National Park Service Paleontological Research

Edited by Vincent L. Santucci and Lindsay McClelland
Technical Report NPS/NRGRD/GRDTR-99/03

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Cover Illustration
Life reconstruction of *Metamynodon planifrons* and an extinct crowned crane, *Balearica* sp. in a riparian habitat during the early Oligocene. Based on work conducted in Badlands National Park. The original painting was produced by Carl Buell.

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To Dr. Michael Soukup,
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Associate Director for
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INTRODUCTION

During this last year of the century, the list of National Park Service areas identified with paleontological resources has grown to 134. Along with redwoods, grizzlies, geysers, and ancient ruins, the national parks preserve a remarkable record of life extending back over a billion years. The rich paleontological resources found in parks have attracted considerable research interest. Paleontological research from within national parks is reported regularly at scientific conferences and provides numerous graduate students with thesis projects.

This fourth National Park Service Paleontological Research Volume compiles 20 papers representing paleontological research in 12 different National Park Service areas. The individual reports reflect a cross-section of the types of paleontological research being conducted throughout the National Park System by academic scientists, their students, and U.S. Geological Survey staff. The contributions from each of the investigators and their research teams are recognized and acknowledged in this volume.

I am again proud to include reports documenting a wide diversity of paleontological research in the national parks. The volume continues to include a number of papers focusing on the biostratigraphy of Triassic sediments at Petrified Forest National Park. A student from Franklin and Marshall College has prepared a report on his research on the cave fauna uncovered at Timpanogos Cave National Monument. Other papers in this volume include work on the Pleistocene mammoths from Channel Islands National Park, marine reptiles from Badlands National Park, and a description of a new bird from Florissant Fossil Beds National Monument.

Thanks to Sid Ash, Ron Blakey, Ken Carpenter, Bill Cobban, Russell Dubiel, Dave Gillette, Steve Hasiotis, Adrian Hunt, Clay Kyte, Greg McDonald, Steve Mitchelson, Don Prothero, Tom Olson, Kris Thompson, William Wall, and Michael Whalen, for their willingness to review manuscripts. Additional thanks to Dave Shaver, Bob Higgins, Dave McGinnis, Arvid Aase, Kris Thompson, Graeme MacDonald, Erin Retelle, Marikka Hughes and Bianca Santucci for their suggestions and support relative to this research publication. I am indebted to Lindsay McClelland, the co-editor of this volume, for many contributions that helped to promote the management, protection and research of paleontological resources in the national parks.

This volume is dedicated to Mike Soukup, Associate Director for Natural Resource Stewardship and Science in the National Park Service. His leadership in building support for science-based decisionmaking has strengthened the management and protection of all park natural resources. Fossils have been key beneficiaries of these policies, as parks increasingly recognize the importance of paleontological research and the value of paleontological resources.

Finally, through the combined efforts of the women and men already mentioned, along with many others, the NPS Paleontological Resource Program continues to grow. Many research questions remain to be explored within the national parks and monuments. Likewise, the increasing numbers of paleontological inventories being initiated in the parks continue to uncover new evidence about the biological past. A holistic approach to managing paleontological resources, which includes research, is becoming the standard practice in national parks.

Vincent L. Santucci
National Park Service

VERTEBRATE PALEONTOLOGY OF THE PIERRE SHALE AND FOX HILLS FORMATIONS (LATE CAMPANIAN - LATE MAASTRICHTIAN) OF BADLANDS NATIONAL PARK, SOUTH DAKOTA

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Abstract—Recent field investigations were concentrated in the Pierre Shale and Fox Hills formations (Late Cretaceous) exposed in Badlands National Park (BADL). Here we describe the occurrence of vertebrate fossils from the two lithostratigraphic units within BADL. Specimens include a tooth of the sand tiger shark, *Odontaspis*; a teleost tooth and scales; a partial left maxilla and associated dorsal vertebrae of a juvenile *Mosasaurus conodon*; and an isolated anterior caudal vertebra of a large unidentified mosasaur. A rich and varied invertebrate assemblage was also found that includes: ammonites, nautiloids, gastropods, pelecypods, scaphopods, decapods, inarticulate brachiopods, bryozoa, and scleractinian corals.

The juvenile specimen of *Mosasaurus conodon* and the teleost tooth were collected from the *Baculites cuneatus* biozone of the Verendrye Member, Pierre Shale. The teleost scales were associated with *Baculites clinolobatus* and *Hoploscaphites burkelundi*, and were found in the Mobridge Member, Pierre Shale. The *Odontaspis* tooth was collected from the Elk Butte Member, Pierre Shale, whereas the isolated mosasaur caudal vertebra was collected from the upper part of the Fox Hills Formation.

INTRODUCTION

During much of the Late Cretaceous, a vast north-south trending epicontinental sea existed in the Western Interior of North America. The eastern margin of the seaway was formed by the low-lying stable Canadian Shield, while the entire western margin was flanked by an unstable cordilleran highland (MacDonald and Byers, 1988).

Rapid sea level rise during the late Early Campanian resulted in a shift from chalk deposition of the Niobrara Seaway to muds of the Pierre Seaway (McGookey *et al*., 1972). During the existence of the Pierre Seaway, several minor transgressive/regressive events occurred that are recorded in the rocks of the Pierre Shale exposed in Badlands National Park. Retreat of the seaway began in early Maastrichtian time due to an increase in both tectonic activity and rate of coarse clastic deposition (McGookey et al., 1972). The Fox Hills Formation represents a nearshore transition between the marine environments of the Pierre Shale and terrestrial environments of the Hell Creek Formation.

The Pierre Shale and Fox Hills Formation are exposed today in the northern and southern parts of Badlands National Park of southwestern South Dakota (Figure 1). The park is well known for Eocene - Miocene mammalian assemblages in the White River Group. However, little is known about the fossil occurrences, especially of vertebrates, within Cretaceous rocks exposed throughout the park.

