH 12092, AMNH 12094, AMNH 12095, AMNH 12097, AMNH 12099, AMNH 14303, AMNH 14311, AMNH 14327, AMNH 14898, AMNH 14899, AMNH 15908, AMNH 15909, AMNH 15911, AMNH 15913, AMNH 15914, AMNH 15931, AMNH 15935, AMNH 15936, AMNH 15951, AMNH 16008, AMNH 16010, and AMNH 16100; Swain Quarry, "Fort Union Formation" middle Paleocene (Torrejonian), Carbon County, Wyoming.

Age and distribution -- Middle Paleocene, New Mexico.

Referred specimens -- UM 105967, UM 105968, UM 105969, UM 105130, UM 105970, UM 105971, UM 105972, UM 105973, UM 105974, UM 105133, UM 105975, UM 105131, UM 105976, UM 105132, UM 105977, UM 104142, and UM 104143.

These specimens are referred to *Machaerosaurus torrejonensis* on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Maxilla. UM 105130 (Figure 41). Locality; 1129

This specimen consists of a small piece of bone (2.3 mm long), bearing one complete tooth. It is probably a posterior maxilla since the tooth bears two grooves on the crown's lingual surface as in the description by Sullivan (1982). Only the subdental platform and a portion of the exterior surface of the bone are present. The tooth root is laterally compressed and parallel-sided in lingual view, except for an expanded base. The crown tapers to a point. Its central portion is round in cross-section. Blade-like ridges form a carina on the anterior and posterior edges of the crown.

Dentary. UM 105131 (Figure 42). Locality; unknown, Green River Basin

This specimen consists of a portion (3.7 mm) of a left posterior dentary. It contains four complete teeth and one broken one. The first is a root. It is slightly recurved, laterally compressed, parallel-sided in lingual view, and has a replacement pit at the center of its base. The next four teeth have a root similar to the first. The crowns taper to a point. The center has a round cross-section, and the anterior and posterior sides bear a blade-like edge forming the carina. There are striations at right angles to the carina

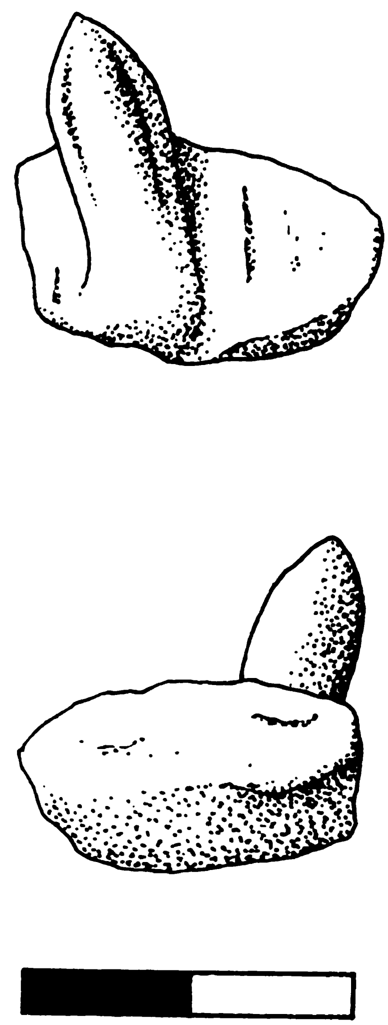

Figure 41. Machaerosaurus torrejonensis. UM 105130. Maxilla, lingual and labial views. Scale bar is 2 mm.

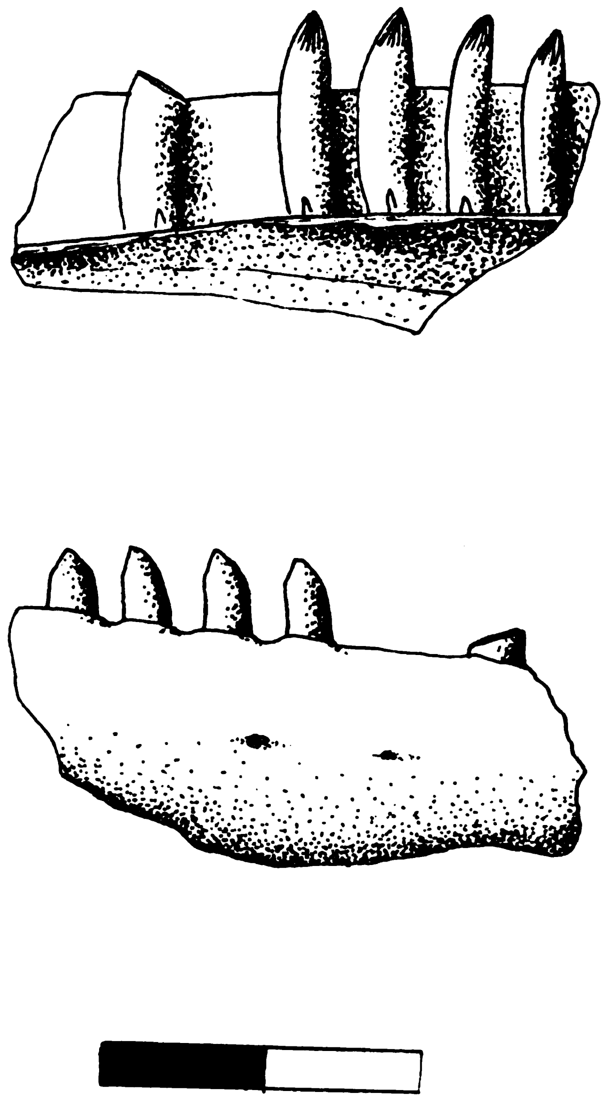

Figure 42. Machaerosaurus torrejonensis. UM 105131. Dentary, lingual and labial views. Scale bar is 2 mm.

over the lingual surface of the crown.

The lingual shelf and ventral edge of the dentary are missing. The sub-dental platform is inclined at 45 degrees from vertical. The Meckelian groove is closed, and infilled by the splenial. In labial view, the dentary is smooth except for two deep, ovoid mental foramina. The dorsal edge of the dentary is irregular, being indented between the teeth. In dorsal view, the lingual and labial edges of the dentary are straight.

Maxilla. UM 105132 (Figure 43). Locality; unknown, Green River Basin

This specimen consists of a portion (5 mm) of a posterior right maxilla that contains four complete teeth and one broken one. The first tooth has a root that is recurved, laterally compressed and parallel-sided in lingual view. The crown tapers to a point. It has a round cross-section except for two blade-like ridges running down the anterior and posterior sides of the crown, forming a carina. It points lingually and posteriorly. Striations occur at right angles to the carina running down the lingual surface of the crown. The second tooth is the same except that it has a worn tip. The third is the same as the first. The fourth also has a worn tip, and the fifth is a partial root.

In lingual view, the maxillary shelf is thin, straight, and horizontal. On its labial side is the dorsal projection

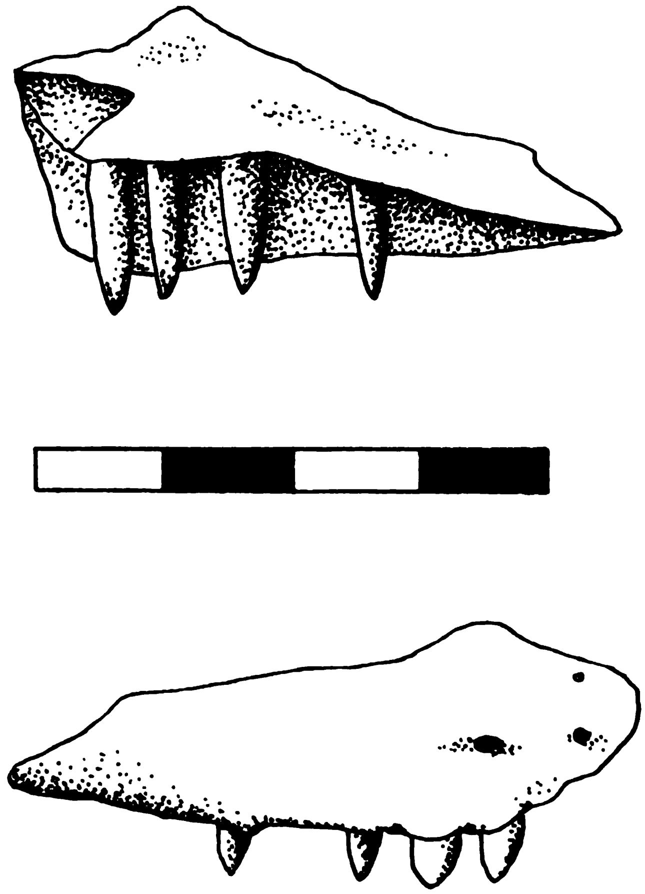

Figure 43. Machaerosaurus torrejonensis. UM 105132. Maxilla, lingual and labial views. Scale bar is 4 mm.

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of the maxilla, which has its dorsal end missing. The maxillary shelf is flat, except for a large ovoid foramen dorsal to the first tooth. The posterior end of the maxilla tapers to a point, the anterior end is missing. In labial view, the surface is smooth except for two mental foramina. The anterior foramen is round and deep and at the anterior end of the specimen. The posterior one is also round and deep and dorsal to the gap between the first and second tooth. In cross-section, the external surface of the maxilla is flat and vertical. In dorsal view, the maxillary shelf is parallel-sided except where it tapers to a point posteriorly, and where it is lingually expanded dorsal to the first and second teeth.

Maxilla. UM 105133 (Figure 44). Locality; 1127

This specimen consists of a portion (5.1 mm) of a left maxilla, containing two complete teeth and one broken one. The anterior most tooth is a partial root with a round cross-section. The next two teeth have roots that are parallel-sided in lingual view, slightly laterally compressed, and have a replacement pit at the center of their bases. The teeth are recurved and point lingually and posteriorly. The crowns taper to a point. They have a round cross-section except where a blade-like ridge runs along the anterior and posterior edges of the crown forming a carina. Striations run at right angles from the carina down the lingual surface of

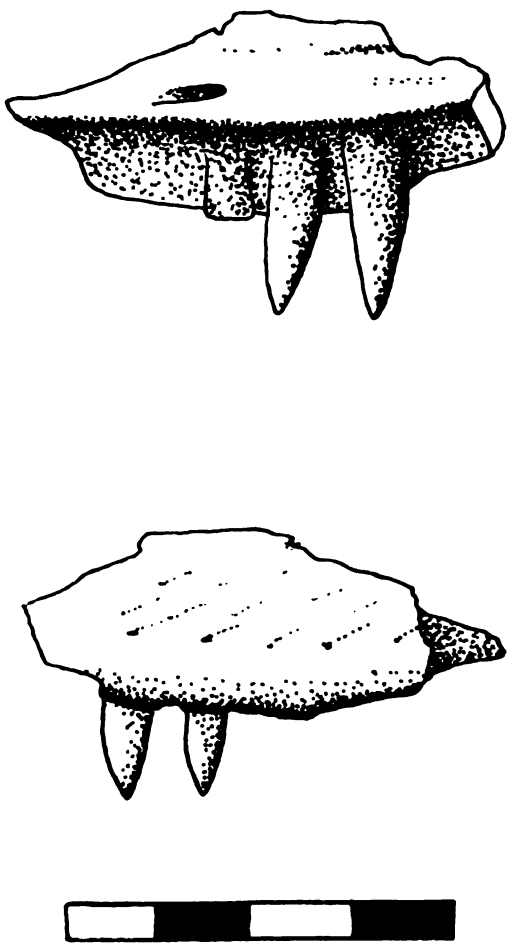

Figure 44. Machaerosaurus torrejonensis. UM 105133. Maxilla, lingual and labial views. Scale bar is 4 mm.

the crown.

In lingual view, the maxillary shelf is thin, straight, and horizontal. On its lingual side is the dorsal projection of the maxilla. It is flat and smooth except for a large, oval foramen dorsal to the alveolus between the first and second teeth. It is deep and distinct, and points anteriorly. The labial surface of the maxilla is smooth except for six irregularly spaced, oval mental foramina. Five lie in a straight line near the ventral edge of the maxilla. One lies dorsal to the line mid-way along the maxilla. Dorsal to the foramina the bone surface is irregular, perhaps showing impressions of the osteoderms. In dorsal view, the exterior edge is straight, while the interior edge is lingually expanded dorsal to the alveolus between the first and second teeth.

<u>Discussion</u> -- This is a group of Paleocene and Oligocene anguids from western North America. <u>Machaerosaurus</u> was first described by Gilmore (1928) as a new species based on a fragmentary skull and lower jaws. He originally assigned <u>M</u>. <u>pawneensis</u> to <u>Xestops</u>? <u>pawneensis</u>. Meszoely (1970) included <u>M</u>. <u>torrejonensis</u> in <u>Pancelosaurus</u>, but Meszoely, Estes and Haubold (1978) showed that <u>M</u>. <u>torrejonensis</u> is closely related to <u>Odaxosaurus</u> on the basis of its simple, conical, unstriated teeth, the extension of the surangular on the labial surface of the jaw anterior to the coronoid, and the similarity in frontal bone sculpture. They also concluded

that M. torrejonensis and M. pawneensis are congeneric, but because of time and climatic differences they retained them as separate species. Sullivan (1982) considered M. pawneensis more closely related to Ophisaurus, and believed that it should be described as a new species of that genus.

Since Machaerosaurus pawneensis is thought to be either conspecific with M. torrejonensis (Meszoely, Estes, and Haubold, 1978), or a species of Ophisaurus (Sullivan, 1982), the University of Michigan specimens are assigned to M. torrejonensis, the only species confidently referred to Machaerosaurus.

Subfamily Anniellinae Nopcsa, 1928

This group includes Anniella and Apodosauriscus. Both are tiny, fossorial lizards having the following shared derived characters; Small size, the splenial is exposed laterally, the tooth number is reduced, the intramandibular septum is reduced, the anterior inferior alveolar foramen (equivalent to the sulcus dentalis in other anguimorphs) is wide, shallow, and lies ventral to the fourth or fifth tooth from posterior, there is a prominent subdental shelf bearing a notch dorsal to the anterior inferior alveolar foramen, the ventral dentary surface is broad and flattened, and the tail is short relative to the body. This group shares some derived features with the anguids - subrectangular, moderately imbricate, sculptured osteoderms, the shape of the frontals,

chisel-shaped, striated, unicuspid, obtusely-pointed teeth, an intramandibular septum with a free posteroventral margin, reduction of the posteroventral margin of the lateral dentary wall, a notch in the subdental shelf marking the position of the anterior inferior alveolar foramen - therefore they are considered a subfamily of the Anguidae (Gauthier, 1982; Estes, 1983). This taxon differs from all other anguimorphs in that the Meckelian groove is visible in lingual view (McDowell and Bogert, 1954; Estes, 1964) and that the dentary is wider than tall for much of its length, with a broad, flattened ventral surface (Gauthier, 1982). Many of the features of the dentary, such as the anterior position of the anterior inferior alveolar foramen and reduced teeth, are related to their fossorial habit (Bellaris, 1950). Also they are limbless, and the high ratio of body to caudal osteoderms found may indicate a short tail typical of burrowing forms, however, this combination of characters occurs only in the anniellids (Gauthier, 1982).

<u>Apodosauriscus</u> Gauthier, 1982

<u>Type species</u> -- <u>Apodosauriscus</u> <u>minutus</u> Gauthier, 1982

<u>Referred species</u> -- None

<u>Diagnosis</u> -- <u>Apodosauriscus</u> differs from <u>Anniella</u> in being twice the size, in having twice as many dentary teeth

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which are lower crowned, less widely spaced, less sharply pointed, and less recurved, in having an intramandibular septum with a small, free ventral border, in having frontals bearing a fused osteodermal crust, in having separate pre- and post-frontal osteoderms, in having relatively large, subrectangular body osteoderms (Gauthier, 1982; Estes, 1983), and in having the anterior inferior alveolar foramen ventral to the fourth and fifth tooth (Gauthier, 1982). The dentary is short and robust and contains thirteen to fourteen teeth. This is a much lower number than in most anguids, and is probably related to their fossorial habit as shown in the study by Edmund (1969) on the relationship between tooth number and increasing fossoriality. Edmund (1969) showed a correlation between low tooth number and fossoriality due to the shorter jaws and skulls in burrowing animals. These characteristics make the skull more robust, a necessary trait in burrowing forms. The teeth project about one third above the parapet of the jaw. They are pleurodont, relatively small, and closely spaced. The roots are slightly anteroposteriorly compressed and are oval in cross-section. The crowns are slightly laterally compressed and may have faint vertical striations on the lingual surface. Tooth apices are pointed posteriorly, and tend to be twisted about the long axis of the teeth (Gauthier, 1982).

Age and distribution -- Lower Eocene, Wyoming, USA.

Apodosauriscus minutus Gauthier, 1982

Figure 45

Type specimen -- UCMP 100125.

Type locality -- Locality V-70246, Oh! locality, Sweetwater County, Wyoming; Wasatch Formation; early Eocene.

Diagnosis -- The dentary is robust, and wider than tall. The ventral surface is broad and flat. The Meckelian groove is widely open posteriorly, closed anteriorly. The coronoid does not extend anteriorly as far as the last dentary tooth. The teeth are pleurodont, small, closely spaced, slightly recurved, and may have faint striae lingually. The splenial extends far forward on the dentary. The maxilla has a steeply rising nasal process. The osteoderms are thin, subrectangular, longer than wide, and may be slightly keeled. The articulation surface lies along the anterior margin and is continuous with the lateral keel (Estes, 1983). The osteoderms of *A. minutus* differ from those of *Eodiploglossus* in being flatter, having a thinner articulating surface along the short edge of the osteoderm which has a straight border with the sculptured area, and in lacking a ridge on the inner surface of the osteoderm.

Previously referred specimens -- UCMP 100056, UCMP 100057, UCMP 100059, UCMP 100103, UCMP 100112,

UCMP 100118, UCMP 100126, UCMP 100128, UCMP 100138, UCMP 100139, UCMP 100145, UCMP 100149, UCMP 100154, UCMP 100155, UCMP 100157, UCMP 100158, and UCMP 116548; Locality V-70246, Oh! locality, Sweetwater County, Wyoming; Wasatch Formation; early Eocene.

Age and distribution -- Early Eocene, Wyoming (USA).

Referred specimens -- UM 105978, UM 105123, UM 105979, UM 105980, UM 105981, UM 105982, UM 105124, UM 105983, and UM 105984.

These specimens are referred to Apodosauriscus minutus on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Dentary. UM 105124 (Figure 45). Locality; 1127

This specimen consists of a small portion (4.2 mm) of a dentary. It contains four partial roots and one alveolus. The teeth are closely spaced and anteroposteriorly compressed, with oval cross-sections and parallel sides in lingual view. Small replacement pits lie at the center of their expanded bases. The dentary is robust, and wider than tall. The lingual shelf is narrow in dorsal view. The Meckelian groove

Figure 45. <u>Apodosauriscus minutus</u>. UM 105123. Osteoderm, exterior and interior views. UM 105124. Dentary, lingual and occlusal views. Scale bar is 4mm.

is closed, indicating that this specimen represents a portion of the anterior part of the jaw. The surface of the dentary is smooth except for one ovoid mental foramen on the labial surface. The ventral surface is broad and flat.

Body osteoderm. UM 105123 (Figure 45) Locality; 2145

This specimen is 3 mm long. It is subrectangular, with a slightly raised center. On the dorsal surface, articulation surfaces occur on two sides. One lies along one short edge. It is narrow and has a straight border with the sculptured area. The second lies along the lateral edge, and is beveled and triangular. It is relatively wide where it contacts the first surface. From here, it tapers to a point that ends before the corner of the osteoderm. The sculpture pattern consists of many short, vermiculate, ridges and grooves. The ventral surface is smooth and slightly concave.

Discussion -- Only three dentaries and a few osteoderms are present in the collection, which is probably a result of collection bias due to the exceedingly small size of the lizard, which is the smallest found in the assemblage. Gauthier (1982) discussed the diagnostic characters for *Apodosauriscus minutus*, all of which were associated with the skull and jaws, except for size. Most of the characteristics of the skull and jaws are related to the size of the lizard, and its fossorial habit (Gauthier, 1982). Although all three dentaries in the assemblage are poorly preserved, their features agree with those given by Gauthier (1982). The size of the osteoderms is the only good indication that they belong to _A_. _minutus_, and they could belong to any anguid. However, I tentatively assign them to _A_. _minutus_, following Gauthier (1982), as they have an identical morphology to the osteoderms associated with the skull material referred to _A_. _minutus_ in that paper.

Subfamily Glyptosaurinae Marsh, 1872

This genus may be distinguished from all other anguids on the basis of size and the form of the sculptured surface of the osteoderms (Gauthier, 1982). The glyptosaurines generally have robust, obtuse cheek teeth. The crowns have a horizontal cutting edge and are striated lingually and labially, the shafts are expanded lingually. Osteoderms on the body are subrectangular, keeled or unkeeled, with poorly developed lateral bevels and rugose or interdigitating lateral margins. Osteoderms of the head and body have tubercular sculpture (Estes, 1983).

Tribe Melanosaurini Sullivan, 1979

This taxon is definable only by primitive character states and is therefore probably paraphyletic. Genera retain a regular pattern of epidermal scales underlying the osteoderms (Estes, 1983).

Xestops Cope, 1873.

Type species -- Xestops vagans Marsh, 1872.

Referred species -- Xestops? gracilis (Oreosaurus gracilis, Xestops gracilis Cope, 1873), Xestops? lentus (Oreosaurus minutus), Xestops? microdus (Oreosaurus microdus), Xestops? minutus (Oreosaurus minutus) Marsh, 1872; Xestops abderhaldeni (Placosauriodes abderhaldeni), Xestops weigelti (Placosauriops weigelti) Kuhn, 1940; Xestops stehlini Hoffstetter, 1962.

Diagnosis -- This taxon is made up of Eocene glyptosaurines from North America and Europe. It is the most primitive of the glyptosaurine genera to achieve the specializations of the subfamily Glyptosaurinae given above, yet still retain the primitive anguid frontal and parietal osteoderm pattern and epidermal scale impressions (Estes, 1983). Xestops differs from Odaxosaurus and Proxestops in having some keeled osteoderms.

The osteoderms have bevelled lateral edges and prominent keels. The osteoderms of the body and head are tuberculate. The frontals are paired. The labial extent of the surangular is at the same level as the anterior extent of the coronoid. The dentary reaches the anterior surangular foramen. On the lingual side, the coronoid extends anteriorly to the most posterior tooth. The teeth are pleurodont, with small bases and crowns that are bluntly wedge-shaped with a strong bevel on their external surfaces. Tooth crowns have striations meeting the tooth edge at right angles and at the tip is a low longitudinal ridge. The tooth shaft is sometimes flattened on the anterior and posterior sides. The teeth are generally indistinguishable from <u>Peltosaurus</u>. The vertebrae are distinguished by the presence of a deep, longitudinal, broad groove on the ventral surface of the centrum, and in having the chevrons attatched on either side of a prominent ridge (Gilmore, 1928).

<u>Age and distribution</u> -- Middle Eocene; Wyoming, USA, Germany to late Eocene; Switzerland.

<u>Xestops</u> <u>vagans</u> Marsh, 1872.

Figures 46, 47, 48, and 49

(<u>Synonyms</u> -- <u>Oreosaurus</u> <u>vagans</u> Marsh 1872; <u>Xestops</u> <u>vagans</u> Cope, 1873; <u>Dimetopisaurus</u> <u>wyomingensis</u> Hecht, 1959.)

Type specimen -- USNM 16532

Type locality -- Uinta County, Wyoming, Bridger Formation, middle Eocene.

Diagnosis -- *Xestops vagans* differs from *X. stehlini* in having paired frontals; and from *X. abderhaldeni* and *X. weigelti* in being larger, having pronounced tuberculation of the osteoderms, and having more parallel-sided frontals. The tooth crowns are expanded, spatulate and bilobate with a central bulbous cusp where the tip points lingually. Some exhibit a strong bevel on their external surfaces. Tooth crowns have few but very distinct striations meeting the tooth edge at right angles, where there is a low longitudinal cutting ridge.

Previously referred specimens -- AMNH 3819 and AMNH 3834; Sublette County, Wyoming; Bridger Formation; Middle Eocene.

Age and distribution -- Middle Eocene, Wyoming.

Referred specimens -- UM 105985, UM 105986, UM 105987, UM 105988, UM 105989, UM 105990, UM 105991, UM 105992, UM 105993, UM 105994, UM 105995, UM 105996, UM 105997, UM 105998, UM 105999, UM 106000, UM 106001, UM 106002, UM 106003, UM 106004, UM 106005, UM 106006, UM 106007,

UM 106008, UM 106009, UM 106010, UM 106011, UM 106012, UM 105126, UM 105125, UM 106013, UM 106014, UM 106015, UM 106016, UM 106017, UM 106018, UM 106019, UM 106020, UM 106021, UM 106022, UM 106023, UM 106024, UM 106025, UM 106026, UM 106027, UM 106028, UM 106029, UM 106030, UM 106031, UM 106032, UM 106033, UM 103785 (in part), UM 102835 (in part), UM 103535 (in part), UM 102998 (in part), UM 102905 (in part), UM 103184 (in part), UM 98741, UM 100575, UM 103495, UM 102914, UM 102758, UM 102839, UM 103236, UM 102366, UM 102143, UM 103243, UM 103241, UM 102350, UM 102260, UM 103222, UM 102758, UM 102839, UM 103027, UM 102914, UM 102933, UM 102760, UM 102690, UM 102361, UM 102690, UM 102933, UM 102760, UM 102361, UM 100700, UM 104471, UM 104511, UM 104621, UM 104641, UM 104712, UM 104866, and UM 104899.

These specimens are referred to Xestops vagans on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- The dentary and maxillary teeth are pleurodont, with small bases and slender, parallel-sided shafts. The crowns are expanded and bluntly wedge-shaped, with their tips pointing lingually and exhibiting a strong bevel on their external surfaces. Tooth crowns have striations meeting the tooth edge at right angles, and a low longitudinal ridge at the tip of some specimens (UM 105985,

UM 105986, UM 105991, UM 105999, UM 106004, UM 106005, UM 106006, UM 106007, UM 106008, UM 106010, UM 106011, UM 106013, UM 105125, UM 106016, UM 100575, and UM 100700). The teeth extend above the jaw parapet by about one-quarter of their length and decrease in size posteriorly. At the anterior tip of the dentary the teeth decrease sightly in size and are inclined anteriorly (UM 106005). The tooth shaft is sometimes flattened on the anterior and posterior sides (UM 105985, UM 105986, UM 105988, UM 105989, UM 105991, UM 105992, UM 105993, UM 105994, UM 105995, UM 105999, UM 106004, UM 106005, UM 106006, UM 106007, UM 106008, UM 106010, UM 106011, UM 106013, UM 105125, UM 106016, and UM 100575). The most posterior tooth of UM 105985 and the teeth of UM 105999 are conical. UM 105985, UM 105989, and UM 105999 have a constriction at the base of each crown. UM 105987 has teeth with a horizontal groove running below the crown. The teeth of UM 105989 are recurved, pointing posteriorly. UM 105996 has osteoderms like Xestops, but its teeth are more pointed.

Only two maxillae are represented in the collection, UM 105999 and UM 106013. The teeth of UM 106013 are of the same type as those of the dentary while those of UM 105999 have a slightly different morphology. They lack striations and are not straight sided, however their crowns conform to the type description of X. vagans with respect to their shape and the longitudinal ridge at their tips.

The dentary is robust and slightly curved along its length in dorsal view and curves inwards slightly where it meets the opposing dentary. In ventral view, it has a shallow but open Meckelian groove, and on the exterior surface a row of mental foramina. Both UM 105999 and UM 106013 are badly broken but UM 105999 shows that the maxilla is straight on its external surface and has unevenly spaced foramina.

Dentary. UM 105125 (Figure 46). Locality; 2413

This specimen consists of the anterior portion (4.9 mm) of the right dentary, with the posterior end missing. It bears three complete and four broken teeth and two teeth are missing. All teeth are slender, parallel-sided and anteroposteriorly compressed. The crowns are expanded and project above the jaw parapet, and bear striations only on the lingual side. The most anterior tooth is a partial root with a triangular cross-section. It points anteriorly, as do all the teeth, and is probably the first one in the tooth row. The next tooth is missing. The third tooth is complete. The crown is spatulate and bilobate with a central bulbous cusp. A ridge runs longitudinally across the crown and down its anterior and posterior sides. At the center, labial to the central cusp, it forms an apex pointing lingually over the cusp so that the ridge, in dorsal view, is made up of two lunate halves. Striations run at right angles from the ridge to the base of the crown. The fourth tooth is similar to the

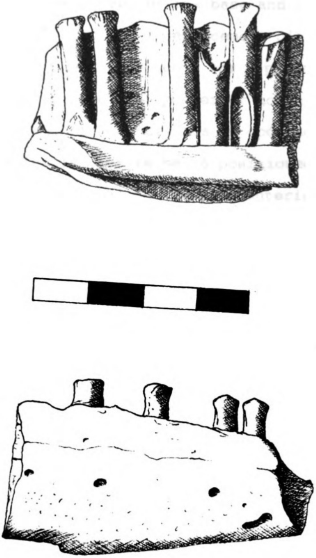

Figure 46. Xestops vagans. UM 105125. Right dentary, lingual and labial views. Scale bar is 4 mm.

third, the fifth is missing. The sixth tooth has a replacement pit at the center of its base and its tip is worn. The next tooth also has a replacement pit but it is broken at the root. The eighth tooth has a partially broken root and a broken tip. The most posterior tooth has no crown.

In lingual view, the dentary has an open Meckelian groove which is visible despite being positioned close to the ventral surface. The lingual shelf thins anteriorly, while in dorsal view it remains the same thickness for the length of the jaw except for the lingually expanded anterior tip which forms a triangular area at the symphysis. The tip is partially broken but the symphysis is present. The jaws would have met at an angle of about 55 degrees. In labial view, the dentary has four mental foramina. Three lie on the midline of the dentary. They are evenly spaced, subrounded, and shallow. The fourth lies near the ventral edge. It is deep and has an hourglass shape. The external surface of the dentary is pitted ventrally, but this, and the series of cracks on the surface, are probably post-mortem. There is no gap between the external surface of the dentary and the teeth where they project above the parapet of the jaw. In ventral view, the Meckelian groove is open and shallow and ends near the anterior tip of the dentary.

Maxillae, vertebrae, osteoderms and postcrania. UM 100575 (Figure 47 and Figure 48). Locality; BI 20

Left maxilla (Figure 47):

This specimen consists of a portion (20.3 mm) of the left maxilla. It bears six complete and five broken teeth. They are all parallel-sided and anteroposteriorly compressed except for slightly expanded crowns and occasional expanded bases. There are faint striations near the cutting edge. In ventral view the central cusp forms the acute angle of the cutting edge which has a double 'U' shape. The apex points lingually.

The most anterior four teeth are broken below their crowns. The roots have a circular cross-section and a central replacement pit at the center of their bases. The base of the fourth tooth is expanded. The base of the fifth tooth is missing, the crown is worn. A longitudinal ridge runs across the tip of the crown from anterior to posterior. At the center of the tip is a small bulbous central cusp. A longitudinal ridge runs along the base of the crown on the lingual side. The sixth tooth is complete, with a crown like the preceding tooth. The root has an expanded base with a replacement pit at the center. The seventh tooth is broken below the crown. The eighth and ninth teeth are like the fifth but without the ridge at the base of the crown. The tenth tooth bears an expanded crown but is broken at the

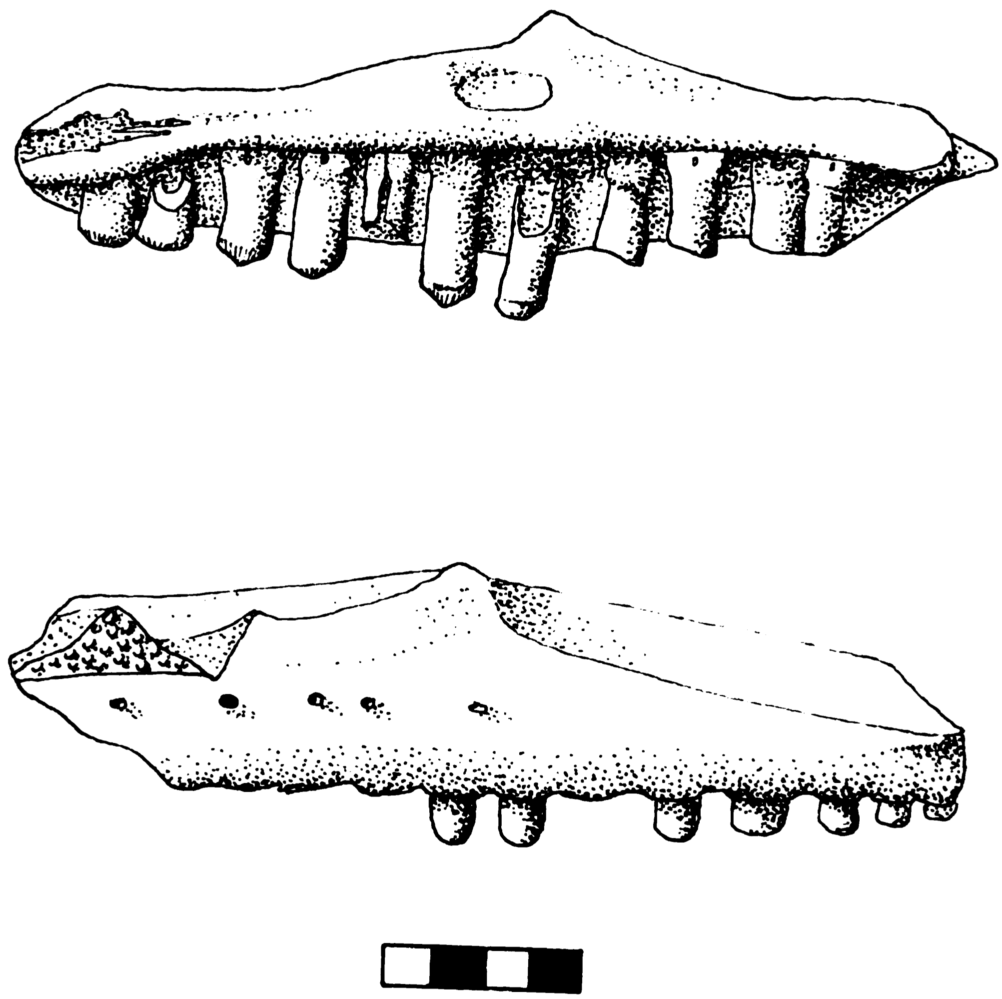

Figure 47. Xestops vagans. UM 100575. Left maxilla, lingual and labial views. Scale bar is 4 mm.

base. The most posterior tooth is likewise broken but the crown is only slightly expanded. Posteriorly the teeth reduce in size. The tips of the teeth are in a straight row of equal height.

The maxillary shelf is thin and expanded lingually. This lingual expansion increases from the anterior to the fourth tooth, then tapers to the posterior end. Anteriorly, the shelf is more dorsal where the teeth attach, posteriorly it is ventral. Dorsal projections of the maxilla are broken dorsal to the maxillary shelf. In dorsal view, the shelf is smooth with an ovoid depression dorsal to the sixth tooth. In lingual view, there are five mental foramina. The anterior four are round, the most posterior one ovoid. They are regularly spaced between the first and fifth teeth. The maxilla's external surface is smooth, flat, and slightly concave. There is a partial osteoderm attached at the anterior end. The posterior tip of the maxilla is broken, but bears a groove running towards the tip.

Right maxilla:

The right maxilla is represented by a small fragment (10.1 mm) bearing one complete tooth, one root, and two alveoli. The teeth have the same morphology as those in the left maxilla. The exterior surface has one mental foramen. The maxillary shelf is broken at the bases of the teeth.

Vertebrae (Figure 48):

There are three fragmentary vertebrae. Two consist of only the centrum, condyle, and partial cotyle. The third also has one synapophysis. In dorsal view, this vertebra has a short, wide, anteriorly expanded centrum. The cotylar opening is exposed, and lateral to this is the synapophysis. In anterior view, the cotyle is a depressed ovoid. The synapophysis is wide, and there is no paracotylar foramen. In posterior view, the condyle is a depressed ovoid. In lateral view, the centrum is depressed. The synapophysis is shelflike, and projects at right angles from the midline. Its surface is subrectangular, being thin anteroposteriorly and tall dorsoventrally. The condyle points slightly dorsally.

Osteoderms (Figure 48):

Each osteoderm is rectangular, with a bevelled lateral edge and a raised keel. The tuberculation is roughly concentric around the keel, which is positioned towards the side opposite the bevelled edge.

Postcrania:

There are a number of fragmentary pieces of postcrania, including the distal end of a limb bone (possibly the humerus), and the ball joint of another.

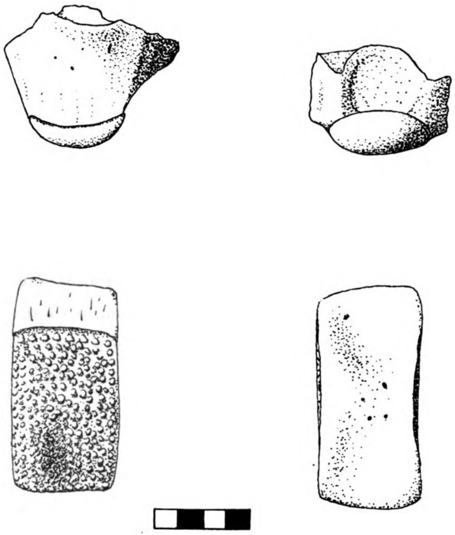

Figure 48. Xestops vagans. UM 100575. Vertebra, ventral and posterior views. Osteoderm, exterior and interior views. Scale bar is 4 mm.

Dentary, splenial, coronoid. UM 105126 (Figure 49). Locality; 1139

This specimen consists of a portion (8.5 mm) of the right mandible. It contains five complete teeth, and five broken ones. They are slender, closely spaced, and the same height. They are parallel-sided in lingual view, anteroposteriorly compressed, and oval in cross-section. The base of the first tooth is missing. The crowns are bluntly wedged shaped, with their tips pointing lingually. Tooth crowns have striations meeting the tooth edge at right angles and at the tip a carina runs anteroposteriorly. There is a small central cusp, where the carina forms the tip of the cutting edge, from which runs a prominent ridge down the lingual surface of the crown. The crown is slightly concave on the anterior and posterior sides of this ridge. The second tooth is similar except that an expanded base is present and the crown is slightly expanded anteroposteriorly. The third tooth is a partial root. The next six teeth are similar to the first. The tenth tooth is a partial root.

In lingual view, the dentary forms the anterior portion of the thin lingual shelf. The coronoid forms the posterior portion. The contact between these two bones is ventral to the sixth tooth. In dorsal view, the lingual shelf is broad. Ventral to the dentary and coronoid is the large splenial covering the Meckelian groove. It is slightly concave and smooth except for two anterior inferior alveolar foramen. The

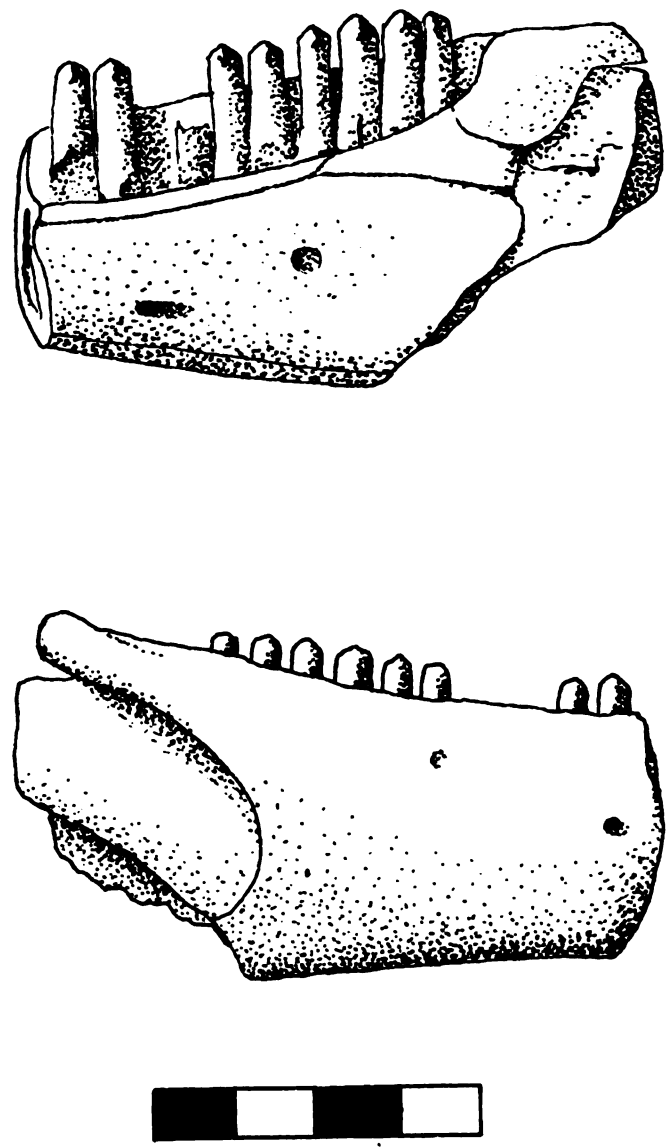

Figure 49. Xestops vagans. UM 105126. Right dentary, lingual and labial views. Scale bar is 4 mm.

most anterior foramen is near the ventral edge of the splenial, oval, and deep. It is ventral to the third tooth. The posterior foramen is ventral to the sixth tooth, and is midway down the splenial, round, and deep. Posterior and ventral to this is a small slitlike foramen. The dentary is visible along the ventral edge of the mandible.

In labial view, the anterior portion of the dentary is smooth and convex, and contains one round, deep mental foramen. Posteriorly, the anterior extent of the coronoid is indicated by an arcuate depression, extending to a point ventral to the seventh tooth. Ventrally, the dentary is broken, and dorsally the coronoid ends 1.4 mm from the parapet of the jaw.

Discussion -- Gauthier (1982) stated that, in xenosaurids and varanids, the sulcus dentalis, or anterior inferior alveolar foramen, lies entirely within the splenial, this being the primitive condition. However, in the anguids it lies at the junction of the dentary and splenial, with the dentary forming the dorsal and anterior border, and the splenial forming the ventral and posterior border of the foramen. This is a derived character (Estes, 1964). Meszoely (1970) stated that the diploglossines also have a foramen lying within the splenial, directly ventral to a notch in the dentary, but that this notch indicates the previous position of the sulcus dentalis, and that this is also a derived state. UM 105126 is assigned here to *Xestops vagans* on the basis of tooth morphology, which is very distinctive, but the anterior inferior alveolar foramina lie entirely within the splenial, a condition not typical of anguids (Estes, 1964). Despite the fact that the position of the foramina is a large variable, the other characteristics of this specimen clearly indicate that UM 105126 is referrable to Xestops vagans. Therefore, the anterior inferior alveolar foramen position is only useful as a general rule, and should not be used to diagnose subfamilies of the Anguioidea.

Tribe Glyptosaurini Sullivan, 1979a

These lizards develop a pattern of small, subequal, hexagonal osteoderms covering the skull. They differ from the Melanosaurini in that all Glyptosaurini have numerous subequal polygonal head osteoderms (Estes, 1983).

The Glyptosaurini have been defined and redefined many times, creating confusion in the nomenclature. Below, in Table 5 and Table 6, is a summary of the most important changes since the original classifications of Marsh (1871b; 1872), Douglass (1903; 1908), and Loomis (1907). For the most part I have followed the classification of Sullivan (1986; 1989), these being the most recent and comprehensive studies. Many of the original names have been discarded once more material was available for study, and intraspecific variation could be assessed. I have used the description of Glyptosaurus sylvestris by Sullivan (1989), and

Paraglyptosaurus hillsi by Sullivan (1986). Sullivan (1989) considered G. donohoei a junior synonym of G. sylvestris except for AMNH 7431, which he renamed Proglyptosaurus huerfanensis on the basis of its obtuse, blunt, robust teeth.

Table 5. The classification of Glyptosaurus and Paraglyptosaurus by Marsh (1871b; 1872), Gilmore (1928), Estes (1983), and Sullivan (1986; 1989).

Marsh 1871b and 1872	Gilmore 1928	Estes 1983	Sullivan 1986	Sullivan 1989
Glyptosaurus sylvestris	G. sylvestris	G. sylvestris		G. sylvestris
Glyptosaurus ocellatus	G. sylvestris	G. sylvestris		G. sylvestris
Glyptosaurus brevidens	G. sylvestris	G. sylvestris		G. sylvestris
Glyptosaurus princeps	G. princeps	Paraglyptosaurus princeps	G. sylvestris	G. sylvestris
Glyptosaurus rugosus	G. rugosus	P. princeps	G. sylvestris	G. sylvestris
Glyptosaurus nodosus	G. nodosus			G. sylvestris
Glyptosaurus sphenodon	G. sylvestris			
	G. hillsi	P. princeps	P. hillsi	

Table 6. The classification of Glyptosaurus, Helodermoides, Proglyptosaurus, Eoglyptosaurus, and Paraglyptosaurus by Douglass (1903; 1908), Loomis (1907), Gilmore (1928), White (1952), Sullivan (1979; 1989), and Estes (1983).

Original	Gilmore 1928	White 1952	Sullivan 1979	Estes 1983	Sullivan 1989
Helodermoides tuberculatus Douglass 1903	G. tuberculatus			H. tuberculatus	
Glyptosaurus montanus Douglass 1908	G. montanus			H. tuberculatus	
Glyptosaurus obtusidens Loomis 1907	G. obtusidens			?G. obtusidens	
	G. giganteus			H. tuberculatus	
		G. donohoei	Eoglyptosaurus donohoei	E. donohoei	Proglyptosaurus huerfanensis G. sylvestris
			Paraglyptosaurus yatkolai		

Glyptosaurus Marsh, 1871b.

Type species -- *Glyptosaurus sylvestris* Marsh, 1871b.

Referred species -- *Glyptosaurus sphenodon* Marsh, 1872; *Glyptosaurus*? *obtusidens* Loomis, 1907; cf. *Glyptosaurus sylvestris*, *Glyptosaurus* sp., *Glyptosaurus macrodon*, (*Peltosaurus macrodon*) Brattstrom, 1955.

Diagnosis -- *Glyptosaurus* differs from *Helodermoides* in having flattened osteoderms that form fewer rows across the interorbital region of the frontal; from *Placosaurus* in having a frontal that is not strongly convex in lateral view; and from *Paraglyptosaurus* in having a straight maxilla and dentary.

The Meckelian groove is covered by the splenial and closed except at the anterior end. The teeth are obtuse, pleurodont, and molariform, though less so than in *Paraglyptosaurus*. They have transversely compressed crowns with bevelled edges leading to the outer face of the jaw. Posterior teeth are short and rodlike with each crown blunt and exhibiting a low, longitudinal ridge. The crowns are short and can be smooth or striated. The vertebrae have no zygosphene (Estes, 1983). The vertebrae differ from those of *Saniwa* in having no precondylar constriction.

Age and distribution -- Lower to middle Eocene; Wyoming, middle Eocene; Utah and late Eocene; California, USA.

Glyptosaurus sylvestris Marsh, 1871b.

Figures 50, 51, 52, 53, 54, 55, and 56

(Synonyms -- Glyptosaurus ocellatus, Glyptosaurus nodosus Marsh 1871b; Glyptosaurus brevidens, Glyptosaurus rugosus, Paraglyptosaurus princeps (Glyptosaurus princeps), Glyptosaurus rugosus Marsh 1872; Eoglyptosaurus donohoei (Glyptosaurus donohoei (in part)) White 1952).

Type specimen -- USNM 16523.

Type locality -- Uinta County, Wyoming; Bridger Formation; middle Eocene.

Diagnosis -- The teeth are robust, with moderate anteroposterior compression. Crowns are short with many distinct striations leading away from a straight carina, running from anterior to posterior and continuing to the base of the crown.

Previously referred specimens -- YPM 521, YPM 522, YPM 523, YPM 1073, AMNH 5902, AMNH 6054, AMNH 7590, AMNH 11045, USNM 18316, USNM 16520, and USNM 18317; Huerfano Formation, Gardner, Colorado; early Eocene, YPM 524 and

AMNH 5113; Horizon B, Bridger Formation, middle Eocene, near Grizzly Buttes, Uinta County, Wyoming, AMNH 1614; Bridger Formation, middle Eocene, Buck Springs, Alkali Creek, Uinta County, Wyoming, YPM 525; Horizon B, Bridger Formation, middle Eocene, near Grizzly Buttes, Uinta County, Wyoming, USNM 16539; Bridger Formation, middle Eocene, Uinta County, Wyoming, AMNH 1617, AMNH 5196, AMNH 7446, AMNH 7454, AMNH 7592, AMNH 7595, AMNH 7596, AMNH 7598, and AMNH 7599; Huerfano Formation, early Eocene, Colorado, AMNH 5109; Wind River Formation, early Eocene, Wyoming, AMNH 11044; Wasatch Formation, early Eocene, Wyoming, PU 13271; Willwood Formation, early Eocene, Park County, Wyoming, YPM 7581, YPM 7583, YPM 7584, YPM 7588, YPM 7595, YPM 7598, YPM 7599, and USNM 215018; Bridger Formation, middle Eocene, Wyoming, AMNH 7454; Huerfano Formation, early Eocene, Wyoming, UCMP 118364; Wasatch Formation, early Eocene, Sublette County, Wyoming, YPM 8422; Willwood Formation, early Eocene, Wyoming.

Age and distribution -- Lower and Middle Eocene, Wyoming.

Referred specimens -- UM 106034, UM 106035, UM 106036, UM 106037, UM 106038, UM 106039, UM 106040, UM 106041, UM 106042, UM 106043, UM 106044, UM 106045, UM 106046, UM 106047, UM 106048, UM 106049, UM 106050, UM 106051, UM 106052, UM 106053, UM 106054, UM 106055, UM 106056,

UM 106057, UM 106058, UM 106059, UM 100645, UM 101436, UM 100554, UM 101064, UM 101418, UM 102920, (UM 101482), UM 104183, UM 104192, UM 104366, UM 104679, WPM 67, WPM 129, WPM 136, WPM 203, WPM 226, WPM 287, WPM 295, WPM 310, WPM 322, WPM 332, and one unnumbered WPM specimen.

These specimens are referred to Glyptosaurus sylvestris on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- The teeth are robust, with moderate anteroposterior compression. Crowns are short with many distinct striations leading away from a carina at the tip, running from anterior to posterior, and continuing to the base of the crown. The crowns are upright. The center striation is more pronounced giving the tooth a bilobed appearance (except in UM 106035). UM 106048, UM 106050, UM 106051, UM 106052, UM 106053, and UM 106057 exhibit a horizontal groove at the base of the crown just above the point where the striations stop. UM 106036 has a slightly flared crown. In those specimens that show the posterior portion of the dentary (UM 106039 and UM 106051) tooth size diminishes towards posteriorly. The shape, striations, and horizontal groove at the base of the crown of specimens UM 106043 and UM 106044 are present, but their crowns are more obviously pointed.

Dentary. WPM 295 (Figure 50). Locality; unknown, Green River Basin

This specimen consists of the anterior portion (16.1 mm) of a right dentary, with the anterior tip missing. It contains one complete tooth, eight broken teeth, and four missing teeth. The first tooth is a partial root with a small replacement pit at the center of the base. It has parallel sides with a subcircular cross section and is inclined anteriorly. The second tooth is like the first, but with a slightly expanded base. The teeth posterior to this are not inclined, but have a similar morphology to the first. The third has a large replacement pit, the fourth a slightly expanded base. The fifth has only the labial root wall present. The sixth has an expanded base. The seventh is like the first. The eight tooth is complete. It is anteroposteriorly compressed and parallel sided in lingual view. It has a large replacement pit at the center of its base. Just ventral to the crown the root is expanded lingually. The crown projects only slightly above the jaw parapet. It bears distinct striations on its lingual and labial surfaces that radiate from a carina running across the crown. The tip points lingually. The ninth tooth is like the first.

In lingual view, the ventral edge of the dentary is convex. It has an open Meckelian groove on its ventral surface that is exposed posteriorly. The lingual shelf thins

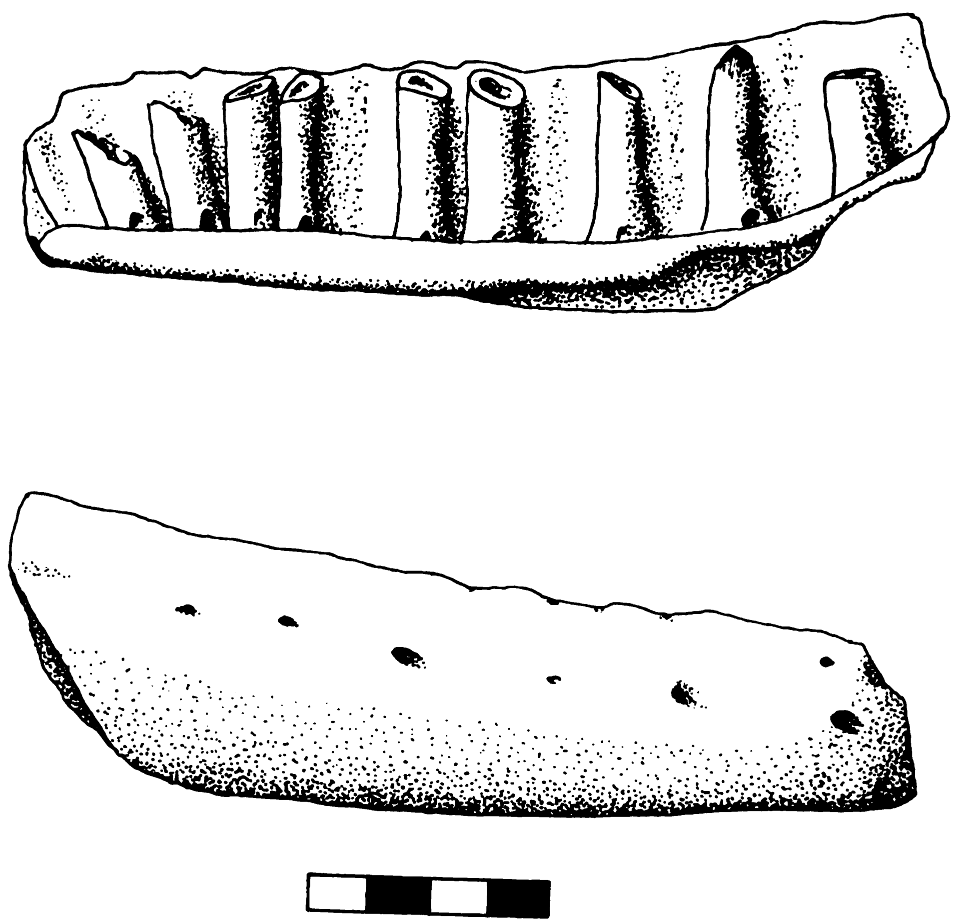

Figure 50. <u>Glyptosaurus</u> <u>sylvestris</u>. WPM 295. Right dentary, lingual and labial views. Scale bar is 4 mm.

posteriorly. In dorsal view, the lingual shelf is narrow except where it is anteriorly expanded. The area of symphysis is missing. In labial view, the bone is slightly pitted, probably due to post-mortem processes. There are five nutritive foramina. They are regularly spaced, ovoid, and lie slightly dorsal to the midline, in a straight line. In ventral view, the dentary is straight except at the anterior tip where it curves lingually. The Meckelian groove runs along the center of the ventral surface of the dentary. It is deep posteriorly but shallows and becomes narrower anteriorly. Its lingual and labial sides are vertical and flat.

Dentary. UM 101436 (Figure 51). Locality; SP 2

This specimen consists of the posterior portion (11 mm) of the left dentary. It contains five complete teeth. The first is anteroposteriorly compressed, parallel sided in lingual view, and slightly recurved. A small replacement pit is present at the center of the base. Dorsal to this are two smaller pits, possibly of post-mortem origin. The crown is blunt and very short, being only one-tenth the length of the root. Faint striations on both lingual and labial sides radiate from a lunate carina running along the tip of the crown. The second tooth is similar to the first except that it has a larger replacement pit, the crown is longer (one-fifth the length of the root) and the striations are more

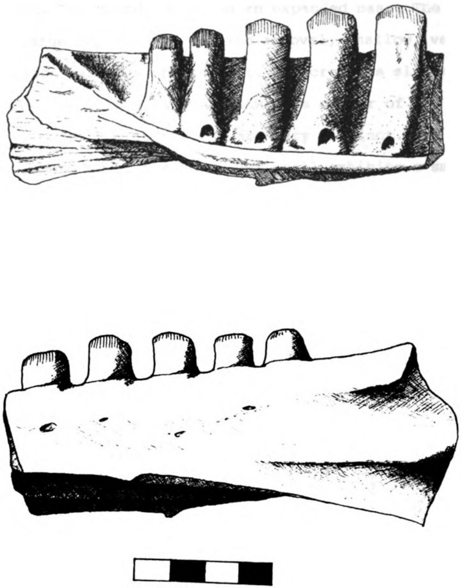

Figure 51. Glyptosaurus sylvestris. UM 101436. Left dentary, lingual and labial views. Scale bar is 4 mm.

distinct. The third tooth has an expanded base. The fourth has a large replacement pit and an oval, shallow, vertical depression half way up the root. The crown is slightly expanded and points lingually. At the center of the carina is a small cusp. The striations are very distinct. The fifth tooth is eroded at its base, but still exhibits a small replacement pit. The crown bears a center cusp like that of the preceding tooth, but has faint striations. The teeth become smaller along the tooth row posteriorly.

In lingual view, the lingual shelf is thin and rises dorsally towards the posterior. Ventral to the shelf the bone is missing. In labial view, the bone is slightly pitted and striated and bears two small mental foramina ventral to the first and third teeth. Anteriorly the external surface of the dentary is flat and vertical, posteriorly it is slightly concave. In dorsal view, the lingual shelf is narrow and is the same width throughout its length. Anterior teeth occur near the labial margin of the dentary, posterior teeth occur more lingually.

Maxilla. WPM 129 (Figure 52). Locality; unknown, Green River Basin

This specimen consists of a portion (16.7 mm) of the left maxilla. It bears one complete tooth and three broken ones. Two teeth are missing. The first tooth is a partial root. It is parallel-sided in lingual view and has a small

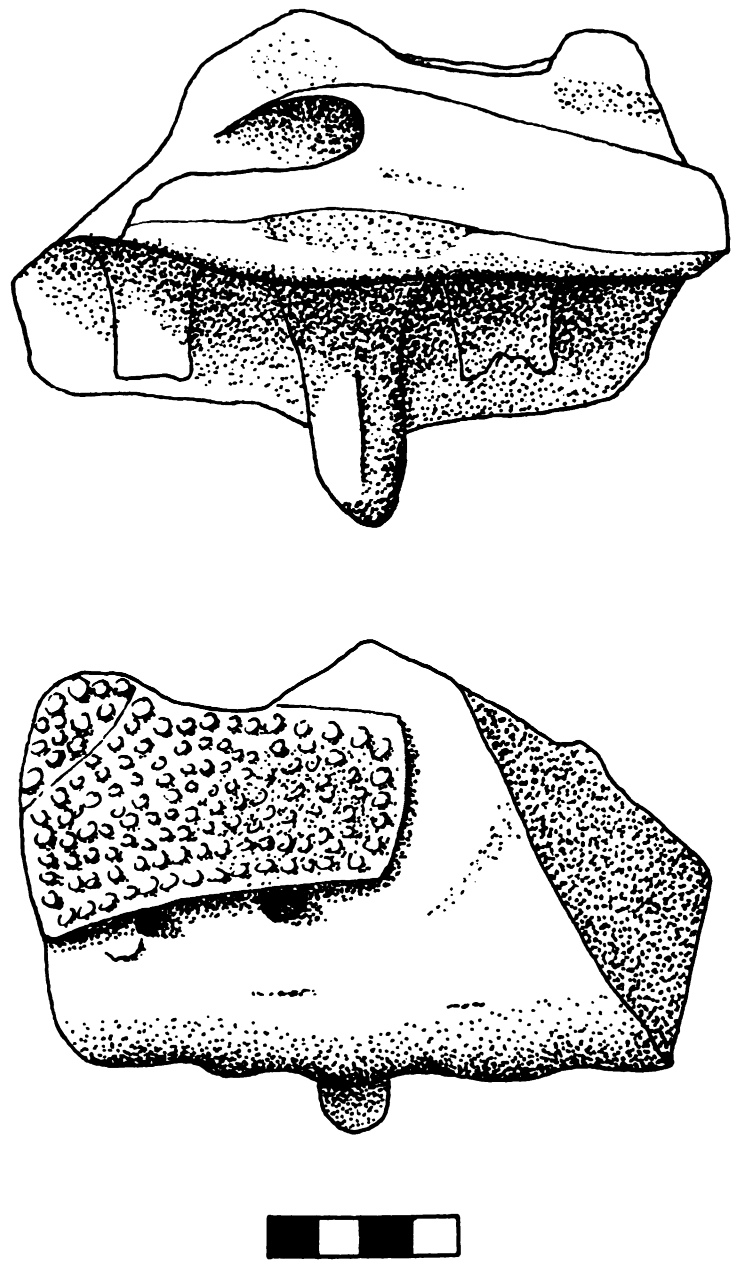

Figure 52. Glyptosaurus sylvestris. WPM 129. Left maxilla, lingual and labial views. Scale bar is 4 mm.

replacement pit at the center of its base. The second tooth has the same morphology. The third tooth is complete and is quite slender (7.1 mm base to tip, 2 mm root width and 1.6 mm crown width). The shaft is anteroposteriorly compressed with parallel sides in lingual view. It is expanded at the base where there is a central replacement pit. The shaft is also lingually expanded half-way up the shaft. Running down the center of the lingual surface of the shaft is a vertical slit-like depression extending from the base of the crown to the midline of the shaft. Ventral to this is a similar depression ventral and anterior to the replacement pit. The crown is slightly tapered with a blunt tip. Very faint striations radiate from a straight carina running along the crown tip, which points slightly lingually. The fourth tooth is a partial root. It is anteroposteriorly compressed and bears a small replacement pit. The fifth tooth is similar.

In lingual view, the maxillary shelf is narrow, with a portion of it expanded dorsal to the third tooth. In labial view, the bone is generally smooth except for slight pitting which is probably post-mortem. There are two osteoderms on the external surface. One is complete. It is raised in the center, roughly triangular and bears a concentric tubercular pattern. The second is a fragment. Ventral to the osteoderms are two nutritive foramina positioned on the ventral edge of the osteoderms. The anterior one is round (1.2 mm diameter) and pierces the bone pointing posteriorly. The posterior one is ovoid and points anteriorly into the bone. They are 2.1 mm apart and 3.5 mm from the ventral edge of the maxilla. This edge is straight, except between teeth where it is indented.

In ventral view, the maxillary shelf is expanded dorsal to the third tooth. In dorsal view, the maxillary shelf is flat and smooth except for a dorsal projection on its labial side and a depression between this and the flat portion of the maxillary shelf in the center of which is a large foramen. The posterior edge of the foramen is distinct, the anterior edge missing. In ventral view it is ovoid, but in cross-section it is circular. It extends into the bone at a small angle from the horizontal, pointing anteriorly and dorsally. Its anterior edge is a thin overhanging roof while the posterior side slopes gradually towards a flat ventral area.

Maxilla. UM 102920 (Figure 53). Locality; SP 6

This specimen is the anterior portion (16.4 mm) of the left maxilla, with the anterior tip and posterior area missing. It bears seven broken teeth and three teeth are missing. The anterior six teeth are partial shafts, with little of the tooth remaining. Replacement pits are visible on some at the center of their bases. They are parallel sided in lingual view. The seventh tooth is a complete shaft with the crown and base missing. It is oval in cross-section and is parallel sided in lingual view with two slitlike depressions running down the center of its lingual surface.

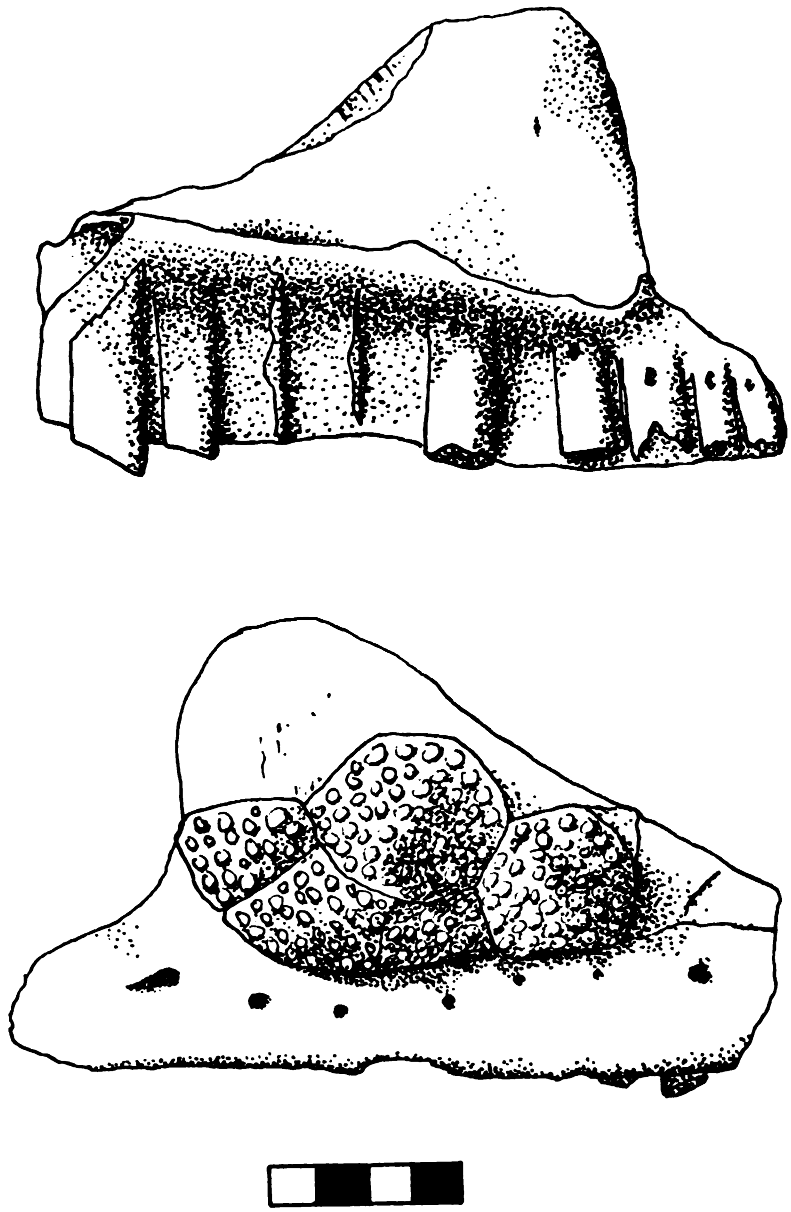

Figure 53. <u>Glyptosaurus</u> <u>sylvestris</u>. UM 102920. Left maxilla, lingual and labial views. Scale bar is 4 mm.

In lingual view, the maxillary shelf thins anteriorly. The dorsal projection of the maxilla is smooth and has a concave internal surface. The dorsal tip points lingually. Its anterior edge is vertical until it meets the maxillary shelf where it becomes horizontal. The posterior edge slopes at about forty-five degrees to the maxillary shelf. In labial view, there are five osteoderms. They are hexagonal or polygonal, with raised centers and a roughly concentric tubercular pattern. Ventral to the osteoderms are seven mental foramina. All but the anterior foramen are positioned in a straight, horizontal line. The most anterior foramen is slightly dorsal to this line. It is ovoid and deep. The five central foramina are subcircular and shallow. The most posterior foramen is circular and deep. The foramina are regularly spaced. They are a distance of 0.5 mm from the ventral edge of the osteoderms, and 1.1-1.8 mm from the ventral edge of the maxilla.

The ventral edge of the maxilla is straight except between the teeth where it is indented. The anterior edge tapers to a point, the posterior edge is missing. In cross-section, the external surface of the main body of the maxilla is straight and vertical. The exterior surface of the dorsal projection is convex, the interior concave.

Premaxilla. WPM 226 (Figure 54). Locality; unknown, Green River Basin

This is a complete premaxilla (11.9 mm in length) with three badly worn and broken teeth and five missing ones. They have parallel sides in lingual view, oval cross-sections, and are slightly anteroposteriorly compressed. They lie along the concave interior edge of the premaxilla. Lingual to the teeth is a shelf on which is a central projection pointing ventrally. It is 1.9 mm wide (laterally) and 2.6 mm high. In labial view, the external surface of the premaxilla is convex. There are two small dorsal projections, the nasal process, on the upper edge of the premaxilla directly above two large mental foramina. These foramina lie symmetrically on either side of the midline, half-way down the premaxilla's external surface. In anterior view, the left one is filled with sediment, while the right one pierces the bone completely. They are 5.2 mm apart. Dorsal to the right one is a smaller, ovoid foramen. In dorsal view, the premaxilla is a flat surface punctured by four fenestrae. The right one connects with the foraminae on the external surface of the premaxilla, the left one probably connects with the left outer foramen. Between these are two smaller foramina lying on the midline. All anguimorphs tend to have two foramina on either side of the nasal process that close with age. Although Sullivan (1979) used them, according to Gauthier (1982) they are not good characters for diagnosis of genus.

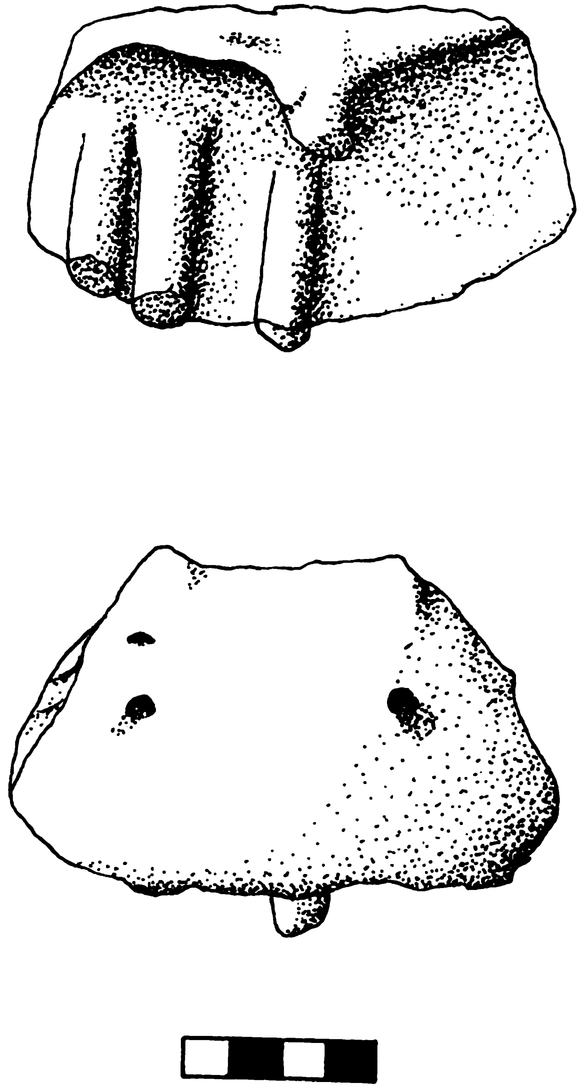

Figure 54. Glyptosaurus sylvestris. WPM 226. Premaxilla, lingual and labial views. Scale bar is 4 mm.

However, only anguids have premaxillary fenestrae at the palatal junction between the maxilla and premaxilla (Gauthier, 1982), as seen in this specimen. The maxillary suture surfaces bear three ridges separated by grooves.

Associated fragments. UM 101064 (Figure 55). Locality; BB 91

This specimen consists of the anterior tip of the right dentary, the posterior portion of the same dentary, a left frontal, an unidentifiable skull fragment, three body osteoderms and nine unidentifiable postcranial fragments.

Osteoderms:

The osteoderms are rectangular and all are partial. They have a concentric pattern of tubercles and one bears the flat articulating surface.

Right dentary (Figure 55):

The anterior dentary has one complete tooth, five broken teeth and a missing one. It is 14.5 mm long. The first tooth is complete and the most anterior. It is inclined anteriorly, anteroposteriorly compressed, and parallel-sided in lingual view. A carina runs along the slightly pointed tip of the crown, from which very faint striations radiate on the

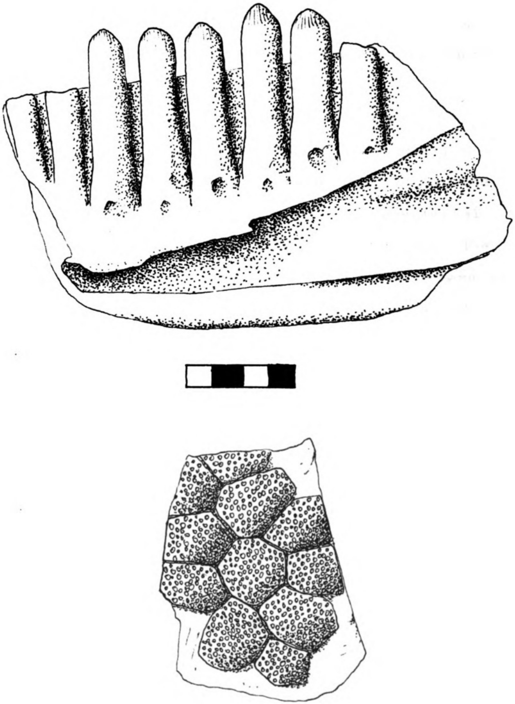

Figure 55. Glyptosaurus sylvestris. UM 101064. Right dentary, lingual view. Frontal, exterior view. Scale bar is 4mm.

lingual side. The remaining teeth are partial roots, all broken ventral to the crown. They are inclined anteriorly and are subcircular in cross-section. The second tooth has a replacement pit at the center of its base while the others are covered in sediment.

In lingual view, the dentary has a convex ventral profile. The lingual shelf thins anteriorly and the open Meckelian groove is visible ventrally. In labial view, the bone is smooth except for four, irregularly spaced mental foramina. They are ovoid and are in an irregular line. The dorsal edge of the dentary is straight except for between the teeth where it is indented. In dorsal view, the external surface is convex, the internal surface concave. The teeth point slightly lingually. The lingual shelf is narrow, and the same width along the jaw. The anterior tip is broken before the symphysis. In ventral view, the Meckelian groove is shallow. It becomes more shallow anteriorly and ends ventral to the second tooth. The groove lies in the center of the ventral surface of the dentary.

An area is missing between the above fragment, and the posterior part of this right dentary. The posterior portion of the right dentary has five complete teeth and three broken ones. The two most anterior teeth are partial roots. They are oval in cross-section, slightly anteroposteriorly compressed and are parallel-sided in lingual view. The third tooth has an eroded base. The root is anteroposteriorly compressed and lingually expanded ventral to the tapered crown. The tip of the crown points lingually. Here, a carina runs along the tip and down the anterior and posterior sides of the crown. Fine striations radiate from the carina. The fourth, fifth and sixth teeth are slightly recurved and point posteriorly. They are anteroposteriorly compressed and parallel-sided in lingual view. There is a small replacement pit at the center of each base. Their roots are lingually expanded ventral to the crown which tapers to a point. The crown resembles that of the third tooth. The eighth tooth is a partial root.

In lingual view, the ventral edge of the dentary is missing. There is a wide, open Meckelian groove with the splenial lining the interior surface. Its dorsal edge is straight except for between the teeth where it is indented. There is one ovoid mental foramen midway up the dentary. In ventral view, the Meckelian groove is visible on the lingual side of the ventral surface.

Left frontal (Figure 55):

The left frontal is broken along its external, anterior and posterior borders. The midline suture is complete and straight. The dorsal surface of the frontal is flat. There are eleven osteoderms, with evidence of a twelfth. Three lie along the suture, with evidence of one more osteoderm anterior to these three. Three more lie in an arc lateral to these. Six more lie towards the lateral edge of the frontal. The osteoderms are polygonal, raised in the center, and bear a concentric tubercular pattern. The ventral surface of the frontal is smooth. The frontal is thin at the suture, but thickens towards the outer edge where the subolfactory process lies. Most of the process is missing. Its interior edge is vertical, its outer edge tapers to the border of the frontal.

Skull fragment:

The unidentifiable skull fragment bears one complete, and one broken osteoderm. They are hexagonal, raised in their centers, and have a concentric pattern of tuberculation. One edge of the bone is thin, the other ventrally expanded to form a ridge. It resembles the ridge on the frontal and is probably an anterior part of that bone.

Postcrania:

There are a number of postcrania, including the articular ends of limb bones, but these are too fragmentary to be identified.

Associated fragments. UM 100645 (Figure 56). Locality; BI 26

This specimen consist of 16 cranial osteoderms, 22 body osteoderms, 3 partial vertebrae, 10 fragments of dentary of

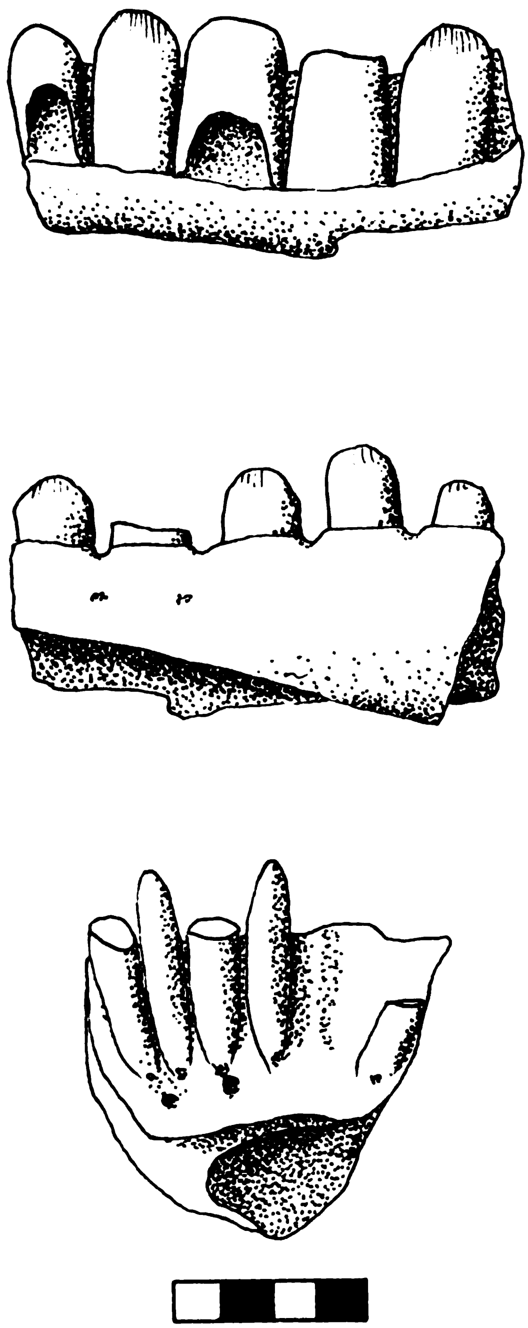

Figure 56. Glyptosaurus sylvestris. UM 100645. Dentary, lingual and labial views. Premaxilla lingual view. Scale bar is 4 mm.

maxilla, 11 skull fragments, 3 possible skull fragments and a partial premaxilla.

Dentary fragment (Figure 56):

The first jaw fragment has three complete teeth and two broken teeth. The first tooth is a partial root with base and crown missing. It has a round cross-section and is parallel-sided in lingual view. The second tooth is complete. It is parallel-sided and slightly anteroposteriorly compressed. The crown tapers to a blunt point. A horizontal groove runs along the base of the crown. A lunate carina runs along the tip of the crown and down the anterior and posterior sides of the crown from which striations radiate on lingual and labial sides. The tip points slightly lingually. The third tooth is similar except the base is missing and it bears a short, expanded crown. The fourth is a partial root. The fifth tooth is similar to the third with very fine striations at the base. Most of the bone is missing. Seven small jaw fragments bear teeth of similar morphology.

Maxilla fragment:

A fragment of maxilla contains two broken teeth and has one missing tooth. The teeth are recurved and point lingually. They are parallel sided in lingual view and have small replacement pits at the center of their bases. In lingual view, the outer surface of the maxilla is smooth except for one nutritive foramen.

Maxilla fragment:

Another fragment of maxilla contains two teeth of similar morphology, one complete and one broken. In labial view, there is one partial osteoderm. Ventral to this is a nutritive foramen, lying at the edge of the osteoderm. The distance from the foramen to the ventral edge of the maxilla is 2.4 mm.

Premaxilla (Figure 56):

The premaxilla contains two complete teeth, three broken teeth, and one missing tooth. In anterior view, the bone is complete on the left side, but missing on the right. The first tooth, on the extreme left, is a partial root. It is parallel-sided in lingual view, anteroposteriorly compressed with an oval cross-section, and has a small replacement pit at the center of its base. The tip of the second tooth is missing. It is similar to the first tooth except that the root is lingually expanded ventral to the crown. The third tooth is a root of the same morphology as the first tooth. The fourth tooth is complete and resembles tooth two except it bears a carina running across the crown. The fifth tooth is the only tooth from the right side of the premaxilla. It is a partial root of the same morphology as the first tooth.

All the teeth are attached to the concave inner surface of the premaxilla. Lingually the bone is broken, thus the ventral projection seen on WMP 226 is missing. The premaxillary shelf is horizontal and flat and bear two nutritive foramina dorsal to teeth three and five. In labial view, the premaxilla is convex and smooth except for one large foramen. It pierces the premaxilla to connect with a large foramen on the dorsal surface. The left edge of the premaxilla is present and bears the same pattern of ridges as seen in WPM 226. In dorsal view, there is a small flat horizontal area bearing two very small foramina.

Skull fragments:

There are eight unidentifiable skull fragments bearing hexagonal osteoderms. Two further fragments are lacking osteoderms but their morphology resembles that of a partial frontal or parietal in that they possess a flat dorsal surface and have a ridge running along the ventral surface. One fragment bears two osteoderms and has a distinct, sharp ridge on its ventral surface suggesting it is probably a parietal. Another fragment bears four osteoderms and has a similar ridge. From comparison with other specimens it most resembles the anterior left portion of the parietal. Another piece has five small, hexagonal osteoderms. The ventral

surface is irregular, with a central foramen and a sharp ridge beside it. This is probably the parietal foramen and the bone is therefore the central portions of the right and left parietal. The final skull fragment has four osteoderms in a row along a suture. On the ventral surface is a ridge, which is probably the subolfactory process. It has a concave internal surface as the tip of the projection points lingually. This is, therefore, probably a right frontal.

Discussion -- I have assigned these specimens to Glyptosaurus sylvestris since they most closely fit the descriptions of Estes (1983) and Sullivan (1986; 1989). They differ from Paraglyptosaurus in lacking molariform crushing teeth. Placosaurus is thus far only found in the Oligocene, and was considered by McDowell and Bogert (1954) to be a senior synonym of Glyptosaurus. Without additional specimens I do not feel I can justifiably extend its range into the Eocene. The teeth of Proglyptosaurus are more robust than those in these specimens. Eoglyptosaurus was included in the Tribe Glyptosaurini by Estes (1983), but was redescribed by Sullivan (1989) as Proglyptosaurus.

WPM 129 (Glyptosaurus sylvestris) can be compared to WPM 377 (glyptosaurine "indet A"). Both are maxillae bearing at least one complete tooth, two osteoderms, mental foraminae and a large foramen on the ventral surface of the maxillary shelf. Neither specimen is complete, so it is difficult to compare the sizes of the specimens, and no suggestion is made that this is a statistically significant sample. Measurements were made of tooth characteristics present on four specimens (Table 7, Table 8, and Table 9). Table 7 shows that the teeth of glyptosaurine "indet A" are more robust than those of G. sylvestris. Table 8 shows that the mental foramina lie closer to the osteoderms in G. sylvestris. This is also the case in UM 100645, but not in UM 102920. Table 9 shows that the large foramen is more circular in G. sylvestris.

Table 7. Comparison of tooth dimensions of glyptosaurine "indet A" (gl. "indet A") and Glyptosaurus sylvestris (G. s.).

Specimen	tooth length, base to tip (average)	root width	crown width
WPM 377 (gl. "indet A")	6.8 mm	2.2 mm	2.2 mm
WPM 129 (G. s)	7.1 mm	2 mm	1.6 mm

Table 8. Comparison of measurements of the position of mental foramina relative to osteoderms and the ventral edge of the maxilla of glyptosaurine "indet A" and _Glyptosaurus sylvestris_.

Specimen	Distance between mental foramina (average)	Distance from mental foramina to the ventral edge of the maxilla (average)	Distance from the mental foramina to the ventral edge of the osteoderms
WPM 129 (_G. s_)	2.1 mm	3.5 mm	0 mm
UM 100645 (_G. s_)	n/a	2.4 mm	0 mm
UM 102920 (_G. s_)	1.5 mm	1.5 mm	0.5 mm
WPM 377 (_gl._ "indet A")	2.3 mm	2.4 mm	0.6 mm

Table 9. Comparison of the dimensions of the large foramen in the ventral surface of the maxillary shelf of glyptosaurine "indet A" and _Glyptosaurus_ _sylvestris_.

Specimen	Length (ant-post) of large foramen	Width of large foramen
WPM 377 (_gl._ "indet A")	5.3 mm	2.4 mm
WPM 129 (_G. s_)	4.6 mm	3.1 mm

The osteoderms of glyptosaurine "indet A" and *Glyptosaurus* *sylvestris* have different morphologies, WMP 129 having flat rectangular osteoderms, WPM 377 having raised, hexagonal osteoderms. However, it is unclear how significant osteoderm shape is in diagnosing glyptosaurine species. Measurements were made of the Recent species *Heloderma suspectum* and *H. horridum* from the Carnegie Museum and the Michigan State University Museum (Table 10). All Carnegie Museum (CU) specimens, and MSUH 12975, MSU 1447, and MSU 3952 are *H. suspectum*, MSU 1440 and MSU 1873 are *H. horridum*. *Heloderma* was used because it is an anguimorph of similar size to the glyptosaurines found in this assemblage, with similar cephalic osteoderms and resemblances in skull structure. Since the study is only concerned with intraspecific variation in any taxon, it is not important that the Helodermatidae lies within the Superfamily Varanoidea as any intraspecific variation seen casts doubt on classifications based on the features measured.

Table 10. Measurements of osteoderm number, height, and arrangement in Heloderma horridum and Heloderma suspectum. Fractions denote osteoderms lying partially on the measured line. Descriptions of pattern names are given below.

Specimen	Osteoderm number on midline	Osteoderm number on anterior edge	Osteoderm number between orbits	Osteoderm number on posterior edge	Osteoderm height/ diameter (mm)	Osteoderm pattern
CM144967	5	2 1/2	4 1/2	4 1/2		irregular
CM112039	5	1/2 3 1/2	5	4		arc
CM144969	3	3	3	5		rows
CM125928	4 3/2	2	5	6 1/2		rows
CM125927	4 2/2	4	4	6 1/2		arc
CM123211	8 1/2	3	4	7 1/2		irregular
CM114381	8 1/2	4	5	7		irregular
CM144968	5 1/2	3	4	7		irregular
CM37481	8 1/2	2	6	6		irregular
CM37475	8	3	5	6		arc
CM69905	8	2 1/2	5	8		arc
CM51768	6 2/2	4	6	8		irregular
MSU1440	2	1 2/2	2 2/2	2 1/2	1.5/5.4	rows
MSU1873	3	1 2/2	2 2/2	1 2/2	1.5/4.9	rows
MSUH12975	3	1 2/2	1 3/2	1 1/2	0.9/3.8	arc
MSU1447	2/2	2	1 4/2	3	1.6/2.2	irregular
MSU3952	1	3	3 2/2	1	1.5/4.7	arc

Table 10 shows that the osteoderms occur in several patterns (Figure 57). Their heights are also variable, as is the relationship between height and diameter, thus showing that diagnoses based on these characteristics are not valid. The method of counting osteoderms is given in Figure 57.

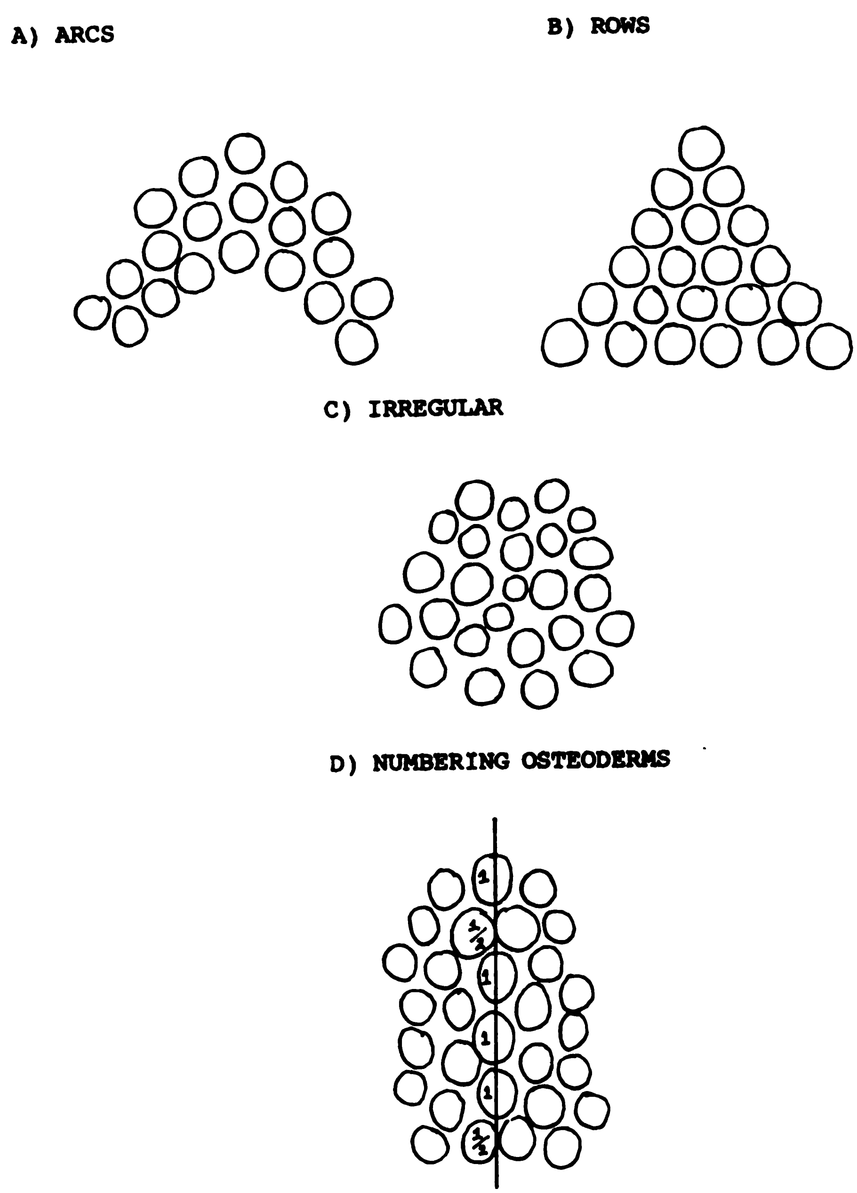

Figure 57. Patterns of osteoderms in Heloderma. A) Rows. B) Arcs. C) Irregular. D) Numbering system for ostoederms. Total is 4 2/2.

<u>Paraglyptosaurus</u> Sullivan, 1979.

<u>Type species</u> -- <u>Paraglyptosaurus</u> <u>princeps</u> (<u>Glyptosaurus</u> <u>princeps</u>, <u>Glyptosaurus</u> <u>rugosus</u>) Marsh 1872; <u>Glyptosaurus</u> <u>hillsi</u> Gilmore 1928).

<u>Referred species</u> -- <u>Paraglyptosaurus</u> <u>yatkolai</u> Sullivan 1979; <u>Paraglyptosaurus</u> <u>hillsi</u> Sullivan 1986.

<u>Diagnosis</u> -- This is a group of middle Eocene glyptosaurines from Wyoming and Colorado. They differ from <u>Glyptosaurus</u> in having fused frontals, bulbous crushing teeth, curved maxillae, very robust dentaries and smaller osteoderms. Paraglyptosaurus differs from <u>Eoglyptosaurus</u> and <u>Helodermoides</u> in having flattened osteoderms, curved maxillae, and bulbous crushing teeth, and from <u>Placosaurus</u> in having flat frontals (Estes, 1983).

<u>Age and distribution</u> -- Early Eocene; New Mexico, middle Eocene; Wyoming and Colorado, USA.

<u>Paraglyptosaurus</u> <u>hillsi</u> Sullivan, 1986.

Figures 58 and 59

(<u>Synonyms</u> -- <u>Glyptosaurus</u> <u>princeps</u> Marsh 1872; <u>Glyptosaurus</u> <u>hillsi</u> Gilmore 1928; <u>Paraglyptosaurus</u> <u>princeps</u> Sullivan, 1979; <u>Paraglyptosaurus</u> <u>princeps</u> Estes 1983.)

Type specimen -- USNM 6004.

Type locality -- Muddy Fork of Huerfano River, above Gardiner, Huerfano County, Colorado; Upper Huerfano Formation; Eocene.

Diagnosis -- _P_. _hillsi_ has anisodont, slender to obtuse teeth posteriorly, and a broad flat skull. _P_. _hillsi_ differs from _P_. _yatkolai_ in having more flattened osteoderms, and in lacking enlarged anterior frontal osteoderms.

Previously referred specimens -- USNM 10606; Muddy Fork of Huerfano River, above Gardiner, Huerfano County, Colorado; Upper Huerfano Formation; Eocene.

Age and distribution -- Middle Eocene, Colorado.

Referred specimens -- UM 105127 and WPM 293

These specimens are referred to _Paraglyptosaurus_ _hillsi_ on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Maxilla. WPM 293 (Figure 58). Locality; unknown, Green River Basin

This specimen consists of the posterior portion (10 mm) of a left maxilla. It bears three short, squat, anisodont teeth, which decrease in size posteriorly. The most anterior tooth is strongly anteroposteriorly compressed. It is 4.75 mm wide (lingual-labial), 2.55 mm long (anterior-posterior), and 2.46 mm high. The anterior and posterior sides are straight and vertical, the lingual side convex, sloping gradually to the tip of the crown, and the labial side is convex and vertical. It exhibits slight crenulations at its base. The crown is a flat, oval crushing surface. Its lunate, anteroposterior cutting ridge is present only on the anterior side of the tip of the crown, and is positioned centrally on the crown. Fine striations radiate from this ridge over the entire crushing surface. In lingual view, the crown is slightly expanded. There is a replacement pit at the center of the base. The middle tooth also shows slight anteroposterior compression in cross-section. It is 2.54 mm wide, 1.72 mm long, and 1.55 mm high and is subrectangular. The anterior and posterior sides are straight and vertical, the lingual side convex, vertical and broken, and the labial side is also convex and vertical. The crown is subrectangular and flat. Its cutting ridge is slightly to the labial side of

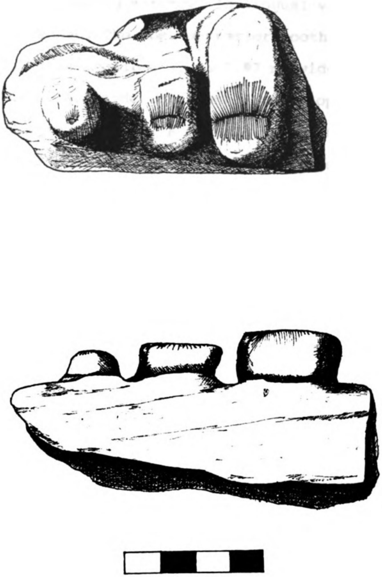

Figure 58. Paraglyptosaurus hillsi. WPM 293. Left maxilla, occlusal and labial views. Scale bar is 4 mm.

the crown. Fine striations radiate from the ridge over about one-half of the crushing surface. In lingual view, the crown is slightly expanded. The most posterior tooth is conical and subrounded in cross-section. It is 1.97 mm wide, 1.49 mm long and 1.28 mm high. All sides are convex and slope gradually to the convex crushing surface. A carina is present at its tip in the center of the crown. Fine striations radiate from the lingual side of the ridge over the crushing surface.

Part of the maxillary shelf is present. It is thin dorsal to the anterior tooth, but thicker dorsal to the most posterior tooth. In labial view, the external surface is worn and bears grooves running anteroposteriorly. In dorsal view, the maxilla's external surface is slightly concave. There is a deep groove running the length of the maxillary shelf on its labial side. The rest of the bone is worn and broken. In cross-section, the maxillary shelf is triangular. The dorsal surface is horizontal, the external surface vertical, and the area of tooth attachment inclined at about 45 degrees, with the acute angle lingually. The teeth are short and squat, and the carinae are slightly raised. In posterior view, the slope of the attachment surface is less pronounced.

Maxilla. UM 105127 (Figure 59). Locality; 1139

The specimen consists of the posterior portion (3.5 mm) of a right maxilla. It bears one complete and three broken teeth. The most anterior tooth is broken along a vertical

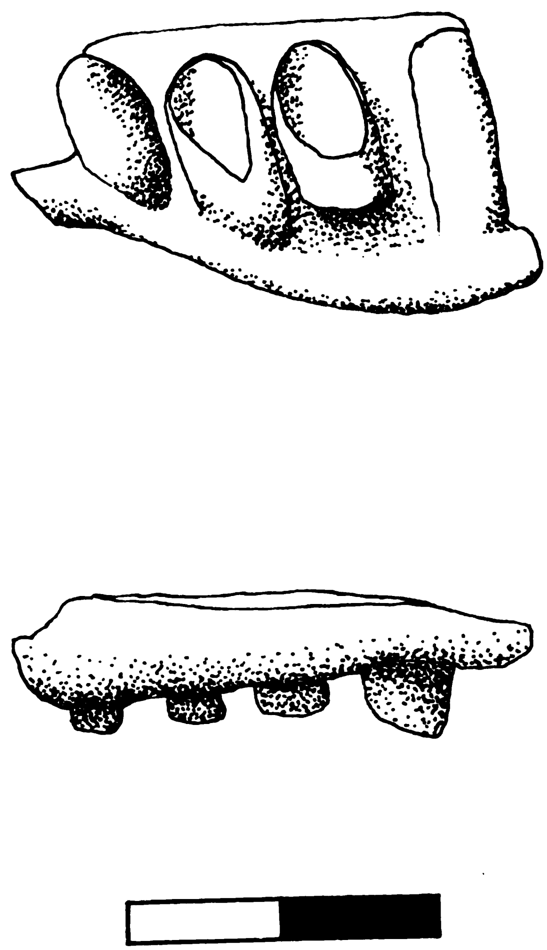

Figure 59. Paraglyptosaurus hillsi. UM 105127. Right maxilla, occlusal and labial views. Scale bar is 2 mm.

midline from base to tip. It is oval in cross-section and, in lingual view, has the same profile as the anterior tooth of WPM 293, its lingual surface slopes gradually to the tip of the crown. The base of the next tooth is missing and the tip is broken. It has an oval cross-section. It is very incomplete but seems similar to the previous tooth. The tip of the third tooth is broken. It is oval in cross-section and has a gradually sloping lingual surface. The most posterior tooth is complete. The lingual side slopes gradually to the tip which points labially. Its anterior and posterior sides are flat and vertical, its lingual and labial sides convex. There is a slight carina at the tip of the crown. Although not strictly a crushing tooth, the crown is pointed labially so a flat area of the tooth, lingual to its tip, would have been in occlusion with the opposing dentary tooth.

In ventral view, the maxillary shelf is expanded lingually. The lingual edge is thin and rounded, the labial edge thicker, flat, and vertical. It is smooth, with anteroposterior grooves. In dorsal view, the maxilla is flat except for a groove running the length of the shelf on the labial side, and a ridge running down its center lingual to the groove. In cross-section, the maxillary shelf profile resembles that of WPM 293 in being triangular, and with its attachment surface inclined at about 45 degrees from vertical.

Discussion -- *Paraglyptosaurus* differs from *Glyptosaurus* in being larger and having bulbous, expanded teeth and a curved maxilla. However, these features may be size-related and *Paraglyptosaurus* may be synonymous with *Glyptosaurus* (Estes, 1983). Sullivan (1979) and Estes (1983) use fused frontals as a defining character of the glyptosaurines, although Sullivan (1986) states that this is not a reliable character. In studies of modern *Heloderma* specimens, it was found that there is considerable intraspecific variation, including fused frontals, partially fused or sutured frontals, sutured frontals, and separate frontals (Table 11). Osteoderm shape, arrangement, and number were also highly variable (Table 11). None of these characters are related to the size of the specimen and are therefore not age, or size related, but an expression of variation (Bartels, pers. com.). All Carnegie Museum (CU) specimens are *Heloderma suspectum*. MSU 12975, MSU 1447, and MSU 3952 are *H. suspectum*, MSU 1440, MSU 1873, and MSU 4218 are *H. horridum*. MSU 4218 is a juvenile.

Table 11. Measurements of frontal dimensions and co-ossification of specimens of *Heloderma horridum* and *Heloderma suspectum*.

Specimen	Length of frontal	Width of anterior edge of frontal	Width between the orbits	Width of posterior edge of frontal	Frontal co-ossification
CM144967	16.1 mm	7.9 mm	11.9 mm	16.2 m	Indistinct suture
CM112039	19.9 mm	11.6 mm	18 mm	20.4 mm	Visible suture
CM144969	15.4 mm	N/A	N/A	N/A	Separate
CM125928	20.5 mm	8.7 mm	16.1 mm	18.4 mm	Visible suture
CM125927	24.1 mm	N/A	N/A	17.2 mm	Indistinct suture
CM123211	27.6 mm	N/A	N/A	21.4 mm	Indistinct suture
CM114381	28 mm	N/A	N/A	20.1 mm	Fused
CM144968	23.6 mm	N/A	N/A	N/A	Indistinct suture
CM37481	30.2 mm	N/A	N/A	N/A	Separate
CM37475	27.7 mm	N/A	N/A	N/A	N/A
CM69904	14.6 mm	N/A	N/A	N/A	Separate
CM69905	13.5 mm	N/A	N/A	N/A	Separate
CM51768	34 mm	N/A	N/A	N/A	Visible suture
MSU1440	21.5 mm	9.8 mm	15.5 mm	23.6 mm	Separate
MSU1873	24.1 mm	11 mm	16.6 mm	26.7 mm	Fused
MSU4218	8.4 mm	4.4 mm	7.4 mm	10 mm	Separate
MSU12975	19.1 mm	9.2 mm	12.6 mm	17.7 mm	Visible suture
MSU1447	19.5 mm	7.7 mm	12.9 mm	18.2 mm	Separate
MSU3952	19.7 mm	8.7 mm	14.1 mm	19.7 mm	Separate

Table 11 shows that there is significant intraspecific variation in the state of the frontals and that this is not related to the size or age of the individual. Therefore diagnoses based solely on this character are suspect.

Glyptosaurine "indet A"

Figures 60 and 61

Diagnosis -- All specimens have large, robust teeth with blunt tips bearing a slight, raised carinae from which very faint striations radiate on the lingual and labial surfaces. Some specimens bear sub-equal, hexagonal osteoderms typical of the glyptosaurines. The teeth of all specimens are more robust than in Glyptosaurus sylvestris, with crowns that are more blunt and have a lower longitudinal carina. No specimens bear the extreme molariform teeth seen in Paraglyptosaurus.

Referred specimens -- UM 106060, UM 106061, UM 95703, UM 102815, UM 102043, UM 100813, UM 101648, UM 104045, WPM 103, WPM 296, WPM 320, WPM 372, WPM 376, and WPM 377.

These specimens are referred to glyptosaurine "indet A" on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Dentary. UM 100813 (Figure 60). Locality; BI 38

This specimen consists of the posterior portion (7.3 mm) of a right dentary. It bears three complete teeth and one broken tooth. All teeth are robust, with parallel sides in lingual view, and are anteroposteriorly compressed. The crown is slightly expanded and there is a small replacement pit at the center of each base. In dorsal view, the center of the crown bears a lunate carina with very faint striations radiating from it to the base of the crown. The apex of the carina points lingually and slightly posteriorly. The most anterior tooth points posteriorly. It has a flat, vertical anterior and posterior sides. The lingual side of the tooth slopes gradually from the lingual shelf to the tip of the crown, the labial side slopes rapidly to the tip and is almost vertical. The base of the root is eroded away. The second tooth is similar except the base is expanded and the tip is less worn, making the striations easier to see. The third tooth is the same only smaller. The most posterior tooth is a partial root.

In lingual view, the dentary has a thin lingual shelf. It is more ventral at the anterior end, sloping dorsally at the posterior end to a level about one-third the way up the most posterior tooth. The ventral portion of the dentary is missing, so the Meckelian groove is not present. In labial

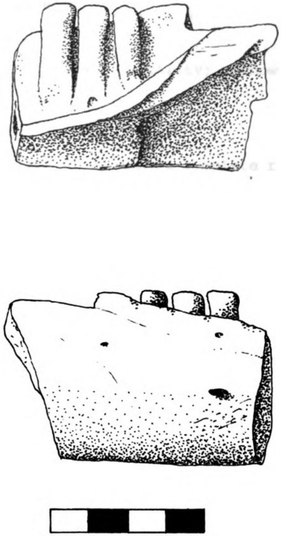

Figure 60. Glyptosaurine "indet A". UM 100813. Right dentary, lingual and labial views. Scale bar is 4 mm.

view, there is one deep, oval mental foramina midway up the dentary. In cross-section, the dentary is roughly triangular, with the concave tooth attachment surface sloping gradually dorsally from the lingual edge.

Maxilla. WPM 377 (Figure 61). Locality; unknown, Green River Basin

This specimen consists of an almost complete right maxilla (23.8 mm in length). It bears three complete and four broken teeth and has two missing ones. All teeth are very slightly recurved and point posteriorly. There is a replacement pit at the center of each base. The crown is blunt and rounded with very faint striations. Crenulations occur at the base of the root. The most anterior tooth is a partially broken root, with its tip missing. The next tooth is missing. The third tooth is also a partial root with part of the crown present. The crown is slightly pointed, with a distinct, straight carina from which striations radiate over the lingual and labial surfaces of the crown. The fourth tooth is similar to the preceding tooth. It is slender (7 mm base to tip, 2 mm root width, and 1.9 mm crown width). The lower half of the root bears crenulations. The crown bears striations but only on the lingual side of the carina. The fifth tooth is a broken root with crown. The crown is slightly expanded and blunt, with faint striations on the labial side of the carina. The next tooth is quite slender

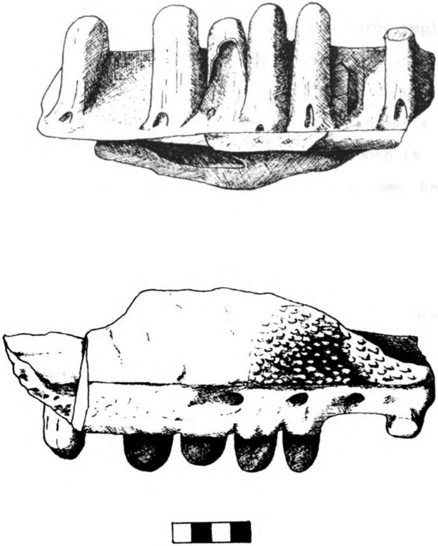

Figure 61. Glyptosaurine "indet A". WPM 377. Right maxilla, lingual and labial views. Scale bar is 4mm.