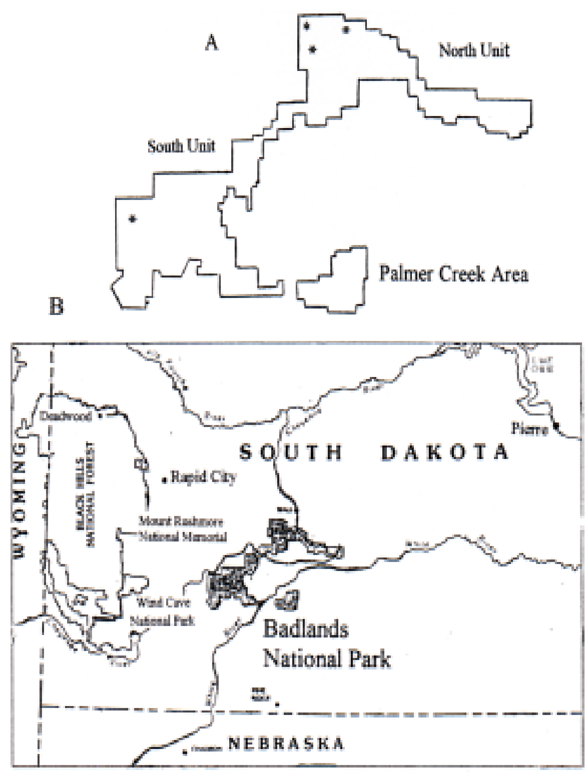

FIGURE 1— A, Map of Badlands National Park. Symbols indicate vertebrate fossil localities; B, Map of southwestern South Dakota showing the location of the park. B modified from U.S.G.S. 1:50,000-scale map of Badlands National Park.

Abbreviations - **BADL**, Badlands National Park, **SDSM**, Museum of Geology, South Dakota School of Mines and Technology. All specimens are stored in the Museum of Geology. Precise stratigraphic and geographic information is on record at Badlands National Park.

HISTORY OF COLLECTING

Very little is known about the fossil resources of Cretaceous rocks exposed in BADL. Meek and Hayden (1862) were the first to recognize the presence of the "Fort Pierre Formation" (Pierre Shale) in the Sage Creek area of the Park (North Unit). Since then, this formation has received little attention. However, recent field research has documented fossils within Cretaceous strata of BADL, including ammonites, pelecypods, gastropods, scaphopods, crustaceans, brachiopods, nautiloids, bryozoans, corals, scaphopods, and belemnites (Table 1). The majority of the fossils are from the Pierre Shale, but several ammonites and the belemnites, as well as a lobster tail, were recovered from the Fox Hills Formation. Meager vertebrate remains, consisting of isolated teleost scales and teeth, a single mosasaurine caudal vertebra, and vertebrae and jaw fragment of *Mosasaurus conodon*, were also discovered. This small assemblage probably reflects a collecting bias (as exposure surface is limited), rather than actual low abundance.

Several important marine reptile discoveries have been made outside the park boundary. The type specimen of *Prognathodon overtoni* (KU 950) was collected from "... near the top of the Pierre deposits of the Cheyenne River of South Dakota" (Russell, 1967; Williston, 1897, p. 95), and an additional specimen (SDSM 3393) was recovered from "... the Virgin Creek Member, Upper Pierre Shale Formation ... southwest of Cuny Table, Shannon County, South Dakota" (Russell, 1967). The preservation of SDSM 3393 indicates that the bones were collected from the Yellow Mounds Paleosol.

An additional mosasaur skeleton, probably *Mosasaurus*, was collected by SDSMT personnel over 30 years ago north of Scenic, South Dakota. The specimen consists of a nearly complete skeleton. Unfortunately, only the skull, limbs, and part of the tail were collected at the time of discovery. The bones are encased in hard, yellowish limestone derived from the Yellow Mounds Paleosol. This material has been prepared with acetic acid to dissolve the limestone. Several teeth of the dogfish, *Squalus*, were also discovered in the limestone. This association may indicate, as has been documented from the Pierre Shale of the Missouri River area of South Dakota, that the mosasaur carcass was scavenged by a school of dogfish (Bell et al., in press).

In 1926, a stratodont osteichthyan, probably *Stratodus* (SDSM 2674 and 2675), was collected from Cuny Table, Shannon County, by the Museum of Geology. The remains consist of a complete dentary, premaxilla, edentulous jaw fragments with a double row of equally sized alveoli, isolated teeth, and scales. Some of the bones are encased in hard yellow and pink phosphatic nodules that are characteristic of the Yellow Mounds Paleosol.

CRETACEOUS STRATIGRAPHY OF BADLANDS NATIONAL PARK

Cretaceous rocks of BADL consist of the Pierre Shale, and bluish, fine-grained glauconitic sandstone of the Fox Hills Formation. Extensive outcrops of the Pierre Shale are found throughout the Sage Creek Wilderness area of the North Unit and within tributaries of the Cheyenne River in the South Unit. Overlying the Pierre Shale is a yellow weathered unit, variously referred to as the "Interior Zone", "Interior Formation", Rusty Member" (Stoffer *et al.*, 1998), and "Yellow Mounds Paleosol" (Pettijohn, 1965). Dunham (1961) recognized that pre-Eocene weathering was responsible for the bright yellow sediments of the "Interior Formation". However, it was uncertain as to whether these sediments belonged to the Pierre Shale or Fox Hills Formation (Agnew and Tychsen, 1965). Recent work by Stoffer *et al*. (1998) has established that the "Yellow Mounds Paleosol" is the result of meteoric weathering of both the upper Pierre Shale and Fox Hills Formation. Exposures of the Fox Hills Formation are

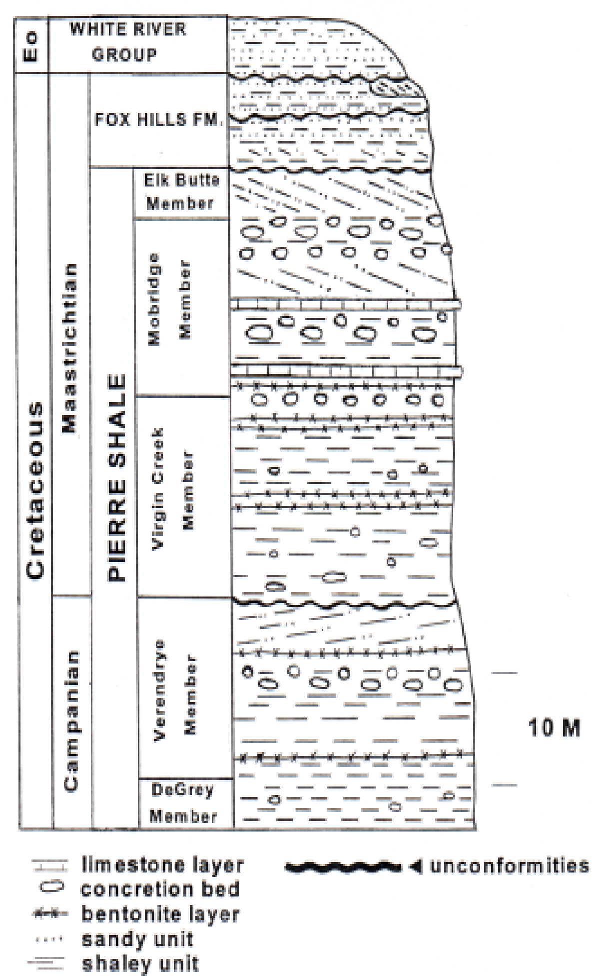

FIGURE 2— Composite stratigraphic section of Cretaceous rocks of Badlands National Park. Eo = Eocene. Modified from Stoffer *et al*. (1998).

found throughout the North Unit of BADL.

Collecting efforts have been concentrated in the Pierre Shale during the past several years, and several ammonite biozones have been recognized, including: *Didymoceras cheyennense*, *Baculites compressus*, *B. cuneatus*, *B. reesidei*, *B. jenseni* and *B. eliasi*, *B. baculus*, *B. grandis*, *B. clinolobatus*, and *Hoploscaphites burkelundi* (oldest to youngest). These biozones have been used to subdivide the Pierre Shale into several biostratigraphic units. In BADL, the lithologic composition correlates with the DeGrey, Verendrye (Crandall, 1958), Virgin Creek, Mobridge, and Elk Butte (Searight, 1937) members of the Pierre Shale of central South Dakota (Figure 2).

Fossils are scarce in the Fox hills Formation, but this may reflect a collecting bias because this unit has largely been neglected. Those fossils that do occur are generally in poor condition because they have been subjected to several episodes of subaerial exposure. The Fox Hills Formation of BADL has been divided into lower and upper units (Stoffer *et al*., 1998), although correlation of the Fox Hills with the type area in Central South Dakota (Waage, 1961) is hindered by the poor preservation of invertebrate fossils. The lower unit is no older than late early Maastrichtian, because this interval overlies the *Baculites clinolobatus* biozone of the Pierre Shale (Cobban *et al*., 1994). Sr^{87}/SR^{86} values of belemnites found in the upper unit yielded an age of 67 mya (Stoffer *et al*., 1998).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880
Order Lamniformes Berg, 1958
Family Odontaspididae Muller and Henle, 1839
Genus *Odontaspis* Agassiz, 1838

Odontaspis sp.
Figure 3, A-C

Referred Specimens - BADL 9935, lower anterior tooth found as float in the Elk Butte Member, Pierre Shale.

Description - The tooth possesses a tall, narrow cusp with a pointed apex. The cusp is slightly sigmoid in lateral profile, and distally inclined. Its labial crown face is smooth and nearly flat, whereas the lingual face is smooth and greatly convex. The cutting edges are smooth and continuous. The enameloid of the labial face extends basally onto root lobes. The lingual dental band is wide and a prominent lingual boss bears a nutritive groove. The root is incomplete, but was bilobate with meso-distally thin lobes and a u-shaped interlobe area. Several foramina are located on the boss and within nutritive groove.

Discussion – Broken surfaces indicate that at least one pair of lateral cusplets was originally present at the base of each side of the central cusp. This character distinguishes BADL 9935 from lower anterior teeth of the Mitsukurinidae (goblin sharks). Also, the smooth crown faces separate the tooth from both mitsukurinids and striated odontaspids ("*Synodontaspis*"). The crown morphology is similar to *Odontaspis hardingi* from the Upper Campanian of New Jersey (Cappetta and Case, 1975), but one specimen is not adequate for precise taxonomic assignment.

Teeth of *Odontaspis* are well suited for a piscivorous diet. The lower teeth pierce and hold, while the upper teeth cut into the prey (Cappetta, 1987). Recent odontaspids are found in shallow bays and coastal waters, to a depth of 200 meters (Tricas *et al*., 1997).

FIGURE 3— Lower anterior tooth of *Odontaspis* sp. (A-C), BADL 9935. A, Labial view; B, Mesial view; C, Lingual view. Scale bar = 3 cm.

Class Osteichthyes
Order indeterminate
Figure 4, A-C

Referred specimens - BADL 8189, single tooth found as float in the *Baculites cuneatus* biozone, Verendrye Member, Pierre Shale; BADL 8172, BADL 8179, BADL 8181, BADL 8182, BADL 8183, BADL 8184, BADL 8185, BADL 8186, BADL 8187, BADL 8188, all isolated scales collected *in situ* from the *Baculites clinolobatus* biozone, Mobridge Member, Pierre Shale.

Description - The tooth is laterally compressed and bisected into equal labial and lingual faces by unserrated anterior and posterior carinae. Fine striations are located on the lower half of the tooth. The posterior carina is vertical, whereas the anterior carina is strongly sloping. The apex is broken and there is a deep basal pulp cavity. Enamel covers only the upper two thirds of the crown.