(7.2 mm base to tip, 2.4 mm root width, and 2.4 mm crown width). It has crenulations on the lower two-thirds of the root. The base is slightly bulbous around a large replacement pit. The crown has no striations. The next tooth is missing. The most posterior tooth is parallel-sided in lingual view with a slightly expanded crown. Where the tooth meets the alveolar wall the boundary between bone and tooth is indistinct. The tooth has crenulations on its lower half and a large replacement pit at the center of the base. The crown is blunt and has striations on the lingual and labial sides of the lunate carina.

In lingual view, the lingually expanded maxillary shelf thickens anteriorly. In dorsal view, at its posterior end, there is a deep groove on the labial side where the shelf meets the maxilla's external surface. The labial border of the groove is vertical, and the lingual border is a gradual slope to the lingual edge of the maxillary shelf. In the center is a large foramen, 5.3 mm long and 2.4 mm wide in dorsal view, and circular in cross-section. The foramen extends into the bone at a small angle from the horizontal, pointing anteriorly and dorsally. Its anterior edge forms a thin overhanging roof while the posterior side slopes gradually towards a ventral floor. Here, on the labial side, there are two smaller foramina pointing ventrally into the bone. The maxillary shelf anterior to the large foramen is flat with a slight, but wide, groove on the labial side.

In labial view, two osteoderms cover part of the external surface of the maxilla. They are raised at their centers and bear a roughly concentric tuberculate pattern. The boundary between the two is indistinct. Their ventral edges are straight and form a distinct, horizontal border dorsal to three mental foramina. These foramina are regularly spaced. The anterior one is tear-shaped, the central foramen is round, and the posterior foramen is oval in labial view, but points anteriorly at an angle into the bone and is subrounded in cross-section. The central foramen is 2.2 mm from the anterior foramen and 2.4 mm from the posterior one. The foramina lie in an horizontal line 0.6 mm ventral to the osteoderms and 2-2.7 mm from the ventral edge of the maxilla.

The ventral edge of the maxilla is straight except between the teeth where the bone is indented. Where the bone meets the teeth, the boundary varies from indistinct to a distinct groove. In ventral view, the external surface of the maxilla is slightly concave and smooth except for the indented areas near the teeth. The maxilla has portions missing dorsally, anteriorly, and posteriorly. In posterior view, the lingual edge of the maxillary shelf is thin. The bone is slightly concave where the teeth attach.

Discussion -- These specimens are assigned to the Tribe Glyptosaurini on the basis of their hexagonal cephalic osteoderms. The glyptosaurines consist of *Glyptosaurus*, *Paraglyptosaurus*, *Helodermoides*, *Placosaurus*, and *Proglyptosaurus* (Sullivan, 1989). *Paraglyptosaurus* is distinguished from the other genera by its flat osteoderms, molariform crushing teeth, straight maxilla, and broad, flat skull, and is the most easily identifiable. *Helodermoides* is known only from the Oligocene, and has obtusely pointed, subconical, slightly recurved teeth (Estes, 1983). *Placosaurus* is known only from Eurasia and has been given by McDowell and Bogert (1954) as a senior synonym of *Glyptosaurus*. *Proglyptosaurus* has subconical osteoderms, obtuse, homodont teeth, and a narrow, high skull (Estes, 1983). The description given by Sullivan (1989) of *Proglyptosaurus huerfanensis* most closely resembles these specimens, in that they have obtuse homodont teeth, but Sullivan did not give a detailed description, or diagrammatic representations of the teeth so I am unable to assign these specimens to *P. huerfanensis*.

Glyptosaurine indet.

Figures 62, 63, and 64

Referred specimens -- UM 106062, UM 106063, UM 106064, UM 106065, UM 106066, UM 106067, UM 106068, UM 106069, UM 106070, UM 106071, UM 106072, UM 106073, UM 106074, UM 106075, UM 106076, UM 106077, UM 106078, UM 106079, UM 106080, UM 106081, UM 106082, UM 106083, UM 106084, UM 106085, UM 106086, UM 106087, UM 106088, UM 106089, UM 106090, UM 106091, UM 106092, UM 106093, UM 106094, UM 106095, UM 106096, UM 106097, UM 106098, UM 106099,

UM 106100, UM 106101, UM 106102, UM 106103, UM 106104, UM 106105, UM 106106, UM 106107, UM 106108, UM 106109, UM 106110, UM 103300 (in part), UM 103822 (in part), UM 103431 (in part), UM 103846 (in part), UM 103229 (in part), UM 102930 (in part), UM 102905 (in part), UM 102905 (in part), UM 102787 (in part), UM 102787 (in part), UM 102835 (in part), UM 103803 (in part), UM 103044 (in part), UM 101433 (in part), UM 103173 (in part), UM 103785 (in part), UM 101482 (in part), UM 102835 (in part), UM 95703 (in part), UM 103000, UM 102930, UM 102998 (in part), UM 102821, UM 103023, UM 102984, UM 103006, UM 102711, UM 102932, UM 102265, UM 102829, UM 102740, UM 101585, UM 103218, UM 103299, UM 103419, UM 102123, UM 102204, UM 102338, UM 102132, UM 102207, UM103707, UM 102136, UM 102217, UM 102243, UM 102147, UM 102222, UM 102251, UM 102177, UM 103211, UM 103697, UM 102201, UM 103178, UM 103471, UM 103232, UM 103227, UM 103191, UM 103430, UM 103925, UM 103531, UM 102289, UM 102367, UM 102368, UM 103771, UM 102334, UM 103695, UM 103295, UM 103743, UM 103180, UM 103189, UM 103204, UM 102369, UM 103365, UM 103533, UM 102221, UM 103908, UM 100918, UM 98781, UM 100527, UM 103275, UM 103340, UM 103339, UM 102716, UM 100431, UM 100438, UM 104024, UM 104187, UM 104240, UM 104272, UM 104274, UM 104306, UM 104322, UM 104363, UM 104452, UM 104466, UM 104508, UM 104522, UM 104618, UM 104619, UM 104708, UM 104713, UM 104718, UM 104848, WPM 9, WPM 294, and WPM 337.

These specimens are assigned to glyptosaurine indet. on the basis of their size and shape, their similarities to the descriptions of Estes (1983) and Sullivan (1986; 1989), and the morphology of their cephalic osteoderms.

Description --

Right and left frontal. UM 100918 (Figure 62). Locality; BI 40

The specimen is a robust, thick fragment, broken on all its edges except where it forms a portion of the median upper boundary of the orbital. The dorsal surface is flat and covered with closely spaced osteoderms that appear to have a roughly concentric arrangement around two central osteoderms. These are of similar size and are surrounded by seven smaller osteoderms, which are in turn surrounded by several larger osteoderms in a more irregular pattern. There are five rows of osteoderms between the orbits. In ventral view the frontal appears undivided, with no median suture, and has two broad ridges - the subolfactory processes - running its length on either side. These are slightly infolded at the anterior end.

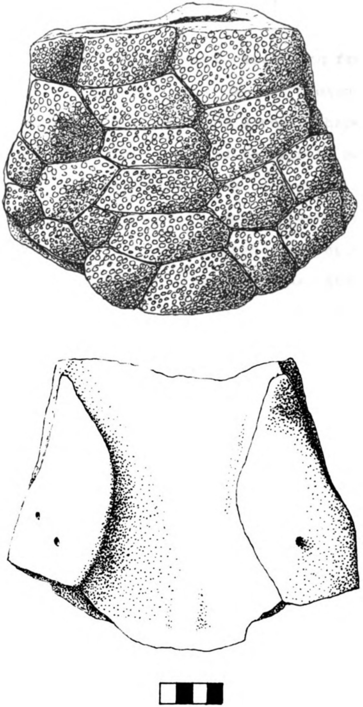

Figure 62. Glyptosaurine indet. UM 100918. Frontal, exterior and interior views. Scale bar is 4 mm.

Parietal. UM 100527 (Figure 63). Locality; BI 15

This specimen is a parietal fragment, extending from the frontoparietal suture to the posterior edge, but broken laterally making it impossible to tell the overall shape of the bone. It is thin for the most part and appears to be undivided. Posteriorly, the parietal tapers to a sharp edge that is slightly irregular transversely. The posterior border at the center is indented by a V-shaped notch. Most of this suture is missing on the right side of the midline, and it is entirely missing on the left. The frontoparietal suture is only present on the right side and slopes posteriorly from the midline for 5 mm (unlike that of the type of Glyptosaurus - USNM 16523 - which is straight). It has a slightly thickened rugose sutural surface.

The dorsal surface of the parietal table is only partly covered with polygonal osteoderms indicating incomplete fusion to the underlying bone (Sullivan, 1986). The cranial osteoderms are covered with raised tubercular mounds arranged in concentric patterns around a raised point at or near the center of the osteoderm. The posterior border of the area covered with osteoderms is an irregular line, 8 mm from the posterior edge of the parietal. From here the osteoderms continue to within 3 mm of the anterior border. They form a roughly concentric pattern with one small osteoderm at the center. This osteoderm is lower than those surrounding it and forms a small depression. The small, distinct pineal foramen

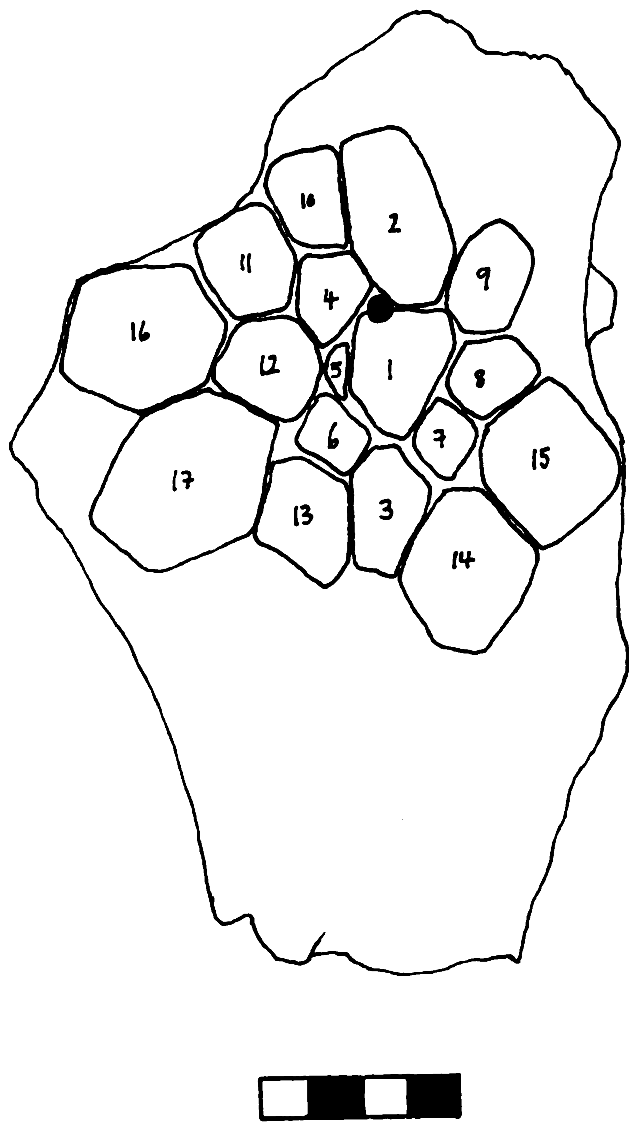

Figure 63. Glyptosaurine indet. UM 100527. Parietal, showing numbered osteoderms. Scale bar is 4 mm.

lies on the midline between this osteoderm and the one immediately anterior to it which is of approximately the same size. Figure 63 shows the numbered osteoderms. Eight osteoderms form a ring around the central one (number 1). Numbers 2 and 3 are on the midline and are larger than the others. Numbers 4 to 8 are small with 9 being slightly larger. Numbers 2 through 9 have one edge in contact with number 1. Around this is another circle of larger osteoderms (10-15). These are polygonal with the most anterior two (10 and 11) being smaller than the rest; 12-15 are of approximately the same size. On the left side, two larger osteoderms are located lateral to 11, 12 and 13 (numbers 16 and 17). Osteoderms 17, 13, 3, and 14 form the posterior border and 2, 9, and 10 form the anterior border of the plated area. The specimen is assigned to the Tribe Glyptosaurini due to the presence of the characteristic pattern of small, subequal, polygonal osteoderms covering the skull.

On the ventral posterior portion of the parietal are three prominent ridges. The two lateral and divergent ones extend backwards and would have given support to the slender processes that extend backward to meet the tabulare. However, this specimen does not show the full extent of these ridges. The median ridge, which is high at the center, rapidly subsides to the posterior border where a V-shaped notch occurs. Its ventral border is narrow and grooved in the center posteriorly, while to the anterior, the walls of the groove diverge to form deep lateral ridges that contribute to the formation of the posterior walls of the brain case. A deep, round pit lies on the midline, 5 mm anterior to the point where the ridges diverge, and the pineal foramen perforates the bone at the bottom of the depression between the anterior extensions of these ridges. It is a 3 mm by 1 mm slit, and lies 5 mm forward of the deep pit. The depression is roughly rectangular and slopes towards the frontoparietal suture.

These anterior diverging ridges, running roughly parallel to each other, and forming a rectangular depression where the pineal foramen is located, are similar to the type specimen of *G. hillsi* described by Gilmore (1928). Similarly, this specimen exhibits an inclined frontoparietal suture as in *G. hillsi*. The fact that the pattern of the dermal armor is different could be due to intraspecific variation. *G. hillsi*, as described by Gilmore (1928), is now a synonym of *Paraglyptosaurus hillsi* (Sullivan, 1986), and is the closest to this specimen. However, the characteristics on which this is based are not strong enough in my opinion to warrant a designation other than glyptosaurine indet.

Parietal. UM 98781 (Figure 64). Locality; BB 83

This specimen is the right half of the bone. The frontoparietal suture is intact, but the bone is broken posteriorly and laterally making it impossible to ascertain

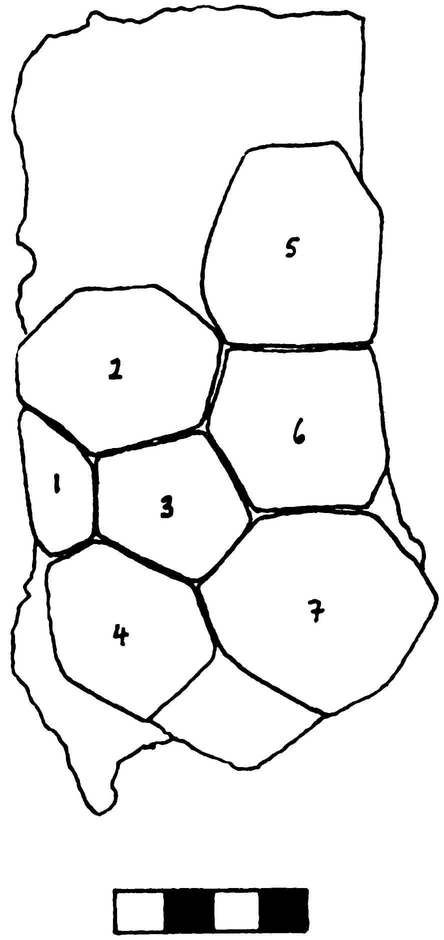

Figure 64. Glyptosaurine indet. UM 98781. Parietal, showing numbered osteoderms. Scale bar is 4 mm.

its original shape. The parietal is more robust than UM 100527, and thickens towards the frontoparietal suture which is rugose. Since the fragment includes the midline, the bone was presumably undivided.

The dorsal surface of the parietal is only partly covered with polygonal osteoderms which are absent from the most anterior part of the bone. The osteoderms are covered with raised tubercular mounds arranged in concentric patterns around a raised central point. The pattern of the tubercles is more regular than in UM 100527 and the osteoderms themselves are more equal in size, and are more regularly placed around the central osteoderm, which lies posterior to the pineal foramen. Osteoderm 1 (Figure 64) is slightly smaller than those lateral to it. Osteoderms 2, 3, and 4 are of roughly equal size and form an inner ring around osteoderm 1. Osteoderms 5, 6, and 7 are the largest present and probably formed part of an outer ring. Since the specimen is broken along the midline the pineal foramen is represented in dorsal view by a semi-circular indentation anterior to osteoderm 1 and probably was either between this osteoderm and the one immediately forward of it, or within this second osteoderm. The pattern, size, and shape of the osteoderms is different from UM 100527 but closely resembles the type of _G. hillsi_ described by Gilmore (1928), thus providing evidence of intraspecific variation.

Two prominent ridges occur on the posterior ventral portion of the parietal. The right lateral ridge runs from the posterior edge to its intersection with the central ridge. It is slightly higher and more prominent than those on specimen UM 100527. The central ridge is narrow and high and runs for 5 mm from the broken posterior edge to the point at which it diverges. Only a small part of the left extension of the median ridge is present. Here, a semi-circular indentation marks the position of the deep pit seen in UM 100527. In cross-section, this pit extends about two-thirds of the way into the bone forming a V-shape. Anterior to this pit, in ventral view, the right diverging anterior ridge forms one side of a roughly rectangular depression which contains the slitlike pineal foramen. Seen in cross-section, this foramen continues though the bone, inclined posteriorly, until it emerges on the dorsal surface anterior of osteoderm 1. Gilmore (1928) described the type for _G. hillsi_ which is identical to this specimen with respect to the parallel anterior diverging ridge and the inclined frontoparietal suture, but as with UM 100527 these characteristics are not robust, so I place this specimen in glyptosaurine indet.

Discussion -- The glyptosaurine species have been distinguished by a number of characters that are now in doubt, such as the fusion of the frontal, and osteoderm shape and pattern (Sullivan, 1979; Estes, 1983). Since there seem to be no reliable characters on which to base the diagnosis of a single skull element, I cannot assign these specimens to species within the Glyptosaurini. A fourth species is not indicated.

Anguidae indet.

<u>Referred specimens</u> -- UM 106111, UM 106112, UM 106113, UM 106114, UM 106115, UM 106116, UM 106117, UM 106118, UM 106119, UM 106120, UM 106121, UM 106122, UM 106123, UM 106124, UM 106125, UM 106126, UM 106127, UM 106128, UM 106129, UM 106130, UM 106131, UM 104601, UM 104689, UM 104689, UM 102835 (in part), WPM 192, and WPM 198.

<u>Description</u> -- These specimens include a number of small, sculptured osteoderms. They can be rounded, rectangular or triangular, depending on their position on the body. The dentaries are incomplete, and lack whole teeth. They are assigned to Anguidae indet on the basis of their ventral, open Meckelian groove, robust jaws, robust teeth, and their similar overall shape to known anguid specimens.

Subfamily Diploglossinae Bocourt, 1873-1879

These are anguids found today in South and Central America, and the Antilles. They are found in Wyoming in the Eocene and in some Pleistocene localities in Dominican Republic and Puerto Rico. They have thin, cycloid or subrectangular osteoderms with an extensive overlap, reduced internal arbor, and an unusual peaked articulation surface possibly reflecting a skink-like habitus. The teeth are closely spaced, less recurved, and fewer in number than in gerrhonotines. The tooth crowns are coarsely striated. Some species have blunt-conical crushing molariform teeth, others pointed conical teeth (Estes, 1983).

Eodiploglossus Gauthier, 1982.

Type species -- Eodiploglossus borealis Gauthier, 1982.

Referred species -- None.

Diagnosis -- Eodiploglossus differs from other diploglossines in retaining subrectangular body osteoderms, although the derived peaked gliding surface has been achieved. Also, the frontoparietal osteoderms are closer to the midline, and the teeth are less robust (Estes, 1983). They have a robust dentary with a less prominently developed coronoid process than in other diploglossines. They have stout, pleurodont, slightly recurved teeth. Their crowns have coarse striations lingually, but never have striations labially (Gauthier, 1982). A small anterior cusp is developed on posterior teeth. The maxilla shows evidence of osteoderm attachment. The osteoderms are usually subrectangular, but occasionally ovoid. They are thin, with no keel. They are deeply imbricated with a smooth gliding surface on the anterior portion of the osteoderm. This derived peaked osteoderm gliding surface indicates that this species belongs to the Diploglossinae, but it is unique in retaining some primitive anguid character states not present in Holocene forms (Estes, 1983).

Age and distribution -- Lower Eocene, Wyoming, USA.

Eodiploglossus borealis Gauthier, 1982.

Figure 65

Type specimen -- UCMP 100100

Type locality -- Sweetwater County, Wyoming; Wasatch Formation; early Eocene.

Previously referred specimens -- UCMP; several.

Diagnosis -- The osteoderms are subrectangular, with a raised center. They have one articulation surface along one short edge. It is broad, and has an irregular border with the tuberculated area. A second articulation surface lies along one long edge. It is relatively narrow, laterally bevelled, has a straight border with the sculptured area, and is triangular, having a broad contact with the other articulation surface, and then tapering to a point at the far corner. The osteoderms of E. borealis differ from those of

Apodosauriscus minutus in being more domed, in having an irregular border between the articulation surface and the tuberculated area, in having a longer lateral articulation surface and broader surface along the short edge, and in having a ridge on the inner surface.

Age and distribution -- Early Eocene, Wyoming.

Referred specimens -- UM 105128, UM 106132, UM 106133, UM 106134, UM 106135, UM 106136, UM 106137, UM 106138, UM 106139, UM 106140, and UM 106141.

These specimens are referred to Eodiploglossus borealis on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Osteoderms. UM 105128 (Figure 65). Locality; 1127

This specimen consists of several unassociated osteoderms ranging from 2 mm to 3 mm in length. They are subrectangular, with a slightly raised center. On the dorsal surface there is a short, broad articulation surface. It is smooth, flat, and has a straight outer edge. The border with the sculptured area is straight, except close to the contact with the second articulation surface, where it projects onto

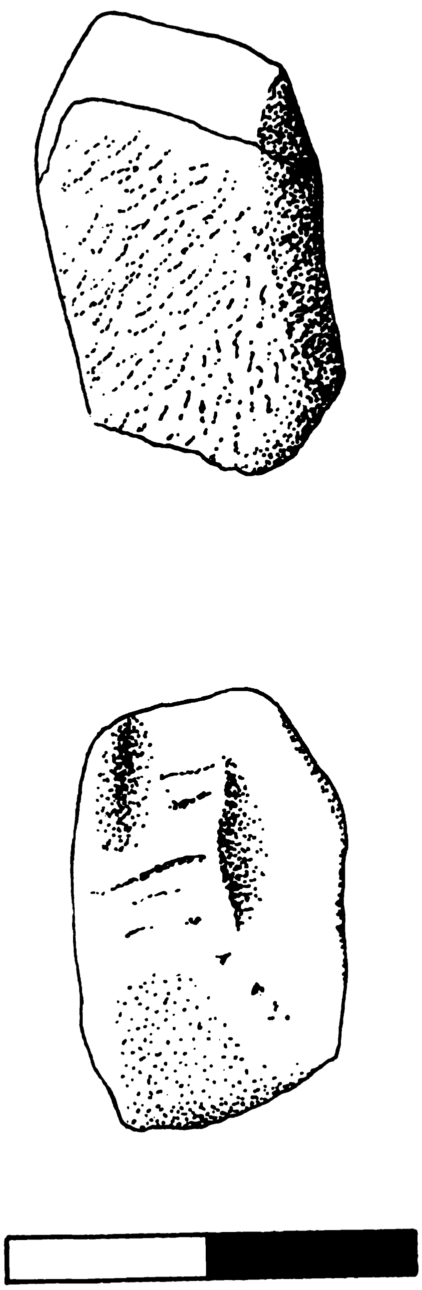

Figure 65. Eodiploglossus borealis. UM 105128. Osteoderm, exterior and interior views. Scale bar is 2 mm.

the tuberculated area. The second articulation surface is long, thin, bevelled, and triangular. It tapers from its contact with the first surface to a point at one corner. The sculpture pattern consists of many, short, vermiculate, ridges and grooves. The ventral surface is smooth and concave. A low ridge radiates from the center, to the corner where the second articulation surface tapers to a point on the outer surface.

Discussion -- Only osteoderms are present in the assemblage. This is probably due to the size of the animal. All other skeletal elements would have been too small and fragile for preservation. Few specimens are present in the collection, which is probably a result of collection bias, again due to size. Other minute osteoderms occur in the assemblage. Some have similar sculpture patterns, but lack the irregular articulation surface border, and the ridge on the inner surface.

Superfamily Varanoidea Fitzinger, 1826

This group includes the Necrosauridae, Helodermatidae, Varanidae, Aigialosauridae, Mosasauridae and Dolichosauridae. The skull is usually moderately long and slender with the external nares greatly extended posteriorly. The nasals are usually slender and fused, the maxilla short. The teeth usually have expanded, crenulated bases, except in the

Necrosauridae. Articulations between the vertebrae are usually oblique. The cervical hypapophyses have free epiphyses (Estes, 1983). The vertebral centra are depressed. In ventral view, the condylar surface is barely exposed (Gilmore, 1928).

Family Varanidae Gray, 1827

Today this group exists only in the Old World, but at the height of tropicality during the Eocene and Miocene varanids occured in northern Eurasia and North America. The teeth are usually trenchant, keeled and sometimes have serrated edges. Tooth bases are expanded, exhibiting labyrinthine folding (Estes, 1983). The ventral surface of the centrum is broad, flat, and occasionally rounded, with no carina (Gilmore, 1928).

Saniwa Leidy, 1870.

Type species -- Saniwa ensidens Leidy, 1870.

Referred species -- Saniwa agilis (Thinosaurus agilis); Saniwa crassa (Thinosaurus crassa); Saniwa grandis (Thinosaurus grandis); Saniwa paucidens (Thinosaurus paucidens) Marsh, 1872; Saniwa australis Marsh, 1899; Saniwa orsmaelensis Dollo, 1923; Saniwa, aff. Kuhn, 1940; Saniwa sp.

Hoffstetter, 1943; Saniwa brooksi Brattstrom, 1955; cf. Saniwa sp Sullivan, 1982.

Diagnosis -- Saniwa represents a group of Eocene and Oligocene varanids from North America and Europe that differ from Varanus only in having a larger number of primitive character states. Two specimens tentatively referred to Saniwa are from the middle Paleocene of Wyoming (Estes, 1983).

The presence of a zygosphene and zygantrum and the reduction of the cervical intercentra are derived character states relative to Varanus. Romer (1956) placed Saniwa in the subfamily Saniwinae to distinguish it from Varanus; Estes (1983) puts both in the Family Varanidae as all differences are slight. I have kept Saniwa in the Varanidae.

The skull is open, light, elongate, and narrow. The dentary is large. The teeth are pleurodont, sharply pointed, trenchant, recurved, and with splayed, crenulated bases. Palatine and pterygoid teeth are present. Their are six teeth in the premaxilla. The vertebrae are procoelous with a depressed condyle and cotyle. The condyle is orientated dorsally, the cotyle ventrally. The centrum is subtriangular. There is a weak ventral keel anteriorly, with a weak transverse convexivity posteriorly. Rudimentary zygosphenes are present. The first cervical rib is on the fifth vertebrae. The cervical hypapophyses have free epiphyses. Caudal vertebrae have a midventral groove. The neural spines are low and broad, especially in the caudals. The caudal intercentra have an intercentral articulation which is closer to the condyle than in *Varanus*. Percondylar constriction is less well-marked than in *Varanus* (Estes, 1983).

Age and distribution -- ?Middle Paleocene, Wyoming; early Eocene, Wyoming, New Mexico, Belgium and France; middle Eocene, Wyoming; late Eocene, California and Utah; early Oligocene, Wyoming; middle Oligocene, Nebraska.

Saniwa ensidens Leidy, 1870.

Figure 66

(*Synonyms* -- *Thinosaurus leptodus* Marsh, 1872, *Saniwa leptodus* Gilmore, 1922.)

Type species -- USNM 2185.

Type locality -- Sweetwater County, Wyoming; Bridger Formation; middle Eocene.

Diagnosis -- *Saniwa ensidens* differs from *Saniwa agilis* in having a higher neural spine and a neural arch with a straight posterior border; from *Saniwa brooksi* in that two times the height of the condylar ball is greater than its width; from *Saniwa crassa* in being smaller and having a less flattened ventral centrum surface; from *Saniwa grandis* in being much smaller, having a more flattened ventral centrum surface, and lacking the medial inflection of the 'zygosphenes'; and from Saniwa paucidens in having a lesser longitudinal cavity of the ventral centrum surface (Estes, 1983).

Previously referred specimens -- AMNH 5169; early Eocene, Wasatch Formation, Clark's Fork Basin, Wyoming. YPM 612; middle Eocene, Bridger Formation, Grizzly Buttes, Uinta County, Wyoming. AMNH 6056, USNM 4128, and USNM 4199; middle Eocene, Bridger Formation, Uinta County, Wyoming. YPM 1064, YPM 1070; no data.

Age and distribution -- Early Eocene to middle Eocene, Wyoming.

Referred specimens -- UM 106142, UM 106143, UM 106144, UM 106145, UM 106146, UM 106147, UM 106148, UM 106149, UM 106150, UM 106151, UM 106152, UM 106153, UM 106154, UM 106155, UM 106156, UM 106157, UM 106158, UM 106159, UM 106160, UM 106161, UM 106162, UM 106163, UM 106164, UM 106165, UM 106166, UM 106167, UM 106168, UM 102930 (in part), UM 102080, UM 102309, UM 100431, UM 101021, UM 103588, UM 102158, UM 103523, UM 103774, UM 100475, UM 100483, UM 102275, UM 102968, UM 103325, UM 102202, UM 103558, UM 103463, UM 103462, UM 103205, UM 103272, UM 102208, UM 104027, UM 104134, UM 104267, and UM 104328.

These specimens are referred to Saniwa ensidens on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Vertebrae. UM 102080 (Figure 66). Locality; BB 56

This specimen consists of 20 associated vertebrae. None are complete. The dimensions of the most complete vertebra are; length of the neural arch: 12 mm, width of the cotyle: 8.2 mm, width of the condyle: 8.6 mm, length between the prezygapophyses and postzygapophyses: 16 mm, width of the prezygapophyses: 16.3 mm, width of the postzygapophyses: 13.9 mm, height: 11.5 mm.

In dorsal view, this vertebra has a sub-rectangular neural arch. The prezygapophyses point at about 45 degrees anterolaterally, and have oval facets. A low, sharp neural arch runs the length of the neural arch. The postzygapophyses project laterally, almost at right angles from the midline. The posterior edge of the neural arch is roughly straight. In ventral view, the centrum is sub-triangular and expanded anteriorly. It has a smooth, flat ventral surface with two lateral foramina lying nearer the anterior edge than the posterior. They are very small relative to the large size of the vertebra. The cotylar opening is exposed. The shelf-like synapophyses lie ventral to the prezygapophyses.

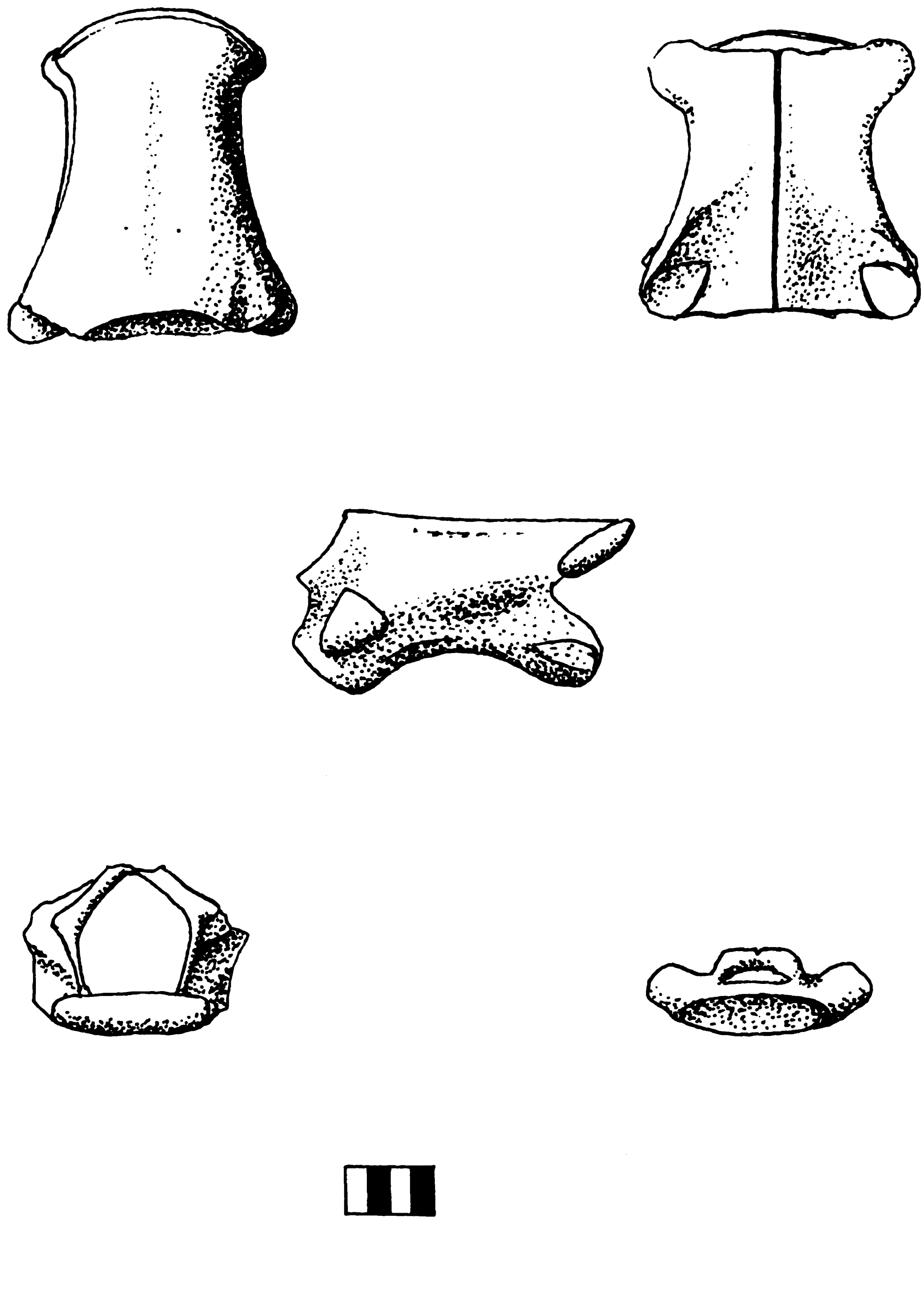

Figure 66. Saniwa ensidens. UM 102080. Vertebra, ventral, dorsal, lateral, posterior, and anterior views. Scale bar is 4 mm.

In anterior view, the cotyle is a depressed ovoid. The neural arch is low, and the neural canal is sub-triangular. The prezygapophyses point slightly dorsally, and ventral to them are the synapophyses. No part of the vertebra projects as far ventrally as the ventral edge of the cotyle. In lateral view, the vertebra is elongate. It has a flat ventral surface and a large distance between the pre- and postzygapophysial facets. In posterior view, the vertebra is incomplete. Two other specimens have condyles which are depressed ovoids. There is a slight precondylar constriction. The postzygapophysial facets point slightly dorsally.

Discussion -- *S. ensidens* is the only adequately known species of *Saniwa*. The differences given in the diagnosis above are seen in the specimens in this assemblage. Where present, the neural spine is high, unlike *S. agilis*. They also have a roughly straight posterior edge to the neural arch. The dimensions of the cotyle are always consistent with *S. ensidens*, i.e. two times the height is less than the width of the condyle, as opposed to the condition found in *S. brooki*, where two times the height is more than the width. *S. crassa* is larger than *S. ensidens*, but the figures given by Estes (1983), for the length of the centrum are: *S. ensidens*; 11.6 mm to 15.9 mm, *S. crassa*; 16 mm and above. These could be the same species, or distinct. There are not enough specimens in this assemblage to determine this, and only one is longer than 16 mm. Further characteristics that distinguish S. ensidens from S. crassa are the flatter ventral surface and less distinct precondylar constriction found in S. crassa. However, the specimen that exceeds 16 mm in length has a similar degree of precondylar constriction as the other vertebrae, and the ventral surface of many of the smaller specimens is flat. The ventral surfaces of the vertebrae of UM 102080 vary. The smaller ones tend to have convex surfaces, the larger ones are flat. S. grandis is much larger than any of the specimens found here, having a centrum 20 mm long. Also, the ventral surface of S. grandis is strongly convex, a condition not found in these specimens. S. paucidens has a concave ventral surface is lateral view, which is not seen in these vertebrae.

Saniwa indet.

Figures 67 and 68

Referred specimens -- UM 105129, UM103558, and UM 103927

These specimens are referred to Saniwa indet. on the basis of the possession of a large dentary and maxilla, with pleurodont, sharply pointed, recurved, tenchant teeth with splayed, crenulated bases.

Description --

Dentary. UM 103927 (Figure 67). Locality; Foster Reservoir

This specimen consists of a portion (9.8 mm) of a posterior right dentary. It bears one complete tooth and two broken ones. The root of the first tooth is parallel sided in lingual view, slightly anteroposteriorly compressed, and oval in cross-section. It has an expanded and crenulated base containing a central replacement pit. The second tooth is recurved, to point posteriorly. Its root is similar to the first. The crown is a worn, simple, blunt point. The third tooth is a partial base.

The lingual shelf, and ventral portion of the dentary, are missing, giving the Meckelian groove an open appearance. The labial surface of the dentary is slightly pitted, and contains one ovoid, distinct mental foramen midway down the dentary, ventral to the second tooth. In cross-section, the dorsal portion of the exterior dentary is flat and vertical until the position of the foramen, where the dentary becomes convex.

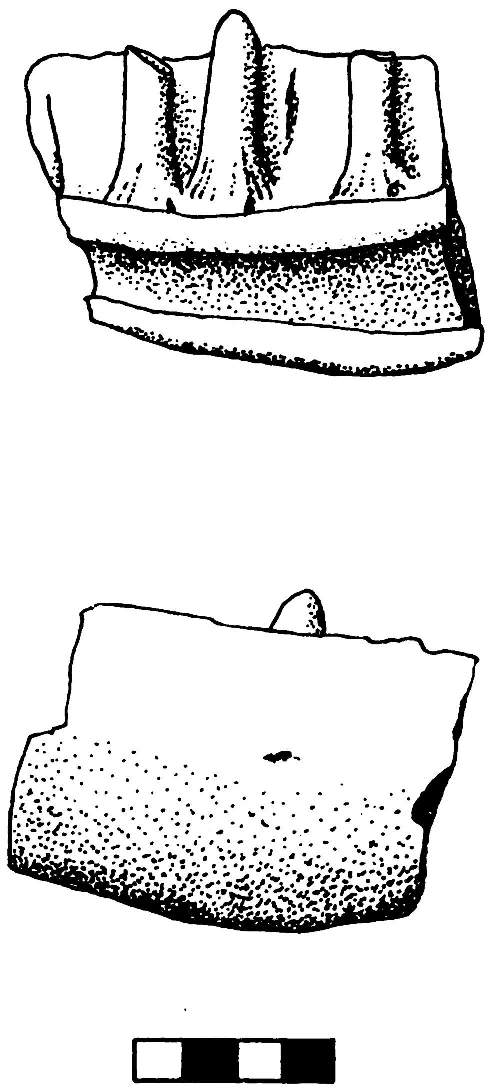

Figure 67. Saniwa ensidens. UM 103927. Right dentary, lingual and labial views. Scale bar is 4 mm.

Maxilla. UM 105129 (Figure 68). Locality; 1139

This specimen consists of a portion (3.3 mm) of a maxilla containing one complete tooth. The tooth is recurved, slender, and points lingually. The base is crenulated, and expanded lingually and anteroposteriorly, producing a splayed effect where the tooth meets the sub-dental platform. The tip of the tooth is missing.

Little of the maxilla is present making it impossible to determine if this is a right or left maxilla. In lingual view, the sub-dental shelf is sloped, the maxillary shelf missing. The external surface is vertical, flat, and smooth except for one large, oval mental foramen half-way down the bone.

Discussion -- The dentary of *Saniwa* is not sufficiently known to be able to assign these specimens to a species. Their teeth have a distcintive shape and splayed, crenulated bases, which allow their assignment to *Saniwa* indet.

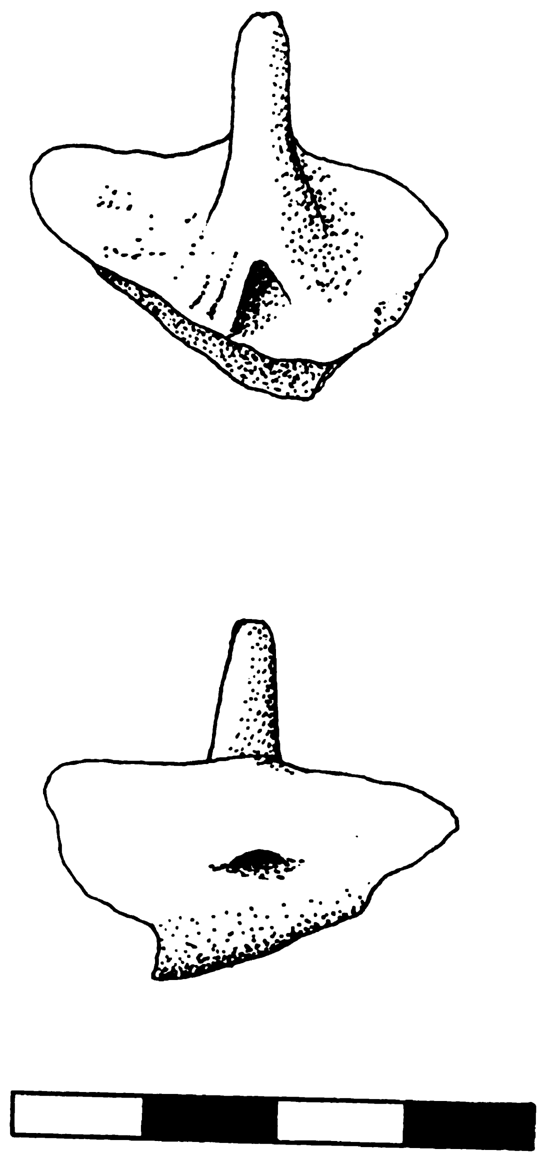

Figure 68. Saniwa ensidens. UM 105129. Maxilla, lingual and labial views. Scale bar is 4mm.

Sauria indet.

Referred specimens -- UM 106169, UM 106170, UM 106171, UM 106172, UM 106173, UM 106174, UM 106175, UM 106176, UM 106177, UM 106178, UM 106179, UM 106180, UM 106181, UM 106182, UM 106183, UM 106184, UM 106185, UM 106186, UM 106187, UM 106188, UM 106189, UM 106190, UM 106191, UM 106192, UM 106193, UM 106194, UM 106195, UM 106196, UM 106197, UM 106198, UM 106199, UM 106200, UM 106201, UM 106202, UM 106203, UM 106204, UM 106205, UM 106206, UM 106207, UM 106208, UM 106209, UM 106210, UM 106211, UM 106212, UM 106213, UM 106214, UM 106215, UM 106216, UM 106217, UM 106218, UM 106219, UM 106220, UM 106221, UM 106222, UM 106223, UM 106224, UM 106225, UM 106226, UM 106227, UM 106228, UM 106229, UM 106230, UM 106231, UM 106232, UM 106233, UM 106234, UM 106235, UM 106236, UM 106237, UM 106238, UM 106239, UM 106240, UM 106241, UM 106242, UM 106243, UM 106244, UM 106245, UM 106246, UM 106247, UM 106248, UM 106249, UM 106250, UM 106251, UM 106252, UM 106253, UM 106254, UM 106255, UM 106256, UM 106257, UM 106258, UM 106259, UM 106260, UM 106261, UM 106262, UM 106263, UM 106264, UM 106265, UM 106266, UM 106267, UM 106268, UM 106269, UM 106270, UM 106271, UM 106272, UM 106273, UM 106274, UM 106275, UM 106276, UM 106277, UM 106278, UM 106279, UM 106280, UM 106281, UM 106282, UM 106283, UM 106284, UM 106285, UM 106286, UM 106287, UM 106288, UM 106289, UM 106290, UM 106291,

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part), UM 102876 (in part), UM 103441, UM 103778 (in part),
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UM101472 (in part), UM 103038 (in part), UM [illegible] (in part),
UM 103250, UM 104122, UM 104132, UM 104136, UM [illegible] and
UM 104286.

Description -- The dentaries are assigned to Sauria indet. on the basis of their robust nature, and their pleurodont teeth which are larger than those found in the Amphibia. The vertebrae are assigned because they are procoelous, have undivided synapophyses, lack a zygosphene-zygantrum articulation, have a centrum with unparallel lateral borders, and lack a prezygapophysial process.

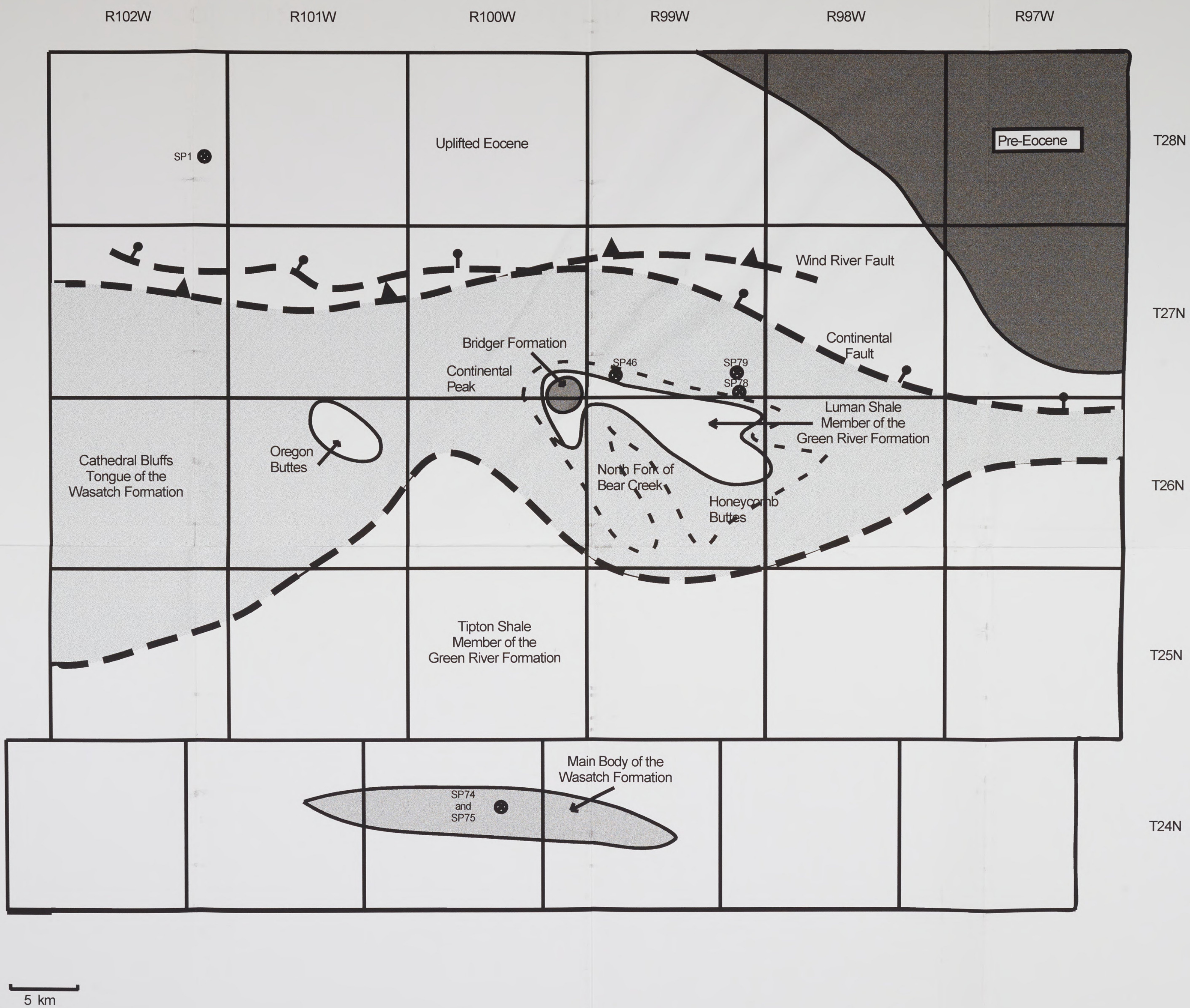


Plate 1. Geologic map of the South Pass area, northern Green River Basin, with localities (SP1, SP46, SP74, SP75, SP78, and SP79), the Wind River and Continental faults, and geographic features shown.

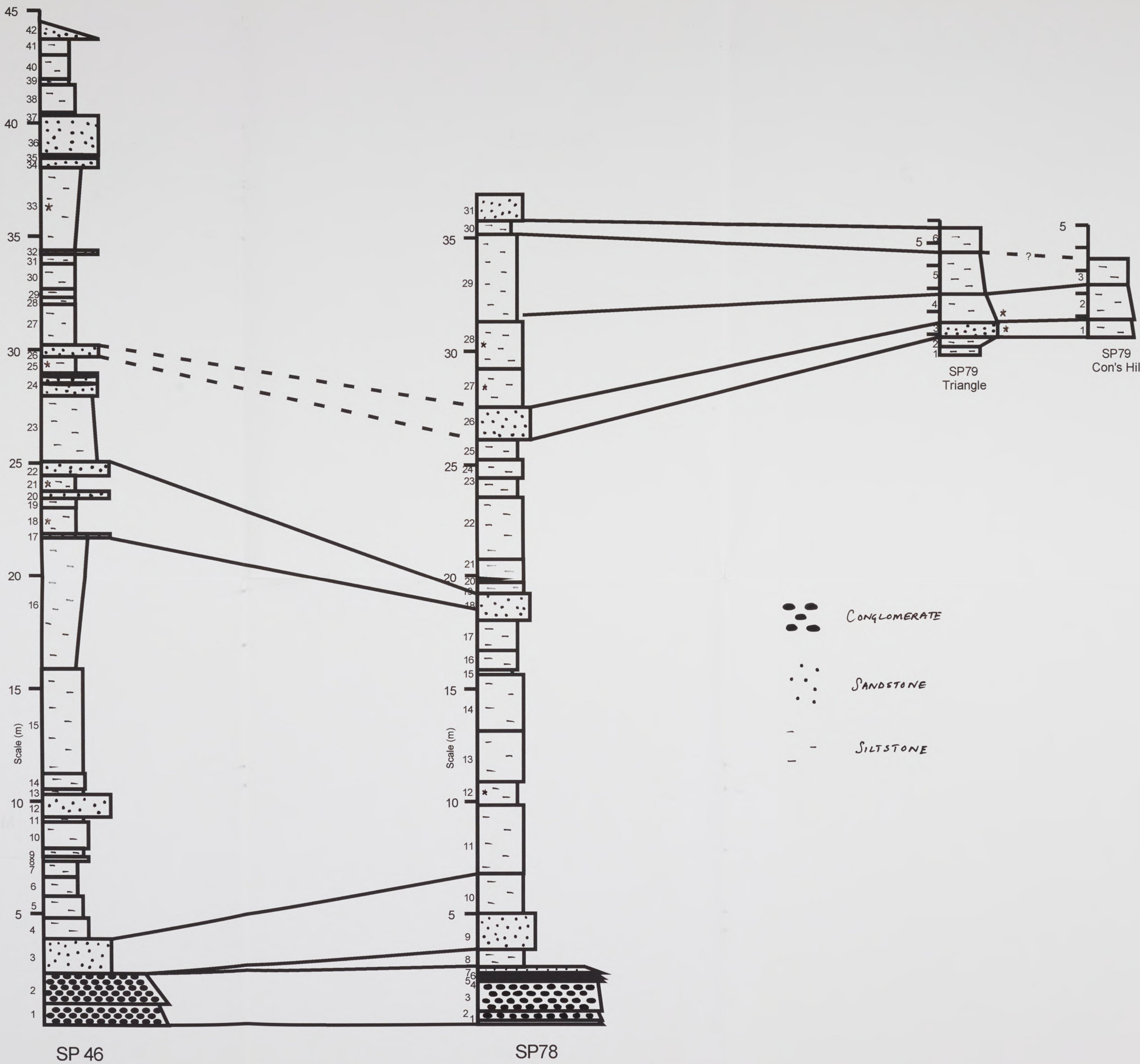
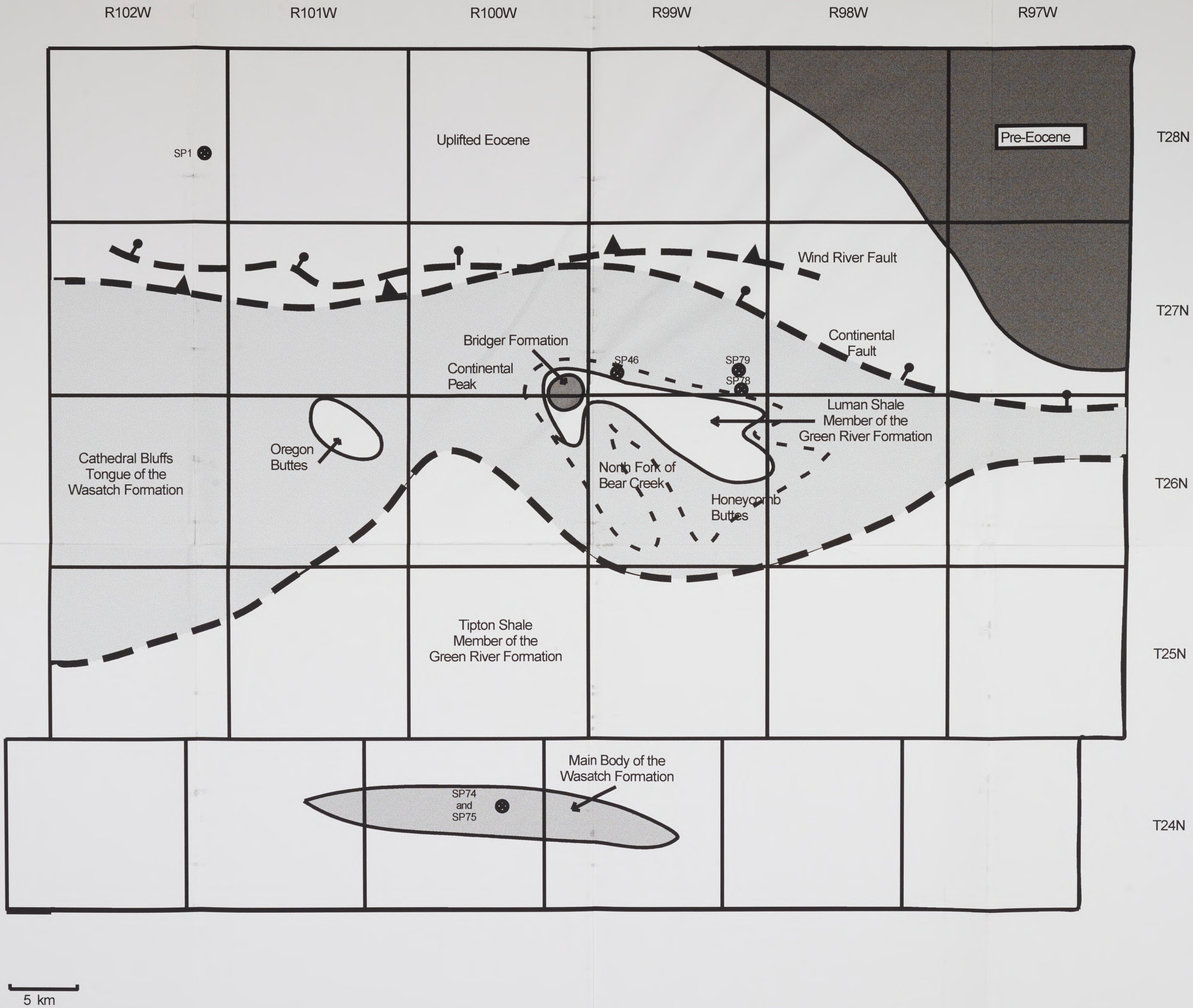


Plate 2. Stratigraphic sections from SP46, SP78, SP79 (Triangle), and SP79 (Con's Hill). Numbers correspond to numbered beds in text. * indicates fossiliferous beds.