Two types of cycloid scales have been collected. One is oval and is taller than long (Figure 4-B). The other type is subequal in length and height, and has three "denticles" on the posterior edge (Figure 4, C).

Discussion - An enamel-free basal section and deep pulp cavity indicates the tooth belonged to a fish with a thecodont dentition. The tooth came from a bioturbated limestone and was associated with broken *Inoceramus* and

Lucina. This specimen was collected near Blindman Table, South Unit.The scales were collected from a limestone bed and are associated with inarticulate brachiopods (*Lingula*). BADL 8180 is similar to scales of the Ichthyodectidae described by Bardack (1965, p. 51). However, the lack of associated skeletal material makes taxonomic assignment difficult. These scales were collected from just north of the Sage Creek Primitive Campground, North Unit.

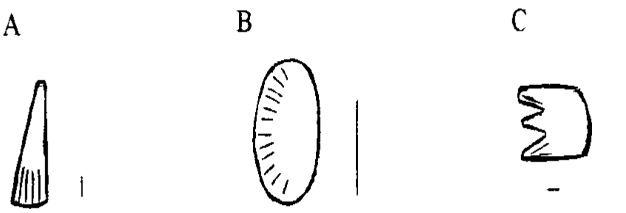

FIGURE 4— Osteichthyes tooth (A) and scales (B-C). A, Lateral view of tooth, BADL 8189. Scale bar = 1 mm; B, Type 1 scale, BADL 8180. Scale bar = 1 cm; C, Type 2 scale, BADL 8186. Scale bar = 1 mm. Anterior is left for all specimens.

Class Reptilia Linnaeus, 1758
Order Squamata Oppel, 1811
Family Mosasauridae Gervais, 1853
Genus *Mosasaurus* Conybeare, 1822

Mosasaurus conodon (Cope, 1881)
Figure 5

Referred specimen - BADL 9831, partial left maxilla and seven dorsal vertebrae collected as float from the *Baculites cuneatus* biozone, Verendrye Member, Pierre Shale. Collected approximately one half mile south of the Sage Creek Primitive Campground, North Unit.

Description - Only the middle portion of the left dentary, including seven teeth, is preserved. Seven foramina are located near the ventral border of the maxilla. This edge of the jaw is wide to accomodate the teeth. The bone thins dorsally and curves strongly medially. A small portion of the external naris is preserved.

The teeth are bicarinate and divided into nearly equal labial and buccal parts. Irregular serrations are uniformly distributed along the length of the anterior and posterior carinae. Both the labial and buccal crown faces are convex and weakly faceted. The teeth are recurved and the apices are internally inclined, becoming more pronounced anteroposteriorly. Crown height decreases anteroposteriorly; labial and buccal convexity increases.

Each dorsal vertebra measures 4.6 cm in length. The cotyle is deeply concave and has a sharp perimeter. The condyle is convex with a circular ventral border, and has flat dorsal and dorsolateral sides. The neural spines are tall, broad, nearly flat walled, and posteriorly inclined. Synapophyses are dorsoventrally compressed and broad based, taper distally to a smooth rounded end, and project slightly anteriorly. The prezygopophyses are narrow with a smooth, ovate, upward oriented articulation.

Discussion – Preservation of the vertebrae inhibits description of postzyopophyses, and the presence of zygosphenes and zygantra are unknown. However, the length of the synapophyses suggests that the vertebrae are medial or posterior dorsals. In addition, the length of the vertebrae and the size and fibrous texture of the maxilla indicates that the specimen was a juvenile. Serrations and faceting are less developed than in more derived mosasaurines such as *Mosasaurus dekay*, *M. maximus*, and *M. missouriensis* (Goldfuss, 1845; Russell, 1967). BADL 9831 is geologically younger than specimens of *M. conodon* collected by the Museum of Geology from the Pierre Shale of central South Dakota.

FIGURE 5— *Mosasaurus conodon*, juvenile, BADL 9831. View of concretion showing incomplete left maxilla (bottom) and five dorsal vertebrae. Neural spine of a sixth vertebra can be seen at left. Scale bar = 10 cm.

Subfamily Mosasaurinae (Gervais, 1853) Williston, 1897
Gen. et sp. indet.
Figure 6, A-C

Referred Specimen - BADL 9934, isolated anterior caudal vertebra found as float from the Fox Hills Formation just south of Robert's Prairie Dog Town, North Unit.

Description - Maximum length of the centrum is 4.1 cm, whereas maximum width and height are equal at 3.2 cm. The cotyle and condyle have a sub-triangular shape. The neural spine is tall (7.8 cm as preserved) and nearly vertical, with convex sides. Transverse processes are dorsoventrally compressed, anteroposteriorly narrow, slightly posteriorly inclined, and ventrally oriented. The haemal arch is incomplete, but the base was fused to the midlength of the centrum's ventral surface.

Discussion - Anterior-most mosasaur caudal vertebrae have long transverse processes but lack haemal arches. Size and length of the centrum and transverse prosesses diminishes posteriorly. The orientation and morphology of the transverse processes of BADL 9934 indicate that it is an anterior caudal vertebra with a haemal arch. The haemal arch was fused to the centrum, indicating a taxon within Mosasaurinae.

CONCLUSIONS

Cretaceous vertebrate fossils of Badlands National Park consist of an isolated mosasaur caudal vertebra, a partial maxilla and dorsal vertebrae of *Mosasaurus conodon*, an isolated tooth of the sand tiger shark, *Odontaspis*, and a tooth and scales of osteichthyes. The paucity of vertebrate material may reflect a collecting bias, as prospectable exposures of Cretaceous rocks generally occur as near-vertical sections.