Prior to here: 2 Plates



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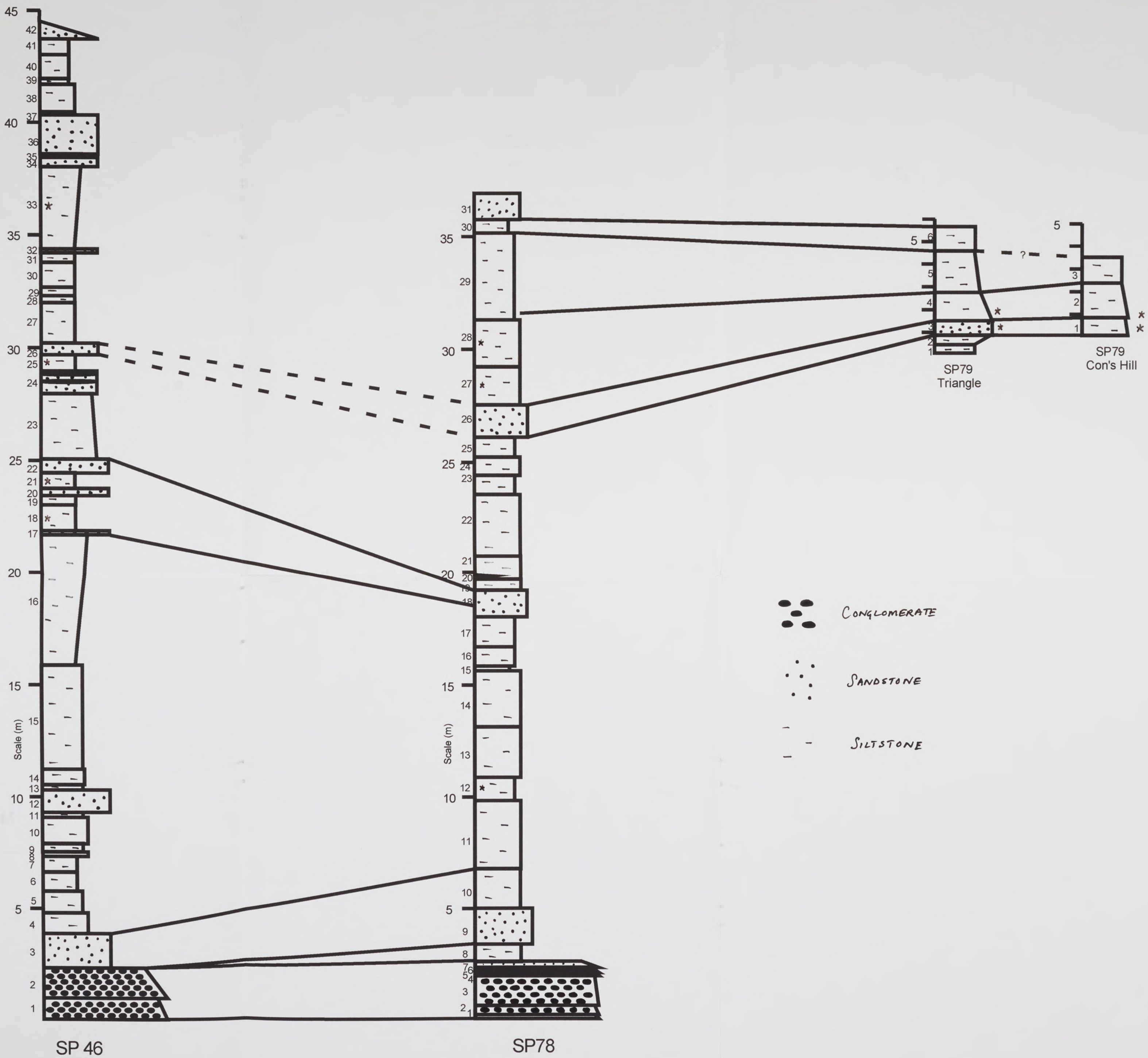

Plate 2. Stratigraphic sections from SP46, SP78, SP79 (Triangle), and SP79 (Con's Hill). Numbers correspond to numbered beds in text. * indicates fossiliferous beds.

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AN ANALYSIS OF THE HERPETOFAUNA AND PALEOENVIRONMENT OF THE WASATCH AND BRIDGER FORMATIONS (MIDDLE EOCENE), AT SOUTH PASS, WYOMING

VOLUME 2

By

Rachael J. Walker

A DISSERTATION

Submitted to

Michigan State University

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

Department of Geology

1999

Order Amphisbaenia Gray, 1844

Amphisbaenians are squamate reptiles with shared-derived characters including; extremely solid skull, with a complex, interdigitating pattern of anterior bones, median enlarged premaxillary tooth, very large, fused orbitosphenoid-pleurosphenoid plate, enclosed anterior braincase, high number of trunk vertebrae, low number of caudal vertebrae (Estes, 1983). Their vertebrae can be distinguished from lizards on the basis of the presence of prezygapophysial processes, and from snakes due to the lack of a zygosphene-zygantrum articulation (Hoffstetter and Gasc, 1969). Their vertebrae are depressed, with a transversely widened, oval condyle without a spinous process except on the first vertebra (Gilmore, 1928). They are stout and solid, with a flat ventral surface of the centrum. They are wider anteriorly than posteriorly, and constricted medially. The centrum is procoelous and parallel sided in ventral view. The neural arch of the trunk vertebrae may be high, but they lack a distinct neural spine (Gans, 1978). The vertebrae in the cloacal region bear hemapophyses (Zangerl, 1945; Hoffstetter and Gasc, 1969) that may unite to form chevrons (Hoffstetter and Gasc, 1969). The atlas-axis complex is distinctive and unlike those found in the squamata. It is totally fused, hourglass shaped, with a concave arc-shaped odontoid process anteriorly, and a condyle posteriorly (Hoffstetter and Gasc, 1969).

Their relationship within the squamata is uncertain, but recent work done on the most primitive amphisbaenian yet found, Sineoamphisbaena hexatabulosis, from the Upper Cretaceous of China, indicates a close relationship to the Scincomorpha (Wu et. al., 1996). However, since the group is poorly known I retain them as a separate order within the Squamata.

Amphisbaenia indet.

Figures 69 and 70

Referred specimens -- UM 106381, UM 106382, UM 106383, UM 106384, UM 106385, UM 106386, UM 106387, UM 106388, UM 106389, UM 106390, UM 106391, UM 105149, UM 103493, UM 101482 (in part), UM 103436 (in part), UM 101472 (in part), UM 101472 (in part), UM 101482 (in part), UM 102835 (in part), UM102835 (in part), UM 103257 (in part), UM 103300, UM 103335, UM 102960, UM 103721, UM 103288, UM 103516, UM 103413, UM 101168, UM 103031, UM 103183, UM 103614, UM 103586, UM 103267, UM 103202, UM 104166, UM 104565, UM 104105, UM 104270, UM 104834, UM 104568, UM 104104, UM 104383, and UM 104657

Description --

Trunk vertebra. UM 105149 (Figure 69). Locality; BB 7

This specimen is an almost complete vertebra, missing both postzygapophyses, and part of the anterior and posterior neural arch. Its dimensions are; length of centrum: 4.1 mm, width at the prezygapophyses: 3.9 mm, width of the condyle: 1.5 mm, height of the condyle: 0.8 mm, width of the cotyle: 1.5 mm, height of the cotyle: 1.1 mm

In anterior view, the vertebra is depressed, with a depressed, oval cotyle. The prezygapophyses point dorsolaterally at about 40 degrees from the horizontal. The neural canal is depressed and oval. The diapophyses are barely exposed. In posterior view, the condyle is a depressed oval. The neural canal is not as low as in the anterior view.

In dorsal view, the prezygapophyses have oval facets, and point posterolaterally at about 45 degrees from the midline. The neural arch is smooth, except for a prominent ridge on the midline and a series of longitudinal ridges and grooves on the posterior neural arch. The vertebra is medially constricted. In ventral view, there is no hemal spine, and the lateral sides of the centrum are parallel. The diapophyses are simple, circular mounds, and the cotylar depression is exposed. In lateral view, the ventral surface is flat and horizontal, the dorsal surface concave.

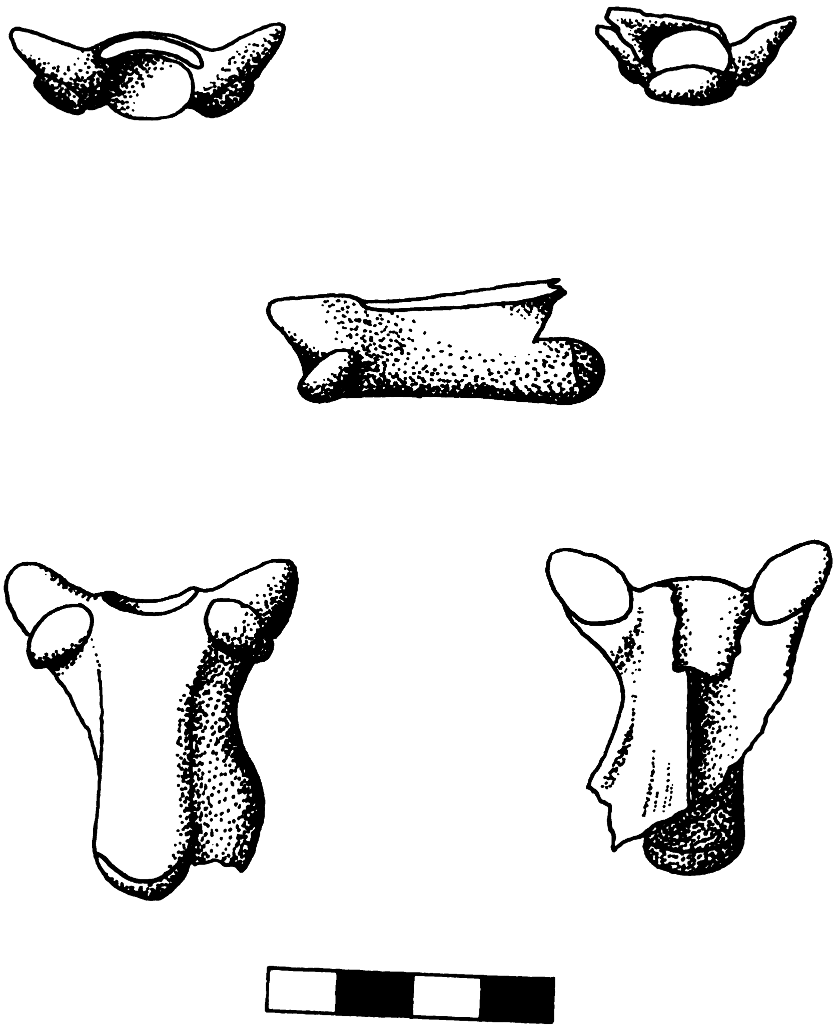

Figure 69. Amphisbaenia indet. UM 105149. Trunk vertebra, anterior, posterior, lateral, ventral, and dorsal views. Scale bar is 4 mm.

Atlas-axis. UM 104568 (Figure 70). Locality; SP 79

This specimen is a complete centrum with a portion of the neural arch attached. Its dimensions are; length: 4.4 mm, width of odontoid process: 3.6 mm, height of odontoid process: 2.2 mm, width of condyle: 2 mm, height of condyle: 1.6 mm, width of neural arch at its base: 2.2 mm.

In anterior view, the dorsal and ventral edges of the odontoid process are parallel and straight. Between them is a concave area that wraps around the anterior tip of the vertebra. In posterior view, the condyle is a slightly depressed oval, with a flattened dorsal edge. The hemapophyses are exposed ventrally. The base of the neural arch extends dorsally from the dorsolateral edges of the condyle.

In dorsal view, the vertebra is fan-shaped anteriorly. Posterior to this is the neural arch which is parallel sided. There is distinct precondylar constriction. In ventral view, the vertebra resembles a blunt arrow. The anterior border is convex. posterior to this is a lunate, flattened area, and posterior to this the centrum. The hemapophyses lie along the midline extending from the flat area of the odontoid process almost to the condyle. There are a number of foramina on the anterior flattened area, and lateral to the hemapophyses. The ventral edge of the centrum is flat and horizontal, and the dorsal edge of the neural arch is missing. The condyle points posteriorly and very slightly dorsally.

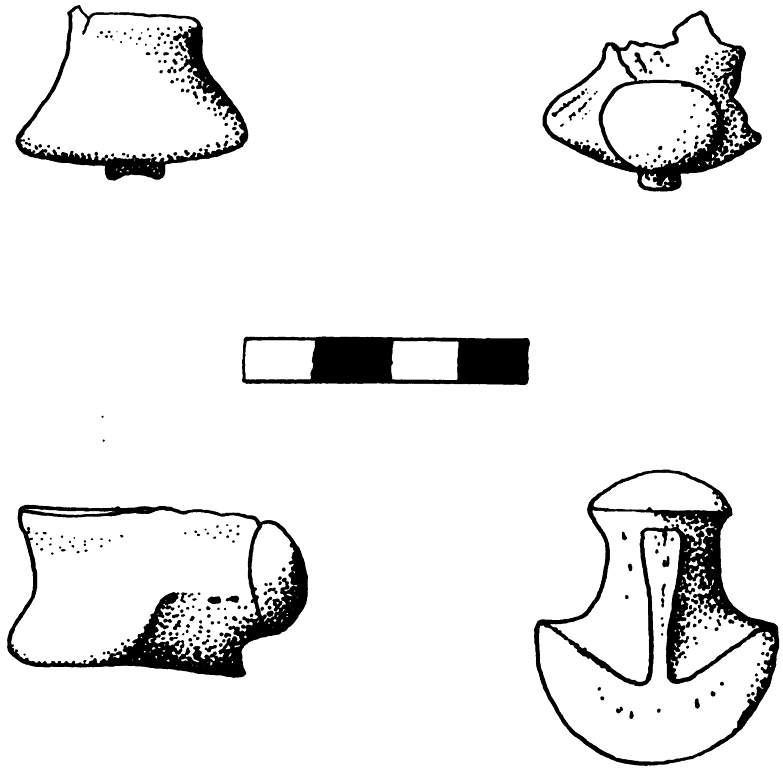

Figure 70. Amphisbaenia indet. UM 104568. Atlas-axis,
anterior, posterior, lateral, and ventral views.
Scale bar is 4 mm.

Discussion -- There are five known genera from the Eocene of North America. Spathorhynchus fossorium, from the early to mid Eocene, Bridger Formation and Wind River Formation of Wyoming, Ototriton solidus from the early Eocene, Wind River Formation, Wyoming, known only from a skull, Lestophis anceps and Lestophis crassus from the middle Eocene, Bridger Formation, Wyoming, both of doubtful validity, and Jepsibaena minor, from the early Eocene, Wind River Formation in Wyoming, known only from skull material (Berman, 1976). All of the University of Michigan specimens are vertebrae. Amphisbaenian vertebrae have changed little since the Eocene and are, therefore, not good for generic diagnosis (Berman, 1973; Berman, 1976). However, Berman (1973) noted that vertebrae of the family Rhineuridae bear longitudinal ridges on the dorsal surface of the neural arch. This feature is possibly present in specimen UM 105149, but I hesitate to make a diagnosis based on one specimen. Therefore, I assign all the specimens to Amphisbaenia indet. on the basis of the presence of one or more of the diagnostic characters above.

Order Serpentes Linnaeus, 1758

The snakes were originally divided into four infraorders by Hoffstetter (1939), the Cholophidia, Scolecophidia, Henophidia, and Caenophidia. This has subsequently been revised, on the basis of phylogenetic evidence (McDowell 1974; Rage 1978). Two suborders are recognized, the Scolecophidia, and the Alethinophidia. The Alethinophidia is further divided into five superfamilies. The Superfamily Simoliopheoidea corresponds to the abandonned Cholophidia, the Aniliidea and Booidea correspond to the Henophidia. The Colubroidea includes all the Caenophidia except those few now found in the Superfamily Acrochordoidea (Rage 1984). The classification of the Serpentes is shown in Table 12.

Table 12. Classification of Serpentes by Hoffstetter (1939), McDowell (1974), and Rage (1978).

Hoffstetter, 1939	McDowell, 1974 and Rage, 1978	
Infraorder	**Suborder**	**Superfamily**
Scolecophidia	Scolecophidia	
Cholophidia	Alethinophidia	Simoliopheoidea
Henophidia		Aniliidea Booidea
Caenophidia		Colubroidea Acrochordoidea

The Serpentes are distinguished by many features in their highly specialized skulls. The dentaries are not rigidly united at the symphysis (Rage, 1984). The vertebrae are highly specialized, bearing additional articulation points. Although some lizards (the Iguanidae, Teiidae, Cordylidae, and Lacertidae) have facets similar to the zygosphene-zygantrum complex, they differ in the following ways. The zygosphene is wide dorsally, with each facet overhanging the prezygapophyses. There is less than a 90 degree angle between the zygosphene and prezygapophysial facets, which are separated by a non-articular area. The anterodorsal lip of the centrum is straight, sinuous, or concave, but never deeply notched, as in lizards (Hoffstetter and Gasc, 1969).

Many features of the teeth of vertebrates are related to function, and are therefore unreliable for a diagnosis. However, authors such as Auffenberg (1963) have shown that the vertebrae can be used in the identification of snakes, since some characters do remain stable throughout the vertebral column. Since all but three of the specimens in this collection are vertebrae, I use them to distinguish genera. I do not believe I have enough evidence to assign many of my specimens to species, more detailed work on snake vertebrae is needed to find reliable characters that are present throughout the vertebral column.

Suborder Alethinophidia Nopcsa, 1923a

This is one of the two suborders of snakes. It contains the majority of snakes in five superfamilies. Characters include; mesokinetic joint absent, prokinetic hinge absent, mobility of the maxilla variable, poison fangs present in some, and vertebral morphology variable.

Superfamily Anilioidea Fitzinger, 1826

This group shares the following characteristics; a narrow, elongate braincase, large vomerine processes on the premaxilla, a nasal-frontal articulation between the snout and braincase, well developed frontals fused to the parietals, a short, vertical quadrate, limited mobility of the maxilla, an ascending process of the maxilla that meets the prefrontals, a coronoid, and depressed vertebrae with slanting zygapophysial facets, and lacking hypapophyses on the mid and trunk vertebrae, and paracotylar foramina (Rage, 1984).

Family Aniliidae Fitzinger, 1826

(Synonym -- Ilysiidae; Fitzinger, 1826. Includes Coniopheidae Hoffstetter, 1955)

This is a group of extant burrowing snakes which includes the fossil genera *Colombophis*, *Coniophis*, and *Eoanilius*. They have a short supratemporal, an odontoid process on the axis, an optic foramen between the parietal and frontal, an occipital condyle with a *fovea dentis*, depressed vertebrae with a flattened, poorly developed neural spine, and caudal vertebrae without hemapophyses (Rage, 1984).

Coniophis Marsh, 1892

Type species -- Coniophis precedens Marsh, 1892

Referred species -- Coniophis carinatus Hecht, 1959, Coniophis cosgriffi, Armstrong-Ziegler, 1978, Coniophis platycarinatus, Hecht, 1959.

Diagnosis -- The posterior border of the neural arch lacks a median notch, the centra are widened anteriorly, they have a round condyle and cotyle, and a distinct hemal keel (Rage, 1984).

Age and distribution -- Upper Cretaceous (Campanian), New Mexico and Wyoming, USA, and Canada to middle Eocene, Wyoming, USA.

Coniophis indet.

Figure 71

Referred specimens -- UM 102730 and UM 101472 (in part).

These specimens are referred to Coniophis indet. on the basis of the possession of one or more of the above diagnostic characteristics.

<u>Description</u> --

Caudal vertebrae. UM 102730 (Figure 71). Locality; SP 35

This specimen is an almost complete caudal vertebra. Its dimensions are; height: 3.3 mm, width at the postzygapophyses: 3.8 mm, length between the pre- and postzygapophyses: 3.4 mm, width of the condyle: 1.3 mm, width of the cotyle: 1.3 mm, length of the neural spine: 1.7 mm.

In anterior view, the cotyle is round. The synapophysial area is wide and a paracotylar foramen lies on either side of the cotyle. The prezygapophyses point slightly dorsally, and have a distinct accessory process. The zygapophysial facets point dorsolaterally at about 60 degrees from the horizontal. In posterior view, the condyle is round. The neural arch is low and bears a low spine. The zygantrum is deep.

In dorsal view, the postzygapophyses are wide and the prezygapophyses are narrow. The neural arch is indistinct from the centrum. The prezygapophysial facet is oval. There is no medial notch in the posterior border of the neural arch. The neural spine runs along half the length of the neural arch and slightly overhangs its posterior border. The zygantral facets are exposed, and the postzygapophyses have a distinct accessory process which is smaller than those on the postzygapophyses. In ventral view, there is a low, broad hemal spine. The postzygapophysial facets are oval. Hemapophyses are present but broken. The centrum widens

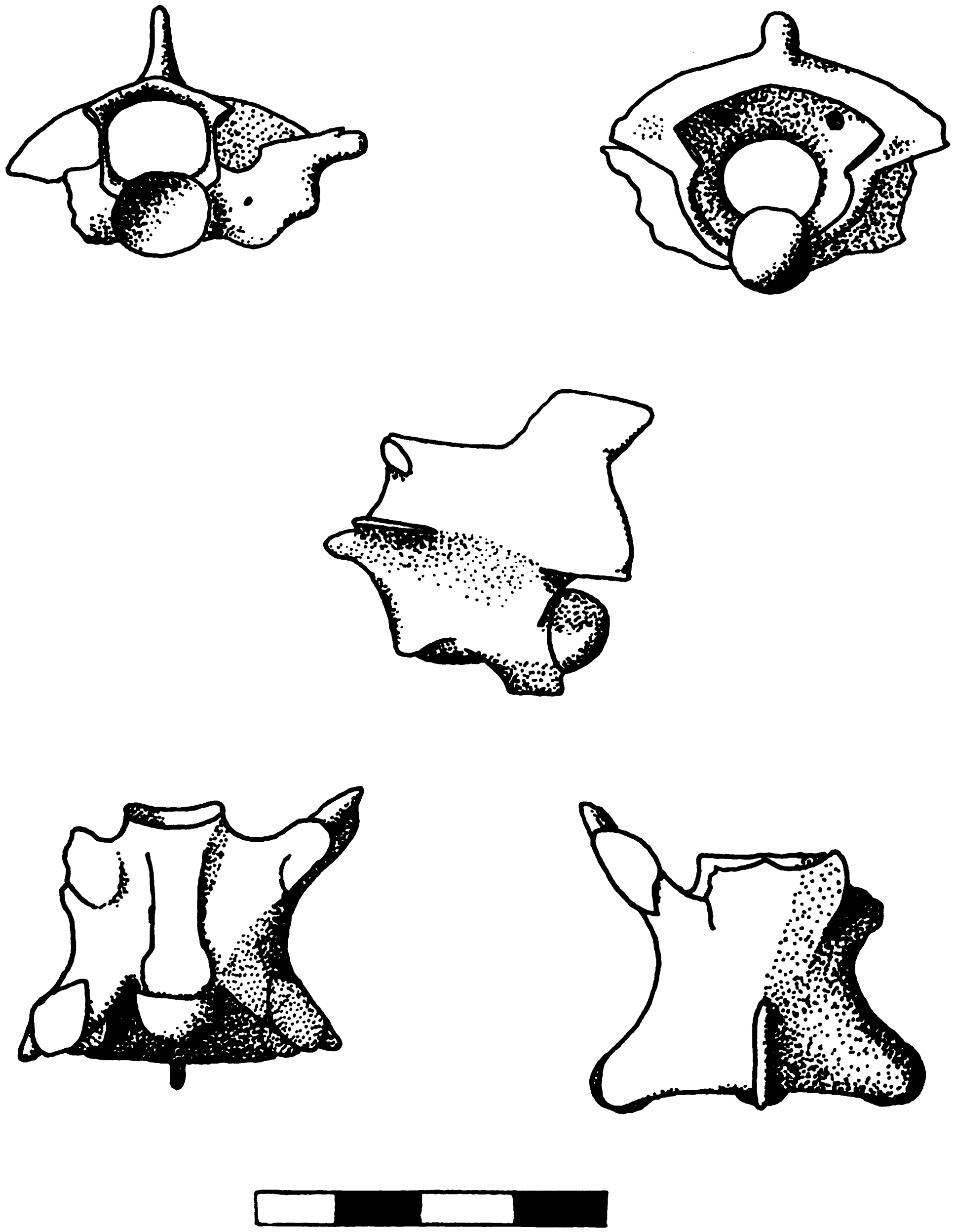

Figure 71. <u>Coniophis</u> indet. UM 102730. Vertebra, anterior, posterior, lateral, ventral, and dorsal views. Scale bar is 4 mm.

anteriorly. In lateral view, the dorsal edge of the neural spine is more dorsal posteriorly. The ventral edge of the centrum is flat and horizontal.

Discussion -- This vertebra resembles Coniophis in all its features except the presence of paracotylar foramina. Since the other features are so characteristic of Coniophis I tentatively assign this specimen to that genus.

Superfamily Booidea Gray, 1825

The braincase is widened posteriorly, behind the orbits and generally does not narrow anteriorly from this region. The maxilla is often very mobile. The vertebrae are short and wide with a higher neural arch than the Anilioidea, and a well developed neural spine. The paracotylar foramina is usual absent, the lateral foramina, present. The caudal vertebrae possess paired hemapophyses (Holman and Case, 1988).

Family Boidae Gray, 1825

The vertebrae are short, wide and massive with short and wide centra. They are higher than long, and shorter than wide. The zygosphene is narrow and thick. The subcentral ridges are arched dorsally. The postzygapophysial part of the neural arch is upswept. The neural spine is thick (Holman, 1976). Hypapophyses are present only on the anterior trunk vertebrae (Rage, 1984). There is little or no additional ornamentation (Holman and Case, 1988). The pelvic vestiges are almost always present in males while being more commonly absent in females (Rage, 1984).

Rage (1984) states that it is not always possible to distinguish the tribes of the Boiidae based on vertebral morphology alone. Since only isolated vertebrae are present in this assemblage, many are assigned to Boidae indet. because of this difficulty. Some, however, fall into distinct groups that closely resemble species of Boidae. For this reason, I tentatively refer these specimens to *Boavus*, *Ogmophis*, or *Dunnophis*.

Subfamily Boinae Gray, 1825

This group has variable cranial features. The neural arch is usually not flattened and lacks additional processes. The prezygapophysial process is greatly reduced but always present. The neural spine is well developed (Rage, 1984). Posterior hypapophyses are usually present (Underwood, 1967). It is not possible to distinguish all the boine tribes based on vertebral morphology.

Boavus Marsh, 1871a.

(Synonym -- Protagras Cope, 1872.)

Type species -- Boavus occidentalis Marsh, 1871a.

Referred species -- Boavus brevis Marsh, 1871a, Boavus idelmani Gilmore, 1938 and ?Boavus affinis Brattstrom, 1955.

Diagnosis -- The vertebrae are large and robust. Both the cotyle and condyle are round. The zygosphene is wider than the cotyle. In lateral view, there is a wide gap between the prezygapophyses and postzygapophyses. The prezygapophyses are barely visible in ventral view, anterior to the paradiapophyses. The neural arch and neural spine are high. The hemal keel is distinct.

Age and distribution -- Middle to late Eocene, USA.

Boavus occidentalis Marsh, 1871a.

Figures 72 and 73

(Synonyms -- Boavus agilis Marsh, 1871a, Protagras lacustris Cope, 1872.)

Type specimen -- PMNH 511

Type locality -- Grizzly Buttes, Wyoming, Bridger Formation, middle Eocene.

Diagnosis -- Both the cotyle and condyle are round. The vertebrae have a thick zygosphene, which is wider than the cotyle. The paradiapophyses project further ventrally than the cotyle. The ventral surface of the centrum is flat, with a sharp, distinct hemal keel which ends just anterior to the condyle (Gilmore, 1938). The neural arch is massive and elevated, the zygosphene is convex in anterior view, concave in dorsal view, and lacks a median tubercle. The neural canal has a distinct median epapophysis on its floor (Marsh, 1871a). In lateral view, the prezygapophysis obscures no part of the zygosphene facet. The pre- and postzygapophysial facets are relatively widely spaced (Rage, 1984). The neural spine is high, and sometimes capped by a slightly laterally expanded, horizontal process. In ventral view, the prezygapophyses are barely visible anterior to the paradiapophyses.

B. occidentalis differs from B. brevis in being larger and longer, with a more massive zygosphene and sharper hemal keel; from ?B. affinis in lacking paracotylar foramina. The vertebrae of B. idelmani are not known.

Previously referred specimens -- None.

Age and distribution -- Middle Eocene, Wyoming, USA.

Referred specimens -- UM 106392, UM 106393, UM 106394, UM 106395, UM 106396, UM 106397, UM 106398, UM 106399, UM 106400, UM 106401, UM 106402, UM 106403, UM 106404, UM 106405, UM 106406, UM 106407, UM 106408, UM 106409, UM 106410, UM 106411, UM 106412, UM 106413, UM 106414, UM 106415, UM 106416, UM 106417, UM 106418, UM 106419, UM 106420, UM 106421, UM 106422, UM 106423, UM 106424, UM 105134, UM 106425, UM 106426, UM 106427, UM 106428, UM 106429, UM 105135, UM 106430, UM 95714, UM102853, UM 102782, UM 103008, UM 102754, UM 103365, UM 99643, UM 103785, UM 105535 (in part), UM 102682 (in part), UM 101483 (in part), UM 102930 (in part), UM 102953 (in part), UM 102787 (in part), UM 101435 (in part), UM 103773, UM103396 (in part), UM103506, UM 104340, UM 104614, and UM 104695.

These specimens are referred to Boavus occidentalis on the basis of the possession of one or more of the above diagnostic characteristics.

Description -- All specimens are massive, and resemble the descriptions of Gilmore (1938) and Rage (1984). The zygosphenes of UM 106408, UM 106412, UM 106418, UM 106421, UM 106423, UM 105134, UM 106427, UM 106429, UM 106425, and UM 105135 are slightly thinner than the others. All have a sharp hemal keel, except UM 106394, UM 106395, UM 106400, UM 106405, UM 106407, UM 106408, UM 106409, UM 106410,

UM 106411, UM 106412, UM 106413, UM 106414, UM 106420, UM 106429, and UM 106430. No specimens have paracotylar foramina.

Vertebra. UM 105134 (Figure 72). Locality; 2406

This specimen is an almost complete trunk vertebra. Its dimensions are; height: 6.1 mm, width at the prezygapophyses: 6 mm, width at the postzygapophyses: 6.5 mm, length between the pre- and postzygapophyses: 5.6 mm, width of the condyle: 2.1 mm, width of the cotyle: 2.4 mm, greatest width of the neural canal: 2.2 mm, length of the neural spine: 2.6 mm.

In dorsal view, the prezygapophyses are wide and robust, projecting anterior of the anterior edge of the neural arch. Their facets are ovoid. The postzygapophyses are fairly wide and more robust, projecting posteriad as far as the posterior edge of the condyle. The anterior border of the neural arch is concave and missing on one side. The neural spine occupies about three quarters of the length of the neural arch. It is wide posteriorly, and tapers to a point anteriorly, dorsal to the zygosphene facets. The tip is missing.

In ventral view, the centrum is triangular, tapering to the condyle. There is no precondylar constriction. The ventral surface is flat and horizontal, with a narrow, sharp hemal keel running the length of the centrum. On either side are the lateral foramina. The cotylar opening is visible. At the anterior end the paradiapophyses are relatively small,

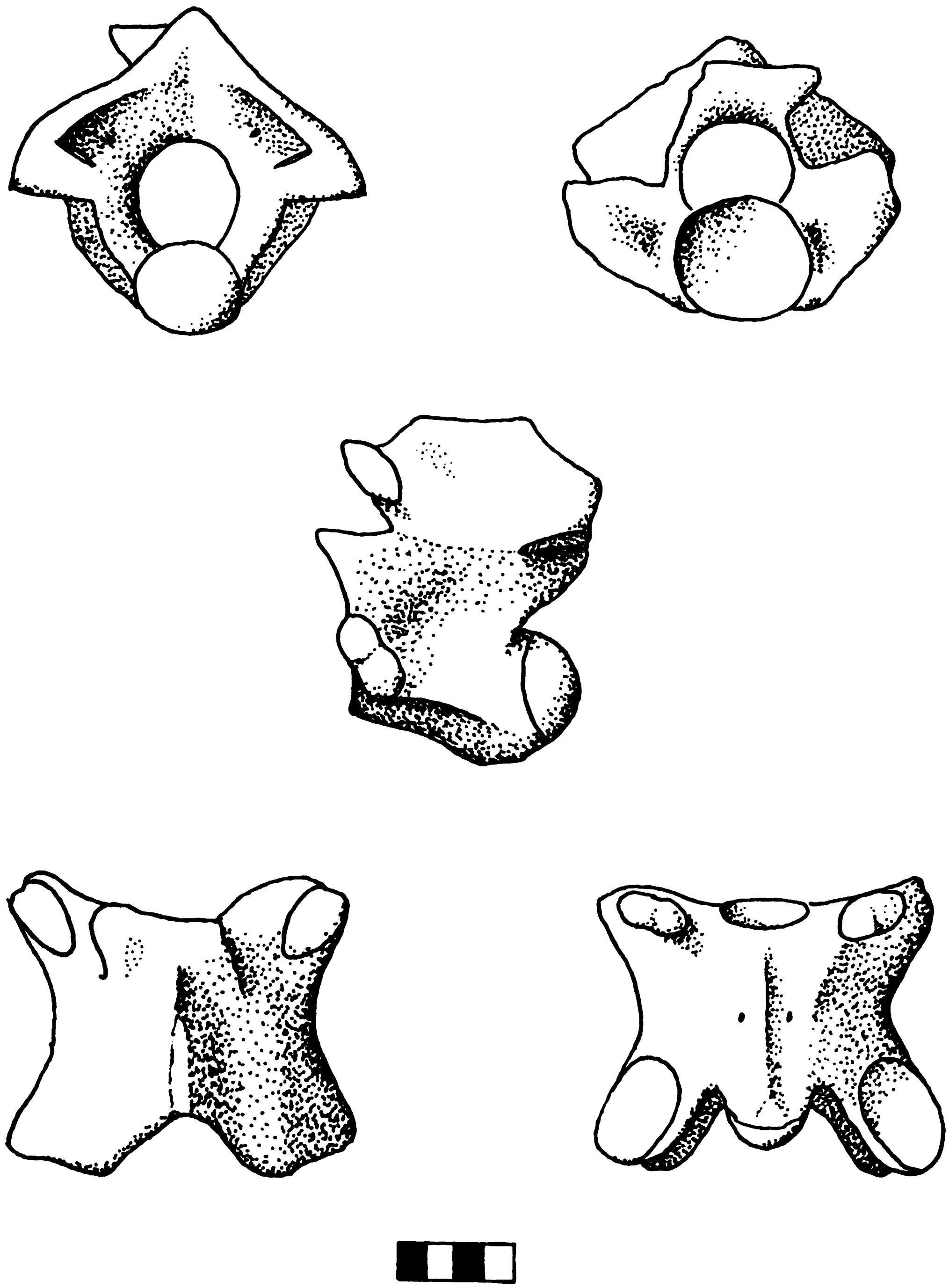

Figure 72. Boavus occidentalis. UM 105134. Vertebra, anterior, posterior, lateral, dorsal, and ventral views. Scale bar is 4 mm.

and form an anteroposteriorly compressed oval. Barely visible anteriorly and laterally to the paradiapophyses are the prezygapophyses, bearing reduced prezygapophysial processes. The postzygapophyses are wide, and project posterolaterally at 45 degrees from the midline. Their facets are ovoid.

In anterior view, the cotyle is round, with the hemal keel visible ventrally. To either side of the cotyle are the robust prezygapophyses. There are no paracotylar foramina. The prezygapophysial facets point slightly dorsally. There is no indentation between the paradiapophyses and the prezygapophyses. Dorsal to the cotyle is the narrow and thick zygosphene. One side is missing. The facet points dorsolaterally at about 45 degrees from the midline. The neural arch is high, wide, and robust. The neural canal is a simple arch and is slightly narrower than the cotyle. The neural spine is wide.

In posterior view, the condyle is round, with the hemal keel visible ventrally. Dorsal to the condyle is the neural canal, which is slightly wider than the condyle. On either side of the neural canal are the postzygapophyses which are wide and robust, and have facets pointing slightly dorsally. The zygantrum is deep.

In lateral view, the vertebra is narrow and tall. The neural arch is high, and the neural spine prominent. Although the vertebra is narrow, the gap between the pre- and postzygapophyses is relatively wide. The prezygapophysial facet and zygosphene are far apart, and separated by a wide non-articular area. The hemal keel is distinct, and the subcentral groove is concave and arched dorsally.

Vertebra. UM 105135 (Figure 73). Locality; 1139

This specimen has a complete neural spine. In lateral view it is tall. Its anterior edge slopes dorsally, at about 45 degrees, from the neural arch. The posterior edge is almost vertical. The dorsal edge is straight and slightly laterally expanded. It slopes posteroventrally at about 30 degrees from the horizontal. Other specimens have neural spines with horizontal or concave dorsal edges.

Discussion -- Since the diagnostic characters given for the species of *Boavus* are few, and are possibly due to differences within the vertebral column of one taxa, I tentatively assign these specimens to *B. occidentalis*. The specimens with a less massive zygosphene, and blunt hemal keel should possibly be assigned to *B. brevis*, but I hesitate to do so based on only one characteristic, when the vertebrae themselves are very similar in every other respect. V64 has what appears to be sediment filled paracotylar foramina, but since the sediment cannot be removed, this is unclear. The only species of *Boavus* that has this feature is ?*B. affinis*, which, for this reason, is only tentatively assigned to *Boavus*.

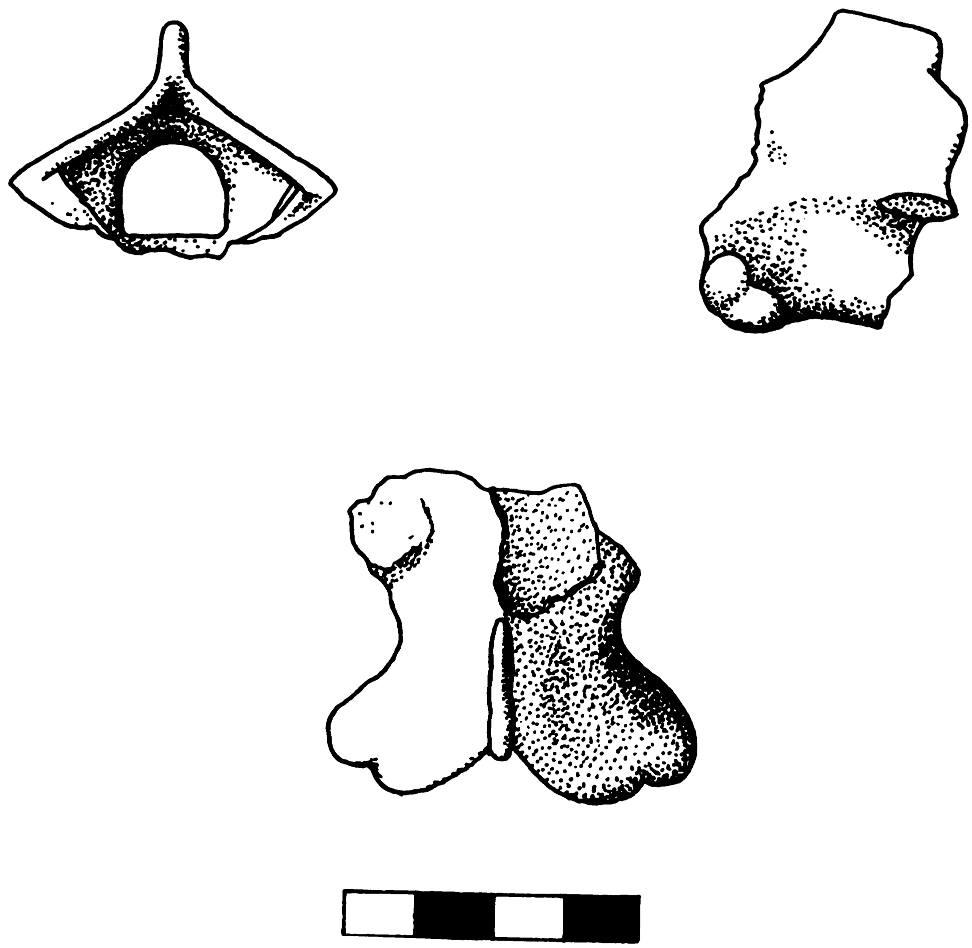

Figure 73. Boavus occidentalis. UM 105135. Vertebra, posterior, lateral, and dorsal view. Scale bar is 4 mm.

Subfamily Erycinae Bonaparte, 1831

The neural arch is flattened, the neural spine of the trunk vertebrae usually low. The caudal vertebrae are very shortened and have a swollen neural spine and additional complex processes. The prezygapophysial processes are greatly reduced but present.

Calamagras Cope, 1973.

(*Synonym* -- *Aphelophis* Cope, 1873.)

Type species -- *Calamagras murivorus* Cope, 1873.

Referred species -- *Calamagras angulatus*, *Calamagras talpivorus* (*Aphelophis talpivorus*) Cope, 1873; *Calamagras primus* Hecht, 1959; *Calamagras floridanus* Auffenberg, 1963; *Calamagras weigeli* Holman, 1972; *Calamagras platyspondyla* Holman, 1976 and *Calamagras gallicus* Rage, 1977.

Diagnosis -- The neural spines of the trunk vertebrae are short, occupying less than half the length of the neural arch. The only known caudal vertebra is short, not very high, with the only additional processes being the very small pterapophyses. Many of the species cannot be confidently distinguished (Rage, 1984).

Age and distribution -- Early Eocene to early Miocene, North America and Europe.

Calamagras primus Hecht, 1959

Figures 74 and 75

Type specimen -- AMNH 3828

Type locality -- Elk Mountain area, Wyoming, Upper Bridger Formation, middle Eocene.

Diagnosis -- The neural spine rises sharply, and occupies less than half the length of the neural arch. The zygantral facets are not visible in dorsal view. There is a distinct, narrow hemal keel running the length of the centrum. Both the para- and diapophyses lie along the anterior edge of the neural arch. They do not extend ventrally further than the ventral border of the cotyle and are not distinct from the prezygapophyses.

Previously referred specimens -- None.

Age and distribution -- Middle Eocene, Wyoming, USA.

Referred specimens -- UM 106431, UM 106432, UM 106433, UM 105137, UM 106434, UM 106435, UM 106436, UM 106437, UM 106438, UM 106439, UM 106440, UM 106441, UM 106442,

UM 106443, UM 106444, UM 106445, UM 106446, UM 106447, UM 106448, UM 106449, UM 106450, UM 106451, UM 106452, UM 106453, UM 106454, UM 106455, UM 105136, UM 106456, UM 106457, UM 106458, UM 106459, UM 106460, UM 106461, UM 106462, UM 106463, UM 106464, UM 106465, UM 106466, UM 106467, UM 106468, UM 106469, UM 106470, UM 106471, UM 106472, UM 106473, UM 106474, UM 106475, UM 106476, UM 106477, UM 106478, UM 106479, UM 106480, UM 106481, UM 106482, UM 106483, UM 106484, UM 106485, UM 104599, UM 104832, UM 101472 (in part), UM 106486, and UM 106487.

These specimens are referred to Calamagras primus on the basis of the possession of one or more of the above diagnostic characteristics.

Description --

Vertebra. UM 105136 (Figure 74). Locality; 1139

This specimen is an almost complete thoracic vertebra. Its dimensions are; height: 3.8 mm, width at the postzygapophyses: 4.1 mm, length between the pre- and postzygapophyses: 3.7 mm, width of the condyle: 1.5 mm, greatest width of the neural canal: 1.1 mm, length of the neural spine: 1.3 mm.

In dorsal view, the vertebra is squarish. The zygosphene, condyle, and one prezygapophysis are missing. The

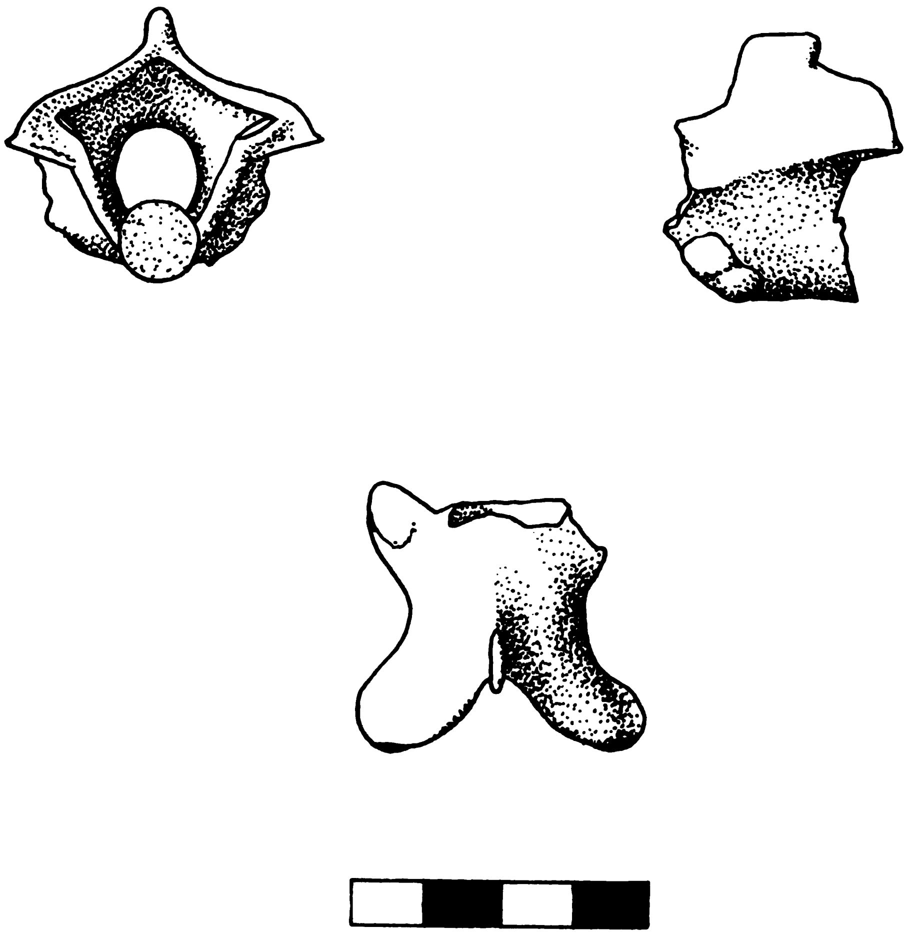

Figure 74. Calamagras primus. UM 105136. Vertebra, posterior, lateral, and dorsal views. Scale bar is 4 mm.

neural spine is short, worn at the tip, and rises sharply from the neural arch. It occupies less than one-half of the neural arch, which has a length of 2.5 mm from its posterior edge, to the broken edge of the zygosphene. There is no keel anterior to the neural spine. The prezygapophysis is elongate and pointed, with the facet missing. It projects at about 45 degrees, anterolaterally, from the midline. Posteriorly, the postzygapophyses project at about 45 degrees posterolaterally. There are slight zygantral mounds lateral to the neural spine. The zygantral facets are not visible.

In ventral view, there is a distinct, narrow hemal keel running the length of the centrum. Anteriorly, there are two shallow, broad grooves that end at the anterior edge of the centrum between the cotyle and the worn paradiapophyses. Both the para- and diapophyses lie along the anterior edge of the neural arch. The prezygapophysis has no accessory process, but a small mound lies close to its tip.

In anterior view, the cotyle is a slightly depressed oval. Lateral to this are the paradiapophyses. They do not extend ventrally as far as the ventral border of the cotyle. They are not distinct from the prezygapophyses, as is the case in Ogmophis. The neural spine is exposed dorsally. The neural canal is trapezoid, with parallel sides, an arched roof, and slight indentations at the sides of the flat floor. In posterior view, the neural arch is low, the zygantrum deep.

In lateral view, the neural spine rises sharply from the neural arch anteriorly. Posteriorly, it overhangs the posterior border of the neural arch. Its dorsal edge is straight, and slightly sloping posteroventrally. The postzygapophyses point slightly dorsally. The distance between them, and the prezygapophyses is small, being smaller than the length of the facets themselves.

Vertebra. UM 105137 (Figure 75). Locality; 2234

This specimen is an almost complete thoracic vertebra. Its dimensions are; height: 2.6 mm, width at the prezygapophyses: 3 mm, width at the postzygapophyses: 2.7 mm, length between the pre- and postzygapophyses: 2.7 mm, width of the condyle: 1 mm, width of the cotyle: 1.1 mm, width of the zygosphene: 1.5 mm, length of the neural spine: 0.8 mm, length of the neural arch along the midline: 2.2 mm.