Invertebrate fossils were abundant and diverse, especially in the Verendrye Member of the Pierre Shale. This assemblage, as well as heavily bioturbated limestones and shales, indicate well oxygenated water and an abundant food supply. Gill and Cobban (1966) suggested that deposition of the Pierre Shale was relatively fast, preventing the dissolution of mollusc shells, thus allowing their fossilisation. The shells of ammonites became hardgrounds for bryozoans and gastropods, and living chambers of *Baculites* were found to contain fecal pellets, indicating these were used as homes by some invertebrates. Disturbed bentonites and linearly oriented baculites in concretions provides evidence that bottom currents were active. The substrate was heavily bioturbated which, coupled with current action, led to the disarticulation and chaotic orientation of pelecypod remains. An abundance of invertebrates, including bryozoans, and juvenile mosasaur remains suggest relatively shallow water. Sohl (1966) reported that the presence of ostreid bivalves in some parts of the Pierre Shale indicated a shallow water environment.

The fish tooth and scales were collected from a limestone bed of the Mobridge Member, Pierre Shale. These

FIGURE 6— Mosasaurinae gen. indet. caudal vertebra (A-C), BADL 9934. A, Posterior view; B, Left lateral view; C, Ventral view. Anterior is at left. Scale bars = 10 cm (in A-C).

remains were associated with abundant inarticulate brachiopods (*Lingula*). Craig (1952) noted that extant lingulid brachiopods are shallow water forms that are most common in waters less than 18.7 m, and only rarely occur at depths up to 37.5 m. Abundant ammonites, gastropods, and pelecypods indicate normal marine conditions.

Yellow, thin-bedded sandstones above the Pierre Shale are lithologically equivalent to the Fox Hills Formation. However, invertebrate fossils indicate that these strata are temporally equivalent to the Elk Butte Member of north-central South Dakota. As evidenced by drag and tool marks, current action was strong. The presence of sand tiger shark remains suggests nearshore marine conditions (Tricas *et al*., 1997).

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TABLE 1 — Pierre Shale and Fox Hills Formation invertebrate and vertebrate fossils collected in Badlands National Park, South Dakota.

- Invertebrata
  - Coelenterata
    - Scleractinia
      - Micrabaciidae
        - *Micrabacia* sp.
  - Arthropoda
    - Crustacea
      - Decapoda
        - Dakoticancridae
          - *Dakoticancer* sp.
        - Family indeterminate (shrimp abdomen)
  - Mollusca
    - Pelecypoda
      - Grypaeidae
        - *Pycnodonte* sp.
      - Inoceramidae
        - *Inoceramus* sp.
      - Ostreidae
        - *Lopha* sp.
        - *Ostrea* sp.
      - Lucinidae
        - *Lucina occidentalis*
      - Nuculanidae
        - *Nuculana* sp.
      - Nuculidae
        - *Nucula cancellata*
    - Scaphopoda
      - Dentaliidae
        - *Dentalium* sp.
    - Gastropoda
      - Naticidae
        - *Natica* sp.
      - Family indeterminate
        - *Turris contortus*
      - Vanikoridae
        - *Vanikoro ambiqua*
        - *Vanikoropsis* sp.
      - Aphorridae
        - *Drepanochilus nebrascensis*
      - Siphonariidae
        - *Anisomyon* aff. *borealis*
    - Cephalopoda
      - Nautilidae
        - *Eutrephoceras dekayi*
      - Belemnitellidae
        - *Belemnitella* sp.
      - Placenticeratidae
        - *Placenticeras meeki*
      - Nostoceratidae
        - *Didymoceras cheyennense*
      - Scaphitidae
        - *Hoploscaphites burkelundi*
        - *Jeletzkytes nodosus*
      - Baculitidae
        - *Baculites compressus*
        - *B. cuneatus*
        - *B. reesidei*
        - *B. jenseni*
        - *B. eliasi*
        - *B. grandis*
        - *B. baculus*
        - *B. clinolobatus*
  - Brachiopoda
    - Inarticulata
      - Lingulidae
        - *Lingula* sp.
  - Bryozoa
    - Gymnolaemata
      - Order indeterminate
  - Ichnites (trace fossils)
    - *Diplocraterion* sp.
    - *Nerites* sp.
- Vertebrata
  - Elasmobranchii
    - Odontaspididae
      - *Odontaspis* sp.
  - Osteichthyes
    - Order indeterminate (tooth and scales)
  - Reptilia
    - Squamata
      - Mosasauridae
        - *Mosasaurus conodon*
      - Family indeterminate (caudal vertebra)

LOCOMOTOR ADAPTATIONS IN *METAMYNODON PLANIFRONS* COMPARED TO OTHER AMYNODONTIDS (PERISSODACTYLA, RHINOCEROTOIDEA)

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Abstract—The association of *Metamynodon* specimens with channel sandstones (particularly with the Orellan section exposed in the southern unit of Badlands National Park) has contributed heavily to the common perception that all amynodontid rhinoceroses were semi-aquatic. An analysis of anatomical traits in a variety of amynodontids was conducted to determine the most likely mode(s) of life for these extinct perissodactyls. The characters providing the most useful information on life habits in amynodontids are: orbital position on the skull (high or low); relative development of the nuchal ligament (as determined by thoracic spine size); the relative size of the olecranon process compared to the length of the radius; and reconstruction of hindlimb musculature with reference to locomotor adaptations. Based on these results primitive amynodontids were subcursorial terrestrial mammals similar to a variety of Eocene ungulates. Cadurcodontines were tapir-like terrestrial mammals. Only one group of amynodontids, the Metamynodontini, was adapted to a semi-aquatic mode of life. The genus *Metamynodon* possibly represents the extreme stage in amynodontid evolution toward this mode of life. Middle Eocene metamynodontines are found in both North America (*Megalamynodon*) and Asia (*Paramynodon*). Migration between these two areas may be a significant factor in tracing the lineage culminating in the hippo-like *Metamynodon*.