In dorsal view, the vertebra has a squarish outline. The anterior edge of the zygosphene is sigmoidal, with a convex central portion. The prezygapophyses are elongate, with ovoid facets, and rounded tips. They project anterolaterally, at about 45 degrees from the midline. Posteriorly, there is a short neural spine, with a short, slight hemal keel anterior to it. The posterior edge of the neural arch is indented at the midline. Laterally, it has a roughly straight border, running at right angles to the centrum. The postzygapophyses have rounded tips, and project at about 45 degrees

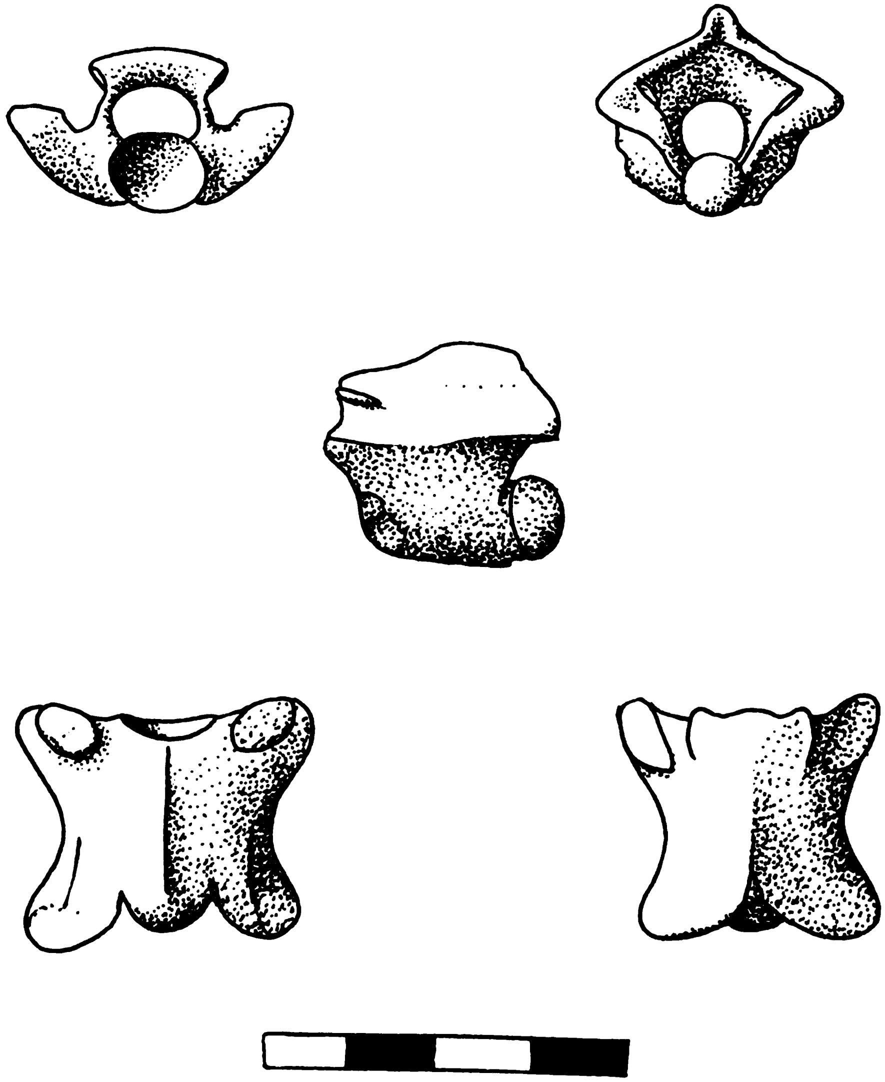

Figure 75. Calamagras primus. UM 105137. Vertebra, anterior, posterior, lateral, ventral, and dorsal views.
Scale bar is 4 mm.

posterolaterally. The zygantral facets are not visible.

In ventral view, the centrum is narrow, and roughly parallel-sided laterally. The cotylar opening is visible anteriorly. A thin, distinct hemal keel lies along the midline of the centrum. The centrum is not separated from the neural arch by grooves. The paradiapophyses are worn, and lie along the anterior edge of the neural arch. They project, at about 45 degrees, anterolaterally. The postzygapophyses have rounded tips and project at about 45 degrees posterolaterally.

In anterior view, the cotyle is slightly depressed, and sub-rounded. Lateral to this are the paradiapophyses. They are not distinct from the prezygapophyses and project ventrally to the same level as the cotyle. The prezygapophysial facets point slightly dorsally. The zygosphene is thin, and straight. Its facets overhang by about 45 degrees, and are separated from the prezygapophysial facets by a non-articulated area which lacks the notch seen in <u>Ogmophis</u>. The neural spine, and hemal keel are barely visible. In posterior view, the condyle is round and worn. The neural arch is low, with very slight zygantral mounds. The prezygapophysial facets point slightly dorsally. The zygantrum is obscured by sediment. In lateral view, the zygosphene facets clearly visible dorsal to the prezygapophyses. The distance between the pre- and postzygapophyses is small.

Discussion -- These specimens are assigned to Calamagras based on a combination of characters given by Gilmore (1938), Hecht (1959), and Rage (1984). Having compared them with the type specimens of C. primus, C. murivorus, C. talpivorus, and C. angulatus I assign them to C. primus, based on the similarity in morphology, and their age and distribution.

Ogmophis Cope, 1884.

Type species -- Ogmophis oregonensis Cope, 1884.

Referred species -- Ogmophis arenarum Douglass, 1903; Ogmophis compactus Lambe, 1908; Ogmophis pauperrimus Vanzolini, 1952; Ogmophis pliocompactus Holman, 1975; Ogmophis miocompactus Holman, 1976; Ogmophis parvus Rogers, 1976; Ogmophis voorhiesi Holman, 1977 and Ogmophis europaeus Szyndlar, 1982,.

Diagnosis -- The neural spine is low and occupies about one half the length of the neural arch. There is no hemal keel, or hypapophyses on the mid-thoracic vertebrae. In dorsal view, they have a squarish outline, slightly longer than broad (Hecht, 1959). Ogmophis differs from Calamagras in having longer neural spines which occupy about one-half the length of the neural arch. Different species of Ogmophis are often distinguished using doubtful characters so their validity is uncertain (Rage, 1984). This genus only occurs in the southeast United States, whereas Calamagras and Helagras occur in the southwest and central United States.

Age and distribution -- Late Eocene to Upper Miocene, North America and Europe.

Ogmophis indet.

Figures 76 and 77

Referred specimens -- UM 106488, UM 106489, UM 106490, UM 106491, UM 106492, UM 106493, UM 106494, UM 105138, UM 106495, UM 106496, UM 106497, UM 106498, UM 106499, UM 106500, UM 106501, UM 106502, UM 106503, UM 106504, UM 106505, UM 106506, UM 106507, UM 106508, UM 106509, UM 106510, UM 106511, UM 106512, UM 106513, UM 106514, UM 106515, UM 106516, UM 106517, UM 106518, UM 106519, UM 106520, UM 106521, UM 106522, UM 106523, UM 106524, UM 106525, UM 106526, UM 106527, UM 106528, UM 106529, UM 106530, UM 106531, UM 106532, UM 106533, UM 106534, UM 106535, UM 106536, UM 106537, UM 106538, UM 106539, UM 106540, UM 105139, UM 102856, and UM 103482.

These specimens are referred to Ogmophis indet. on the basis of the possession of one or more of the following diagnostic characteristics - the neural spine is about half the length of the neural arch; the zygantral facets are visible in dorsal view; the parapophyses lie on the anterior edge of the neural arch, while the diapophyses lie posterodorsally, a little posterior of the anterior edge; in anterior view, the paradiapophyses project further ventrally than the cotyle, and are distinct, separated from the cotyle and prezygapophyses by indentations.

<u>Description</u> --

Vertebra. UM 105138 (Figure 76). Locality; 2234

This specimen is a complete thoracic vertebra. Its dimensions are; height: 3.4 mm, width at the prezygapophyses: 4.5 mm, width at the postzygapophyses: 4.3 mm, length between the pre- and postzygapophyses: 4.2 mm, width of the condyle: 1.5 mm, width of the cotyle: 1.6 mm, width of the zygosphene: 1.8 mm, length of the neural spine: 1.4 mm, length of the neural arch along the midline: 3.1 mm.

In dorsal view, the vertebra has a squarish outline. The neural spine is about one-half the length of the neural arch. It is worn, and the tip is missing. Anterior to the spine is a slight, short hemal keel. The anterior edge of the zygosphene is sigmoidal, with a convex central part. The facets are slightly convex, arching laterally, and form a low ridge on either side of the zygosphene's dorsal surface. The anterior portion of the zygosphene is laterally expanded, with a slight constriction posterior to the facets, where it joins the neural arch. The prezygapophyses are elongate, with

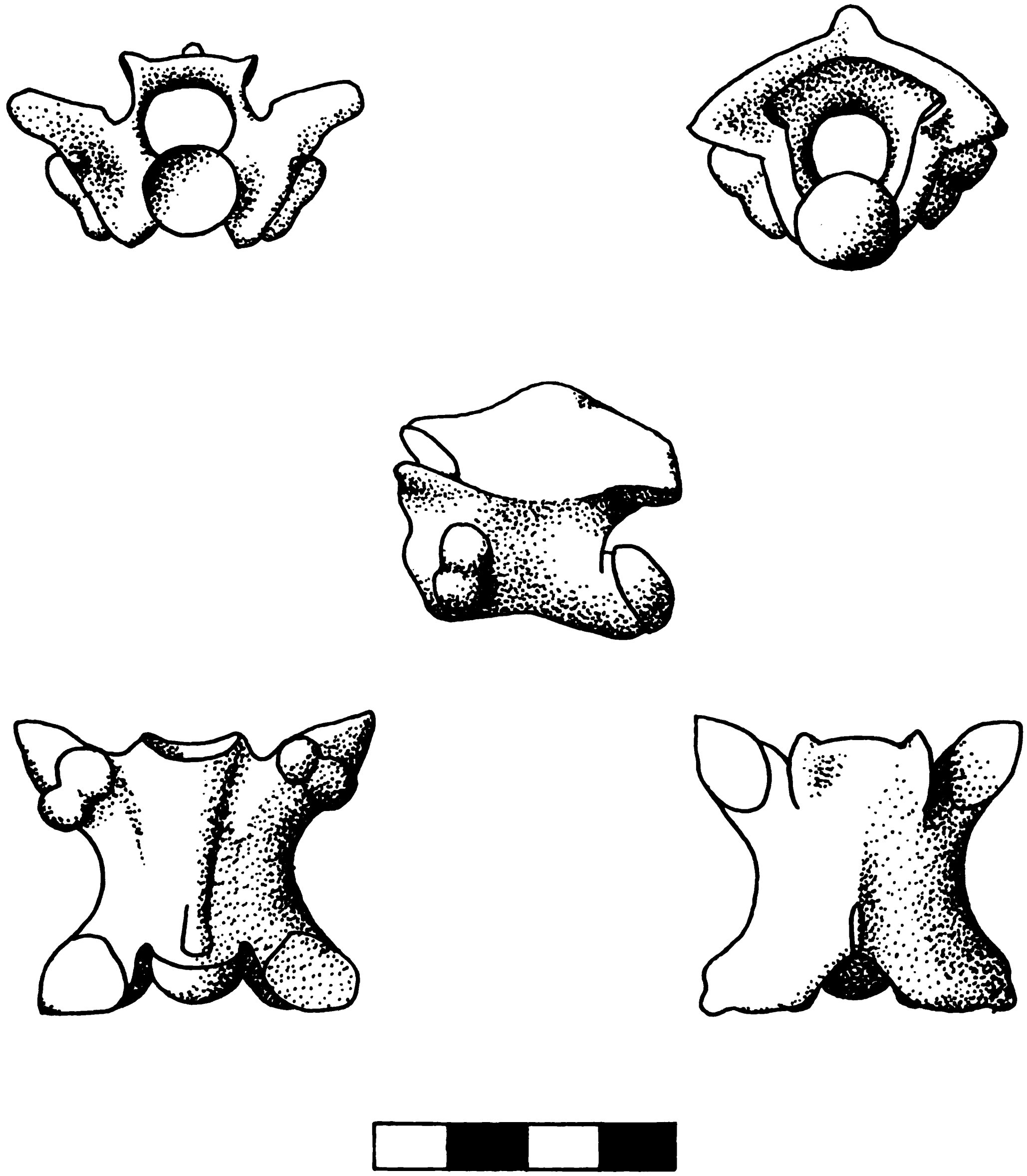

Figure 76. Ogmophis indet. UM 105138. Vertebra, anterior, posterior, lateral, ventral, and dorsal views.
Scale bar is 4 mm.

oval facets, and project at about 45 degrees, anterolaterally, from the midline. The postzygapophyses have blunt tips and project at about 45 degrees posterolaterally. At the midline, the posterior border of the neural arch is incized. Lateral to this, the border is roughly straight, and at right angles to the midline. There are very slight zygantral mounds on either side of the neural spine. The zygantral facets are visible.

In ventral view, the centrum is narrow, with roughly parallel lateral borders. There is a shallow, broad, and distinct hemal keel running the length of the centrum. On either side, midway along the centrum, are two small, round lateral foramina. Anteriorly, two shallow, broad grooves lie on either side of the centrum, separating it from the neural arch. They end at the anterior border of the centrum, between the cotyle and paradiapophyses. The paradiapophyses are worn. The parapophyses lie on the anterior edge of the neural arch, while the diapophyses lie posterodorsally, a little posterior of the anterior edge. Anterolateral to them the prezygapophyses project at roughly 45 degrees. They do not bear accessory processes, but have a small mound near their tips. The postzygapophyses have oval facets and project at about 45 degrees posterolaterally. The cotylar opening is visible.

In anterior view, the condyle is round. Lateral to this lie the distinct paradiapophyses, which project further ventrally than the cotyle. They are separated from the cotyle and the prezygapophyses by indentations. There are no paracotylar foramina. Dorsal to the cotyle the neural canal is obscured by sediment. The zygosphene is thin and sigmoidal, with a convex central portion. Its facets overhang at about 45 degrees. They are separated from the prezygapophysial facets by a notched non-articular area. The neural spine and hemal keel are visible. In posterior view, the condyle is a slightly depressed oval. Dorsal to this the neural canal and zygantrum are obscured by sediment, although the zygantral facets are just visible. There are slight zygantral mounds in the low neural arch, on either side of the neural spine. In lateral view, the pre- and postzygapophysial facets point slightly dorsally. There is a short distance between them. The prezygapophysis does not obstruct the view of the zygosphene facets.

Vertebra. UM 105139 (Figure 77). Locality; 1125

This specimen is an almost complete thoracic vertebra. Its dimensions are; width at the prezygapophyses: 5.6 mm, width at the postzygapophyses: 5.5 mm, length between the pre- and postzygapophyses: 5.4 mm, width of the cotyle: 2.1 mm, length of the neural spine: 1.6 mm, length of the neural arch along the midline: 3.2 mm, greatest width of the neural canal: 1.5 mm.

In dorsal view, the vertebra has a squarish outline. The zygosphene is missing. The worn neural spine occupies

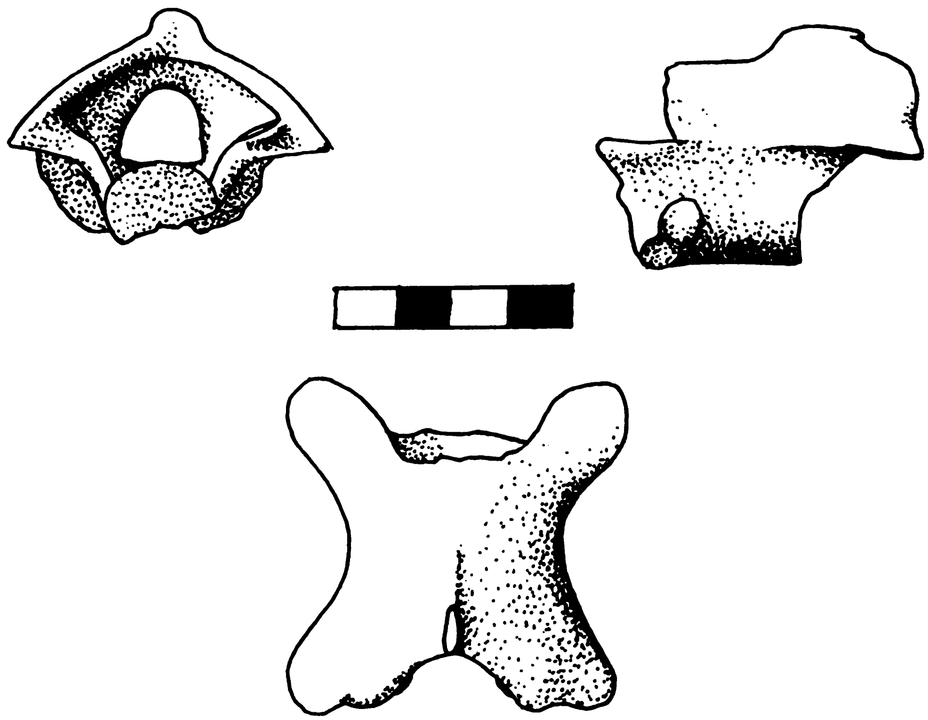

Figure 77. Ogmophis indet. UM 105139. Vertebra, posterior, lateral, and ventral views. Scale bar is 4 mm.

one-half the length of the neural arch. The prezygapophyses are elongate, with oval facets, and project at about 45 degrees, anterolaterally, from the midline. The postzygapophyses have broken tips and project at about 45 degrees posterolaterally. The posterior edge of the neural arch is indented centrally. Lateral to this it is roughly straight and at right angles to the midline. The zygantral facets are barely visible. In ventral view, the condyle and ventral surface of the centrum are missing. The centrum is narrow, and has roughly parallel sides. Anteriorly it is separated from the neural arch by two shallow, broad grooves running to the anterior edge of the centrum between the cotyle and paradiapophyses. The parapophyses are small and ovoid, and lie on the anterior edge of the neural arch. The larger, round diapophyses lie posterodorsal to them. The prezygapophyses are expozed, projecting anterolaterally, at about 45 degrees from the midline. There are no prezygapophysial processes, but a small mound lies near the tip. The postzygapophyses have oval facets and project at about 45 degrees posterolaterally. The cotylar opening is expozed.

In anterior view, the cotyle is a slightly depressed oval. Lateral to it are the paradiapophyses which project further ventrally than the cotyle, and are distinct, separated from the cotyle and prezygapophyses by indentations. The prezygapophysial facets point slightly dorsally. There are no paracotylar foramina. The neural spine is visible. The neural canal is trapezoid, having parallel sides, and arched roof, and slight indentations on either side of the flat floor. In posterior view, the neural arch and spine are low, the zygantrum deep. The postzygapophysial facets point slightly dorsally. In lateral view, the anterior edge of the prezygapophysis is irregular, bearing a small process anterior to the diapophysis. Posteriorly, there is a slight zygantral mound. The distance between the pre- and postzygapophysial facets is small, being smaller than the length of each facet, but slightly larger than that found in UM 105138.

Discussion -- Calamagras and Ogmophis share many characteristics: In dorsal view, the vertebrae are squarish. The prezygapophysis has no accessory process, but a small mound lies close to its tip. In anterior view, the cotyle is a slightly depressed oval. The neural canal is trapezoid, with parallel sides, an arched roof, and slight indentations at the sides of the flat floor. In posterior view, the neural arch is low, the zygantrum deep. In lateral view, the neural spine rises sharply from the neural arch anteriorly. Posteriorly, it overhangs the posterior border of the neural arch.

Rage (1984) states that Ogmophis differs from Calamagras and Helagras in having a neural spine occupying about one-half of the neural arch. Since this is a feature that varies along the vertebral column, it is of doubtful importance. It is possible that Ogmophis, Calamagras, and Helagras are congeneric, but more detailed studies of their vertebrae are needed to verify this. Having studied the type specimens of C. primus, C. murivorus, C. talpivorus, and C. angulatus, and specimens of Ogmophis sp. I conclude that there is a suite of characters that, taken together, suggest that these genera are distinct. Until further work is done, I assign specimens exhibiting all these characters to Calamagras primus, and Ogmophis indet. The latter specimens, based on age and distribution, are possibly O. voorhiesi. Any specimens exhibiting a combination of these characters are assigned to Erycinae indet. as they are clearly members of the Calamagras-Ogmophis group.

Subfamily Tropidopheinae Cope, 1894

The hemal keel is very high in some and may be regarded as a hypapophysis. The neural arch is depressed and the centrum is narrow.

Dunnophis Hecht, 1959.

Type species -- Dunnophis microechinis Hecht, 1959.

Referred species -- Dunnophis matronensis Rage, 1973 and Dunnophis cadurcensis Rage, 1974.

Diagnosis -- The vertebrae are somewhat depressed and elongate with a low neural spine and a low neural arch. The prezygapophysial processes are absent and the centra are low and elongate. The mid and posterior trunk vertebrae lack hypapophyses and have two grooves running lengthwise on the ventral surface of the centrum. The posterior trunk vertebrae lack a hemal keel. The caudal vertebrae possess hemapophyses. The paracotylar foramina may be present or absent. The medial lobe of the zygosphene is narrow. Grooves on the ventral surface of the centrum run from the cotyle to the condyle. The neural spine is short and not anteriorly prolonged by a keel (Rage, 1984).

Age and distribution -- Early to late Eocene, USA and Europe.

Dunnophis microechinis Hecht, 1959

Figures 78, 79 and 80

Type specimen -- AMNH 3830

Type locality -- Elk Mountain area, Wyoming, Bridger Formation, middle Eocene.

Diagnosis -- The vertebrae are somewhat elongate. They have a depressed condyle, and a depressed, and undercut cotyle. The neural arch and spine are low. There are no prezygapophysial processes. The centrum is narrow and elongate. Paracotylar foramina may be present or absent (Rage, 1984). They have no hemal keel, and they bear an incized notch at the posterior border of the neural arch (Hecht, 1959). The paradiapophyses are small and simple. The zygosphene is thin. The prezygapophyses are horizontal. The neural spine rises sharply from the neural arch and does not overhang the condyle.

Previously referred specimens -- None.

Age and distribution -- Middle Eocene, Wyoming, USA.

Referred specimens -- UM 106541, UM 106542, UM 106543, UM 106544, UM 106545, UM 106546, UM 106547, UM 106548, UM 106549, UM 106550, UM 106551, UM 106552, UM 106553, UM 106554, UM 105142, UM 106555, UM 106556, UM 106557, UM 106558, UM 106559, UM 106560, UM 106561, UM 106562, UM 106563, UM 106564, UM 106565, UM 106566, UM 106567, UM 106568, UM 106569, UM 106570, UM 105140, UM 106571, UM 106572, UM 106573, UM 106574, UM 106575, UM 106576, UM 106577, UM 106578, UM 106579, UM 106580, UM 105141, UM 106581, UM 106582, UM 106583, UM 106584, UM 106585, UM 106586, UM 106587, UM 106588, UM 106589, UM 106590, UM 106591, UM 106592, UM 106593, UM 106594, UM 106595, UM 106596, UM 106597, UM 106598, UM 106599, UM 106600, UM 106601, UM 106602, UM 106603, one unnumbered WPM specimen, UM 104180, and UM 104236.

<u>Description</u> -- Although all have a depressed cotyle, only UM 106542, V49, UM 106544, UM 106558, UM 106561, UM 106562, UM 106569, UM 105140, UM 106546, UM 106547, UM 106548, UM 106550, UM 105142, UM 106559, UM 106572, UM 106575, UM 106577, UM 106579, UM 106580, UM 105141, UM 106582, UM 106587, UM 106592, UM 106593, UM 106595, UM 106596, UM 106597, UM 106598, UM 106599, UM 106600, UM 106601, and UM 106603 are undercut. Many others have the ventral part of the cotyle missing, while some have a convex outline. None have prezygapophysial processes. The zygosphenes of all specimens that possess one, are narrow. Some have a smooth ventral surface, others have two grooves running from the anterior edge of the centrum, to a point just anterior to the condyle. The neural spine of all specimens is short, and there is no keel anterior to it.

Vertebra. UM 105140 (Figure 78). Locality; 1098

This specimen is an almost complete trunk vertebra. Its dimensions are; height: 1.9 mm, width at the prezygapophyses: 3 mm, width of the condyle: 0.9 mm, width of the cotyle: 1.2 mm, greatest width of the neural canal: 0.7 mm, width of the zygosphene: 1.1 mm. The posterior end of the neural arch, and the postzygapophyses are missing.

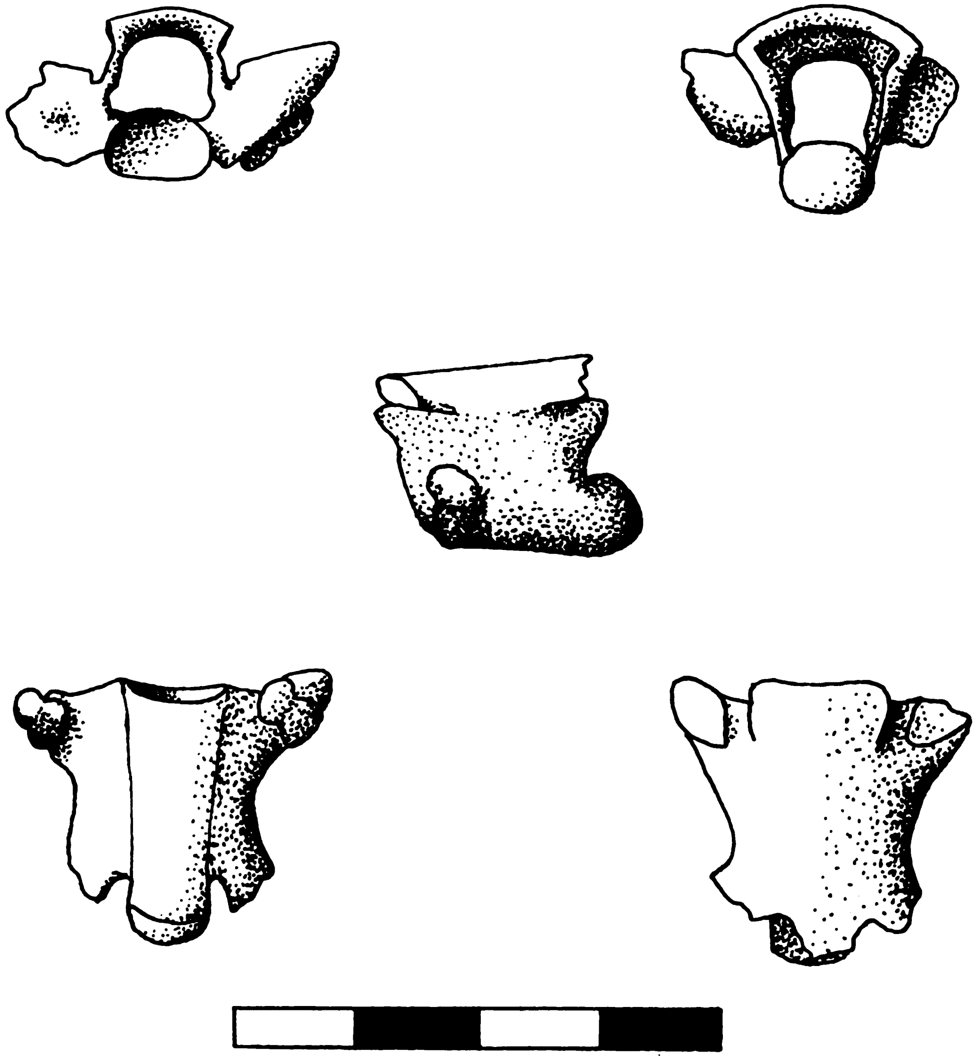

Figure 78. Dunnophis microechinis. UM 105140. Vertebra, anterior, posterior, lateral, dorsal, and ventral views. Scale bar is 4 mm.

In dorsal view, the anterior border of the neural arch is worn, and concave. The neural arch has a flat, horizontal dorsal surface. There is no neural spine. The prezygapophyses are slender, with oval facets, and project anterolaterally at about 45 degrees from the midline, slightly more anteriorly than the cotyle. There are no prezygapophysial processes. In ventral view, the centrum is narrow, with roughly parallel lateral edges. It is distinct, and separated from the neural arch by a groove on either side. The cotylar opening is visible. The ventral surface is flat, smooth, and horizontal, and bears no lateral foramina. The paradiapophyses are small and distinct. Visible anteriorly to them are the prezygapophyses.

In anterior view, the vertebra is depressed, especially the neural canal. The cotyle is oval, with flat dorsal and ventral surfaces. Dorsal to the cotyle is an hemiovaloid neural canal. The zygosphene is thin and narrower than the cotyle, its facets overhang the prezygapophyses at about 45 degrees. On either side of the neural canal, the prezygapophyses project slightly dorsally. Ventral to them are the paradiapophyses. They are distinct from the prezygapophyses and the cotyle, separated from them by small indentations. In posterior view, the condyle is oval and depressed. The zygantrum is mostly missing, its dorsal edge is thin and horizontal. The postzygapophyses are missing.

In lateral view, the centrum is elongate, relatively long for its height, compared with other boids. The subcentral grooves are visible and roughly straight. The postzygapophysis obscures most of the zygosphene facet. The dorsal surface of the neural arch is straight and flat.

Vertebra. UM 105141 (Figure 79). Locality; 1125

This specimen is an almost complete trunk vertebra, with part of the next vertebra attached. Its dimensions are; height: 3.7 mm, width at the postzygapophyses: 4.8 mm, length between the pre- and postzygapophyses: 4.4 mm, width of the condyle: 2 mm, width of the cotyle: 2.1 mm, greatest width of the neural canal: 1.2 mm, length of the neural spine: 0.9 mm. The zygosphene, part of the neural arch, and one prezygapophysis are missing.

The only part of the neural arch present is that bearing the neural spine. It is small and sub-rounded. There is no keel anterior to it. The postzygapophyses slope away from the spine. Their posterior borders are straight, at right angles to the centrum's lateral edge. The prezygapophysis is slender, lacks additional processes, and has an oval facet. It projects anterolaterally at about 45 degrees from the midline, slightly past the anterior edge of the cotyle. In ventral view, the centrum is slender, and has roughly parallel lateral edges. Two small, ovoid foramina lie on either side of the midline, in the flat, smooth ventral surface of the centrum. The cotylar opening is visible. Lateral to the cotyle are the small, distinct

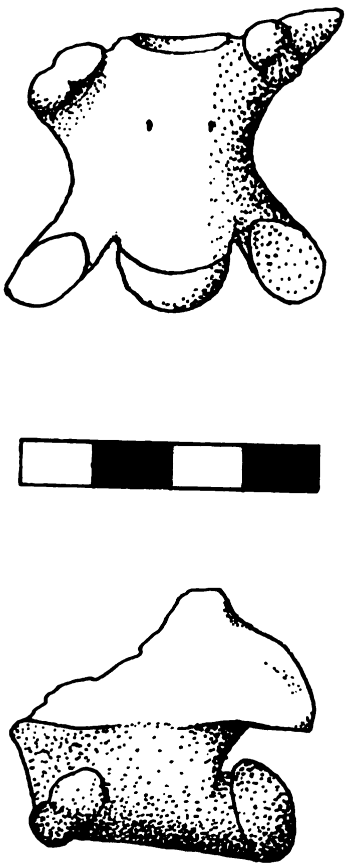

Figure 79. Dunnophis microechinis. UM 105141. Vertebra, ventral and lateral views. Scale bar is 4 mm.

paradiapophyses. Anterolateral to them the prezygapophyses are visible. The tips of the prezygapophyses are thin in the center, with blade-like edges. Slight grooves define the central area.

In anterior view, the vertebra is much wider than tall. The cotyle is depressed and ovoid. Its dorsal edges are horizontal and straight, the ventral edge almost straight. The zygosphene is missing, but the base of the neural canal is present. Lateral to this the prezygapophyses point slightly dorsally. Ventral to them are the paradiapophyses. They are slightly worn. They are distinct from the prezygapophyses and cotyle, separated from them by indentations slightly smaller than those seen in UM 105140. The posterior view is partially obscured by a portion of the next vertebra in the column. The condyle is depressed. Dorsal to this is the depressed neural arch, and the small neural spine. Laterally, the postzygapophysial facets point slightly dorsally. In lateral view, the centrum is elongate. There is only a small gap between the pre- and postzygapophysial facets. The neural arch and spine are low.

Vertebra. UM 105142 (Figure 80). Locality; 2406

This specimen is an incomplete caudal vertebra, exhibiting most of the diagnostic features. Its dimensions are; height: 3.6 mm, width of the cotyle: 2 mm, greatest width of the neural canal: 1.8 mm, width of the zygosphene:

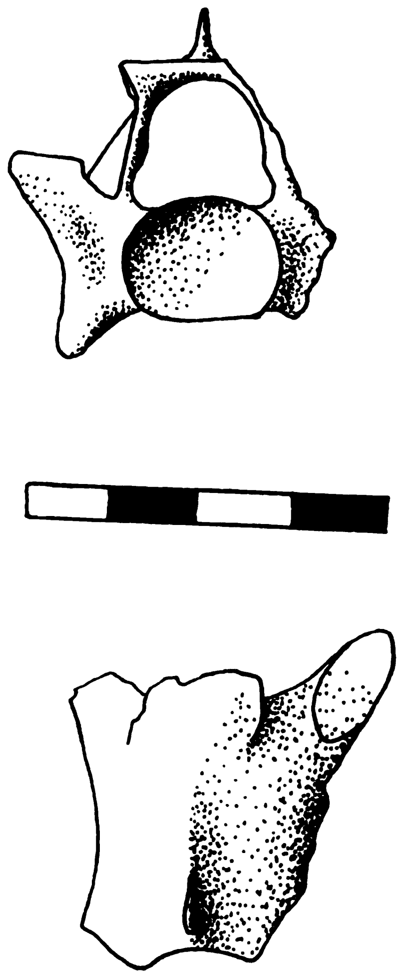

Figure 80. Dunnophis microechinis. UM 105142. Vertebra, anterior and dorsal views. Scale bar is 4 mm.

1.9 mm, length of the neural spine: 1.7 mm.

The dorsal surface is flat, except for the neural spine which lies along one-half of the length of the neural arch. The anterior edge of the neural arch is concave, the posterior edge incized. The prezygapophyses are slender, with oval facets. They point anterolaterally at about 45 degrees from the midline, a little further anteriorly than the cotyle. In ventral view, the centrum is narrow. Its ventral surface is flat, with two small, round foramina on either side of the midline. The posterior end is missing. The cotylar opening is visible. The paradiapophyses are replaced by pleurapophyses, with missing tips. They extend from the anterolateral edges of the centrum. There are no hemapophyses.

In anterior view, the cotyle is a depressed oval, with the ventral edge flat and straight. On either side of the cotyle is the ventral part of the pleurapophyses, projecting ventrally, and slightly laterally. Dorsal are the prezygapophyses, separated from the pleurapophyses by a concave area. Dorsal to the cotyle is the hemiovaloid neural canal, and the narrow zygosphene, with overhanging facets. Between the zygosphene and prezygapophysial facets is a concave non-articular area. The neural spine is visible, dorsal to the zygosphene. The condyle and zygantrum are missing.

Discussion -- Only one species of *Dunnophis* is known from the Eocene of the USA. Hecht (1959) regarded *Dunnophis* as snake incertae sedis, but Bogert (1968) stated that the genus closely resembles the extant genera *Charina*, *Exiliboa*, and particularly *Ungaliophis*, therefore he assigned *Dunnophis* to the Tropidopheinae.

Boidae indet.

Referred specimens -- UM 106604, UM 106605, UM 106606, UM 106607, UM 106608, UM 106609, UM 106610, UM 106611, UM 106612, UM 106613, UM 106614, UM 106615, UM 106616, UM 106617, UM 106618, UM 106619, UM 106620, UM 106621, UM 106622, UM 106623, UM 106624, UM 106625, UM 106626, UM 106627, UM 106628, UM 106629, UM 106630, UM 106631, UM 106632, UM 106633, UM 106634, UM 106635, UM 106636, UM 106637, UM 106638, UM 106639, UM 106640, UM 106641, UM 106642, UM 106643, UM 106644, UM 106645, UM 106646, UM 106647, UM 106648, UM 106649, UM 106650, UM 106651, UM 106652, UM 106653, UM 106654, UM 106655, UM 106656, UM 106657, UM 106658, UM 106659, UM 106660, UM 106661, UM 106662, UM 106663, UM 106664, UM 106665, UM 106666, UM 106667, UM 106668, UM 106669, UM 106670, UM 106671, UM 106672, UM 106673, UM 106674, UM 106675, UM 106676, UM 106677, UM 106678, UM 106679, UM 106680, UM 106681, UM 106682, UM 106683, UM 106684, UM 106685, UM 106686, UM 106687, UM 106688, UM 106689, UM 106690, UM 106691,

UM 106692, UM 106693, UM 106694, UM 106695, UM 106696, UM 106697, UM 106698, UM 106699, UM 106700, UM 106701, UM 106702, UM 106703, UM 106704, UM 106705, UM 106706, UM 106707, UM 106708, UM 106709, UM 106710, UM 106711, UM 106712, UM 106713, UM 106714, UM 106715, UM 106716, UM 106717, UM 106718, UM 106719, UM 106720, UM 106721, UM 106722, UM 106723, UM 106724, UM 106725, UM 106726, UM 106727, UM 106728, UM 106729, UM 106730, UM 106731, UM 106732, UM 106733, UM 106734, UM 106735, UM 106736, UM 106737, UM 106738, UM 106739, UM 106740, UM 106741, UM 106742, UM 106743, UM 106744, UM 106745, UM 106746, UM 106747, UM 106748, UM 106749, UM 106750, UM 106751, UM 106752, UM 106753, UM 106754, UM 106755, UM 106756, UM 106757, UM 106758, UM 106759, UM 106760, UM 106761, UM 106762, UM 106763, UM 106764, UM 106765, UM 106766, UM 106767, UM 106768, UM 106769, UM 106770, UM 106771, UM 106772, UM 106773, UM 106774, UM 106775, UM 106776, UM 106777, UM 106778, UM 106779, UM 106780, UM 106781, UM 106782, UM 106783, UM 106784, UM 106785, UM 106786, UM 106787, UM 106788, UM 106789, UM 106790, UM 106791, UM 106792, UM 106793, UM 106794, UM101472 (in part), UM 101472 (in part), UM 101472 (in part), UM 103822 (in part), UM 103803 (in part), UM 103846 (in part), UM 103032, UM 103326, UM 104273, UM 104278. UM 104327, and UM 104816.

All specimens are fragmentary but are referred to Boidae indet. on the basis of the possession of one or more of the following diagnostic characteristics - the vertebrae are higher than long, and shorter than wide; when present, the zygosphene is narrow and thick; the sub-central ridges are arched dorsally; the postzygapophysial part of the neural arch is upswept; the neural spine is thick; the vertebrae lack additional processes. The specimens are too fragmentary to make a more detailed identification.

Serpentes indet.

Figure 81

Referred specimens -- UM 106795, UM 105143, UM 106796, UM 106797, UM 106798, UM 106799, UM 106800, UM 106801, UM 106802, UM 106803, UM 106804, UM 106805, UM 106806, UM 106807, UM 106808, UM 106809, UM 106810, UM 106811, UM 106812, UM 106813, UM 106814, UM 106815, UM 106816, UM 106817, UM 106818, UM 106819, UM 106820, UM 106821, UM 106822, UM 106823, UM 106824, UM 106825, UM 106826, UM 106827, UM 106828, UM 106829, UM 106830, UM 106831, UM 106832, UM 106833, UM 106834, UM 106835, UM 106836, UM 106837, UM 106838, UM 106839, UM 106840, UM 106841, UM 106842, UM 106843, UM 106844, UM 106845, UM 106846, UM 106847, UM 106848, UM 106849, UM 106850, UM 106851, UM 106852, UM 106853, UM 106854, UM 106855, UM 106856, UM 106857, UM 106858, UM 106859, UM 106860, UM 106861,

UM 106862, UM 106863, UM 106864, UM 106865, UM 106866, UM 106867, UM 106868, UM 106869, UM 106870, UM 106871, UM 106872, UM 106873, UM 106874, UM 106875, UM 106876, UM 106877, UM 106878, UM 106879, UM 106880, UM 106881, UM 106882, UM 106883, UM 106884, UM 106885, UM 106886, UM 106887, UM 106888, UM 106889, UM 106890, UM 106891, UM 106892, UM 106893, UM 106894, UM 106895, UM 106896, UM 106897, UM 106898, UM 106899, UM 106900, UM 106901, UM 106902, UM 106903, UM 106904, UM 106905, UM 106906, UM 106907, UM 106908, UM 106909, UM 105663, UM 101455 (in part), UM 103803 (in part), UM 102787 (in part), UM 103778 (in part), UM 102768 (in part), UM 10300 (in part), UM 101433 (in part), UM 101482 (in part), UM 103535 (in part), UM 101472 (in part), UM 101472 (in part), UM 103014 (in part), UM 102787 (in part), UM 102858, UM 103009, UM 103212, UM 104140, UM 104249, UM 104293, UM 104456, UM 104469, and UM 104782.

All specimens are fragmentary, and cannot be assigned to suborder or below. The zygosphene is wide dorsally, with each facet overhanging the prezygapophyses. There is less than a 90 degree angle between the zygosphene and prezygapophysial facets, which are separated by a non-articular area. The anterodorsal lip of the centrum is straight, sinuous, or concave, but never deeply notched (Hoffstetter and Gasc, 1969). The teeth are ankylozed to the rims of a shallow, crater like depression, and are constantly being resorbed and replaced (Gans et.al., 1969).

Description --

Right dentary. UM 105143 (Figure 81). Locality; 1139

This specimen is a portion (2.4 mm) of an anterior right dentary which bears one tooth without its tip, and has three alveoli. The tooth is conical, sharply pointed, slender and slightly anteroposteriorly compressed. It is recurved to point posterolingually. There is a small pit at the center of the base on the lingual side. It is set in a sub-thecodont socket.

In lingual view, the dentary has a deep Meckelian groove which shallows posteriorly. In labial view, the bone is smooth except for one large foramen ventral and slightly anterior to the tooth. Anterior to the foramen is a longitudinal, broad, shallow depression. In dorsal view, the alveoli are ovoid and deep, and vary in size. The dentary is concave lingually.

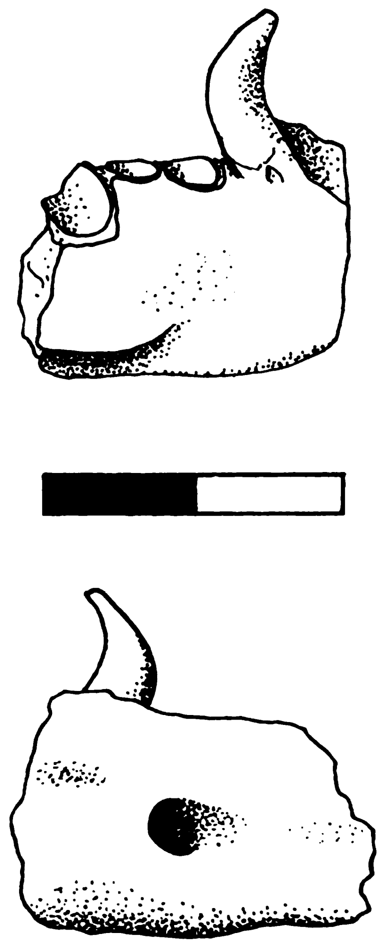

Figure 81. Serpentes indet. UM 105143. Right dentary, lingual and labial views. Scale bar is 2 mm.

Discussion -- No dentaries are known of *Coniophis*, *Calamagras*, *Ogmophis*, and *Dunnophis*. The known dentaries of *Boavus* are more tapered than UM 105143 or UM 106795. Both the Boidae and Aniliidae have an open Meckelian groove (Cope, 1900). It is, therefore, not possible to assign these specimens further.

Romer (1956) described snake teeth as being acrodont. However, Gans et. al. (1969) stated that the teeth are ankylosed to the rims of shallow, crater like depressions, and are constantly being resorbed and replaced. The Aniliidae have simple, solid, compressed teeth, whereas the Boidae have long, recurved, conical, non-compressed teeth (Gans et. al., 1969). It is therefore most likely that these teeth belong to a boid snake.

BIOSTRATIGRAPHY

The North American Eocene has been subdivided into four biochronological ages (NALMA's), the Wasatchian, Bridgerian, Uintan and Duchesnean (Wood et. al. 1941). Gunnell et. al. (1993) added the early Chadronian. The Wasatchian and Bridgerian have been further subdivided into subages by various authors.

The Wasatchian was subdivided by Granger (1914) into the Sand Couleean, Graybullian, Lysitean, and Lostcabinian. Gingerich (1989) redivided the Wasatchian into eight biostratigraphic zones (Wa0 - Wa7), with each of Granger's divisions containing two of the new zones (Zonneveld, 1994). This study is concerned only with the Lostcabinian (Wa7) (see Table 13).

Robinson (1966) defined a new zone, the Gardnerbuttean, between the Lostcabinian and "Bridgerian A", from fossils found in the Huerfano Valley of Colorado. A similar fauna was found by Stucky (1984) in the Wind River Basin. The Gardnerbuttean has since been renamed as the Br0 by Gunnell and Bartels (1994).

The Bridger Formation spans most of Bridgerian time and was subdivided by Matthew (1909) into lithostratigraphic units A through E using nine calcareous tuffs or "white layers" as stratigraphic markers, because of their lateral persistance (Figure 2, page 4). He further subdivided these units into basal, lower, middle, upper, and top layers, but these are not clearly defined. Osborn (1929) renamed the Sage Creek White Layer as the Cottonwood Creek White Layer, but this had already been used by Matthew (1909) as a subdivision of the Bridger B, and so has been abandoned (Evanoff et. al., 1998). Wood (1934) grouped Bridger A and B as the Blacks Fork Member, and Bridger C and D, as the Twin Buttes Member, because of difficulties in correlation between his area and the type section. He also indicated that there are distinct differences between the faunas of the two members. West and Hutchison (1980) named the Bridger B the Cedar Mountain Member. However, this is already used in Utah, and Evanoff et. al. (1998) proposed the name Turtle Bluff Member for this unit. Gunnell and Bartels (1994) recognized four biostratigraphic zones corresponding to the units of Matthew (1909); Br0 (Gardnerbuttean), Br1 (Bridgerian A), Br2 (Bridgerian B) and Br3 (Bridgerian C, D and E).

Evanoff et. al. (1998) have re-examined the section in the Bridger Basin. They have redefined and redescribed the marker units used by Matthew (1909), as they are of a more varied lithology than originally thought. They have also placed the fossil localities of R. M. West in stratigraphic context. Table 14 summarizes the various terminologies used.

These terms were not intended to be used as rock stratigraphic units and stratigraphers have consistently avoided these units, prefering to base their work on lithostratigraphic differences (Sullivan, 1980). Koenig

(1960) simply divided the Bridger into Lower (A and B), Middle and Upper, separated repectedly by the Sage Creek White Layer and the Upper White Layer . Underlying the Bridger throughout much of the area is the Wasatch Formation.

Table 13. Stratigraphic and biostratigraphic nomenclature for the Wasatchian.

Hayden, 1869	Granger, 1914 Robinson, 1966	Gingerich, 1989 biostratigraphic zones Gunnell et. al., 1992
	Gardnerbuttean	Br0
Wasatch Fm.	Lostcabinian	Wa7
	Lysitean	Wa6
	Graybullian	Wa5
		Wa4
		Wa3
	Sandcouleean	Wa2
		Wa1
		Wa0

Table 14. Stratigraphic and biostratigraphic nomenclature for the Bridgerian.

<table>
<tr><th>Hayden 1869</th><th>Matthew 1909</th><th>Osborn 1929</th><th>Wood, 1934 West and Hutchison 1981</th><th>Evanoff et. al. 1998</th><th>Gunnell and Bartels 1994 biostrati-graphic zones</th></tr>
<tr><td rowspan="11">Bridger</td><td>Bridger E</td><td>Bridger E</td><td>Cedar Mountain Member</td><td>Turtle Bluff Member</td><td rowspan="7">Br3</td></tr>
<tr><td rowspan="3">Bridger D</td><td rowspan="3">Bridger D</td><td rowspan="6">Twin Buttes Member</td><td>Upper</td></tr>
<tr><td>Middle</td></tr>
<tr><td>Lower</td></tr>
<tr><td rowspan="3">Bridger C</td><td rowspan="3">Bridger C</td><td>Upper</td></tr>
<tr><td>Middle</td></tr>
<tr><td>Lower</td></tr>
<tr><td rowspan="3">Bridger B</td><td rowspan="3">Bridger B</td><td rowspan="4">Blacks Fork Member</td><td>Upper</td><td rowspan="3">Br2</td></tr>
<tr><td>Middle</td></tr>
<tr><td>Lower</td></tr>
<tr><td>Bridger A</td><td>Bridger A</td><td>Bridger A</td><td>Br1</td></tr>
</table>

STRUCTURAL HISTORY OF THE GREEN RIVER BASIN

During the Paleocene and Eocene the Laramide Orogeny caused fragmentation of the crust into fault bounded, basement cored blocks which moved vertically along reverse faults. Major detrital basins developed between these uplifted blocks (Frazier and Schwimmer 1987). One such basin formed between the Uinta Mountains to the south, the Wind River and Granite mountains to the north and east, the Sierra Madres to the southeast and the Wyoming Overthrust Belt to the west. This basin was divided in the middle to late Eocene by the anticlinal Rock Springs Uplift, into the Washakie and Great Divide basins to the east, and the Green River Basin to the west. Downwarping in these basins began in the early Tertiary and continued intermittently throughout the Eocene (Love 1960). This occured due to both tectonic subsidence and sediment loading of the highly compressible, fine-grained, Tertiary sediments. The low stream gradient between this region and the ocean prevented the margins of the basin from being cut downward (Bradley 1964).

The Green River Basin has a general north-south synclinal form parallel in strike to the folded pre-Tertiary rocks of the Overthrust Belt, but changes to a northwest-southeast trend in the north, along the Wind River Mountains (Love 1961; Koenig, 1960). The structure of the basin is complex, as it was affected by many independent, vertically moving, tectonic blocks. In the south, a thick sequence of alluvial fan deposits formed in response to uplift of the adjacent Uinta Mountains (Crews and Ethridge 1993). Steeply dipping strata occur due to drag along the large, sinuous Uinta fault running parallel to the basin rim. In the north, the Wind River thrust fault and Continental normal fault formed downdropped graben blocks and local folding which results in the middle Eocene rocks of the area outcropping at the same level as the older Wasatch and Green River formations (Bradley 1964).

The Wasatch and Bridger formations were laid down during Laramide uplifting which resulted in the deposition of thick, fluvial sediments in intervening basins. In the central part of the basin the beds are essentially horizontal, but in a narrow belt around the margin the layers can be tilted up to 12 degrees and locally the Bridger contacts the Wasatch without a stratigraphic break. Downwarping and compaction of the highly compressible, fine-grained sediment have, in places, accentuated the original depositional dip (Bradley 1964).

STRUCTURAL HISTORY OF THE SOUTH PASS REGION

The main focus of this study is the South Pass region in the northern Green River Basin, about 16 km south of Atlantic City. The area was first extensively studied by Nace (1939), and then again by Zeller and Stephens (1969). Middle Eocene deposits unconformably overlie the Precambrian basement. These are, in ascending order, the Main Body of the Wasatch Formation, the Tipton Shale Tongue of the Green River Formation, the Cathedral Bluffs Tongue of the Wasatch Formation, the Wilkins Peak and Laney Shale members of the Green River Formation, and the Bridger Formation (Zeller and Stephens, 1969) (Figure 82).

To the north, the Wind River Range formed by overturn folding followed by faulting on the Wind River thrust fault, with its northern side upthrown (Berg, 1963). To the south, Lake Gosiute deposited the Green River Formation. The areal extent of this formation reflected the expansion and contraction of ancient Lake Gosiute (Nace, 1939), which was in turn controlled in the north by movement of the Wind River and Continental faults. The Wasatch and Bridger formations were deposited on the margins of the lake basin. Early faulting of the Wind River Fault controlled the deposition patterns and lithologies of the Main Body of the Wasatch Formation, the Tipton Shale Tongue, and the Cathedral Bluffs Tongue (Steidtmann et. al., 1983). The Continental Fault,

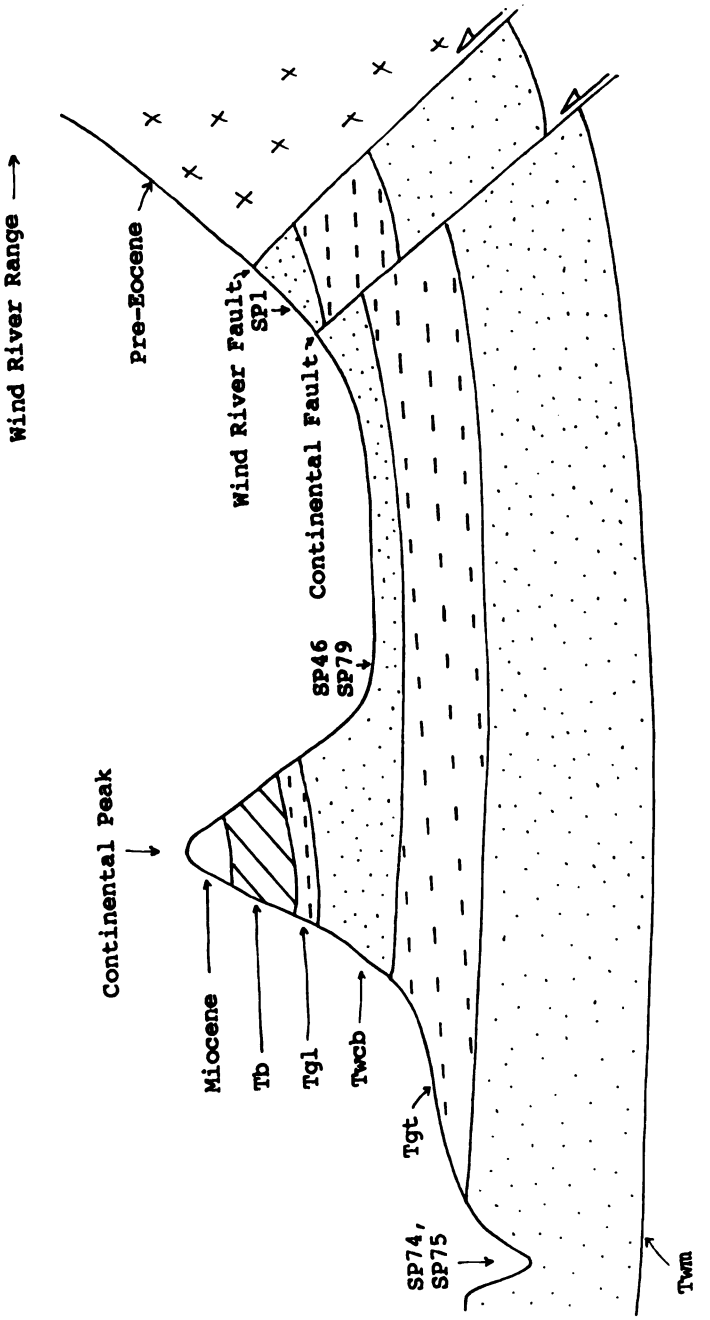

Figure 82. Cross section of the South Pass areas showing lithological units and positions of major localities. Twm (Main Body of the Wasatch Formation), Tgt (Tipton Shale Member of the Green River Formation), Twcb (Cathedral Bluffs Tongue of the Wasatch Formation), Tgl (Laney Shale Member of the Green River Formation), Tb (Bridger Formation).

first named by Nace (1939), is a normal fault, cropping out in the northern part of the study area. Steidtmann et. al. (1983) propose Eocene movement on the Continental Fault because of the 5 m diameter boulders found in the sediments of the Cathedral Bluffs Tongue adjacent to the fault. Since the Pliocene the Continental Fault has been upthrown on its south side, but during the Eocene, the north side was upthrown. The Wind River Fault consists of a number of segments which moved seperately throughout its history. It does not crop out in the area, but is exposed to the northwest (Steidtmann et. al., 1983).

Late faulting, west of the study area, folded pre-Laney Shale sediments into the Red's Cabin Monocline. Subsequently, the Laney Shale was deposited as a drape over the monocline. Overlying Bridger deposits show no evidence of folding indicating that fault movement had ceased by this time (Steidtmann et. al., 1983). In the study area folding is slight, with most beds being near horizontal except those in direct contact with the Continental Fault. The relationship between the movement on the faults and the lithology in the area is shown in Figure 83.

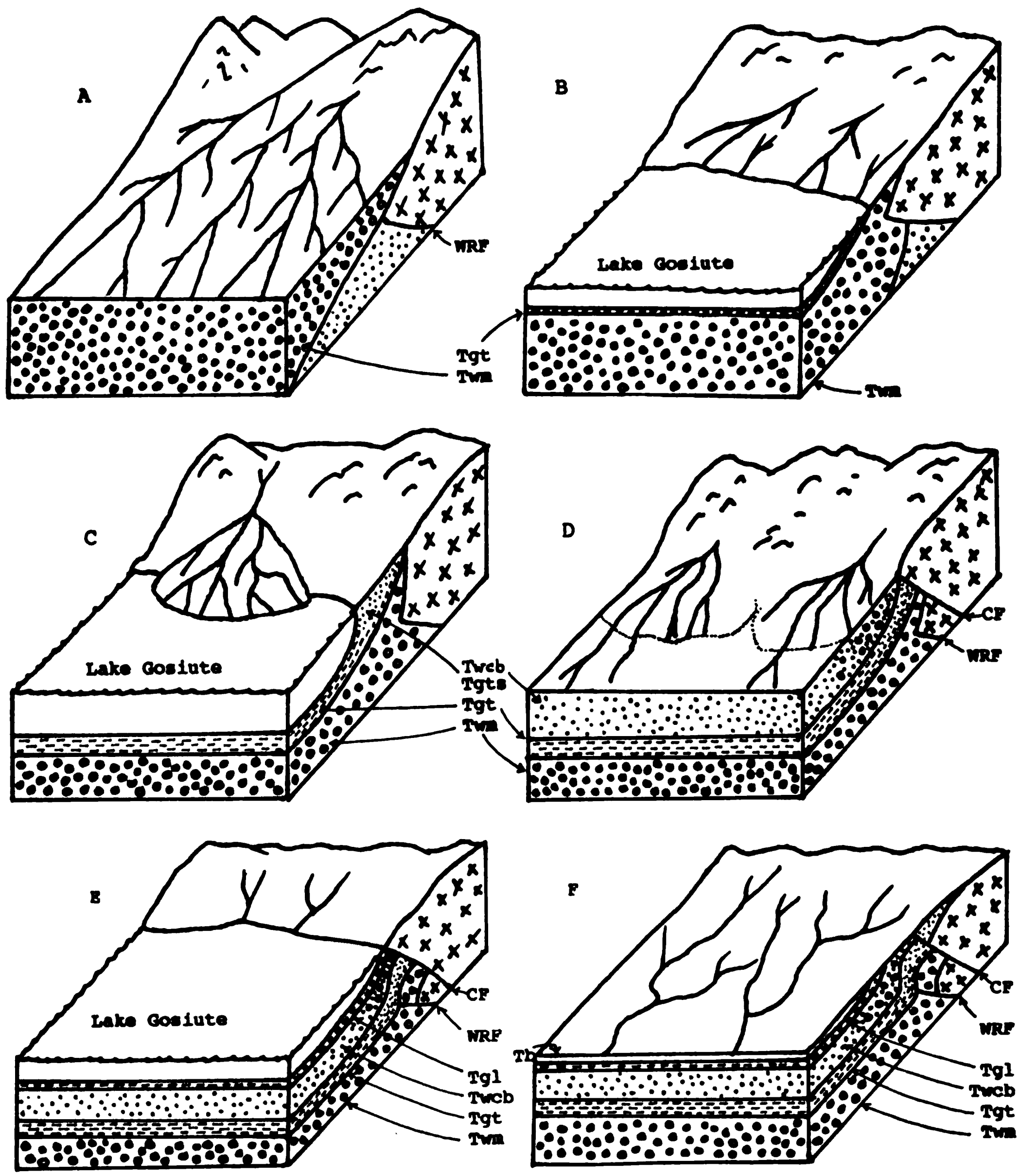

Figure 83. Schematic diagrams showing depositional and structural events related to fault movement from Steidtmann et. al. (1983). A. Deposition of the Main Body of the Wasatch Formation (Twm). B. Continued motion on the Wind River Fault (WRF) controlling the position of the lake margin, with deposition of the Tipton Shale Member (Tgt). C. Deposition of fluvial and deltaic sandstone of the Tipton Shale Member (Tgts). D. Uplift of the Continental Fault (CF) and deposition of the Cathedral Bluffs Tongue (Twcb). E. Last motion on the Wind River Fault, folding of Red's Cabin Monocline, and subsequent deposition of the Laney Shale Member (Tgl). F. Present configuration after collapse of the Continental Fault, with Bridger Formation (Tb) shown.

STRATIGRAPHY

Three localities were studied in detail, University of Michigan localities SP46, SP78 and SP79. In all sections, beds were numbered from 1 at the base, upward to the highest level. Beds were assigned a facies code (see Appendix A) after Miall (1978). High concentrations of fossil remains were found at SP46 and SP79, but it was not possible to precisely correlate these localities due to the difference in sedimentary facies present at the two localities, and the fact that SP79 consists of only 5 m of deposits. SP78 represents a section including levels found at SP46 and SP79, and was used to correlate these localities with respect to each other, and to the main section through the Wasatch Formation at South Pass.

Locality SP78

Three stratigraphic sections were taken at SP78 (Circle Bar Lake Quadrangle, NE 1/4, SE 1/4, NW 1/4, NW 1/4, Section 35, T27N R99W), within the Cathedral Bluffs Tongue of the Wasatch Formation (see Appendix B). A composite section is shown in Plate 2. The locality consists of about 37 m of variagated sediment, capped by a covered interval underneath the first paper shales of the Laney Shale Member of the Green

River Formation (Figure 84). The outcrop forms steep cliffs and gullies, rising from the surrounding flat plains.

The base consists of a series of conglomerates and sandstones (Figure 85). Beds vary from 0.11 m to 1.4 m in thickness, with a total thickness of 3.03 m. The conglomerates are clast supported, containing granule to cobble sized, rounded quartz, deeply weathered gray schist and tan sandstone, with a gray, very coarse sand matrix. Some layers contain imbricated clasts and all layers fine upward. Some layers are impersistant, with a lateral extent of about 30 m. They are interbedded with layers of gray, very coarse sandstone. These contain grains of the same composition as the conglomerates. They fine upwards, are poorly sorted - containing quartz granules - and have a silty matrix. The contact between the conglomerate and sandstone layers varies from a gradational grain size change, to a sudden grain size change.

Above these layers is a thick section of fine grained deposits (Figure 86). Beds can be laterally extensive - several kilometers in extent - or impersistant - several meters in extent. In some instances it is possible to trace a bed using its sedimentary characteristics, despite a color change in different areas within the locality. Most of the beds were found to be correlatable within SP78.

The fine grained deposits are made up of siltstone, mudstones, and some fine to very fine sandstones. The sandstones vary in color from gray-green near the base of the

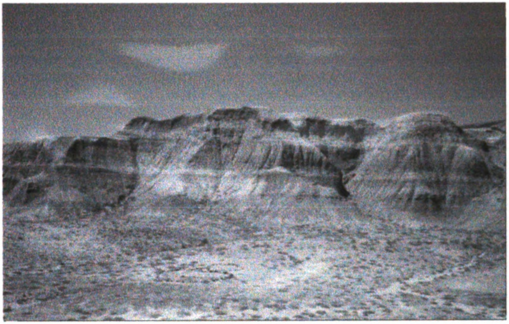

Figure 84. Photograph of the outcrop at SP78.

Figure 85. Photograph of the conglomerates and sandstones at SP78

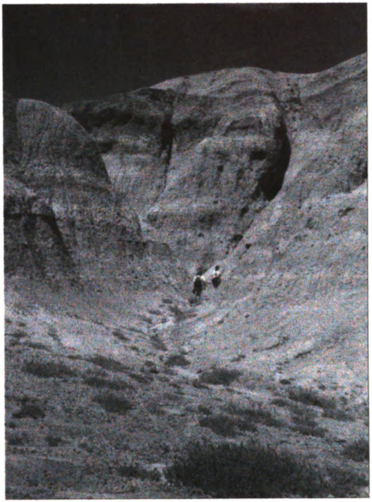

Figure 86. Photograph of the fine grained deposits at SP78.

section, to red-brown near the top. The lowest of these layers occurs above a coarse siltstone that marks the first fine grained bed above the conglomerate and sandstone sequence. This sandstone is similar in composition and grain size to the sandstones below, and is probably related to the coarse grained sequence. Sandstones higher in the section are red-brown, and finer grained, and were deposited as part of the fine grained sequence. These sandstones are mottled with gray-green areas, contain quartz, are moderately to poorly sorted and moderately to poorly consolidated, with a silty matrix. At 20.3 m up the section there is an impersistant layer of white very fine sandstone that is well consolidated and contains mafic grains.

The majority of the beds in the section are siltstones. They vary in color from gray-green, to orange, to red-brown. Near the base of the section the majority of the siltstones are poorly sorted, and contain sub-rounded to sub-angular granules of quartz. Nearer the top, well sorted siltstones predominate. Most are moderately consolidated, and are mottled.

Several distinctive layers are present in the section. At 21.13 m from the base of the section two layers of brown-green siltstone occur that weather a distinctive orange. They were laterally persistant and were used for correlation within SP78. At 19.72 m and 31.59 m above the base similar layers occur. Both are green, moderately consolidated siltstones. They have a characteristic "popcorn" weathering and form distinctive flat benches in outcrop. These benches were very useful in correlation within the locality. At 16.08 m up the section there is a layer of gray-green, well consolidated fine siltstone that forms a resistant layer. The bed probably has a silica cement as it lacks orange lichen, which would indicate the presence of calcium, and lacks the red coloration associated with iron-bearing cements. This layer was used in correlation between different areas within the locality.

A 0.63 m thick mudstone layer occurs 35.4 m from the base. It is dark green, poorly consolidated, and clayey. It has a distinctive "popcorn" weathering but does not form a bench in outcrop.

Fossils were found in beds 12, 27, and 28 (see Appendix B). These were crocodylian and turtle remains, and were most abundant in beds 27 and 28. Surface collection at SP78 was not extensive, but a number of specimens were obtained. These were an associated hyaenodontid skeleton in bed 12, an unidentified lizard atlas, a tooth from *Scenopagus*, a paramyid, and *Hyopsodus* from unknown levels.

Locality SP46

Six sections were measured at SP46 (South Pass Quadrangle, NE 1/4, SW 1/4, NE 1/4, Section 30, T27N R99W) within the Cathedral Bluffs Tongue of the Wasatch Formation (see Appendix B). A composite section is shown in Plate 2.

The locality consists of about 40 m of mainly gray-green sediment capped by a covered interval which lies underneath the first paper shale of the Green River Formation. The outcrop forms prominent cliffs on either side of a wide drainage running to Sand Creek to the north. The base consists of interbedded conglomerate and sandstone. Individual beds vary in thickness from 0.04 m to 1.5 m, and make up the bottom 3.81 m of the section. Beds are impersistant and often measure only tens of centimeters in lateral extent.

The conglomerates are clast supported, with a very coarse sandstone matrix. The clasts are granule to pebble sized, and consist of sub-angular quartz, sub-rounded and platy, deeply weathered gray biotite rich schist, and rounded tan sandstone. The clasts are occasionally imbricated. Some beds contain sandstone lenses within them. Each bed fines upwards, and in some cases very coarse sandstone occurs at the top. These finer parts of the unit often have parallel laminations, and can contain lenses of granule-sized conglomerate. The sandstone layers occur at the top of, and between, the conglomerate beds. They are gray-green, very coarse, and the grains consist of the same components as the conglomerates. Some layers have parallel laminations, some have ripple cross-bedding, and some contain conglomerate lenses. Many of the beds are lens- or wedged shaped.

Above these units is a sequence of fine grained deposits. They vary from red-brown, and brown-green near the base, to predominantly gray-green near the top of the section. The lower units are mainly siltstones, with some mudstones and one sandstone bed, and are grouped into a number of fining upward sequences. This sandstone is very fine grained, brown, poorly sorted, poorly consolidated, and slightly clayey. The mudstones are interbedded with the siltstones. They are brown to green, with a muddy matrix. They are well sorted, poorly consolidated, and clayey. Mudrock is most common near the base of the section, with beds becoming less clayey higher in the section. Siltstones are the most common lithology in the lower part of the section. They vary from red-brown, to gray-green, and most are mottled red or green. They are generally well sorted lower in the section, and poorly sorted farther up where abundant quartz granules occur within the siltstones.

Sandstone predominates in the upper part of the section, and the beds are grouped into coarsening upward sequences. The boundary between the lower fining upward groups and upper coarsening upward groups is marked by a 0.22 m thick resistant sandstone layer at the 14.14 m level. It is tan colored, weathers red, is well sorted, fine grained, and has subrounded quartz grains, and a silty matrix. Similar layers occur at the 15.86 m, 16.83 m and 20.33 m levels. They are all laterally persistant within the locality.

Between these sandstone beds are layers of green, well sorted, moderately consolidated, muddy siltstone. They continue to occur above the highest resistant sandstone bed. They are, at some levels, finely interbedded with gray-white calcareous beds, which occur as both laterally persistant, and impersistant layers through the sequence. The green siltstones range from 0.06 m to 3.8 m in thickness. They are moderately to very poorly sorted, containing quartz granules, and coarsen upwards. Some layers form prominant, laterally persistant cliffs, that were used in correlation. Between these siltstones are very fine grained to fine grained sandstones. They are light green, poorly sorted and coarsen upward.

The majority of fossils were found in beds 18, 22, 26, and 34, they will be discussed in the paleoenvironment section (p443).

Locality SP79

Three sections were measured at SP79 (Circle Bar Lake Quadrangle, SE 1/4, SW 1/4, NW 1/4, Section 26, T27N R99W) within the Cathedral Bluffs Tongue of the Wasatch Formation (see Appendix B). Two sections from SP79 are shown in Plate 2. The locality consists of about 5 m of siltstone and sandstone layers. The lowest unit at SP79 is a reddish brown, very fine sandstone which contains a few sub-angular quartz granules. It is moderately consolidated and has a silty matrix. Above this is a gray, well sorted, moderately consolidated coarse siltstone with a silty matrix. Above this is a dark gray, very poorly sorted, unconsolidated, very fine sandstone. Above this layer occurs a greenish-gray, poorly sorted, moderately consolidated coarse siltstone, which has "popcorn" weathering. The highest bed at SP79 is a dark green mudstone layer, which is poorly consolidated, well sorted, and clayey.

At Con's Hill, a small knob near the center of SP79, a detailed section was measured, and quarrying helped determine the position of the most fossiliferous layers. The section was made up of three units, a lower red and green mottled, fining up coarse siltstone, a middle red and green mottled, fining up medium to coarse siltstone with quartz granules, and an upper gray-green medium siltstone with rare quartz granules. Fossiliferous layers were found at 0.34 m, 0.57 m, and 0.85 m from the base. The first two of these zones occur within the lower unit. The third, and most prolific, zone occurs at the boundary between the lower and middle units. The gray-green unit is almost entirely unfossiliferous throughout SP79. Fossils recovered from SP79 will be discussed in the paleoenvironment section.

A section in the North Fork of Bear Creek, about 2 km south of SP78, was made by W. S. Bartels in 1996 (see Plate 1). This consists of 32.5 m of the Cathedral Bluffs Tongue of the Wasatch Formation, and 16.5 m of the Laney Shale Member of the Green River Formation (Figure 87). The lowest unit is a gray-green conglomeratic very fine sandstone, with pebble grains. Above this is an orange siltstone and a gray quartz

Figure 87. Photograph of the North Fork of Bear Creek.

arenite. The rest of the section is made up of gray, red, purple, and orange siltstones until the first paper shale of the Green River Formation. There are two thin ash layers within the Wasatch units. Throughout this area, fossils were mainly found in the upper green beds of paleosol units.

CORRELATION WITHIN THE SOUTH PASS AREA

Correlated beds are shown on Plate 2. The coarse grained beds at the bases of the sections at SP46 and SP78 are very similar in color and lithology. At SP46 they have a finer grain size, as would be expected from a locality situated farther from the source area, the Wind River Mountains. In both sections they are overlain by a series of finer grained sediments, that are of similar color and composition until the occurence of the resistant sandstone unit at SP46. At SP78 the upper beds are similar to those below and continue to occur in fining upward sequences. At SP46 the upper beds are grouped into coarsening upward sequences of green siltstones and sandstones, with thin calcareous beds found throughout. Sandstone bed 3 of SP46 can be correlated with beds 9 and 10 at SP78. Beds 17 through 22 of SP46 is correlated with bed 18 of SP78. Bed 26 of SP46 is correlated with bed 26 of SP78, and bed 3 of the "Triangle" section at SP79.

At SP78 beds 26, 27, and 28 can be correlated with beds 3 and 4 of the "Triangle" section at SP79, and beds 1 and 2 of the "Con's Hill" section (see Appendix B and Plate 2). Beds 29 and 30 of SP78 correlate respectively with beds 5 and 6 of the "Triangle" section, and bed 29 correlates with bed 3 of the "Con's Hill" section. Sequences at both localities consist of i) a red-brown very fine sandstone at the base,

ii) a reddish-brown coarse siltstone, iii) a greenish very fine sandstone (SP79) or brown-green coarse siltstone (SP78), iv) a greenish coarse siltstone (SP79) or greenish medium siltstone (SP78), and v) a dark green clayey mudstone at the top. This last layer is particularly characteristic as it occurs nowhere else in the SP78 section. At both localities the top two layers exhibit popcorn weathering, and form distinct benches in outcrop. Layers 1 and 2 of the "Con's Hill" section, and layers 27 and 28 at SP78 were highly fossiliferous. At SP78, the level of layer 29 was compared to the section at SP79 using a Brunton compass, and was found to occur at the level of layer 4 of the "Con's Hill" section. Beds at SP79 are found to be coarser grained than their equivalents at SP78 due to their closer proximity to the source area.

Using correlation between SP78 and SP46, and between SP78 and SP79 it is possible to approximately correlate SP46 and SP79. It is found that the fossiliferous layers occur at roughly the same horizon, although they occur in different facies.

The section in the North Fork of Bear Creek consists of 32.5 m of the Cathedral Bluffs Tongue. Its base is made up of a gray-green conglomeratic sandstone, of a similar type as the conglomerates at SP46 and SP78. The rest of the section is predominantly siltstones, and it is not possible to correlate between this section and those to the north. The North Fork of Bear Creek is about 2 km further from the

Continental Fault than the other three localities. It is possible that the conglomerates of SP46 and SP78 correlate with the conglomeratic sandstone from the North Fork of Bear Creek, which would simply be a more distal facies. Similarly, the siltstone and sandstone sequences of SP46, SP78, and SP79 may correlate with the predominantly siltstone sequence of North Fork of Bear Creek. SP78 is the most complete section and consists of 55 m of the Cathedral Bulffs Tongue, SP46 consists of about 45 m of the Cathedral Bluffs Tongues. The 32.5 m of the Cathedral Bluffs Tongue of the North Fork of Bear Creek is consistant with its more distal position. However, I hesitate to correlate this section with the others to the north, except in suggesting possible correlation between the conglomerates of SP46 and SP78 and the conglomeratic sandstone of the North Fork of Bear Creek, and the fine grained sequences of all sections.

DEPOSITIONAL ENVIRONMENT OF THE GREEN RIVER BASIN

The principle depositional environments of the Green River Basin are lacustrine (fresh and saline), alluvial, and paludal (Roehler, 1965). Lacustrine sediments were deposited by Lake Gosiute which first formed during the latest Wasatchian due to climate changes and the lack of an outlet from the basin (Roehler, 1993). The Sheggs Bed of the Tipton Shale Member and the upper Laney Shale Member of the Green River Formation were deposited under freshwater conditions and consist primarily of two lithologies; deep water oil shale and shore line facies. The Rife Bed of the Tipton Shale Member, the Wilkins Peak Member, and the LaClede Bed of the Laney Member were deposited under saline conditions. Facies include dark brown and black dolomitic oil shale, and shore facies such as mudflat mudstones (Roehler, 1993).

At the basin margins, alluvial fans dominate comprised of conglomerates, sandstones, and siltstones. Basinward, they interfinger with alluvial plain or lacustrine deposits. These alluvial plain deposits consist of channel and sheet sandstones within sequences of siltstone, mudstone, and shale. Coal and carbonaceous shale deposits represent paludal environments (Roehler, 1993).

Deposition during the Wa7 involved the Main Body of the Wasatch Formation which is formed primarily of alluvial fans and plains. Close to the basin margins, the sediments are red or variegated and represent well aerated paleosols, while near the center they are gray and green as paleosol formation was hindered by the permanently waterlogged soils. During the Br0, the Cathedral Bluffs and Desertion Point tongues of the Wasatch Formation were deposited as a series of coalescing alluvial fans while the Wilkins Peak Member of the Green River Formation was being deposited by the small, saline Lake Gosiute (Roehler, 1993).

Deposition during the Br1 consisted of a transgression of Lake Gosiute across an alluvial floodplain in a humid environment and contains many laterally continuous calcareous marker horizons. Volcanism from the Absaroka Range became increasingly important during this time (Gunnell and Bartels, 1994). Deposition during Br2 occurred during a semi-humid, better drained, regressional period and accordingly, few green to brownish-red beds are found here. Br3 was deposited during a return to humid conditions as Lake Gosiute expanded for the last time (Gunnell and Bartels, 1994). This part of the section closely resembles that of the Br1 but has a larger number of volcanic layers as volcanism to the north increased until finally these deposits filled the basin. By this time, Lake Gosiute no longer existed and the upper part of the Bridger Formation is made up of fluvial volcaniclastic deposits. In the central and southwest parts of the basin Br1, Br2, and Br3 occur. In South Pass only zones Wa7, Br0 and Br1 are thought to be represented (West, 1969), and along the western margin of the basin, only Wa7 and Br0 (Zonneveld, 1994).

SEDIMENTARY INTERPRETATION OF THE SOUTH PASS AREA

The sediments measured at SP46, SP78, and SP79, and those observed at SP1 fall into four categories which can be interpreted to represent facies within an alluvial fan. Facies (i) and (ii) correspond to the "pediment facies" of Roehler (1965). Facies (iii) corresponds to the red-bed fluviatile facies of Roehler (1965). Facies (iv) is a local lacustrine deposit that possibly corresponds to the non-red fluviatile-paludal facies of Roehler (1965).

A diagramatic representation of the alluvial fan environment is given in Figure 88. Localities SP46, SP78, SP79, and the North Fork of Bear Creek are given approximate locations in relation to the fan.

i) At SP1 a conglomerate occurs with up to 1 m clasts. It is clast supported and consists of subangular, boulder-sized quartz, metamorphic and igneous rocks from the Wind River Mountains to the north. The bed exhibits a rapid decrease in grain size upwards at the boundary with an overlying sandstone. The bed lacks sorting, stratification, or channel filling features. It is non-stratified, has a non-erosive base, lacks grading, has no imbrication or other fabrics. Above the conglomerate a red-brown sandstone occurs which is coarse grained, massive, and contains sub-angular quartz, feldspar, mafics, and rock fragments.

SP1 is located between the Continental and Wind River

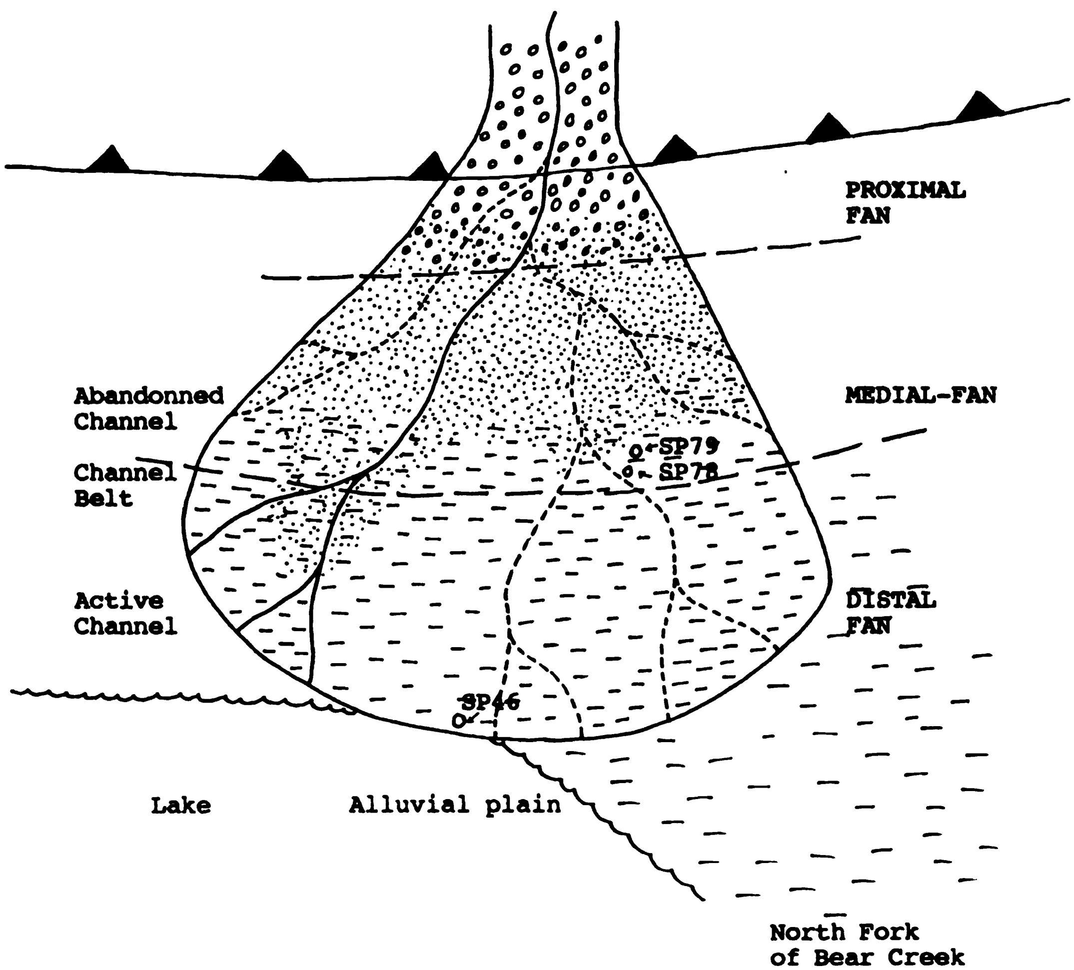

Figure 88. Depostional evironments of the alluvial fan in the South Pass area, with positions of localities shown.

faults, and can therefore not be correlated with other South Pass localities. The presence of boulder-sized, poorly sorted, unstratified conglomerates is consistant with its close proximity to the Wind River Fault. Heward (1978) described similar conglomerates from the section at La Magdalena, northern Spain. The coarseness, rapid variation in grain size, lack of sorting, stratification, and channel filling features suggest these beds were deposited by major, erosive flood events in a medial alluvial fan environment corresponding to sediments of the medial-fan lobe association of Heward (1978). Alluvial fans have high slopes and high flow conditions resulting in deposition by sheetfloods, rock slides, rock avalanches, and debris flows.

The unconfined nature of the depositional surface results in a rapid decrease in sediment velocity and rapid deposition, leading to angular or sub-angular, poorly sorted, coarse grained sediments. Conversely, rivers have lower slopes, and are characterized by thick, cross-bedded or lenticular sandstones and floodplain sequences, consisting of better sorted sediments with more rounded grains and clasts (Blair and McPherson, 1994). The clast supported, non-stratified conglomerates at SP1 suggest deposition by debris flow because of their non-erosive bases, sub-angular clasts, well-defined units, lack of sorting, imbrication and grading. These features are not found in reworked sediments or stream deposits (Beaty, 1963; Blair and McPherson, 1994). The non-erosive bases suggest limited turbulence, and laminar flow

(Rodine and Johnson, 1976). These beds were, therefore, deposited by large flood events associated with torrential precipitation, and by sediment and fluid gravity flows associated with movement on the Wind River and Continental faults. The sandstones found within and above conglomerate beds represent the declining floodwater stage that characteristically succeeds debris flow (Beaty, 1963) or sheetflooding (Blair and McPherson, 1994).

ii) At the base of sections at SP46 and SP78, a series of conglomerates and sandstones occurs with beds varying from 0.11 m to 1.4 m in thickness (Figure 89). The conglomerates at SP46 and SP78 are clast supported, containing granule- to cobble-sized, rounded quartz, gray schist and tan sandstone, with a gray, very coarse sandstone matrix. Some layers contain imbricated clasts and all layers fine upwards. Some layers are impersistant, with a lateral extent of about 30 m. They are interbedded with layers of gray, very coarse sandstone. These contain grains of the same composition as the conglomerates. They fine upwards, are poorly sorted - containing quartz granules - and have a silty matrix. The contact between the conglomerate and sandstone layers varies from a gradational grain size change, to a sudden grain size change. The conglomerates and sandstones are generally unfossiliferous.

The clast supported, stratified conglomerates and pebbly- and cross-bedded sandstones found at SP46 and S978 are laterally extensive within the localities, and exhibit

Figure 89. Photograph of deposits that make up facies (ii) at SP78.

only minor channeling. They are finer grained and better sorted than those found at SP1 and therefore, were deposited more distally from the source. The lateral extent of the beds suggests depostion on a flat plain lacking discrete channels (Beaty, 1963), probably adjacent to channels on the fan surface.

Alluvial fans are characterized by rapid, intermittent periods of deposition, separated by long periods of erosion and reworking (Blair and McPherson, 1994). The alluvial fan deposits near the Continental Fault were reworked for lengthy periods of time by rivers, and then redeposited during flood events over the fan surface. The series of conglomerates and sandstones at South Pass are indicative of depostion in a medial-fan environment.

iii) Above the conglomerates and sandstones at SP46 and SP78 is a thick series of fine grained laterally extensive, and occasionally impersistant deposits (Figure 90). These deposits fine upwards, and are made up of siltstones, mudstones, and some sandstones. The sandstones are mottled, contain quartz, are moderately to poorly sorted and moderately to poorly consolidated, with a silty matrix. The majority of the beds in the section are siltstones. Near the base of the sections the majority of the siltstones are poorly sorted, and contain sub-rounded to sub-angular granules of quartz. Nearer the top, well sorted siltstones predominate. Mudstones are interbedded with the siltstones. They are brown to green, with a muddy matrix. They are well

Figure 90. Photograph of deposits making up facies (iii) at SP78.

sorted, poorly consolidated, and clayey. At SP46 mudrock is most common near the base of the section, with beds becoming less and less clayey higher up. At SP78 mudrock occurs high in the section. Mottled paleosols occur throughout the section.

The fine grained, fining upwards sequences are laterally extensive within each locality, with rare pinching out beds, no cross-stratification, and they are vertically persistant. The lateral extent of the sandstones, their poor sorting, and the presence of paleosols and discrete fossiliferous horizons within them suggest that they were deposited rapidly, followed by long periods of non-deposition. The finer grained deposits have similar features and represent deposition in a distal fan environment during waning flood events (Heward, 1978). Blair and McPherson (1994) state that fine grained "floodplain" deposits do not occur within alluvial fan complexes. However, rivers reworking the sediments of an alluvial fan during long periods of erosion can redeposit sediments as rounded conglomerates and sandstones proximally on the fan, and poorly sorted sandstones, siltstones and mudstones more distally on the fan (Bartels pers. comm.). Furthermore, the presence of quartz granules in mudrocks is difficult to explain in a purely fluvial (water-lain) environment. The abundant, poorly sorted siltstones found in the lower part of the section at SP78, closely resemble deposits found in alluvial fans in present-day Fresno County, California. Here, mudflow deposits consist of poorly sorted claystones containing sand and gravel grains (Bull, 1964).

The fine grained facies exhibits moderate to strong paleosol formation, while the sandstones and conglomerates of the first two facies lack color banding. At SP46, SP78, and SP79 the coarse grained facies, interpreted as channel or near channel deposits, are gray-green and show little evidence of pedogenic processes, while the fine grained facies are color banded and represent mature paleosols developed on the alluvialplain.

SP79 probably represents a Stage 4 paleosol as described by Bown and Kraus (1987), and Kraus and Bown (1988). This stage is characterized by a thick, red/purple B horizon overlain by a green Ae horizon, and thin dark gray-green, clayey Ao horizon. Color contacts, especially low in the paleosol, are distinct. The A horizons of mature paleosols are often highly fossiliferous (Kraus, 1987). This is the most mature paleosol in the section measured, and corresponds to beds 26, 27, 28, 29, and 30 of the SP78 section. Lower in the section at SP78 color contacts are often diffuse, and soil horizons lack the Ao horizon characteristic of Stage 4 paleosols. Near the base of the section, Stage 1 and Stage 2 palesols predominate with orange, red and green mottled beds. The presence of mottled paleosols in this part of the section is characteristic of immature alluvial soils formed in a wet environment (Bown and Kraus, 1987). These paleosols are generally thinner than those found higher up the section. A

Stage 3 paleosol is represented by beds 22, 23, 24, and 25, which exhibit an orange, red, purple and then green color sequence. Overlying this is the Stage 4 paleosol described above.

Mottling and lack of horizon development are characteristic of alluvial soils, which are evidence of flooding (Costa, 1974). Bown and Kraus (1987) proposed that the maturity of a paleosol is relative to its distance from the sediment source. Deposits representing channel, and near channel sedimentation are frequently inundated with fresh sediment that buries the surface and arrests soil development. Farther from the channel, sediment is exposed for longer intervals and is only buried by thin layers of new sediment allowing the development of mature, color banded paleosols. This is consistant with the stratigraphic sequence at SP78. At the base of the section are sandstones and conglomerates representing depostion on a medial-fan within or near channels. They are gray-green and do not exhibit pedogenic characteristics. Areas proximal to alluvial channels would have been buried frequently by flooding events and would not have had sufficient time to develop distinct soil horizons. Higher up in the sequence, the fine grained deposits are interpreted as alluvial plain deposits on a distal fan, the same distance from channels. These areas would be exposed for significant periods of time, permitting soil development. The sediments found high in the section show increasing paleosol maturity probably due to the migration of the channel belts away from the area (Kraus, 1987).

Fine grained sediments often form channel banks as streams cut into the previously deposited alluvial plain sediments forming trenches and levees (Bull, 1964). Boothroyd and Nummedal (1978) used Alaskan glacial outwash fans as a model for humid, vegetated alluvial fans. Their Figure 12 (p 659) shows a coarse grained channel cutting into a fine grained swamp and marsh environment. Intermittent flow is characteristic of alluvial fan deposition (Hooke, 1968). During high flow, larger clasts could be deposited in the channel adjacent to the channel banks. At times of flood, river banks collapse forming mudflow and crevasse splay deposits. Crevasse splays fine and thin distally, and coarsen upward due to progradation (Etheridge, Jackson and Youngberg, 1981), features not characeristic of these deposits. Mudflows would fine upwards, and be composed of both fine grained deposits and quartz granules close to the channel, with only fines deposited distally (Bull, 1964). Therefore, the similar sediments found in the study area most probably represent mudflows. The presence of quartz granules mainly in the lower part of the section at SP78, corresponds to immature paleosols suggesting rapid burial by successive flooding events. Higher up the section the mature paleosols are well sorted and generally lack quartz granules indicating deposition in an environment distal to the channel where less frequent deposition events permitted paleosol formation.

Medial and distal alluvial fan deposits differ from simple braided stream deposits in being more extensive laterally grading upstream into proximal alluvial fan deposits. However, braided streams may occur on alluvial fans, for example, at the head of the Yellow River, China (Rust, 1978). Alluvial sediments occur in two major facies; sandstones and conglomerates in sheets or ribbons deposited within, or near, the channel, and mudstone, siltstone, very fine sandstone, paleosols, and peat deposited as overbank deposits (Bull, 1964; Bridge and Leeder, 1979; Kelly and Olsen, 1993). Conglomerates can also spread out over the fan surface, proximal to the channels during major flooding events (Rust, 1978). Fining upward sequences represent the establishment of a channel system, and then its abandonment and burial beneath the floodplain, due to channel avulsion. A typical stratigraphic sequence would involve a basal intraformational conglomerate overlain in succession by a fine grained cross-bedded sandstone, a very fine grained, cross-laminated sandstone, and a thick sequence of flat bedded fine grained deposits. Such a sequence represents a steady decrease in stream power (Allen, 1970). Evidence for channel avulsion includes a rapid facies change (Bridge, 1984), and the presence of a laterally extensive sandstone body overlain by a thick, fining upward siltstone layer (Bridge and Leeder, 1979), both of which are seen in beds 7 and 8 at SP78.

iv) Coarsening upward sequences of sandstone, siltstone and shale occur at SP46 above the sequences of fining upward deposits. Where the transition occurs there are a number of resistant, tan colored sandstones. They weather red, are well sorted, fine grained, have subrounded quartz grains, a silty matrix, and are laterally persistant within the locality.

Between these sandstone beds are layers of green, well sorted, moderately consolidated, muddy siltstone. They continue to occur above the highest resistant sandstone bed. They are, at some levels, thinly interbedded with gray-white calcareous beds, which occur as both laterally persistant, and impersistant layers through the sequence. The green siltstones range from 0.06 m to 3.8 m in thickness. They are moderately to very poorly sorted, containing quartz granules and they coarsen upwards. Between these siltstones are very fine grained to fine grained sandstones. They are light green, poorly sorted, and coarsen upwards.

Similar coarsening upward sequences were described by Heward (1978) as a lacustrine association occuring distal to an alluvial fan. Small-scale series occur with green, bioturbated fine siltstones at the base, coarsening upwards into coarse siltstones and fine sandstones. Carbonate layers, nodules, and burrow infillings also occur. No channel features are seen, which might be expected in lake delta deposits. This suggests gradual shoreline progradation in a low-energy lake due to changes in lake level or the infilling of a lagoon (Heward, 1978). Many of the sandstones are well sorted and consist of mostly quartz. The poorly sorted siltstones contain quartz granules, with occasional mafic grains and rare rock fragments. In comparison with SP78 and SP79 they are more mineralogically mature, and probably represent shoreline facies (Hooke, 1972).

A cross section of the area, showing the timing of depoitional events, is given in Figure 91.

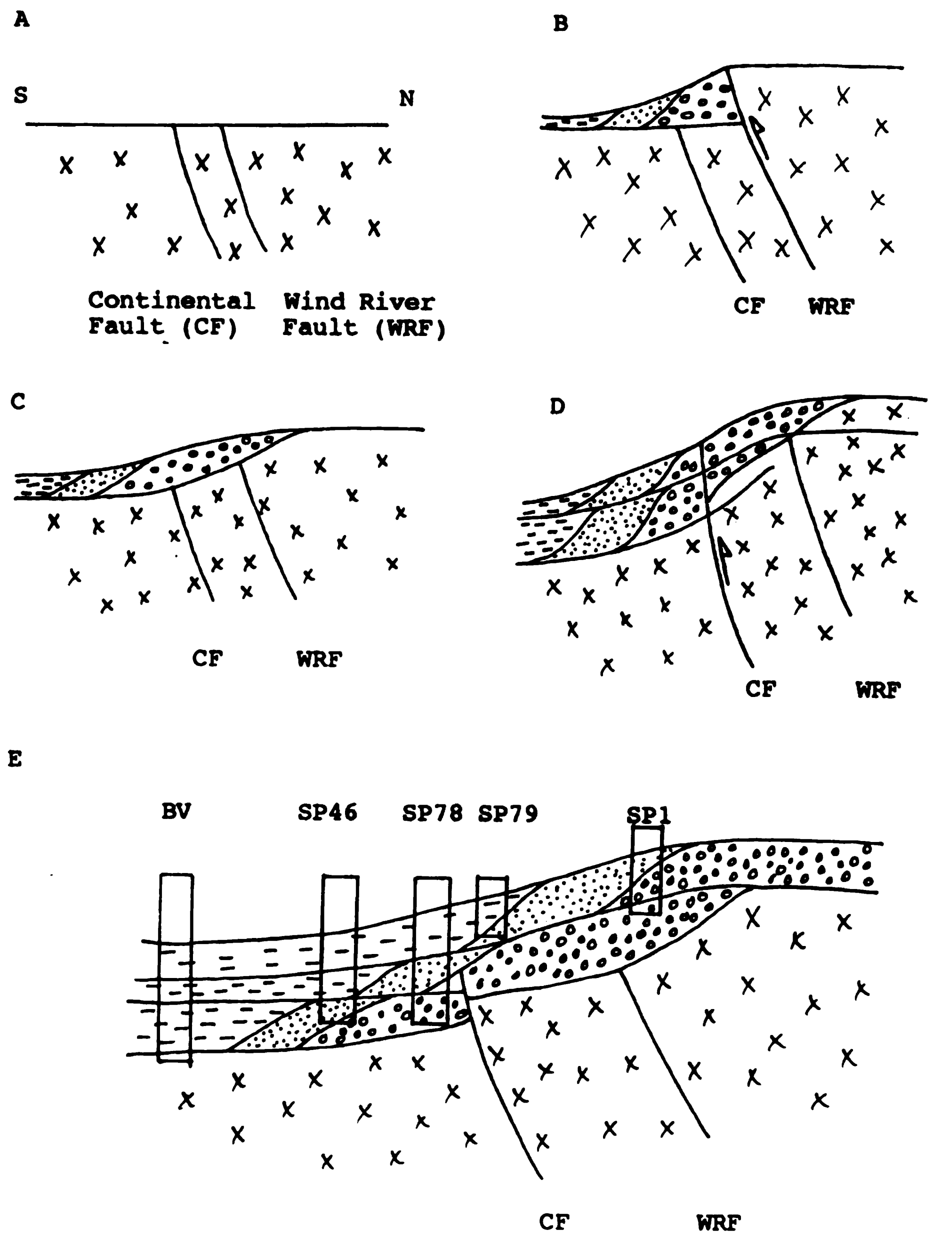

Figure 91. Fault control of alluvial fan formation in the South Pass area, and the positions of South Pass locations.

PALEOENVIRONMENT OF THE CONTINENTAL INTERIOR AND GREEN RIVER BASIN

Interpretations of Paleogene environments have historically used floral remains, as opposed to vertebrates, because many plant genera and families from the Paleocene are alive today, while vertebrate turnover is high (McKenna, 1980; Zonneveld, 1994). The Eocene was a period of major evolutionary and biogeographic change in floras. Three trends are apparent; the development of phytogeographic provinces in contrast to the more homogeneous Paleocene pattern, the diversification of plants important in the present day flora, and the first appearances of many extant angiosperms as ancient Cretaceous and Paleocene forms disappeared. Concurrent with this is the spread of broad-leaved evergreen forests to 60°N latitude (during the Wasatchian and early Bridgerian) in response to global warming, and the subsequent (late Bridgerian) fragmentation of this flora into more open forest due to a decrease in precipitation (Wing, 1987).

Paleogene climates are characterized by low mean annual range of temperature, moderate to high mean annual temperature, and abundant precipitation (Wolfe, 1980). Wasatchian and Bridgerian floras contain taxa that are presently associated with temperate and subtropical/ paratropical climates (Wing, 1987). From Paleocene to Wasatchian time climatic trends include general warming, an increase in entire margin leaves, and an increase in thick textured leaves all of which indicate increased tropicality (Wing, 1987). In the Bridgerian low-stature subhumid forests replaced those of the Wasatchian due to the drier, cooler climate (Wolfe, 1978). In general during the middle Eocene, temperatures were increasing, and precipitation decreasing in the continental interior (Wolfe, 1975).

MacGinitie (1969) analyzed floras from the Green River Formation of Utah and Colorado, using the concept of floristic analogy to interpret the area's paleoenvironment. Although the requirements of Paleogene plants must have been somewhat different from those of today, such analyses are accurate in a general sense (Wing, 1987). MacGinitie (1969) used plant families, as opposed to species, to lessen this problem. Even though the Utah/Colorado flora is somewhat unique, its setting in a large, lowlying basin surrounded by high mountain ranges is similar to that found in the Green River Basin of Wyoming, so comparisons can be made. MacGinitie (1969) described four vegetational types (lake margin-high water table, lake margin-low water table, moderate elevation, and high elevation), which have distinct characteristics suggesting different environmental preferences. Similar plant assemblages probably occurred in the Green River Basin near the lake, and at the basin margins respectively. The lake margin-high water table environment contained plant families that today prefer high summer temperatures, and a season of low humidity. The lake-margin-low water table assemblage contains plant families that today live under subhumid conditions in areas of seasonal rainfall. The moderate elevation assemblage contains plant families that suggest mesic, warm temperate environments similar to the southern Appalachians today. The high elevation assemblage lived under cool conditions, probably over 1000 m. This demonstrates the high variability that is characteristic of the Eocene on a spacially small and large scale (Wing, 1987).

To account for these climatic implications, MacGinitie (1969) proposed a warm temperate to subtropical environment for the Eocene of Colorado and Utah, with a mean annual temperature of 18°C, 60-85 cm annual precipitation, and high equability. This is in agreement with Axelrod (1966), who proposed that during the Eocene, the mesophytic warm temperate broadleaved evergreen forest environment was replaced by a subhumid warm temperate savanna-like environment. At low elevations the high water table environment supported a rich savanna-like vegetation, while the low water table areas had a more mesic, subhumid vegetation. These areas would have experienced hot summers with a monsoon-like pattern of precipitation (at least 60 cm annually), and dry winters. Higher elevations would have been cooler and would have received more rainfall (about 95 cm). These areas supported subhumid shrubs and conifer-hardwood forests adapted to cool, subhumid conditions (MacGinitie, 1969). Even at these elevations frost would have been minimal, possibly due to the high humidity (Wilf et. al., 1998).

The area was probably subhumid, as the assemblages lack plants adapted to humid environments, and contain plants suited to subhumid environments (MacGinitie, 1969). MacGinitie (1969) also noted that the leaves of the Utah and Colorado floras are generally small with a heavy texture and 38% have entire margins, suggesting high temperatures, abundant sunshine, and low humidity associated with seasonal dry periods. The varved nature of the Green River Formation, and the presence of evaporites, was also used by MacGinitie (1969) to support the presence of regular seasonal variations in temperature and precipitation, with a maximum for rainfall in the late spring to early summer and a relatively dry autumn and winter.

MacGinitie (1969) compared the Utah and Colorado floras with several in Wyoming. The Wind River Basin flora is Lostcabinian in age and contains a large-leaved mesic flora suggesting a warm temperate environment. The Kisinger Lake flora is basal middle Eocene, and contains many mesic forms also found in the Utah and Colorado floras. However, it contains abundant large-leaved plants and would have been adapted to a humid subtropical environment with abundant precipitation. The Boysen flora of the middle Eocene occurs near Shoshoni, Wyoming, north of South Pass, and represents a swamp environment. The Little Mountain flora in Wyoming from the Wilkins Peak Member contains many plants found in the

Utah/Colorado area, and has a similar small leaf type with heavy textures.

The general trend in the continental interior is increasing humidity towards the north, and temperatures varying with elevation (MacGinitie, 1969). The flora was much more mixed than those of the Gulf and Pacific coasts (MacGinitie, 1969), perhaps because of the greater variation in elevation which is a major factor in controlling the distribution and composition of forests today (Axelrod, 1966).

In contrast to the method of floristic analogy is that of foliar physiognomy used by Wolfe (1975; 1978; 1980; 1994). The concept is based on the fact that physical characteristics of leaves are related to the environment. Wolfe (1978) lists several useful characters including type of leaf margin, leaf size, leaf texture, and leaf shape. In general, increasing temperature and precipitation are indicated by an increase in the number of leaves with entire margins, and an increase in size, thickness, cuticle thickness, and the number of drip tips (Wolfe, 1978; Wing, 1987). The reason for rejecting the use of modern day analogues is that often analogues are not available, or are of uncertain relationship, and the weight given to certain taxa is highly subjective. Leaf characteristics are used because modern day floras from similar environments exhibit similar leaf characters (Wolfe, 1978). Problems with this method are that streamside populations are over-represented in stratigraphic sections, and factors other than temperature and precipitation also affect leaf characteristics (Wing, 1987). Wolfe (1994) utilizes the Climate-Leaf Analysis Multivariate Program in his leaf analysis. Wilf et. al. (1998) attempted to avoid the problem of multiple variables by using only one assumption, that mean annual precipitation correlates with leaf morphology, which produced more constrained results than when using several factors. A problem for any interpretation of paleoenvironment is whether the plants seen today in different areas are wholly adapted to the present environment, or whether populations are still recovering from the Ice Ages (Axelrod, 1966).

The climatic variables that have the most effect on floral assemblages are mean annual temperature, mean annual range of temperature, and warm month mean ie. the mean temperature of the warmest month. For example, the percentage of entire leaves in an assemblage is directly correlatable to mean annual temperature. Wolfe (1978) plotted leaf margin and leaf size for the Eocene Puget Group of western Washington. He found that both variables fluctuated during the middle Eocene, but not concurrently or to the same degree. In the early middle Eocene, while the percent of entire leaf margins remained relatively constant, the leaf size decreased, indicating a decrease in mean annual temperature range (to about half that of present day). During the late middle Eocene, both variables increased, indicating increasing temperature and humidity, reflected by a more tropical rainforest flora.

Wolfe (1978) found great variability during the middle Eocene between the northern and southern Rockies, which is in agreement with MacGinitie (1969) who stated that the south experienced dry conditions, while the north was more mesic. Wilf et. al. (1998), using only one variable, concluded that the continental interior of the Eocene was more humid than today, and that the Green River Basin was drier than others in the area. Therefore, results from both foliar analogy and foliar physiognomy agree in general (Wing, 1987).

Using floral assemblages, MacGinitie (1969) and Axelrod (1966) proposed a warm temperate to subtropical environment for the middle Eocene continental interior, with a mean annual temperature of 18°C, 60-85 cm annual precipitation, and high equability, supporting a savanna-like/woodland vegetation. Wolfe (1978; 1994) agreed with the high mean annual temperature, amount of precipitation, and high equability, but he thought the large size of the leaves indicated a semi-deciduous vegetation (Wolfe, 1985). Wilf et. al. (1998) agreed with the high humidity, and that the Green River Basin was relatively dry.

In summary, oxygen^{18} analysis of benthic and planktonic foraminifera indicates that the early to middle Eocene was the warmest period of the Cenozoic (Miller et. al., 1987), with ocean surface temperatures at tropical latitudes of about 20°C, and about 10°C at 60°N latitude (Donn, 1982). In

North America, the mean annual temperature range was about half that of today. From the middle Eocene to the Oligocene, temperatures decreased, and the mean annual temperature range increased (Wolfe, 1978). The Arctic was warm (10-20°C mean annual temperature), equable (10-15°C mean annual temperature range), had abundant precipitation (Wolfe, 1980), and no permanent ice caps (McKenna, 1980). On the Pacific coast, there was a low temperature gradient, of approximately 0.25°C/1°latitude, and the southeastern coastal plain had a dry tropical climate (Wolfe, 1980). The continental interior was characterized by high humidity, increasing temperatures and decreasing precipitation (Wolfe, 1975), and by its highly variable vegetation (Wing, 1987).

HERPETOLOGICAL EVIDENCE FOR PALEOCLIMATE IN THE GREEN RIVER BASIN DURING THE MIDDLE EOCENE

Workers attempting late Tertiary paleoenvironmental reconstructions typically assume that the amphibian and reptile faunas are the most reliable vertebrate fossils for climatic analysis. In late Tertiary and Holocene, many species have modern day analogues with known geographical ranges and habitat types, making paleoenvironmental reconstructions relatively easy (Gajewski 1993).

An analysis of herpetological extinctions and radiations shows a considerable degree of stasis of individual species, and a relatively stable rate of species turn-over through time. At the Permo-Triassic extinction, for example, some groups of the small herpetofauna were affected adversely, but many survived intact (Maxwell 1992). A similar pattern appears to apply at the Cretaceous-Tertiary boundary (Archibald 1982; Sullivan 1987).