INTRODUCTION

Amynodontids are commonly called swamp rhinoceroses or aquatic rhinoceroses in reference to their presumed amphibious life style. Although aquatic habits for amynodontids are firmly ingrained in the paleontological literature today, this has not always been the case. Marsh's (1877) original description of a skull of *Amynodon advenus* (Uintan, Eocene) made no mention of aquatic habits. Scott and Osborn (1882) likewise did not discuss aquatic habits when they described a skull of *Orthocynodon* (= *Amynodon*) and raised the amynodontids to a separate family within the Rhinocerotoidea. Even when a skull and skeleton of *Metamynodon* was described (Scott and Osborn, 1887, and Osborn and Wortman, 1894) no reference was made to aquatic habits in amynodontids. Osborn (1898), in his monograph on rhinoceroses, stated for the first time that amynodontids were aquatic. Osborn must have assumed that a semi-aquatic mode of life for amynodontids was common knowledge since he did not justify his statement. Taphonomic evidence may have contributed to the interpretation of aquatic habits for amynodontids.

The vast majority of *Metamynodon* specimens are found in or near Orellan (early Oligocene) channel sandstones (see Retallack, 1983, and 1992). These channels are particularly well exposed in the Southern Unit of Badlands National Park (Prothero and Whittlesey, 1998). For twenty-one years prior to Osborn's statement on aquatic habits, amynodontids had never been described in the literature as amphibious animals. Since Osborn's paper, however, no one questioned the aquatic mode of life for all amynodontids until Wall (1980). The purpose of this paper is to look in detail at various lines of anatomical evidence alluding to aquatic habits in amynodontids.

MATERIALS AND METHODS

Fossil specimens used in this study are housed in the American Museum of Natural History (AMNH); Georgia College & State University Vertebrate Paleontology Collection (GCVP); the Museum of Comparative Zoology, Harvard (MCZ); the South Dakota School of Mines and Technology (SDSM); and the University of Florida (UF). Modern mammals from the American Museum of Natural History (AMNH); Georgia College & State University Mammalogy Collection (GCM); and the University of Massachusetts, Amherst (UMA) were used for comparative purposes. All measurements were taken with Helios dial calipers. General information on name, origin, insertion, and function of muscles comes from Sisson and Grossman (1953). Amynodontid taxonomy is based on Wall (1989).

ANATOMICAL EVIDENCE

Previous attempts (Troxell, 1921; Scott, 1941) at analyzing evidence for aquatic habits in amynodontids were based solely on the genus *Metamynodon*. In the discussion below we have analyzed the characters presented by Troxell and Scott (as well as others they did not mention) from a broader perspective, looking at the entire range of anatomical features present in amynodontids. Where appropriate we have included two well known sympatric North American Miocene rhinocerotids that are generally regarded as having distinctly different life habits, *Aphelops*, a terrestrial browser, and

Teleoceras, an amphibious grazer (see Prothero, 1998), to test the general applicability of our biomechanical interpretations.

Dentition

Scott (1941) stated that resemblance between the large canine tusks of *Metamynodon*, *Hippopotamus*, and *Astrapotherium* was probably due to their similar aquatic life style. Scott did not mention why large canines would be indicative of aquatic habits in mammals. Recent hippos use their canines as weapons and for intraspecific display (Herring, 1975), a function that is also true of many terrestrial mammals including pigs and peccaries (Herring, 1972). Although metamynodontines exhibit an extreme in canine size for the family, large canines are typical of amynodontids in general (including the tapir-like cadurcodontines, Wall, 1980; 1989). Canine size in amynodontids varies in a manner implying sexual dimorphism. If that is the case, canine size probably had a behavioral function independent of the animal's other life habits. The tusk-like lower incisors of the presumably terrestrial *Aphelops* are relatively larger than those of the supposed semi-aquatic *Teleoceras*. Canine size does not appear to be of any value in deciding whether amynodontids were aquatic or terrestrial.

Cranial Characters

There are a series of skull characters that can be used to help determine whether amynodontids were aquatic. Most of these characters have been used with variable success by other authors dealing with aquatic adaptations in fossil vertebrates.

POSITION OF NARIAL OPENINGS

Troxell (1921) believed the shortened preorbital region of the skull and large external nares indicated that *Metamynodon* probably had a prehensile upper lip. Troxell further stated that since *Hippopotamus* had a similar prehensile upper lip the presence of the same structure in *Metamynodon* indicated that it was aquatic as well. Analysis of snout structure in amynodontids (Wall, 1980) is in agreement with Troxell's interpretation of a prehensile upper lip in *Metamynodon*. We do not agree with Troxell, however, that a prehensile upper lip implies aquatic habits. A variety of terrestrial mammals also have a prehensile upper lip, including the black rhinoceros (*Diceros bicornis*).

The position of the external nares on the skull could provide evidence for aquatic habits. Typically, aquatic mammals have external nares, which open high on the snout. Perhaps the best comparison for amynodontids is with *Hippopotamus* (Figure 1A). The nasal bones in the modern hippo skull are retracted and do not overhang the external nares. In addition, the lateral borders of the external nares slope gradually backward. As a result of these cranial modifications the nostrils of *Hippopotamus* open dorsally on the snout. A wide range of snout configurations can be recognized within the Amynodontidae (Wall, 1980). Skulls of *Metamynodon*,