Williams and Bartels (1997) proposed paleoclimatic estimates derived from a GIS based analysis of reptile diversity with respect to climate in present day North America. They used the number of reptile and mammal species in an area, and not the particular species found, to plot regressions against a variety of climatic variables. The number of lizard species was found to be highly dependant on all variables based on temperature, but largely independent of precipitation and relative humidity. Two of the graphs Williams and Bartels (1997) produced are reproduced in Figure 92 as an example of the method used for estimating climatic variables based on the lizard species used in this study. A best-fit line on each graph indicates the most probable estimate, however the minimum was used as this better reflects present-day examples. For the lizards of the Br1 of the Bridgerian, Williams and Bartels (1997) estimated a mean annual temperature (MAT) of at least 13°C, a mean cold month temperature (MCMT) of at least -5°C, a mean annual range of temperature (MART) of at least 10°C, and a mean annual precipitation (MAP) of 406-1524 mm.

The number of species recovered from areas used in this study, the biostratigraphic zones they were recovered from, and the climatic estimates are presented in Table 15 and Table 16. These climate estimates are from the lizard assemblages, and are therefore minimum figures. Where turtles and crocodiles are present they indicate higher minimum temperatures and rainfall. Where appropriate, these species are used to estimate climate in the conclusion.

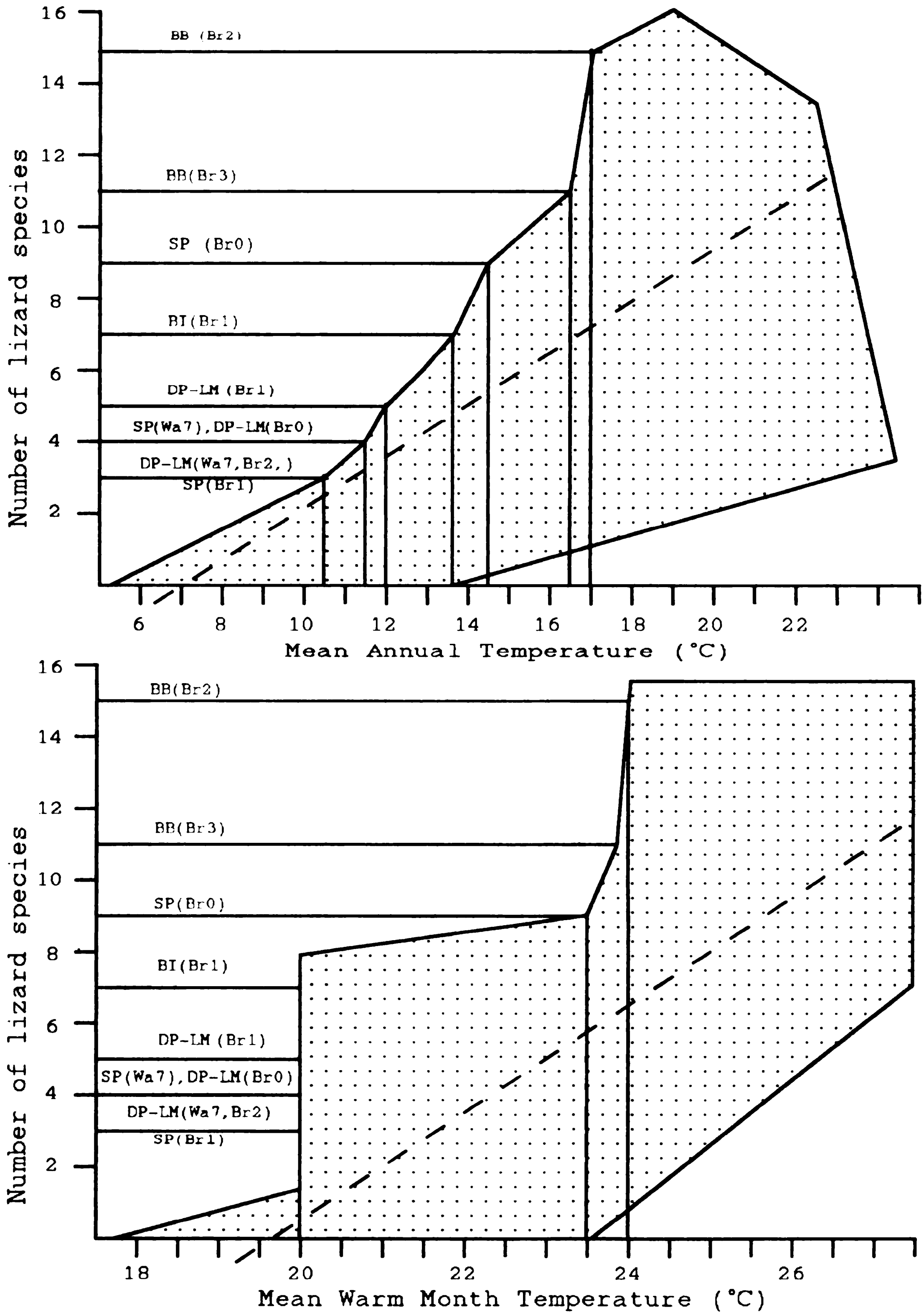

Figure 92. Examples of graphs from Williams and Bartels (1997) used to estimate climatic variables. Dashed line denotes the best-fit for all data. The shaded area denotes all data plotted.

Table 15. Localities, biostratigraphic zones, and number of lizard species found.

Area	Biostratigraphic Zone	Number of lizard species
South Pass	Wa7	4
	Br0	9
	Br1	3
Desertion Point-Little Muddy	Wa7	3
	Br0	4
	Br1	5
	Br2	3
Big Island	Br1	7
Bridger Basin	Br2	15
	Br3	11

Table 16. Paleoclimate estimates for Wa7, Br0, Br1, Br2, and Br3, for South Pass (SP), Desertion Point-Little Muddy (DP-LM), Big Island (BI), and the Bridger Basin (BB). MAT (mean annual temperature), MCMT (mean cold month temperature), MWMT (mean warm month temperature), MART (mean annual range of temperature - equability).

Locality	SP			DP - LM				BI	BB	
Zone	Wa7	Br0	Br1	Wa7	Br0	Br1	Br2	Br1	Br2	Br3
MAT(°C)	11.5	14.5	10.5	10.5	11.5	12	10.5	13.5	17	16.5
MCMT (°C)	-6	-2	-5	-6	-6	-3	-6	-3	5.5	3
MWMT (°C)	20	23.5	20	20	20	20	20	20	24	24
MART (°C)	8	11	8	8	8	8	8	8	18	18
Maximum temp: 30°C or above	2 days	50 days	2 days	2 days	2 days	2 days	2 days	9 days	88 days	77 days
Minimum temp: 0°C or above	130 days	183 days	116 days	116 days	130 days	130 days	116 days	152 days	192 days	190 days
Solar radiation (gcal/cm^2)	230	386	220	220	230	240	220	264	439	412
Cloud cover (%)	48.5	40	48.5	48.5	48.5	47.5	48.5	41.5	40	40

No fossil assemblage represents the complete fauna living at the time of deposition. Biases occurring at the time of death include those due to the species geographical position (where the species lived and died), and how quickly they were covered with sediment before scavengers or bacteria began decomposition. Once buried, the mode of preservation and physical characteristics of the animal dictate what structures will be fossilized, and even if this occurs, the rock may be subsequently weathered away. Sieving in-situ minimizes collection bias, and the careful stratigraphic description, and horizontal and vertical segregation of sampling areas, will indicate the possible degree of mixing of the assemblage with faunas from higher strata.

The localities used in this study must be assessed for completeness. At South Pass, Wa7 was sampled by surface collection and dry screening, and therefore collector bias is minimal. However, there are few exposures at this level in this area, so the numbers of lizard specimens for this level must be regarded as a minimum with the possibility that more species would be found with further collection.

The majority of the localities at South Pass are from Br0, and two localities (SP46 and SP79) were extensively collected by surface collection, quarrying, and wet screening. The fossils found are generally disarticulated, but well preserved. The number of lizard species found in Br0 at South Pass is probably close to the living assemblage, so climatic data derived from these localities is well constrained. Br1 at South Pass has not been extensively collected, and is not represented by many localities, and therefore, climatic data is less reliable.

In the Desertion Point-Little Muddy area, Wa7 is not very fossiliferous. There is little exposure, and fossils were obtained by surface collection only. It is likely that more lizard species existed than are found in the fossil assemblage, however, the numbers found, and their climatic implications, can be taken as a minimum. Br0 is represented by more fossiliferous localities, and therefore climatic data for this zone is more reliable.

The Big Island area has been collected for many years, therefore information for Br1 from this area is relatively well constrained, however few lizards have been recovered. This is also true for the Bridger Basin which has produced a large number of fossils of good preservation. The number of lizard species found in Br2 exceeds the number given on graphs by Williams and Bartels (1997), but a minimum number can be assumed. Extensive collection of Br3 has recovered many, well preserved fossils, therefore climatic implications are well constrained.

The Wa7 is only represented by basin margin localities from South Pass and the Desertion Point-Little Muddy area. Relative to Br0 localities from these areas they had low temperatures and high rainfall. Br0 is also represented by these basin margin localities, but exhibits much higher temperatures and lower rainfall than the Wa7. This indicates that there was a climate change that affected the faunal distribution in the Green River Basin at this time. When comparing variables from the Br1 (the only zone represented by both basin center and basin margin localities) basin margin areas are characterized by lower temperatures, better drainage, a lower number of frost free days, lower solar radiation, and a higher percent cloud cover than basin center localities. This is due to the areas' higher elevation and proximity to surrounding mountain ranges. Br2 is only represented by basin center localities from the Bridger Basin and Desertion Point-Little Muddy area which has not been extensively collected. Minimum values indicate a period of high temperatures compared with previous times zones. Br3 has higher temperatures and lower rainfall than Br1 basin center localities and better drained soils than the Br2.

LIZARD DENTAL MORPHOLOGY AND SQUAMATE CHARACTERISTICS AS INDICATORS OF DIET AND HABITAT

Fewer fossil analogues of modern species are found in progressively older sediments. In the early Tertiary, some modern groups are found, but it would be difficult to make assumptions, within these taxa, concerning their lifestyle or habitat, which may have become specialized recently. Therefore other, more distantly related, but morphologically similar groups, can be used as analogues to represent ancient modes of life. The species' diet and lifestyle can be based on modern analogues and skeletal morphology of the herpetofauna (Hotton, 1955; Naylor and Krause 1981; Sullivan 1982; Bartels 1983; Erickson 1987). It is possible to make some analogies with a degree of certainty, but any paleoenvironmental, paleoecological, or climatic study should take the lack of direct analogues into account (Gunnell and Bartels 1994).

Dental morphology of lizards is strongly influenced by selective factors operating through diet, and therefore provides information about habitat. Prey with different activity levels and integument exert different selective pressures. Large, active, heavily armored insects require teeth to capture them. Heavy armor requires holding and chewing, ant-eating requires little use of the teeth (Hotton, 1955). Hotton (1955) studied the teeth of the Iguanidae using degree of development of accessory cusps, the position of the first multicusped tooth, the dental profile, slenderness of the teeth, and the lateral compression of the teeth, to define four dietary groups (Table 17). These groups were herbivorous, ant-eating, predatory 1 (eating active prey with heavy integuments), and predatory 2 (eating very active prey with intermediate integuments). Even though this study only dealt with iguanids, lizards from other groups are assumed to have adapted teeth of similar morphologies to deal with similar diets (Hotton, 1955).

Table 17. Dentition types, their characteristic morphologies, and the fossil taxa from this study that belong to each type.

Tooth type	Characteristics	Fossil taxa
Herbivorous	Teeth: highly cuspate, laterally compressed, blade like crowns, even crown line	_Tinosaurus stenodon_ _Tinosaurus pristinus_
Ant-eating	Teeth: blunt, conical, peglike, no lateral compression, weak or no cuspation	
Predatory 1 (active prey with heavy integument)	Teeth:sharp, slender, cylindrical, weak to moderate cusps, even crown line	_Palaeoxantusia fera_ _Palaeoxantusia borealis_ _Machaerosaurus torrejonensis_ _Restes rugosus_ _Xestops vagans_ _Saniwa ensidens_
Predatory 2 (very active prey with intermediate integument)	Teeth: moderately sharp, conical, stout, moderate to high cuspation	_Parasauromalus olseni_

In general, carnivorous lizards have tall crowned, sharply pointed, recurved, widely spaced teeth, whereas herbivores have closely spaced multicuspate teeth with laterally compressed crowns. Omnivorous lizards have closely spaced, stout teeth, with blunt crowns, that are the equivalent to mammalian bunodont teeth in being able to process a wide variety of food (Gauthier, 1982). Few lizards are exclusively herbivorous or carnivorous (Pough, 1965).

Large recent iguanids (300 g and above) are herbivorous, small iguanids (50-100 g) are carnivorous, and those weighing between 100 g and 300 g are either herbivorous, carnivorous, or omnivorous. There are few prey items large enough to sustain large lizards. Amphibians are mostly nocturnal, birds and mammals are too agile, and egg-feeding is seasonal. Most must rely on other lizards for prey. In the case of large lizards, there appears to be a selective advantage to herbivory (Pough, 1965). Today, iguanids live in tropical and subtropical areas of North and South America, and on some Pacific islands (Frost and Etheridge, 1989).

The teeth of Parasauromalus olseni resemble those of Basiliscus which feeds predominantly on insects, but eats some vegetation. The teeth are adapted for gripping, piercing, and breaking the integument of their prey. Herbivorous iguanids such as Iguana iguana have crowns with many more accessory cusps (Montanucci, 1968).

Present day agamids inhabit temperate and tropical areas of Eurasia, Africa, Australia, and nearby islands (Frost and

Etheridge, 1989). The teeth of Tinosaurus most resemble those of Uromastix, which are used to shear vegetation, but do not act in gripping food (Throckmorton, 1976), and Sauromalus which is herbivorous but does not grind its food (Pough, 1965).

Restes rugosus has teeth that are blunt and simple or incipiently bilobed, as in all xenosaurids. Present day xenosaurids include Shinisaurus, an amphibious lizard that eats tadpoles, and Xenosaurus, a terrestrial lizard that inhabits mountainous regions (Gauthier 1982).

The sharp, laterally compressed, slightly recurved teeth of Machaerosaurus torrejonensis indicate that it would have fed on insects (Sullivan, 1982). The reduced number of teeth, short dentary, and short tail of Apodosauriscus minutus indicate that the species was fossorial (Gauthier, 1982; Estes, 1983). All burrowing forms today are carnivorous, regardless of their size (Pough, 1965).

Most glyptosaurines are similar to the present day Australian lygosomine scincids Trachydosaurus rugosus and Tiliqua occidentalis, which are also stout bodied and armoured and are herbo-omnivorous (Gauthier, 1982).
During the Eocene the continental interior experienced equable tropical conditions (Wolfe, 1978). Anguids were at their greatest diversity during the early Cenozoic (Gauthier, 1982), and glyptosaurines flourished, probably in response to the large diversity of prey animals living in the luxuriant vegetated habitat (Sullivan, 1979).

Large lizards like _Paraglyptosaurus_ _hillsi_ and glyptosaurine "indet A" were probably at least partly herbivorous like Recent large lizards (Gauthier, 1982). Sullivan (1980) proposed that the large, flat crowned posterior teeth of _P_. _hillsi_ and the stout peglike teeth of glyptosaurine "indet A" are well adapted to crushing land mollusc shells. However, modern mollusc-eating lizards have relatively sharp teeth that are used for piercing the shells of mollusc species similar to those found in the Eocene (Bartels, pers. com.). Although the decline of the glyptosaurines coincides with the extinction of many mollusc species (Gauthier, pers. com.), the end of the Eocene was also characterized by a deterioration of the climate (Wolfe, 1980; Frederickson, 1980; Prothero, 1985) and an increase in volcanism in the Absaroka Range which also contributed to the infilling and extinction of Lake Gosiute (Roehler, 1993). Climate probably had the primary control on the diversity of the glyptosaurines, as the decreasing temperatures of the terminal Eocene event adversely affected their populations (Sullivan, 1979).

The teeth of _Eodiploglossus_ _borealis_ are like those of Recent diploglossines such as _Celestus_ _costatus_ (Gauthier, 1982) which lives under leaf litter and eats insects.

Varanids are highly predatory, large and very active lizards (Carroll, 1988), which often occupy niches similar to those of small carnivorous mammals. Most carnivorous lizards employ a rapid, but short, pursuit tactic when hunting. Only varanids are capable of sustained pursuit due to their high aerobic metabolic rate (Pough, 1965). Carnivorous lizards have two methods of subduing prey. If the prey is smaller than the lizard's head, the head of the prey animal is seized and the animal is immobilized by crushing and piercing. If the prey is larger than the lizard's head, the animal is seized, lifted off the ground and killed by crushing or shaking. The shaking action of Varanus is often so rigorous that it can break its victim's neck, or rupture the visceral cavity. Then the prey is swallowed in a series of gulps. The recurved teeth of varanids makes it easier for the teeth to disengage from the prey during gulping (Gans, 1961). Saniwa is morphologically very similar to Varanus (Estes, 1983), and would have fed in a similar manner.

Recent xantusids are secretive and most active at night, and tend to inhabit rocky crevices and live under debris (Savage, 1963). It is more likely, given the climate of the Eocene, that Palaeoxantusia was more similar to the tropical and subtropical Recent xantusids that live under the leaves of rain forests, rather than the rock-dwelling Xantusia (Estes, 1983).

Aniliid snakes, such as Coniophis, were fossorial, inactive burrowers (Rage 1984). Recent boids can be fossorial, terrestrial, arboreal, or semiaquatic (Carroll, 1988). The tall vertebrae of Boavus, and multiple articulation points indicate that the species, like its modern day counterpart, was arboreal. The vertebrae of

Dunnophis are depressed and elongate with a low neural spine and a low neural arch. The centra are low and elongate, with a depressed condyle, and a depressed and undercut cotyle. The posterior trunk vertebrae lack a hemal keel. _Calamagras_ has a short neural spine, a low neural arch, and the only additional processes are very small pterapophyses. _Ogmophis_ has no hemal keel or hypapophyses on the mid-thoracic vertebrae. The characteristics of _Dunnophis_, _Calamagras_, and _Ogmophis_ indicate that these were terrestrial or fossorial snakes, with _Dunnophis_ being the most adapted for fossorial life.

A COMPARISON AND DISCUSSION OF GREEN RIVER BASIN LOCALITIES, THEIR FAUNAL ASSEMBLAGES, AND ENVIRONMENTAL IMPLICATIONS

The Green River Basin shares important characteristics with the Utah and Colorado basins studied by MacGinitie (1969). Both are lowlying basins containing lakes surrounded by high mountains that would have caused a downward flow of relatively dry air into the center of the basin, limiting rainfall there, and causing higher rainfall at the basin margins (MacGinitie, 1969). The development of volcanic highland regions throughout the Eocene affected the vegetation by dividing lowland areas, and reducing flow of Pacific influenced air (Wing, 1987). The center of the continent would have experienced low air pressure during the summer, causing in-drafts of marine air from the Gulf of Mexico, resulting in afternoon thunderstorms in the warm season (MacGinitie, 1969). Volcanic ash input increased throughout the Eocene, causing changes in soil and groundwater conditions (Wing, 1987). Due to the absence of polar ice caps during the Eocene, polar activity would have been minimal, and the jet stream would have been further north than today (McKenna, 1980). This would also have limited precipitation. Higher continental minimum temperatures and warm oceans would have increased humidity and cloudiness at higher elevations (MacGinitie, 1969).

Lake Gosiute had a lake level approximately 300 m above sea level with an area of about 25,000 km^2 (Bradley, 1964), with surrounding mountains about 500 m higher (MacGinitie, 1969). The South Pass area and the Muddy Creek localities of the Desertion Point-Little Muddy area are near the northern and western margins of the basin respectively. They would have been at moderate to high elevations, and probably represent a variety of habitats. Mature paleosols observed at South Pass indicate that the area was relatively distal with respect to Lake Gosiute. The Desertion Point localities of the Desertion Point-Little Muddy area, the Big Island localities, and the majority of the Bridger Basin localities are from the basin center.

DISCUSSION OF LOCALITIES WITHIN THE GREEN RIVER BASIN

South Pass Localities

SP74 and SP75 are stratigraphically the lowest localities in the South Pass area. They occur in the Main Body of the Wasatch Formation, at level Wa7 (Bartels pers. com.). The fossil assemblage is given in Table 18. The fossils were obtained by surface collection and dry screening. The mammalian fossils obtained from these localities are predominantly terrestrial, such as rodents, artiodactyls, and a miacid carnivore. The presence of Hyopsodus suggests a dry forest or savanna-like environment, while the perissodactyl Hyracotherium indicates a swampy woodland proximal to Lake Gosiute. Three species of primate suggest a forested environment. The presence of a fossorial epoicothere suggests a well drained environment, which is supported by the nature of the substrate; sandstones and siltstones exhibiting mature paleosols (Zonneveld, 1994). The presence of Glyptosaurus sp., Xestops vagans, and Restes rugosus suggests abundant insect life supported by the forested habitat.

Many of these species are highly mobile and are therefore of limited use in small scale paleoenvironment analysis. However, it is likely that the area represents an open forest on well-drained substrate near Lake Gosiute.

Table 18. Comprehensive faunal list for SP74 and SP75, 1997 and 1998.

Level	Taxon
Wa7	Glyptosaurus sp.(anguimorph lizard)
	Xestops vagans (anguimorph lizard)
	Restes rugosus (anguimorph lizard)
	Procaimanoidea (crocodylia)
	Sciuravus (rodent)
	Paramys (rodent)
	Hyopsodus (condylarth)
	Diacodexis (palaeodont artiodactyl)
	Bunophorus (palaeodont artiodactyl)
	Hyracotherium (perrisodactyl)
	Uintacyon (myacid carnivore)
	Microsyops (pro-primate)
	Absarokius (primate)
	Notharctus (primate)
	epoicothere (palaeanodont)
	Diplocynodon (prototherid)
	bird

SP46 is at level Br0 (Bartels pers. com.) in the Cathedral Bluffs Tongue of the Wasatch Formation. Below the principal fossiliferous zone at SP46, the stratigraphic section comprises of a lowest unit of conglomerate overlain by sandstones and siltstones formed on an alluvial fan. From bed 17 to the top of the section a series of coarsening upward sequences occurs that represent gradual shoreline progradation of the distal end of an alluvial fan into a low-energy lake or pond. Paleosols are very immature, and calcareous beds are abundant. The fossil assemblage at SP46 (Table 19) was obtained by extensive surface collection, and contains almost entirely terrestrial forms, with several amphibian specimens, and some crocodilian remains. There are many lizard specimens, and fossorial amphisbaenid remains, abundant turtle and crocodile remains, an epoicothere, and an unidentified palaeanodont.

The presence of an indeterminant amphibian and salamander suggest the proximity of water. Xestops vagans, the glyptosaurine, Palaeoxantusia sp., and Parasauromalus olseni are lizards with diets varying from herbo-omnivorous to carnivorous suggesting a large range of prey and habitat that supported the prey. These species and Calamagras are highly terrestrial. Amphisbaenids lack limbs, are elongate and snake like, and have a robust skull used in digging (Carroll, 1988). The presence of an amphisbaenid suggests well drained soils that were easy to burrow into.

These animals would have lived nearby, on dry, well-drained substrate, and must have been deposited at SP46 by streams traversing the alluvial fan. Primates, rodents, and insectivores are each represented by three species, which suggests a wholly terrestrial environment proximal to SP46. The perissodactyl Hyracotherium is the only species adapted to swampy woodland near a lake or pond, and may represent in situ remains. The total numbers, and percentage of elements found at SP46 are given in Table 20.

Table 19. Comprehensive faunal list for SP46, 1997 and 1998.

Level	Taxon
Br0	amphibian
	salamander
	Xestops vagans (anguimorph lizard)
	glyptosaurine (anguimorph lizard)
	Palaeoxantusia sp. (xantusid lizard)
	Parasauromalus olseni (iguanid lizard)
	amphisbaenid
	crocodylian
	Calamagras sp. (boid snake)
	Sciuravus (rodent)
	Paramys (rodent)
	Microparamys (rodent)
	Hyopsodus (condylarth)
	Antiacodon (palaeodont artiodactyl)
	Hexacodus (artiodactyl)
	Hyracotherium (perrisodactyl)
	Scenopagus (insectivore)
	leptictid (insectivore)
	Apatayms (insectivore)
	Miacis (miacid carnivore)
	Vulpavus (miacid carnivore)
	Viverravus (miacid carnivore)
	mesonychid (ungulate)

Table 19 (cont'd)

Microsyops (pro-primate)

Notharctus (primate)

Omomys (primate)

epoicothere (palaeanodont)

Peratherium (marsupial)

bird

Table 20. Number and percentages of elements found at SP46, 1997 and 1998.

Element	Number collected	Percentage
Isolated teeth	70	65.4%
Claws	2	1.9%
Edentulous dentaries	3	2.8%
Dentaries with teeth	5	4.68%
Maxillae with teeth	2	1.9%
Vertebrae	8	7.48%
Humeri	3	2.81%
Metacarpals	3	2.81%
Astragali	6	5.61%
Calcanea	2	1.9%
Skull fragments	1	0.9%
Radii	1	0.9%
Pisoforms	1	0.9%
Total	107	100%

Most fossils at SP46 show little abrasion, many are found in association, and most jaws contain teeth. This suggests that transport distance was short, and that the fossils did not remain on the surface for long before being washed into the water-logged environment of SP46. The locality represents an alluvial fan entering a lake, and it is likely that a large variety of habitats existed on the alluvial surface and surrounding area. Basin margins had a greater topographical relief than basin centers, and were therefore more ecologically diverse. These environments are characterized by high energy regimes which means that the animals would have inhabited a more stressful environment during life (Gunnell and Bartels, in prep), and that once an animal died it would have been quickly washed to an area of deposition and buried. This agrees with the observation that animals from a wide range of environments were fossilized at SP46 in relatively good condition.

The lithology suggests a beach and pond environment where the remains of terrestrial animals that lived in other proximal environments were deposited. The immature paleosols at SP46 indicate that the locality was poorly drained and proximal to Lake Gosiute. Fossils are best preserved in water logged soils (Retallack, 1990), as is shown at SP46 where the fossiliferous horizons occur exclusively within the green, very fine sandstones and siltstones.

SP79 also occurs at level Br0 (Bartels pers. com.), in the Cathedral Bluffs Tongue of the Wasatch Formation, but in contrast to SP46, the locality consists of a fining upward sequence of very fine sandstone and siltstone exhibiting relatively mature paleosols. The fossil assemblage (Table 21) was recovered by surface collection, quarrying, and wet screening, and differs from that of SP46 in that it contains no amphibian, turtle, or crocodilian remains, few squamates, six species of primate, and a very large number of rodent remains. The terrestrial taxa present were adapted to a variety of habitats; primates and pro-primates indicate an arboreal or semi-arboreal environment; condylarths indicate a dry forest or savanna-like environment (Zonneveld, 1994); perissodactyls indicate a woodland close to the lake; the one fish specimen suggests the presence of water nearby, but the lack of amphibian, turtle, and crocodilian remains suggests that the area was more distal to Lake Gosiute than SP46, and that these fish must have lived in streams and ephemeral ponds.

Machaerosaurus torrejonensis, *Saniwa ensidens*, and *Palaeoxantusia* sp. were carnivores that preyed on a wide range of insects. The presence of glyptosaurine lizards suggest the presence of a well developed forest close to the lake with abundant streams. The presence of a species of *Dunnophis*, a boid, an indeterminate snake, and an amphisbaenian suggest a wholly terrestrial environment with well drained soils nearby.

Table 21. Comprehensive faunal list for SP79, 1997 and 1998.

Level	Taxon
Br0	Fish
	Glyptosaurus sylvestris (anguimorph lizard)
	Machaerosaurus torrejonensis (anguimorph lizard)
	Saniwa ensidens (varanid lizard)
	Palaeoxantusia sp. (xantusid lizard)
	amphisbaenid
	Dunnophis sp. (boid snake)
	boid
	snake
	Sciuravus (rodent)
	paramyid (rodent)
	Thisbemys (rodent)
	Microparamys (rodent)
	Hyopsodus (condylarth)
	Antiacodon (palaeodont artiodactyl)
	Hexacodus (artiodactyl)
	Helaletes (tapiroid perrisodactyl)
	Hyrachyus (tapiroid perrisodactyl)
	Palaeosyops (brontotheroid perrisodactyl)
	Orohippus (equid perrisodactyl)
	Hyracotherium (equid perrisodactyl)
	Scenopagus (insectivore)
	Microsyops (pro-primate)

Table 21 (cont'd)

<u>Omomys</u> (primate)

<u>Notharctus</u> (primate)

<u>Smilodectes</u> (primate)

<u>Washakius</u> (primate)

<u>Uintanius</u> (primate)

<u>Trogosus</u> (tillodont)

<u>Peratherium</u> (marsupial)

<u>Peradectes</u> (marsupial)

palaeanodont

Fossils are often found in specific lithologies, most commonly channel deposits and on ancient land surfaces (Behrensmeyer, 1982; Retallack, 1990). In the North Fork of Bear Creek area, to the south, most fossils are found within the green beds, which represent paleosurfaces where bone could accumulate while the paleosols developed. At SP79 fossil remains are found in three layers within the red beds of the paleosol sequence at Con's Hill, the most fossiliferous locality at SP79. The green, uppermost level of the paleosol, bed 3 of the Con's Hill section, is almost entirely unfossiliferous throughout SP79. This suggests that the fossils found did not accumulate on an ancient land surface at SP79.

During the summer of 1998, the locality was divided into named sections of roughly equal area, and a detailed plan map was made (Figure 93). Fossils found previous to this cannot be precisely located within the locality, although most were found at Con's Hill (Childress, pers. com.), and are used only when comparing total numbers of fossils or elements found. Certain areas within SP79 are much more fossiliferous than other, regardless of the horizon sampled (the number of identifiable fossils found are given in parentheses on Figure 93). Con's Hill and Con's Cove have a relatively small combined area, but produced the most fossils (57 identifiable specimens). Gully, Alcove, and North Valley were relatively large areas, with 34, 22, and 33 identifiable fossils respectively. First Hill and Gregg's Hill produced 22 identifiable fossils each. The eastern and western boundaries of SP79 were relatively unfossiliferous, even though all but the Flats consisted of the same beds, and were well exposed. The Flats is a relatively large area and comprises only the upper green bed. Only one fossil was found here, indicating the unfossiliferous nature of this bed.

The numbers of different elements found at SP79 are shown in Table 22. Isolated teeth make up 84% of the identified specimens. The next most common elements are vertebrae, dentaries, maxillae, metacarpals, and astragali.

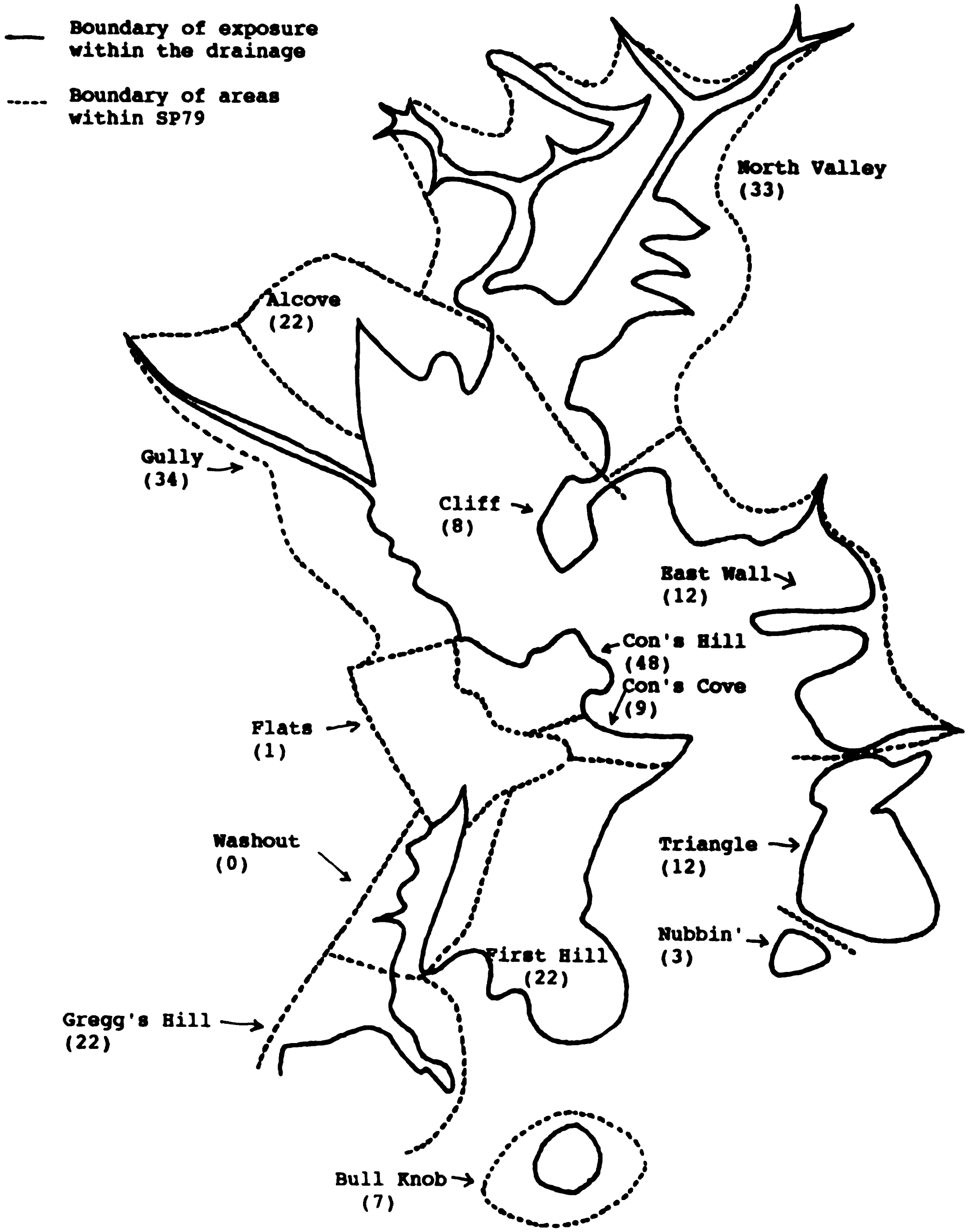

Figure 93. Plan map of SP79, with area names and number of fossils found given in parenthesis.

Table 22. Number and percentages of elements found at SP79, 1997 and 1998.

Element	Number collected	Percentage
Isolated teeth	295	84%
Calcanea	2	0.6%
Astragali	5	1.4%
Radii	2	0.6%
Metacarpals	6	1.7%
Vertebrae	17	4.8%
Unciforms	1	0.3%
Edentulous dentaries	4	1.1%
Dentaries with teeth	7	2%
Edentulous maxillae	7	2%
Maxillae with teeth	1	0.3%
Skull fragments	3	0.9%
Cuboids	1	0.3%
Total	351	100%

Fossil preservation at SP79 is different from that of SP46 where specimens were often found well preserved, in association, and most jaws contained teeth. Most specimens at SP79 are isolated teeth and postcranial elements. Few jaws were found, and no associated bones. The jaws obtained from SP79 generally fall into one of two categories, those that show little sign of weathering, but contain no teeth, and those that are disintigrated and which bear badly damaged teeth. The first group is found near the center of SP79, the second is found close to the western boundary of the locality.

I propose that the majority of the fossils at SP79 belong to animals that died in a variety of habitats near by, and to the north. These bones accumulated on the surface for a period of time sufficient for the bones to disarticulate and for jaws to lose their teeth, but not long enough for disintigration to affect the bone. Disarticulation takes between 13 days and six months, while disintigration of bone takes between one and 15 years depending on size (Behrensmeyer, 1978; Bickart, 1984). Subsequently, during a period of flooding that characterized the alluvial fan surface, the bones were transported south in a shallow, possibly braided, stream through the area now occupied by SP79. Voorhies (1969) classified skeletal elements into two groups, those moved with difficulty by water currents, and those moved relatively easily. Using his element lists only 7% of the specimens obtained at SP79 are easily moveable.

Most of the fossils recovered are of a similar size, and no large bones are found at SP79. This supports deposition by a brief period of increased flow which deposited the majority of the specimens, and washed lighter specimens downstream.

The eastern and western borders of SP78 represent areas not covered with water during the flooding events. The eastern border is relatively unfossiliferous, despite being well exposed. This is also where grain size is largest within SP79 (at Triangle and Bull Knob), whereas in the center of the locality, at Con's Hill, only mudrocks occur. This suggests that the water was moving too quickly to deposit much bone on the eastern bank of the stream.

On the western side of SP79 a large number of fossils are found where the red beds crop out. This is also where the jaws are found that contain teeth but are badly disintigrated. This indicates that the water was moving more slowly here, depositing fossils and finer grained sediment that subsequently covered the bones. Bones from the surface of the alluvial fan became incorporated into the assemblage, as they were also covered by the sediment deposited by the slow moving water.

Few bones show the same preservation state as the highly disintigrated jaws found at Gregg's Hill. Bones on the fan surface may have been washed there by previous floods, or may have belonged to animals that inhabited the fan. Most of these bones would have been destroyed by weathering or scavenging (Voorhies, 1969). During a flood these bones could be incorporated into an assemblage like that at SP79 by being covered with sediment along with the bones being washed in. Their presence on the finer grained western boundary of the locality would correspond to the area of slowest water flow. This would explain the difference in preservation, and the fact that even though the jaws were degraded the teeth and jaws were found in association.

In analyzing a site, one must take into account time averaging of the sediment, which may account for sequentially occurring species appearing in the record contemporaneously (King, 1993; Holz and Barberena, 1994). It is important, therefore, to appreciate, and attempt to quantify, the incompleteness of an assemblage and the degree of reworking. This can be done by taking into consideration the potential for preservation (Voorhies, 1969), and the preservational state of the specimens (Holz and Barberena, 1994), or by studying Recent sediments and their ability to preserve material, and recent bone assemblages (Behrensmeyer, 1978; Behrensmeyer et. al., 1979; Bickart, 1984).

In general, the degree of faunal reworking of an assemblage, or preservation state, can be expressed as a taphonomic grade which reflects the depositional environment, and can be used in reconstructing the depositional history and paleoecology of the strata (Brett and Baird, 1986). The taphonomic grade is based on sedimentologic, paleontologic, and taphonomic data, such as, percentage matrix, size sorting and size grading of the sediment, breakage, articulation, corrasion and orientation of the fossils (Brandt, 1989).

The sedimentology at SP79 suggests a medial area of an alluvial fan where siltstones, and some sandstones were deposited. Flooding is suggested by the poorly sorted nature of the sediment. The specimens found are generally in good condition, exhibiting few abrasions. Transport by water is characterized by abraded and rounded bones, but not by clean breaks which are more likely to be produced by scavenging and trampling (Holz and Barberena, 1994). The specimens at SP79 exhibit little abrasion, and are typically cleanly broken, suggesting that the bones spent a period of time on the surface before being transported by water over a relatively short distance to SP79.

Comparison of all Green River Basin Localities

The distribution of lizard, snake, and amphibian taxa found in the Green River Basin are given in Table 23 and Table 24. Ranges of taxa are given in Table 25, Table 26, and Table 27.

Table 23. Lizard taxa recovered from four areas within the Green River Basin, arranged by biostratigraphic zone. Within the Desertion Point-Little Muddy area, Wa7 is represented by the Little Muddy Fauna, and Br0 is represented by the Desertion Point Fauna of Zonneveld (1994).

	South Pass	Desertion Point-Little Muddy	Big Island	Bridger Basin
Br3				glyptosaurine Xestops vagans Palaeoxantusia fera Palaeoxantusia borealis Tinosaurus stenodon Tinosaurus pristinus Parasauromalus olseni Restes rugosus Saniwa ensidens Machaerosaurus torrejonensis amphisbaenid

Table 23 (cont'd)

	South Pass	Desertion Point-Little Muddy	Big Island	Bridger Basin
Br2		*Glyptosaurus sylvestris* *Saniwa ensidens* *Parasauromalus olseni*		*Glyptosaurus sylvestris* *Paraglyptosaurus hillsi* glyptosaurine "indet A" *Xestops vagans* *Palaeoxantusia fera* *Palaeoxantusia borealis* *Parasauromalus olseni* *Saniwa ensidens* *Tinosaurus stenodon* *Tinosaurus pristinus* *Restes rugosus* *Machaerosaurus torrejonensis* *Apodosauriscus minutus* *Eodiploglossus borealis* amphisbaenid
Br1	*Glyptosaurus* sp. *Xestops vagans* *Saniwa ensidens*	*Glyptosaurus* sp. *Xestops vagans* *Parasauromalus olseni* *Saniwa ensidens* amphisbaenid	*Glyptosaurus sylvestris* *Paraglyptosaurus hillsi* *Xestops vagans* *Parasauromalus olseni* *Saniwa ensidens* *Palaeoxantusia fera* *Tinosaurus stenodon* amphisbaenid	

Table 23 (cont'd)

	South Pass	Desertion Point-Little Muddy	Big Island	Bridger Basin
Br0	*Glyptosaurus sylvestris* *Machaerosaurus torrejonensis* *Saniwa ensidens* *Palaeoxantusia* sp. *Xestops vagans* *Parasauromalus olseni* *Restes rugosus* glyptosaurine "indet A" amphisbaenid	*Glyptosaurus sylvestris* glyptosaurine "indet A" *Xestops vagans* *Parasauromalus olseni*		
Wa7	*Gltptosaurus* sp. glyptosaurine "indet A" *Xestops vagans* *Restes rugosus*			
	South Pass	Desertion Point-Little Muddy	Big Island	Bridger Basin

Table 24. Amphibian and snake taxa recovered from four areas within the Green River Basin, arranged by biostratigraphic zone.

	South Pass	Desertion Point-Little Muddy	Big Island	Bridger Basin
Br3				rhinophrynid *Ogmophis* sp. *Dunnophis microechinis* *Boavus occidentalis* *Calamagras primus* *Cryptobranchus saskatchewanensis* *Necturus krausei* *Scapherpeton tectum* *Piceoerpeton willwoodense*
Br2				*Dunnophis microechinis* *Ogmophis* sp. *Boavus occidentalis* *Calamagras primus* *Piceoerpeton willwoodense* *Cryptobranchus saskatchewanensis* *Necturus krausei* *Scapherpeton tectum*
Br1	*Boavus occidentalis*	*Boavus occidentalis*	*Boavus occidentalis* *Coniophis* sp.	
Br0	*Dunnophis microechinis* *Boavus occidentalis* *Calamagras primus* *Coniophis* sp. rhinophrynid salamander	*Calamagras primus*		
Wa7				

Table 25. Ranges of lizard taxa from the Green River Basin.

	Wa7	Br0	Br1	Br2	Br3
P. olseni		<----	-----	-----	---->
T. stenodon			<----	-----	---->
T. pristinus				<----	---->
R. rugosus	<----	-----	-----	-----	---->
M. torrejonensis		<----	-----	-----	---->
A. minutus				<--->	
X. vagans	<----	-----	-----	-----	---->
G. sylvestris		<----	-----	---->	
P. hillsi			<----	---->	
glyptosaurine "indet A"	<----	-----	-----	---->	
E. borealis				<--->	
S. ensidens		<----	-----	-----	---->
P. fera			<----	-----	---->
P. borealis				<----	---->
amphisbaenid	<----	-----	-----	-----	---->

Table 26. Ranges of snake taxa from the Green River Basin.

```
                                  Wa7   Br0   Br1   Br2   Br3
Coniophis indet                         <------->
B. occidentalis                         <------------------->
C. primus                               <------------------->
Ogmophis indet                                      <--------->
D. microechinis                         <------------------->
```

Table 27. Ranges of amphibian taxa from the Green River Basin.

```
                                  Wa7   Br0   Br1   Br2   Br3

C. saskatchewanensis                                <-------->
N. krausei                                          <-------->
S. tectum                                           <-------->
P. willwoodense                                     <-------->

rhinophyrnid                      <------------------------->
```

From Wa7 sediments the only lizards recovered are Parasauromalus olseni, Restes rugosus, Xestops vagans, glyptosaurine "indet A", and an amphisbaenid. This is, in part, because Wa7 sediments of South Pass and Desertion Point-Little Muddy area are less well exposed, however extensive screening carried out limits collector bias. At South Pass, the fossils occur in a single channel lag sandstone layer, and are therefore hydraulically sorted and probably represent a variety of habitats.

This time is characterized by the limited extent of Lake Gosiute and the presence of mature paleosols, which both indicate favorable environments for lizards. It cannot be determined if the absence of species found higher in the section is due to the fact that these species did not exist at this time, or that they have yet to be collected. No snakes or amphibians have been recovered from Wa7 at South Pass which suggests that further collection is necessary since the environment should have been favorable for these taxa.

Br0 at South Pass exhibits a large increase in the numbers of lizard species found with respect to the Wa7, and with respect to the basin center Desertion Point-Little Muddy area assemblage. Machaerosaurus torrejonensis, Saniwa ensidens, Palaeoxantusia sp., Restes rugosus, and an amphisbaenid are found only in the basin margin localities of South Pass. Both South Pass and the Desertion Point-Little Muddy areas contain specimens of Glyptosaurus sylvestris, glyptosaurine "indet A", Xestops vagans, and Parasauromalus olseni. Dunnophis microechinis, Boavus occidentalis, Calamagras primus, Coniophis sp., a rhinophrynid, and a salamander have been recovered from the Br0 at South Pass. The large number of amphibians and squamates collected at South Pass corresponds with the presence of a variety of suitable habitats at the basin margin, and the extensive collection in the area.

Br1 at South Pass has markedly fewer lizard species (Glyptosaurus sylvestris, Xestops vagans, and Saniwa ensidens) than Br0, although this is probably due to lack of exposure and insufficient collecting. Basin center localities at the Desertion Point-Little Muddy and Big Island areas contain Parasauromalus olseni, Paraglyptosaurus hillsi, Palaeoxantusia fera, Tinosaurus stenodon, and an amphisbaenid, in addition to the species from South Pass. Since these areas are closer to the lake, and should have been less favorable environments for lizards, the appearance of more lizards is probably due to increased collection. With more collecting, these species may be recovered from South Pass in time. Amphisbaenids are not common due to the proximity of Lake Gosiute and associated waterlogged soils. The first occurrences of P. hillsi and T. stenodon are probably an accurate representation of the species' first appearance since one would expect them to have been collected from the the fossiliferous localities of the Br0 at South Pass had they lived at that time. The first appearance of a definitive specimem of Palaeoxantusia fera suggests that the indeterminate palaeoxantusid found in the Br0 at South Pass was also P. fera. Boavus occidentalis and Coniophis sp. are the only snake species found, and there are no amphibians from the Br1. B. occidentalis occurs in all levels at both the basin center and margin, and must be a highly adaptable species.

In general, lizard species are at their maximum number during the Br2, a period of decreased precipitation and minimum extent of Lake Gosiute. The increased terrestrial conditions would have created favorable environments for a variety of lizards from different habitats and with different diets. In the southern basin center localities the first appearances of Palaeoxantusia borealis, Tinosaurus pristinus, Apodosauriscus minutus, and Eodiploglossus borealis indicate more terrestrial conditions. All snake species known from the Wa7 of South Pass are found in the Br2 of the Bridger Basin collection except Coniophis sp. which is extremely rare even at South Pass. There is also an increase in amphibian species. The same number are found in the Br2 as the Br3 which may reflect the proximity of Lake Gosiute or the presence of small ponds nearer the basin margin.

The relatively small lizard assemblage found in the Br3 at the Bridger Basin localities is probably due to the proximity of Lake Gosiute, which would have limited the numbers of habitats available, and driven some species from the area, or to extinction. No new lizard species are seen in the Br3.

Gunnell and Bartels (1998, and in prep) stated that assemblages from basin margins differ in content and composition from time equivalent basin center assemblages. Due to greater relief, habitats are compressed vertically and horizontally. Their work was based mainly on mammalian, turtle and crocodylian species. They found four distinctive characteristics in basin margin assemblages. The first is distinctive taxa, which are those species that are uncommon in the basin center, but common at the margins. In general basin center assemblages are dominated by anguids and iguanids, whereas basin margin assemblages comprise mainly of anguids, varanids, snakes and amphisbaenids. The second characteristic is unique taxa found only in basin margin assemblages. In this study *Machaerosaurus torrejonensis* and *Restes rugosus* are unique to South Pass during the Br0. Among snake and amphibian taxa only *Boavus occidentalis*, *Coniophis* sp., and *Calamagras primus* are found in the basin center before Br2. The absence of amphibians in the basin center until Br2 may be a result of a bias due to limited collection by workers familiar with amphibian remains, however the relatively few snakes in the basin center is to be expected due to their terrestrial nature. The third assemblage characteristic is unique morphological forms, where the same taxa exhibits unusual morphologies. In the South Pass region, anguid lizards are generally much larger than those found in the basin center deposits, with some being twice as large. The fourth characteristic is anachronistic taxa, that is, species that co-occur in basin margin sediments, but occur sequentially at the basin center. Calamagras primus and Boavus occidentalis belong to this category. In the Desertion Point-Little Muddy area C. primus occurs in Br0 sediments while B. occidentalis occurs in Br1, but both taxa occur together at South Pass. Anachronistic lizard taxa are not seen in a strict sense, however several taxa appear for the first time, and all of these appear in basin margin sediments at South Pass. These include Palaeoxantusia fera, P. borealis, and Machaerosaurus torrejonensis. An indeterminate species of Palaeoxantusia appears first in the Br0 at South Pass, and P. fera subsequently appears in the basin center, in Br1 at Big Island, and both P. fera and P. borealis occur in the Br2 and Br3 at the Bridger Basin localities. M. torrejonensis first appears in the Br0 at South Pass, but does not appear in the basin center until the Br2.

To account for the differences seen in basin margin assemblages Gunnell and Bartels (in prep) propose five explanations. Firstly, sampling bias, however this should be biased against basin margin assemblages, and one would therefore expect to see fewer species from these localities. Secondly, time averaging, however other basins show the same characteristics which would be unlikely if time averaging was the only factor. The third is immigration, but these species are not found in adjacent basins just prior to their appearance in the Green River Basin. The fourth is due to the vertical compression of habitat zones. This is poorly understood at present, and may be a factor. The fifth explanation is cladogenesis.

Gunnell and Bartels (in prep) propose that the increased variability within populations, the increased diversity, different community structure, and unique taxa reflect differing habitat utilization, preferences, and actual vertebrate diversity. They propose that marginal areas acted as "species pumps" in that they provided new species and increased genetic variability in the diverse habitats that occur at the basin margin. Increased stresses due to the proximity of different habitats, and their small size would have been favorable for cladogenesis. Greater diversity is seen in the Bridger Basin collection than at any other locality. This is more likely due to a generally improving climate that could support a greater diversity of amphibian, lizard, and snake species, than to the "species pump" idea. However, individual cases such as <u>Palaeoxantusia</u> and <u>Machaerosaurus</u> may fit the pattern exhibited by the mammalian fauna.

CONCLUSION

General Characteristics of the Green River Basin

The Green River Basin is a major detrital basin which developed between the Uinta mountains to the south, the Wind River and Granite Mountains to the north and east, the Sierra Madres to the southeast and the Wyoming Overthrust Belt to the west. The basin was divided in the middle to late Eocene by the anticlinal Rock Springs Uplift, into the Washakie and Great Divide basins to the east, and the Green River Basin to the west. Downwarping in these basins began in the early Tertiary and continued intermittently throughout the Eocene. The Green River Basin has a general north-south synclinal form parallel in strike to the folded pre-Tertiary rocks of the Overthrust Belt, but changes to a northwest-southeast trend in the north, along the Wind River Mountains.

The Eocene sedimentary rocks of the Green River Basin consist of the fluvial Wasatch and Bridger formations (57.5-48 Ma) interdigitating with the lacustrine Green River Formation. The Wasatch and Bridger formations are derived from the mountainous source areas bounding the basin which vary in lithic composition. To the west, the Overthrust Belt is comprised of Paleozoic and Mesozoic marine sedimentary rocks. To the north, the Wind River Mountains are comprised of Precambrian igneous and metamorphic rocks (West 1969). The

Wind River thrust fault and Continental normal fault formed downdropped graben blocks, local folding, and a thick alluvial fan sequence. To the south, a thick sequence of alluvial fan deposits formed in response to uplift of the adjacent Uinta Mountains which consist primarily of Mississippian limestones, sandstones, and metaquartzites. The Green River Formation comprises a huge lens of fine-grained, generally calcareous sedimentary rock of lacustrine origin, representing the continual change in areal extent of Lake Gosiute throughout the late early and early middle Eocene.

According to floral data, during the middle Eocene the continental interior had a warm temperate to subtropical environment, with a mean annual temperature of 18°C, 60-85 cm annual precipitation, and high equability, supporting a savanna-like/woodland vegetation. Climatic variables based on turtle, lizard, and mammal data consistently support higher temperatures and precipitation than those based on the flora.

General characteristics of the amphibian and squamate fauna

Throughout early and middle Bridgerian time an abundant lizard fauna existed in the Green River Basin. Fossil assemblages from South Pass, the Desertion Point-Little Muddy area, Big Island, and the Bridger Basin have included a large number of reptile specimens. Lizards are represented by insect eating and plant eating iguanids, insect eating xantusids, and a large number of insect eating anguids. The lizards ranged in size from species the size as modern day anoles, to large varanids. Snake species are all boids except for Coniophis. Dunnophis, Coniophis, Calamagras, and Ogmophis were all in part fossorial, while Boavus was adapted to a variety of subaerial terrestrial habitats. Amphibians are represented by a rhinophrynid and several salamander species, and the amphisbaenians are represented by one indeterminate species.

Faunal assemblages

This fauna diversified through time from 10 taxa in Wa7 to a maximum of 23 taxa in Br2, a period characterized by better drained substrates and the minimum extent of Lake Gosiute which was due to the interplay of decreasing basin subsidence and decreasing precipitation. The Br1 of Big Island marks the first appearance of Paraglyptosaurus hillsi, Palaeoxantusia fera, and Tinosaurus stenodon. The Br2 of the Bridger Basin marks the first appearance of Palaeoxantusia borealis, Tinosaurus pristinus, Apodosauriscus minutus, and Eodiploglossus borealis, and an increase in the number of amphibian species. The presence of Machaerosaurus torrejonensis in the middle Eocene has not been previously reported, although it occurs in the Paleocene and upper Eocene. This study extends the range of Palaeoxantusia borealis down to the middle Eocene.

Lostcabinian (Wa7) assemblages at South Pass are represented by SP74 and SP75 where the fossil assemblage includes Glyptosaurus sp., Xestops vagans, and Restes rugosus. Lostcabinian assemblages at Desertion Point-Little Muddy area include an indeterminate glyptosaurine, glyptosaurine "indet A", Xestops vagans, and Restes rugosus.

Gardnerbuttean (Br0) assemblages at South Pass include Glyptosaurus sylvestris, Machaerosaurus torrejonesis, Saniwa ensidens, Palaeoxantusia sp., Xestops vagans, Parasauromalus olseni, Restes rugosus, glyptosaurine "indet A", an amphisbaenid, Dunnophis microechinis, Boavus occidentalis, Calamagras primus, Coniophis sp., a rhinophrynid, and an indeterminate salamander. The assemblages from the Desertion Point-Little Muddy area include G. sylvestris, glyptosaurine "indet A", X. vagans, P. olseni, and C. primus.

Bridgerian A (Br1) assemblages from South Pass include Glyptosaurus sp., Xestops vagans, Saniwa ensidens, and Boavus occidentalis. The assemblages from the Desertion Point-Little Muddy area include Glyptosaurus sp., X. vagans, Parasauromalus olseni, S. ensidens, an amphisbaenid, and B. occidentalis. Assemblages from Big Island include Glyptosaurus sylvestris, Paraglyptosaurus hillsi, X. vagans, P. olseni, S. ensidens, Palaeoxantusia fera, Tinosaurus stenodon, an amphisbaenid, Coniophis sp., and B. occidentalis.

Assemblages from the Bridgerian B (Br2) from Desertion Point-Little Muddy area include Glyptosaurus sylvestris, Saniwa ensidens, and Parasauromalus olseni. Assemblages from the Bridger Basin include G. sylvestris, Paraglyptosaurus hillsi, glyptosaurine "indet A", Xestops vagans, Palaeoxantusia fera, Palaeoxantusia borealis, P. olseni, S. ensidens, Tinosaurus stenodon, Tinosaurus pristinus, Restes rugosus, Machaerosaurus torrejonensis, Apodosauriscus minutus, Eodiploglossus borealis, an amphisbaenid, Dunnophis microechinis, Ogmophis sp., Boavus occidentalis, Calamagras primus, Piceoerpeton willwoodense, Cryptobranchus saskatchewanensis, Necturus krausei, and Scapherpeton tectum.

The assemblages from the Bridgerian C (Br3) from the Bridger Basin include a glyptosaurine, Xestops vagans, Palaeoxantusia fera, Palaeoxantusia borealis, Tinosaurus stenodon, Tinosaurus pristinus, Parasauromalus olseni, Restes rugosus, Saniwa ensidens, Machaerosaurus torrejonensis, an amphisbaenid, a rhinophrynid, Ogmophis sp., Dunnophis microechinis, Boavus occidentalis, Calamagras primus, Cryptobranchus saskatchewanensis, Necturus krausei, Scapherpeton tectum, and Piceoerpeton willwoodense.

The Basin Margin at South Pass

Depositional Characteristics

South Pass represents a basin margin environment where a fault controlled alluvial fan deposited conglomerates, channel and sheet sandstones, and fine grained alluvial fan sediments. A large number of habitats were present in the area due to the variation in elevation, proximity of the Wind River Range, and Lake Gosiute. The two localities within the Wa7 contain a fossiliferous channel lag sandstone which represents a channel on the surface of an alluvial fan. This area would have been subject to flooding but was essentially dry. Localities such as SP79, which represents an ephemeral channel in the medial-fan area, were relatively dry, and supported abundant terrestrial taxa. Localities such as the lower beds of the North Fork of Bear Creek section and SP46, which represents the distal end of the fan at the edge of Lake Gosiute, would have had saturated soils and permanent streams. Taxa such as amphibians, turtles, crocodiles would have lived in these areas

Faunal Composition Compared To The Basin Center

Basin margin areas are represented by localities at South Pass (Wa7, Br0, and Br1) and Desertion Point-Little Muddy (Wa7 and Br0). Basin center areas are represented by Desertion Point-Little Muddy (Br1 and Br2), Big Island (Br1), and the Bridger Basin (Br2 and Br3). Complete lizard, amphisbaenid, snake, and amphibian taxa lists are given in Table 23 and Table 24 (page 461 and page 464).

In general, basin center assemblages are dominated by anguids and iguanids, whereas basin margin assemblages comprise mainly of anguids, varanids, snakes and amphisbaenids. Machaerosaurus torrejonensis and Restes rugosus occur at South Pass during the Br0, are absent in the Br1, and present in the Br2 and Br3 of the Bridger Basin. Only Boavus occidentalis, Coniophis sp., and Calamagras primus are found in the basin center before Br2. All other snakes, and all amphibians are found only at the basin margins until the Br2. In the South Pass region, anguid lizards are generally much larger than those found in the basin center deposits, with some being twice as large. Calamagras primus and Boavus occidentalis occur together at South Pass and in the Bridger Basin, but only B. occidentalis is present in the basin center before the Br2. The first appearance of an indeterminate species of Palaeoxantusia is in the Br0 at South Pass. P. fera subsequently appears in the basin center, in Br1 at Big Island, and both P. fera and P. borealis occur in the Br2 and Br3 at the Bridger Basin localities. M. torrejonensis first appears in the Br0 at South Pass, but does not appear in the basin center until the Br2.

Environmental Interpretation

There are five main factors to be considered when studying the assemblages from South Pass, Desertion Point-Little Muddy, Big Island, and the Bridger Basin. Firstly, faunal variation through time, from the Wa7 through Br3. Secondly, climatic variation of the continental interior during the middle Eocene. Thirdly, the difference between basin margin and basin center environments. Fourthly, the consideration of all the animal and plant taxa in the area and how they relate to one another, their habitat, and climate. Fifthly, the taphonomic and sedimentary processes operating on the specimens and local habitat.

Time

The Wa7, Br0, Br1, Br2, are characterized by distinctive faunal assemblages given in Table 28. The mammals are well constrained, and are in bold. The amphibian, lizard, amphisbaenid, and snake taxa given here are based solely on my data. Br3 is defined by the absence of several taxa, which are listed below.

Table 28. Defining taxa of the time zones of the Wasatchian and Bridgerian.

Time Zone	Defining Taxa
Br3	**Uintatherium** (interval-zone)
Br2	**Microsyops elegans** (assemblage-zone) Apodosauriscus minutus, Eodiploglossus borealis (interval zone)
Br1	**Palaeosyops borealis/fontinalis** (lineage-zone) Tinosaurus stenodon, Paraglyptosaurus hillsi Palaeoxantusia fera Coniophis indet (concurrent range zone)
Br0	**Palaeosyops borealis/fontinalis** (lineage-zone) Parasauromalus olseni, Paraglyptosaurus hillsi Palaeoxantusia fera, Coniophis indet Boavus occidentalis Calamagras primus, Dunnophis microechinis (consecutive range zone)
Wa7	**Lambdotherium** (range-zone) Parasauromalus olseni Saniwa ensidens Machaerosaurus torrejonensis, Xestops vagans Restes rugosus, Glyptosaurus sylvestris glyptosaurine "indet A" amphisbaenid rhinophrynid (consecutive range zone)

Br3 is characterized by the absence of Apodosauriscus minutus, Glyptosaurus sylvestris, Paraglyptosaurus hillsi, glyptosaurine "indet A", Eodiploglossus borealis, and Coniophis. Br2 is an interval zone containing the only records of Apodosauriscus minutus and Eodiploglossus borealis. Br1 is a concurrent range zone marking the last appearance of Coniophis and the first appearances of Tinosaurus stenodon, Paraglyptosaurus hillsi, and Palaeoxantusia fera. Br0 is a consecutive range zone characterized by the first appearances of Parasauromalus olseni, Machaerosaurus torrejonensis, Glyptosaurus sylvestris, Saniwa ensidens, Coniophis, Boavus occidentalis, Calamagras primus, and Dunnophis microechinis, while the next zone marks the first appearances of Tinosaurus stenodon, Paraglyptosaurus hillsi, and Palaeoxantusia fera. Wa7 is a consecutive range zone marking the first appearance of Restes rugosus, Xestops vagans, glyptosaurine "indet A", an amphisbaenid and a rhinophrynid. However, since the time zone below is not available it is better to characterize the zone by the absence of Parasauromalus olseni, Machaerosaurus torrejonensis, Glyptosaurus sylvestris, Saniwa ensidens, Coniophis, Boavus occidentalis, Calamagras primus, and Dunnophis microechinis, which all have their first appearances in the Br0.

Climate

Williams and Bartels (1997) proposed paleoclimatic estimates derived from a GIS based analysis of reptile diversity with respect to climate in present day North America. They used the number of reptile and mammal species in an area, and not the particular species found, to plot regressions against a variety of climatic variables. The number of lizard species was found to be highly dependant on all variables based on temperature, but largely independent of precipitation and relative humidity. Turtles are highly sensitive to variables related to precipitation, but less so to temperature. Although only two taxa of crocodiles were available for study, present-day species live in areas with a mean annual temperature in excess of 20°C, and a mean cold month temperature above 10°C. Since crocodiles often live in major rivers in arid regions the number of species found is not useful in estimating precipitation.

A best-fit line was produced for each graph indicating the most probably estimate however, minimum values are used as they are better constrained, and relate to conditions in present-day localities. Williams and Bartels (1997) also compared their data from the Wa1, Wa3, Wa6 and Br1 to see changes through time. These data are reproduced for lizards, turtles, and mammals in Table 29.

Table 29. Climatic variable estimates from turtle, lizard, and mammal species numbers for the Wa1, Wa3, Wa6, and Br1, from Williams and Bartels (1997).

		Wa1	Wa3	Wa6	Br1
Mean Annual Temperature (MAT) (°C)	turtles	11	11	11	17.5
	lizards	11.5	14	14.5	13
	mammals	4	no data	11.5	21
Mean Cold Month Temperature (MCMT) (°C)	turtles	-5	-5	-3	38
	lizards	-7	-1	-1	-5
	mammals	-20	no data	-4	16.5
Mean Annual Range of Temperature (MART) (°C)	turtles	7.5	7.5	7.5	13
	lizards	8	12.5	13	9
	mammals	17.5	no data	17.5	9
Mean Annual Precipitation (MAP) (mm)	turtles	736	736	867	1224
	lizards	432	330	330	406
	mammals	1296	no data	1372	1372

Table 29 shows that figures derived from the different groups vary markedly. For the lizards of the Br1 Williams and Bartels (1997) estimated a mean annual temperature (MAT) of at least 13°C, a mean cold month temperature (MCMT) of at least -5°C, a mean annual range of temperature (MART) of at least 10°C, and a mean annual precipitation (MAP) of 406-1524 mm. Using mammals they estimated a mean annual temperature of at least 21°C, a mean cold month temperature of at least 16.5°C, a mean annual range of temperature of at least 10°C, and a mean annual precipitation of 1372-1524 mm. Using turtles they estimated a mean annual temperature of at least 17.5°C, a mean cold month temperature of at least 9.5°C, a mean annual range of temperature of at least 13°C, and a mean annual precipitation of 1244-1524 mm (Bartels pers. com.).

Generally, lizards indicate cooler temperatures than turtles or mammals, however, since these are minimum temperatures the figures are not in disagreement. Turtles are the most reliable indicators in wet environments where they are abundant, since the majority of the area is wet, and any drier areas are not representative of the overall environment. Where turtles are found, in rocks indicating a wet environment, it can be assumed that the area was often flooded and unsuitable for lizards and mammals. Where xeric conditions predominate, lizards are a more reliable indicator whereas turtles are generally found in small numbers and presumably lived in restricted areas that did not necessarily reflect the overall climate.

For example, at South Pass locality SP79 represents a medial-fan environment that was generally dry, but flooded occasionally. Turtle and crocodile remains are not found here, amphibians are rare, and lizards, snakes, and mammals predominate. At SP46, where the distal end of the fan entered Lake Gosiute, turtle and crocodile specimens are abundant. These taxa presumably lived near and in the lake, while the terrestrial taxa found would have been transported by streams to be deposited in the area. Therefore, at South Pass the overall climate is best represented by the lizard and mammal record, since the majority of the area was an upland environment. In contrast, the Bridger Basin and Big Island localities produce abundant turtles, and their position in the center of the basin suggests an overall wet environment. For these localities turtle data should be used.

In general, however, all estimates based on animal taxa give warmer temperatures than those based on plants. It is difficult to determine which method is more accurate as all species requirements have changed, modern analogues are rare, and species interactions may have changed. However, what is indicated is a general warming trend from the Wa7 through Br3, with the related increase in numbers of turtles, crocodiles, amphibians, and squamates.

Basin margin versus basin center

When comparing different areas and times within the Green River Basin, it is important to take their geographical position into account. Basin margin and basin center environments will contain markedly different habitats due to the differences in factors such as elevation, relief, and soil saturation. Basin margin faunas at South Pass exhibit four characteristics; distinctive taxa, unique taxa, unique morphological forms, and anachronistic taxa.

In general basin center assemblages were dominated by anguids and iguanids, whereas basin margin assemblages comprised mainly of anguids, varanids, snakes and amphisbaenids. In this study *Machaerosaurus torrejonensis* and *Restes rugosus* were unique to South Pass during the Br0. Among snake and amphibian taxa only *Boavus occidentalis*, *Coniophis* sp., and *Calamagras primus* were present in the basin center before Br2. At South Pass many groups, such as the anguid lizards, were generally much larger than those found in the basin center deposits, with some being twice as large. In the basin center localities at Desertion Point-Little Muddy area *C. primus* occurs in Br0 sediments while *B. occidentalis* occurs in Br1, but both taxa occur together at South Pass. *Palaeoxantusia fera*, *P. borealis*, and *Machaerosaurus torrejonensis* appear for the first time in basin margin localities.

Associated Environments

When studying the paleoenvironment of an area, all groups must be taken into account, as they all interact with one another. Lizard species contain herbivorous groups, feeding on a variety of vegetation, omnivores, and carnivores feeding on insects and other lizards. Snake species, and amphisbaenids would have eaten small lizards and mammals. Amphibians would have fed on insects and other invertebrates. Mammals would have preyed on many different groups as well as eating the local plants.

Plant specimens have not been recovered from South Pass, but other collections from Wyoming have been studied. The Wind River Basin flora is Lostcabinian in age and contains a large-leaved mesic flora suggesting a warm temperate environment. The Kisinger Lake flora is basal middle Eocene, and contains many mesic forms also found in the Utah and Colorado floras. However, it contains abundant large-leaved plants and would have been adapted to a humid subtropical environment with abundant precipitation. The Boysen flora of the middle Eocene occurs near Shoshoni, Wyoming, north of South Pass, and represents a swamp environment. The Little Mountain flora in Wyoming from the Wilkins Peak Member contains many plants found in the Utah/Colorado area, and has a similar small leaf type with heavy textures (MacGinitie, 1969).

Localites at South Pass from the Wa7 contain a variety of fauna which together provide a more detailed picture of the paleoenvironment than when taking only one group into account. Hyopsodus suggests a dry forest or savanna-like environment, while the perissodactyl Hyracotherium indicates a swampy woodland proximal to Lake Gosiute. Primates suggest a forested environment, the fossorial epoicothere suggests a well drained environment. The presence of Glyptosaurus sp., Xestops vagans, and Restes rugosus suggests abundant insect life supported by the forested habitat. From this one can predict that the area supported an open forest on well-drained substrate near Lake Gosiute.

Abundant amphibian, turtle, and crocodile remains have been recovered from SP46. An amphisbaenid, an epoicothere, an unidentified palaeanodont, and abundant primates, rodents, and insectivores suggest a wholly terrestrial environment proximal to SP46, with well drained soils. The perissodactyl Hyracotherium is adapted to swampy woodland near a lake or pond. Xestops vagans, the glyptosaurine, Palaeoxantusia sp., and Parasauromalus olseni are lizards with diets varying from herbo-omnivorous to carnivorous suggesting a large range of prey and habitat that supported the prey. These species as well as Calamagras and many of the mammals found, are highly terrestrial. This locality represents a lake shore at the distal end of an alluvial fan, with a poorly drained substrate and abundant streams.

No amphibian, turtle, or crocodilian remains, few squamates, six species of primate, and a very large number of rodent remains have been recovered from SP79. The terrestrial taxa are varied and suggest a large number of habitats and the lack of amphibian, turtle, and crocodilian remains suggests that the area was more distal to Lake Gosiute than SP46, and that fish lived in streams and ephemeral ponds. The fauna suggests a wholly terrestrial environment with well drained soils nearby.

Taking all three areas into account, South Pass was a basin margin environment where a series of alluvial fans existed at the edge of Lake Gosiute. Most environments supported a variety of species, with localities close to the lake exhibiting a higher percentage of amphibious taxa. Terrestrial taxa dominated in areas farther from the lake.

Taphonomy and sedimentary processes

When estimating climate from faunal assemblages the completeness of the assemblage must be estimated. Figure 94 shows the number of amphibian and squamate specimens collected from the four areas used in this study in each time zone. In addition to the numbers of specimens found, it is important to take into consideration the preservation of the specimens, as an indication of distance of transport, length of time on the surface, and hydraulic conditions operating in the area. One must also take into account the depositional

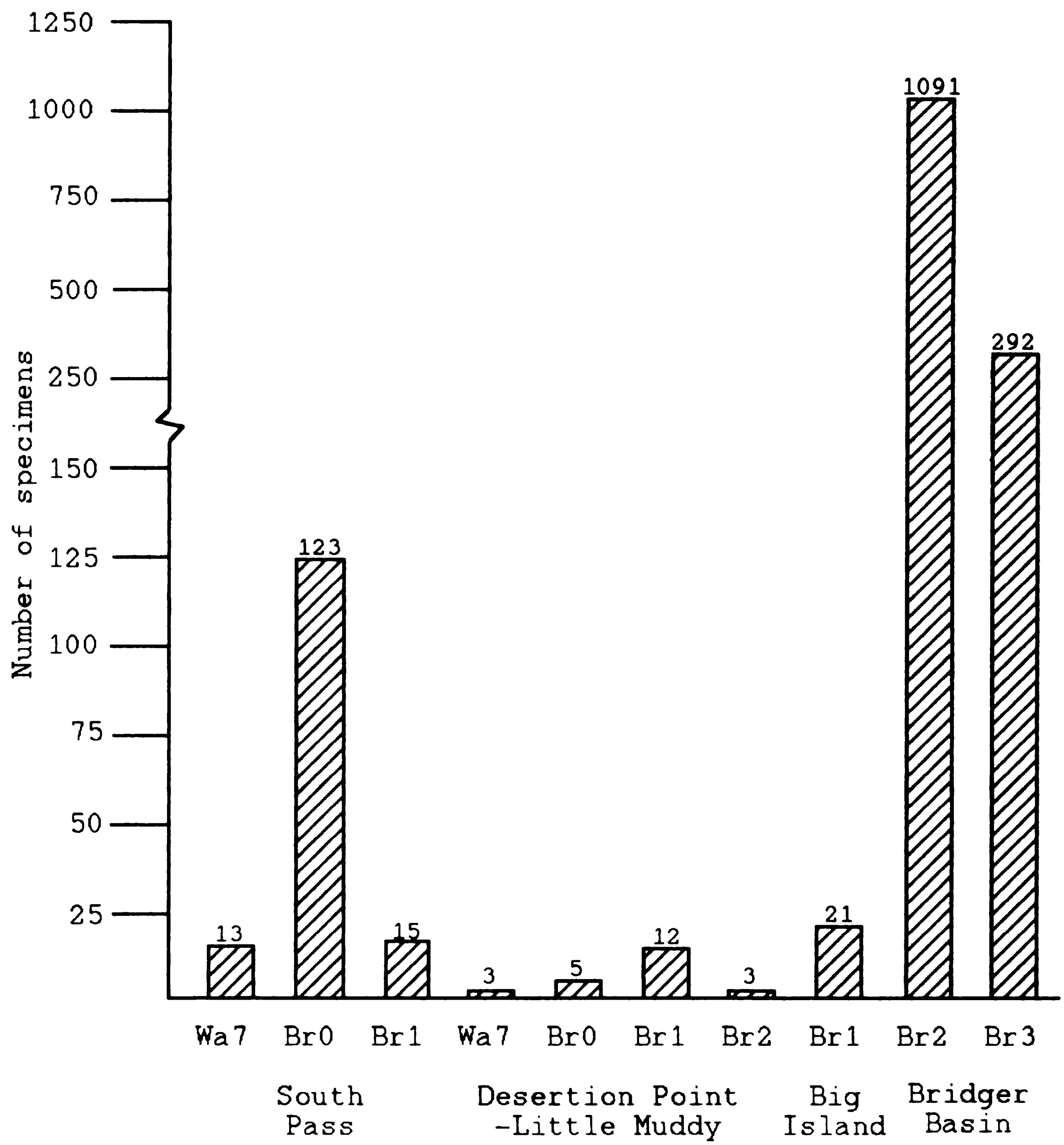

Figure 94. The number of squamate and amphibian specimens recovered from the four study areas, for each time zone, numbers shown above each column.

setting with respects to preferential sorting of certain elements or species. The fossiliferous layer at SP74 and SP75 is a channel lag sandstone, indicating that the assemblage has been hydraulically sorted and represents a variety of proximal and distal habitats. The small sample size, restriction of fossils to one level, and dissarticulated state of the specimens indicate that the Wa7 at South Pass cannot be used in climate estimates with much confidence. However, Br0 localities at South Pass have been extensively collected by surface collection, dry screening, wet screening, and quarrying. The predominantly upland environments of the area would have supported abundant terrestrial groups, and the well drained soils would have been suitable for burrowing species. SP79 represents an ephemeral channel in a mid-fan area of an alluvial fan where siltstones, and some sandstones were deposited. Flooding is suggested by the poorly sorted nature of the sediment. The taphonomic grade of the specimens found suggest deposition by a brief period of increased flow which deposited the majority of the specimens, and washed lighter specimens downstream. These localities give a good approximation of the living assemblage.

Br1 localities at South Pass are rare, and have not been extensively sampled. The sediments represent less well drained substrate, much closer to Lake Gosiute. The fossil assemblage recovered is much smaller than that living during the Eocene.

All the Desertion Point-Little Muddy localities have few fossils. The sample size is small, therefore only surface collection was utilized, and the higher beds represent poorly drained soils close to the lake that would have been unsuitable for terrestrial species. All these localities are of very limited use when making climate estimates.

The Br1 at Big Island has been extensively collected, but its location in the basin center, and poorly drained substrate make this area unsuitable for most of the species in this study except the amphibians. The large number of of specimens of turtles and crocodiles can be used in climatic estimation.

The Bridger Basin has been extensively collected by a variety of collection techniques. Some localities, for example 1129 at Sage Creek, have produced hundreds of specimens of a large number of species. The area is large, thus providing a wide variety of habitats, many very suitable for terrestrial animals. Vertebrate preservation, especially at the very productive sites, is very good. Turtles and crocodiles occur in great abundance, so climatic estimates should use these groups. Table 30 is a summary of each area and time with comments on their completeness.

Table 30. Estimates and comments on completeness of the assemblages used in this study. The main focus being on amphibian, lizard, amphisbaenian, and snake components.

Area	Time zone	Comments	Completeness
Bridger Basin	Br3	large sample size, good preservation, collected by a variety of methods, good habitat for a variety of taxa	Very good
	Br2		Very good
Big Island	Br1	small sample size, unsuitable habitats for terrestrial species, extensive collection	Adequate
Desertion Point-Little Muddy	Br2	small sample size, only surface collection utilized generally unsuitable habitats for terrestrial species	Poor
	Br1		Poor
	Br0		Poor
	Wa7		Poor
South Pass	Br1	small sample size, very little collection	Poor
	Br0	large sample size, multiple collection techniques, suitable habitats for terrestrial species	Good
	Wa7	small sample size, hydraulically sorted	Poor

Synthesis

Fossil assemblages from South Pass, Desertion Point-Little Muddy, Big Island and the Bridger Basin represent basin margin and basin center environments from the Wa7 through the Br3, that have produced a variety of herpetological faunas. These were used to estimate the climates and habitats present during the middle Eocene in the Green River Basin.

During the Wa7, deposition in the basin was largely fluvial, with ephemeral streams and small lakes present near the center, and alluvial fans depositing thick clastic wedges of sediment near the basin margins. South Pass and Desertion Point-Little Muddy represent such alluvial fans at the basin margins, which provided a rich variety of habitats for a highly varied fauna. The assemblages recovered allow only a minimum estimate of climate from lizard species, however, the habitats may be inferred from the species present. A dry forest or savanna-like environment existed on the fan surface, with swampy woodland nearer the lake. Soils were generally well drained, and insects proliferated in the highly vegetated environment. Desertion Point-Little Muddy had a similar environment, though may have been less well drained.

During the Br0 Lake Gosiute filled the Green River Basin. Proximal to the lake turtles and crocodiles would have been abundant, while near the basin margins more terrestrial taxa were dominant. All Br0 localities in this study are from the basin margin. Here, the lizard, turtle, and crocodile species may be used to estimate climate at South Pass, where collections are assumed to be close to the living assemblage. Climatic estimates are; mean annual temperature, 20°C; mean cold month temperature, 10°C; mean warm month temperature, 23.5°C; mean annual range of temperature, 11°C; number of days of 30°C or above, 50; solar radiation, 386 gcal/cm^2; and cloud cover, 40%. Habitats at South Pass during the Br0 were varied, due to their proximity to the Wind River Range. At the margin, alluvial fans and upland areas provided a variety of terrestrial environments. Here arboreal, semi-arboreal, ground dwelling, and fossorial animals proliferated. Closer to the lake, soils were poorly drained, and swampy woodland existed next to Lake Gosiute. Desertion Point-Little Muddy faunas are insufficient for climatic estimates to be made, but habitats would have been similar to those at South Pass.

The Br1 is represented by basin margin localities at South Pass, and basin center localities at Desertion Point-Little Muddy and Big Island. South Pass assemblages are too small to make climate estimates. Sediments and fauna suggest that the area was poorly drained relative to the Br0 at South Pass. Desertion Point-Little Muddy faunas are insufficient for climatic estimates. Big Island faunas, however, can be used. Here turtles and crocodiles predominate. Minimum figures given by Williams and Bartels (1997) are; mean annual temperature, 21°C; mean cold month temperature, 16.5°C, mean annual range of temperature, 13°C; and mean annual precipitation, 1244-1524 mm. Desertion Point-Little Muddy and Big Island were close to Lake Gosiute, and would have had generally poorly drained soils, with some higher areas supporting terrestrial taxa. Turtles and crocodiles are very abundant in sediments indicating close proximity to the lake, while lizards, snakes and mammals occur in better drained sediments indicating that they lived in areas that were at least periodically dry.

The Br2 is represented by basin center localities at Desertion Point-Little Muddy and the Bridger Basin. The assemblage at Desertion Point-Little Muddy is not sufficient for climatic estimates to be made. However, the Br2 of the collection from the Bridger Basin is assumed to be very close to the living assemblage. Climatic estimates, using turtles and crocodiles are; mean annual temperature, 20°C; and mean cold month temperature, 10°C. Here turtles and crocodiles are again abundant, and the sediments indicate Lake Gosiute flooded most of the area. Terrestrial taxa also occur, but these species must have been restricted to a relatively narrow belt of dry land between Lake Gosiute and the Uinta Mountains, which provided a wide variety of habitats for the fauna due to rapid changes in elevation producing condensed habitat sequences. From here, many were washed into Lake Gosiute by large trunk streams on broad, well developed floodplains, while others are found in alluvial sediments proximal to the mountain range.

The Br3 is only present in the Bridger Basin, where it represents a basin center area. Climate estimates using turtles and crocodiles are; mean annual temperature, 20°C; and mean cold month temperature, 10°C. Turtles and crocodiles predominate, with large numbers of lizards, snakes, and mammals being recovered from some localities that were presumably subaerial. As Lake Gosiute receded, and subsequently vanished near the end of the Bridgerian, wholly terrestrial environments would have come to dominate.However, the assemblages available for this study represent lacustrine, and near-lake environments from the Bridgerian B and Bridgerian C. Terrestrial taxa would have been restricted to alluvial areas proximal to the Uinta Mountains until the later Bridgerian.

In summary:

1) There were a minimum of 4 salamanders, 1 frog, 14 lizards, 1 amphisbaenid, and 5 snakes living in the Green River Basin during the middle Eocene (Wa7 - Br3).

2) The fauna diversified from a minimum of 10 taxa during the Wa7, to 23 during the Br2.

3) This collection marks the first record of Machaerosaurus torrejonensis in the middle Eocene, and extends the range of Palaeoxantusia borealis down into the middle Eocene.

4) Basin margin localities contain markedly different assemblages than those from the basin center.

5) Machaerosaurus torrejonensis, Restes rugosus, Palaeoxantusia, Boavus occidentalis, Coniophis, and Calamagras primus occur initially in sediments from the basin margin, and are subsequently recovered from basin center deposits.

6) Many groups display intraspecific variation related to their habitat and diet.

7) Squamate taxa may be used to define the biostratigraphic zones of the middle Eocene as an alternative, or in addition to, the North American Land Mammal Ages.

8) Four major facies are present at South Pass:

(i) A clast supported, non-stratified, unsorted conglomerate.

(ii) A clast supported, stratified, better sorted conglomerate interbedded with very coarse sandstone.

(iii) A series of fining-upward, mottled fine grained sandstones, siltstones, and mudstones.

(iv) A series of coarsening-upward, gray and green fine grained sandstones, siltstones, and mudstones.

9) South Pass represents a basin margin environment where a fault controlled alluvial fan deposited conglomerates, channel and sheet sandstones, and fine grained sediments at the edge of Lake Gosiute.

10) SP46 represents the distal end of an alluvial fan where it entered Lake Gosiute.

11) SP79 represents an ephemeral channel in a medial fan environment where bones were deposited by floodwater on the fan surface.

12) Stratigraphic sections measured at SP46, SP78, and SP79 can be correlated, and show that the fossiliferous beds at these localities occur at roughly the same level.

13) Lizards are good indicators of mean annual temperature, and amount of solar radiation. Lizards tend to indicate

cooler temperatures than turtles, crocodiles, or mammals. Estimates based on the fauna give warmer temperatures than those based on the flora.

14) During the middle Eocene, the Green River Basin experienced an equable, warm, and semi-humid to humid environment with mean annual temperatures consistently above 20°C, mean annual temperature ranges much smaller than today (11-13°C), and generally high annual precipitation rates (1244-1524 mm).

15) At the basin margins, the Br0 was relatively warm compared to the Wa7, and the Br1 had a higher annual precipitation than the Wa7 and Br0.

16) In the basin center, the Br2 was warmer than the Br3 which was warmer than the Br1. Annual precipitation probably remained roughly constant.

17) The Br2 of the Bridgerian was the warmest zone during the Tertiary.

18) The variation in the size of Lake Gosiute was primarily controlled by tectonics and the presence or absence of an outlet. Precipitation was a relatively unimportant factor.

APPENDIX A

Facies Codes (modified from Miall, 1978)

G -	Undescribed gravel.
Gp -	Gravel, stratified, planar cross beds.
S -	Undescribed sandstone.
Sh -	Sand, very fine to coarse, may be pebbly, horizontal laminations.
Sr -	Sand, very fine to coarse, ripple cross-laminations.
Sm -	Sand, fine to coarse, massive, or faint laminations.
F -	Undescribed mudrock.
Fsm -	Silt, mud, massive.
Fsmg -	Silt, mud, massive, contains granules.
Fl -	Sand, silt, mud, fine laminations.
Flg -	Sand, silt, mud, fine laminations, contains granules.
Flf -	Sand, silt, mud, fine laminations, fossiliferous.
Flpf -	Sand, silt, mud, fine laminations, poorly sorted, fossiliferous.
Ls -	Lacustrine sandstone.
Lsp -	Lacustrine sandstone, poorly sorted.
Lsf -	Lacustrine sandstone, fossiliferous.

Lsc -	Lacustrine sandstone, with carbonate layers/nodules.
Lsfc -	Lacustrine sandstone, fossiliferous, carbonate burrows.
Lspfc -	Lacustrine sandstone, poorly sorted, fossiliferous, carbonate burrows.
Lspc -	Lacustrine sandstone, poorly sorted, with carbonate layers/nodules.
Lspfc -	Lacustrine sandstone, poorly sorted, fossiliferous, with carbonate layers/nodules.
Lsg -	Lacustrine sandstone, poorly sorted with granules.
Lspf -	Lacustrine sandstone, poorly sorted, fossiliferous.
Lsgf -	Lacustrine sandstone, poorly sorted with granules, fossiliferous.
Lf -	Lacustrine fine grained.
Lfp -	Lacustrine fine grained, poorly sorted.
Lfg -	Lacustrine fine grained, poorly sorted with granules.
Lc -	Lacustrine carbonate.
Lcp -	Lacustrine carbonate, poorly sorted.
Lcf -	Lacustrine carbonate, fossiliferous.

APPENDIX B

Measured sections from SP46, SP78, and SP79.

1) Measured section. SP46 South Pass.

Continental Peak Quadrangle SE 1/4, SE 1/4, NE 1/4, SW 1/4, NE 1/4, Section 30, T27N R99W.

Unit	Thickness	Code	Description
42	0 - 0.1 m	Lsp	Brown sandstone. Silty matrix, poorly sorted. Weathers red. Very well consolidated with siderite. Forms ball-like structures at the top of the escarpment. Covered with Pleistocene debris from the Wind River Mountains.
41	0.64 m	Lfp	Poorly sorted gray white very fine siltstone.
40	1.06 m	Lf	Dark green very fine siltstone. Moderately consolidated and well sorted. Muddy matrix.
39	0.28 m	Lf	Creamy white very fine siltstone. Very well sorted and consolidated. Red and purple weathering.
38	1.26 m	Lf	Dark green fine silt. Well sorted, slabby weathering with a silty matrix. An impersistant carbonate layer occurs 0.7 m from the base of the bed.
37c	0.05 m	Lf	Gray-green very fine siltstone. Very well sorted and consolidated.
37b	0.05 m	Ls	Dark green very fine sandstone. Very well sorted, slabby weathering with occasional fossils.
37a	0.02 m	Lf	Creamy white very fine siltstone. Very well consolidated and well sorted with occasional black minerals of very fine sandstone grain size. Orange-black weathering.
36	1.75 m	Lsgf	Green very fine sandstone. Poorly sorted with pebble sized quartz and fossil fragments. Silty matrix. Popcorn weathering.
35	0-0.35 m	Lf	Light gray-green fine siltstone. Moderately sorted with occasional

			sandstone sized quartz. Well consolidated, weathers red.
34	0.35 m	Lsgf	Green very fine sandstone. Poorly sorted with pebble sized quartz and fossil fragments. Silty matrix. Popcorn weathering.
33	3.80 m	Lspf	Light green very poorly sorted course siltstone with occasional very fine sandstone sized quartz grains and silty matrix. Gradual increase in grain size and sorting towards the top of the bed to a very well sorted, fine grained sandstone. An impersistant layer of creamy white carbonate of very fine siltstone grain size occurs at 1.36 m above the base of the bed. Concentrations of fossil fragments occur at 0.54 m and 0.74 m above the base of the bed. Throughout the bed burrows occur infilled with poorly consolidated carbonate. They are straight, between 3 cm and 10 cm long and with a circular cross section up to 2 cm in diameter.
32	0.17 m	Lspf	Dark green very fine sandstone with a silty matrix. Very poorly sorted, moderately consolidated, with fossil fragments.
31	0.15 m	Lfp	Light green, well consolidated fine siltstone. Poorly sorted with a muddy matrix.
30f	0.07 m	Lc	Creamy white, moderately sorted carbonate with clay sized grains. Very well consolidated.
30e	0.06 m	Lf	Green coarse siltstone. Moderately sorted with very fine sandstone sized quartz grains. Well consolidated.
30d	0.11 m	Lf	Dark green siltstone. Moderately sorted with very fine sandstone sized quartz grains. Well consolidated with a muddy matrix.
30c	0.03 m	Lcp	Impersistant layer of creamy white carbonate. Very fine siltstone sized grains. Well consolidated and poorly sorted with very fine sandstone sized grains of quartz. Well consolidated, weathers brown.
30b	0.11 m	Lf	Dark green, moderately sorted medium siltstone with very fine sandstone sized quartz grains. Well consolidated with a muddy matrix.

30a	0.03 m	Lcp	Impersistant layer of creamy white carbonate. Very fine siltstone sized grains. Well consolidated and poorly sorted with very fine sandstone sized grains of quartz. Well consolidated, weathers brown.
29	0.28 m	Lfg	Poorly sorted, green brown very fine siltstone with occasional granules of quartz and rock fragments. Well consolidated with a popcorn weathering.
28	0.2 m	Lcp	Creamy white, poorly sorted carbonate with very fine siltstone sized grains. Well consolidated.
27	1.75 m	Lfp	Green very fine siltstone. Poorly sorted with very fine sandstone sized grains of quartz.
26	0.5 m	Lsgf	Brown-green very fine sandstone. Very poorly sorted with granules and pebbles of quartz, and fossil fragments. Well consolidated, popcorn weathering and silty matrix.
25	0.75 m	Lf	Fine, green siltstone with moderate sorting. Well consolidated.
24i	0.03 m	Lc	Light gray, moderately sorted carbonate with medium siltstone sized particles. Very well consolidated.
24h	0.06 m	Ls	Green, well consolidated very fine sandstone. Well sorted.
24g	0.06 m	Lc	Gray, moderately sorted carbonate with very fine sandstone sized grains. Very well consolidated.
24f	0.07 m	Ls	Green, well consolidated very fine sandstone. Well sorted.
24e	0.08 m	Lc	Creamy white, very well consolidated carbonate with medium siltstone sized particles. Occasional very fine sandstone sized grains of quartz and a black mineral. Muddy matrix.
24d	0.14 m	Lsg	Green, very fine sandstone. Moderately sorted with granules of quartz and a silty matrix. Well consolidated.
24c	0.11 m	Lc	Gray, very well consolidated carbonate. Muddy matrix.
24b	0.35 m	Ls	Green, well sorted very fine sandstone. Well consolidated, with a silty matrix.
24a	0.1 m	Lc	Impersistant layer of light gray carbonate with very fine siltstone

			sized grains. Well sorted and very well consolidated. Weathers red.
23	2.85 m	Flg	Gray-green, poorly sorted very fine sandstone. Occasional granules of quartz and rock. Well consolidated with a silty matrix. Better sorting and decrease in grain size towards top of the bed.
22	0.65 m	Flpf	Light gray, poorly sorted fine grained sandstone. Well consolidated with a silty matrix. A concentration of fossil fragments 0.25 m above the base of the bed.
21	0.65 m	Fl	Dark gray-green medium siltstone. Moderately consolidated and well sorted with a muddy matrix. Scraps of bone weathering out.
20	0.32 m	Fl	Very light gray-green fine sandstone. Moderately sorted with a silty matrix. Weathers red, well consolidated.
19	0.3 m	Fl	Gray-green very fine mudstone.
18	1.5 m	Flf	Green-gray very fine silty claystone. Well sorted and moderately consolidated. Slaty weathering, muddy matrix, with abundant fossil fragments.
17	0.22 m	Fl	Tan color fine grained sandstone with a silty matrix. Weathers red. Well sorted, with sub rounded medium sandstone sized grains of quartz.
16	5.85 m	Fsm	Green-gray fine grained siltstone, becoming medium silt towards the top of the bed. Moderately consolidated with a silty matrix. Degree of sorting decreases from well sorted at the base, to poorly sorted towards the top of the bed. Mottled weathering increases towards the top as does the occurence of very fine to fine sandstone sized quartz grains. Possibly two beds but the slope was covered with vegetation and weathered material from above.
15	1.77m	Fsm	Green medium siltstone. Poorly consolidated. Silty matrix.
14	0.63m	Fsm	Brown medium-coarse siltstone. Well sorted. Poorly consolidated. Silty matrix. Contains quartz grains.
13	0.2m	Fsmg	Green medium siltstone. Poorly sorted. Poorly consolidated.

			Contains quartz grains. Silty matrix.
12	1.02m	Flg	Brown very fine sandstone with green mottles. Poorly sorted. Poorly consolidated. Silty matrix. Slightly clayey. Contains rounded quartz, gray sandstone, tan sandstone, and feldspar.
11	0.26m	Fsm	Green medium siltstone. Moderately sorted. Poorly consolidated. Silty matrix. Slightly clayey.
10	1.19m	Fsmg	Brown-green coarse siltstone. Poorly sorted, with some sand-sized grains. Poorly consolidated. Muddy matrix. Clayey.
9	0.31m	Fsm	Green medium siltstone with brown mottles. Poorly consolidated. Well sorted. Muddy matrix. Clayey.
8	0.26m	Fsmg	Brown-green mottled coarse siltstone. Poorly sorted. Poorly consolidated. Silty matrix.
7	0.69m	Fsm	Green fine siltstone. Well sorted. Poorly consolidated. Muddy matrix. Clayey.
6	0.92m	Fsm	Brown fine siltstone with green mottles. Well sorted. Poorly consolidated. Muddy matrix. Clayey.
5	0.95m	Fsm	Gray-green medium siltstone. Well sorted. Poorly consolidated. Silty matrix.
4	0.92m	Fsmg	Red-brown coarse siltstone with gray mottles. Poorly sorted, with a few quartz granules. Poorly consolidated. Silty matrix.
3	1.5m	Sm	Gray-brown fine sandstone. Poorly sorted. Poorly consolidated. Contains quartz and mafics. Silty matrix.
2	1.25m	Gp-Sh	Fining up bed from pebble-sized conglomerate to coarse sandstone. The conglomerate contains sub-rounded and platy clasts of quartz and gray schist. Coarse sandstone matrix. The sandstone contains quartz and lenses of conglomerate. Poorly sorted. Poorly consolidated.
1j	0.12m	Sh	Gray-green coarse sandstone. Well sorted. Poorly consolidated. Some laminations. Silty matrix.
1i	0.1m	Gp	Gray-green pebble-sized conglomerate. Contains rounded and platy quartz, gray schist, and tan sandstone clasts. Contains sandy lenses. Silty matrix.

1h	0.15m	Gp-Sr	Gray-green pebble-sized conglomerate. Subrounded and platy quartz, gray schist, and tan sandstone clasts. Fines up to a very coarse, poorly sorted sandstone. Poorly consolidated. Cross-bedded.
1g	0.8-0.17m	Sr	Gray-green very coarse sandstone. Poorly sorted, with quartz, gray schist, and tan sandstone clasts. Cross-bedded.
1f	0m-0.06m	Gp	Gray-green granule-sized conglomerate. Bed pinches out to the northeast. Fines up. Contains quartz, gray schist, and tan sandstone clasts.
1e	0.4m	Sh	Gray-green coarse sandstone. Silty matrix. Moderately sorted. Poorly consolidated. Parallel laminated.
1d	0m-0.15m	Gp	Gray-green pebble-sized conglomerate. Well rounded and platy quartz, gray schist,and tan sandstone clasts. Fines up.
1c	0.04m	Sh	Gray-green coarse sandstone. Moderately consolidated. Well sorted. Silty matrix. Contains subrounded quartz grains. Parallel laminated.
1b	0.09m	Gp	Gray-green pebble-sized conglomerate Contains subangular quartz, platy gray schist, and subrounded tan sandstone clasts. Imbricated, with long axis dipping to the north. Fines up slightly. Poorly consolidated.
1a	0m-0.3m	Gp	Gray-green pebble-sized conglomerate. Contains subangular quartz, rounded gray schist, and rounded tan sandstone clasts. Fines up to a granule-sized conglomerate with quartz, gray schist, and tan sandstone clasts. Medium sandstone matrix. Poorly consolidated. Parallel laminations at the top of the bed.

Covered interval

2) Measured section. SP78 South Pass.

Circle Bar Lake Quadrangle NE1/4, SE1/4, NW1/4, NW1/4, Section 35, T27N R99W.

Unit	Thickness	Code	Description
31	1.08 m	Fsm	Red and green mottled coarse siltstone. Well sorted. Moderately consolidated. Silty matrix.
30	0.63 m	Fsm	Dark green mudrock. Well sorted. Poorly consolidated. Muddy matrix. Clayey. Popcorn weathering.
29	3.85 m	Fsm	Green-gray medium siltstone. Well sorted. Moderately well consolidated. Silty matrix. Popcorn weathering.
28	2.03 m	Fsm	Brown-green mottled coarse siltstone. Well sorted. Moderately consolidated. Silty matrix.
27	1.7 m	Fsm	Reddish brown mottled coarse siltstone. Moderately sorted. Silty matrix. Moderately poorly consolidated.
26	1.45 m	Flg	Brownish red very fine sandstone with gray mottles. Contains quartz and mafics. Poorly sorted, with subrounded quartz granules. Silty matrix. Moderately to poorly consolidated.
25	0.77 m	Flg	Gray-green medium siltstone with increased red mottling upwards. Poorly sorted, with subangular quartz granules. Silty matrix.
24	0.84 m	Fl	Purplish gray-green coarse siltstone. Silty matrix. Well sorted. Moderately consolidated.
23	0.89 m	Fl	Brown medium siltstone with green-gray mottles. Contains quartz. Moderately consolidated. Moderately sorted. Silty matrix. Weathers a distinctive orange.
22	2.78 m	Fl	Mottled red-green coarse siltstone. Moderately sorted. Moderately consolidated. Silty matrix. Weathers a distinctive orange. The layer becomes impersistant towards the south.
21	0.83 m	Flg	Gray-green coarse siltstone. Poorly sorted, with subangular quartz granules. Silty matrix. Moderately consolidated.

20	0-0.05 m	Fl	Impersistant layer of white very fine sandstone. Contains quartz and mafics. Well consolidated. Silty matrix.
19	0.58 m	Flg	Green coarse siltstone. Moderately well consolidated. moderately sorted, with quartz granules. Silty matrix. No mafics.
18	1.17 m	Fl	Red-brown very fine sandstone mottled with gray-green at the base. Contains quartz. Moderately sorted. moderately consolidated. Silty matrix. No mafics.
17	1.37 m	Flg	Green medium siltstone with red mottles. Poorly sorted, with quartz granules. No mafics. Silty matrix. Moderately consolidated.
16	0.88 m	Flg	Mottled red-green medium siltstone. moderately consolidated. Poorly sorted, with quartz and mafic granules. Silty matrix.
15	0.22 m	Fl	Gray-green fine siltstone. Well sorted. Well consolidated. Silty matrix. No mafics. Silica cement. Forms prominent resistant layer.
14	2.4 m	Flg	Mottled red-green medium siltstone. Poorly sorted, with quartz granules. Moderately consolidated. Silty matrix.
13	2.36 m	Flg	Green medium siltstone. Poorly sorted. Silty matrix. Moderately consolidated. 1.42 m up the layer is an impersistant calcareous layer.
12	1.03 m	Fl	Reddish brown medium siltstone with gray-green mottles. Well sorted. Silty matrix. Moderately consolidated. Contains quartz and small fossil fragments.
11	3.06 m	Flg	Green-gray coarse siltstone with a few red-brown mottles. Moderately consolidated. Silty matrix. Poorly sorted. Mottling and red color increase upwards.
10	1.75 m	Flg	Red-brown very fine sandstone, becoming red-brown/gray-green upwards. Poorly sorted, with rounded quartz granules. Silty matrix. Moderately consolidated. Mottling increases upwards.
9	1.62 m	Flg	Greenish fine sandstone. 50% quartz, 50% mafics. Poorly sorted, with rounded quartz granules. Moderately consolidated. Massive.

			0.8 m from the base is an impersistant layer of poorly sorted fine sandstone with more quartz than mafics. Moderately consolidated. Silty matrix.
8	0.83 m	Fl	Reddish brown coarse siltstone with purple mottles. Moderately consolidated. Well sorted. Contains quartz.
7	0.4 m	Gp-Sh	Pebble-sized gray-green conglomerate at the base. 50% gray schist, 50% quartz. Coarsens or fines up, in different areas. Matrix is a very coarse sandstone. Gradual change to a gray-green coarse sandstone at the top. Poorly sorted, with a few well rounded quartz and sandstone granules. Silty matrix.
6	0.34 m	Sh	Gray-green very coarse sandstone. Contains quartz and some mafics. Poorly sorted, with well rounded quartz and sandstone granules. Silty matrix.
5	0.11 m	Gp	Cobble-sized conglomerate. More gray schist than quartz clasts. Clasts are rounded. Matrix is very coarse sandstone. Poorly consolidated.
4	0.19 m	Gp	Cobble-sized conglomerate at the base. Consistent clast size until half-way up the unit where there is a sudden change to a pebble- and granule-sized conglomerate. Clasts are imbricated, with the long axis dipping to the south.
3	1.4 m	Gp-Sh	Fining up bed, from cobble-sized conglomerate to very coarse sandstone. The conglomerate is impersistant - 30 m lateral extent at the outcrop. It has well rounded quartz, gray schist, and tan sandstone clasts. Very coarse sandstone matrix. The sandstone contains well rounded quarts, gray sandstone, and tan sandstone granules. Well consolidated. the bed dips 20 degrees towards the south (original dip).
2	0.43 m	Gp	Fining up bed from cobble-sized conglomerate to very coarse sandstone. The conglomerate contains quartz, gray schist, and tan sandstone well rounded clasts.

			Very coarse sandstone matrix. Poorly consolidated. The sandstone is poorly sorted, with well rounded quartz and sandstone granules. Well consolidated. Iron (Fe) cement.
1	0.17 m	Gp	Fining up bed from cobble-sized conglomerate to very coarse sandstone. The conglomerate contains well rounded quartz, gray schist, and tan sandstone clasts. Very coarse sandstone matrix. The sandstone is gray-green, and contains quartz.

Covered interval

3) Measured section 1. SP79 South Pass.

Circle Bar Lake Quadrangle NW1/4, SE1/4, SW1/4, NW1/4, Section 26, T27N R99W. From the base of "Bull Knob" to the top of "First Hill".

Unit	Thickness	Code	Description
5		Fl	Dark greenish gray mudstone. Poorly consolidated. Well sorted. Muddy matrix. Clayey. Forms top of "First Hill".
4	0.45 m	Flg	Greenish gray coarse siltstone. Poorly sorted. Moderately consolidated. Silty matrix.
3	0.2 m	Flg	Dark gray very fine sandstone. Very poorly sorted, with quartz granules and fossil fragments. Unconsolidated. Silty matrix. Popcorn weathering.
2	1.45 m	Fl	Mottled red and gray coarse siltstone. Well sorted. Silty matrix. Moderately consolidated.
1	1.4 m	Flg	Reddish brown very fine sandstone, with gray mottles. Poorly sorted, with a very few subangular quartz granules. Silty matrix. Moderately sorted.

Covered interval

4) Measured section 2. SP79 South Pass.

Circle Bar Lake Quadrangle NW1/4, SE1/4, SW1/4, NW1/4, Section 26, T27N R99W. From the base of "Triangle" to the top of "East Wall".

Unit	Thickness	Code	Description
6		Fl	Dark greenish gray mudstone. Poorly consolidated. Well sorted. Muddy matrix. Clayey. Popcorn weathering. Forms top of "East Wall".
5	1.83 m	Flg	Greenish gray coarse siltstone. Poorly sorted, with subrounded quartz granules. Silty matrix. Moderately consolidated. Popcorn weathering.
4	1.28 m	Flg	Brownish, and gray-green coarse siltstone. Becoming redder at the top of the unit. Poorly sorted, with subangular quartz granules, and fossil fragments. Moderately consolidated. Silty matrix.
3	0.58 m	Flg	Brown very fine sandstone. Very poorly sorted, with angular quartz granules and pebbles. Moderately consolidated. Silty matrix. Well cemented, forms a prominent layer.
2	0.45 m	Flg	Brownish red and gray-green mottled medium siltstone. Very poorly sorted, with subrounded quartz granules and pebbles. Silty matrix. Moderately consolidated.
1	0.4 m	Flg	Brownish red and gray-green mottled medium siltstone. Poorly sorted, with a few subrounded quartz and feldspar granules. Silty matrix. Moderately consolidated.

Covered interval

5) Measured section 3. SP79 South Pass.

Circle Bar Lake Quadrangle NW1/4, SE1/4, SW1/4, NW1/4, Section 26, T27N R99W. From the base to the top of "Con's Hill".

Unit	Thickness	Code	Description
3	1.08 m	Fsmg	Green, moderately consolidated medium siltstone. Poorly sorted, with rare subangular quartz granules. Silty matrix.
2	1.53 m	Fsmg	Red and green mottled coarse siltstone. Poorly sorted, containing subangular quartz granules. Moderately consolidated and silty matrix.
1	0.85 m	Fsm	Red and green mottled fining up coarse siltstone. Poorly sorted, moderately consolidated, with a silty matrix. Two fossiliferous layers occur 0.34 m and 0.57 m from the base. A third fossiliferous layer occurs at the boundary between this bed and bed 2.

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