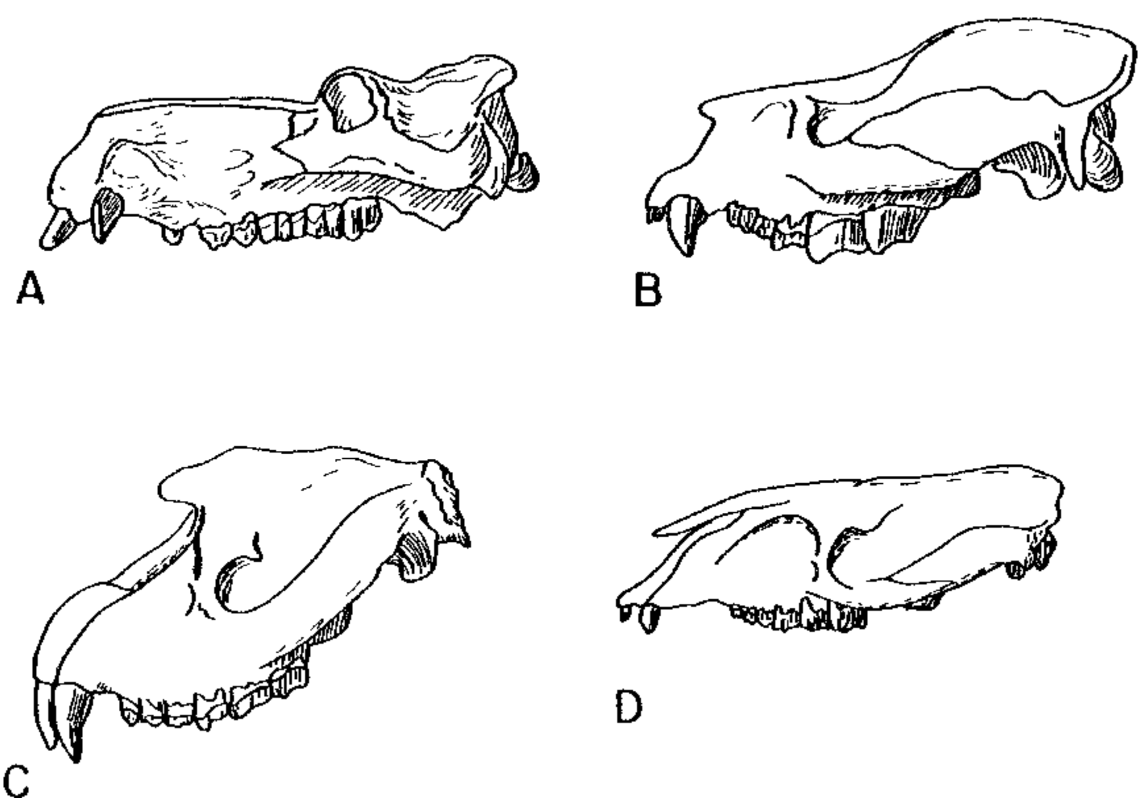

FIGURE 1— Lateral views of skulls of A, *Hippopotamus*; B, *Metamynodon*; C, *Cadurcodon*; and D, *Rostriamynodon.*

Cadurcodon, and *Rostriamynodon* are also illustrated (Figures 1B, 1C, and 1D respectively). *Rostriamynodon*, a primitive amynodontid (Wall and Manning, 1986), has elongate nasal bones, which extend far over the external nares. It is unlikely therefore that the nostrils could have opened dorsally on the skull. A certain amount of nasal retraction is apparent in both *Cadurcodon* and *Metamynodon*, but the overall construction of the snout region in the two amynodontids is different. *Cadurcodon* has a vertically heightened nasal opening that is partially roofed by thickened nasal bones. Numerous cranial features of *Cadurcodon* are convergent with tapir skulls (Wall, 1980) therefore it is likely that advanced cadurcodontines probably had a proboscis. Since the nostril openings are invariably at the distal end of a proboscis, this structure would rule out any possibility that cadurcodontines had a dorsally positioned nasal opening. *Metamynodon*, however, does show some similarity to the snout region of *Hippopotamus*. Figure 1 shows some nasal overhang above the external nares, but this is not always the case in *Metamynodon*. In some skulls the nasal bones do not overhang the external nares at all. The configuration of the snout region in *Metamynodon* does allow for the possibility of a dorsal opening for the nostrils.

Troxell (1921) believed that the far posterior placement of the internal nares in amynodontids was an adaptation to allow a continuous passage of air from nostrils to larynx when the mouth was under water. It is true that in all amynodontids the internal narial opening is far back on the palate (at the level of the M3 protoloph), but this does not in itself prove that the larynx had an unbroken soft tissue connection with the internal nares. A second problem with interpreting the posterior position of the internal nares as an aquatic character is that direct connection of the larynx to the internal nares also may be advantageous in a terrestrial mammal. As Troxell pointed out, horses have direct connections between the larynx and external nares. Troxell believed this adaptation prevented dust from entering the lungs while the horse was eating. Since Troxell realized that the same respiratory arrangement could be found in terrestrial and aquatic mammals, his interpretation of amynodontid internal nares position as an aquatic character was based solely on his prior bias that amynodontids were aquatic.

The only reliable narial character for interpreting aquatic life habits appears to be the relative position of the nostrils. Using this character to interpret amynodontid life habits, three "groups" of amynodontids can be recognized. A primitive group, including *Rostriamynodon*, lacked any modifications beyond the primitive perissodactyl condition in nostril position. Cadurcodontines were derived but the nostrils probably opened low on the face at the end of a short proboscis. Snout structure in metamynodontines does allow for dorsal opening of the nostrils; therefore this is the only amynodontid group showing modifications of the snout for aquatic life.

Reduced olfactory ability in aquatic mammals

Poor sense of smell has commonly been regarded as a by-product of adopting aquatic habits (see Howell, 1930; and Mitchell and Tedford, 1973). Troxell (1921) believed that, because of lateral constriction by preorbital fossae and ventral constriction resulting from a highly concave secondary palate, the snout region of amynodontids could not have provided space for abundant nasal epithelium. Direct evidence on olfactory ability in amynodontids is limited. Amynodontid endocranial anatomy is poorly known; only a single brain cast has been made (that of *Amynodon* figured in Marsh, 1886). Olfactory bulbs in *Amynodon* show no significant reduction in size compared to an endocranial cast of *Hyrachyus* (although the cerebral hemispheres in *Amynodon* were relatively larger than in *Hyrachyus*).

Troxell's indirect evidence regarding reduced olfactory ability in amynodontids is open to interpretation. It is true that laterally positioned preorbital fossae reduce the internal surface area of the snout, but we believe Troxell was mistaken as to the function of the fossae (he believed they were for snout muscle attachment; see Wall, 1980 for snout muscle attachment sites). If amynodontid preorbital fossae housed enlarged nasal diverticula (as asserted by Gregory, 1920a), there still would be ample room for nasal epithelium. Thus, ascertaining the function of preorbital fossae in amynodontids is an integral part of determining whether these animals had reduced olfactory abilities. There are only two likely functions of preorbital fossae in amynodontids: the fossae provided space for either nasal diverticula or scent glands.

Gregory (1920a) argued that preorbital fossae in some extinct horses (such as *Onohippidium*) were developed to allow room for large, laterally directed nasal diverticula. As evidence for his theory, Gregory cited similar fossa development in modern tapirs that (as shown by dissected animals) clearly contain a nasal diverticulum. Gregory applied a nasal diverticula function to a host of fossil mammals exhibiting preorbital fossa. Although this may be true of some fossil mammals, evidence from amynodontids does not entirely support Gregory's viewpoint. In tapirs, the preorbital fossa connects with the external nares via a distinct groove, which provides passage for the nasal diverticulum. No such connection exists in amynodontids; in fact, the large canine root produces a maxillary bulge, which might have formed a barrier to migration of nasal diverticula into the preorbital fossa.

An alternative function for preorbital fossae in amynodontids is that they housed scent glands of some type. Gregory disregarded this idea because the shape of most preorbital fossae were not as circular or as distinctly rimmed as the depression housing the larmier gland in deer and antelopes. Clearly the preorbital fossa in amynodontids is not homologous to the larmier fossa in artiodactyls, however, that does not rule out similarity in function.

Both of the most probable functions for the amynodontid preorbital fossa are associated with a good sense of smell. If the fossa is well developed it can be assumed that olfactory ability was also acute. Figure 2 illustrates the relative development of preorbital fossae in the three tribes within the Amynodontinae. The primitive preorbital fossa condition is seen in *Amynodon*; in this animal the fossa is large but be-

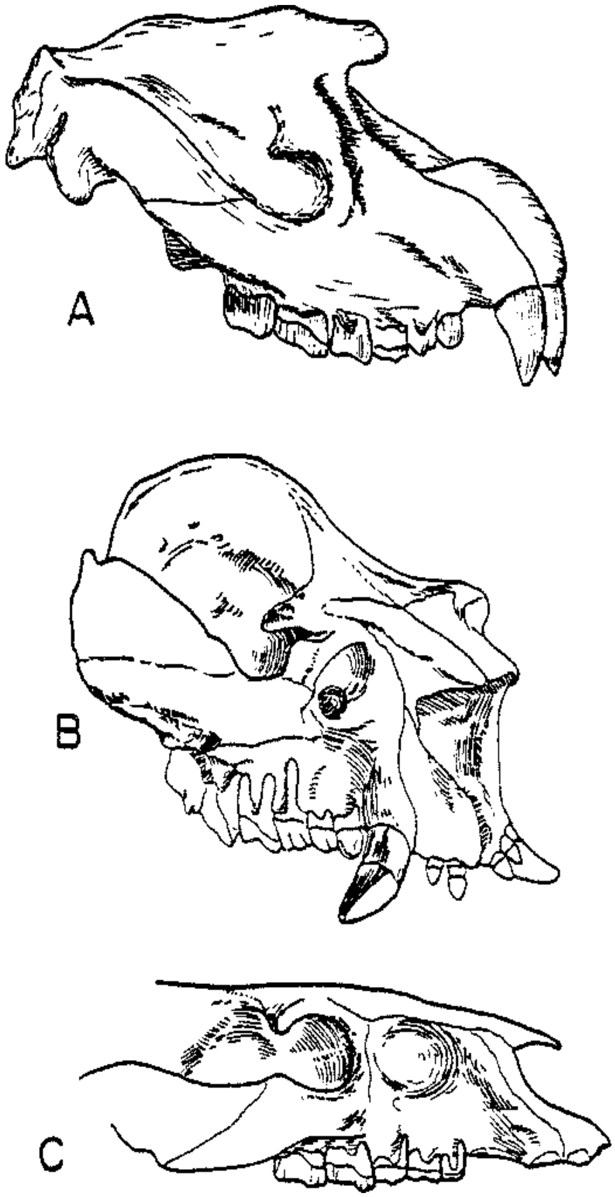

FIGURE 2— Preorbital fossa development in A, *Cadurcodon*; B, *Metamynodon*; and C, *Amynodon*.

cause of the length of the snout it does not extend medial to the orbit. The fossa in *Cadurcodon* remains large, but due to shortening of the snout region, the fossa extends far medial to the orbit. *Metamynodon*, however, has a relatively small preorbital fossa, and in spite of reduction in snout length and hypertrophy of the canines the preorbital fossa does not extend medial to the orbit. Assuming there is a correlation between olfactory ability and preorbital fossa size, metamynodontines had a poorer sense of smell than other amynodontids. The original statement of reduced olfactory ability implying aquatic habits would therefore only apply to the tribe Metamynodontini.

REDUCTION IN SIZE OF THE LACRIMAL BONE

Many aquatic mammals have reduced or lost the lacrimal bone and lacrimal foramen (for a review see Mitchell and Tedford, 1973). Although this character is not universal among aquatic mammals (for example, the hippo, *Hippopotamus amphibius*, has a large lacrimal, see Gregory, 1920b) it may be of some use in amynodontids. A broad contact between the lacrimal and nasal is a primitive character for perissodactyls. A naso-lacrimal contact is retained in most amynodontids but in at least *Zaisanamynodon* and *Metamynodon* (Figure 3) the lacrimal is reduced and its contact with the nasal is broken by a backward extension of the maxilla, which contacts the frontal. If reduction in size of the lacrimal is indicative of aquatic habits this trait applies only to the Metamynodontini.

MUZZLE BREADTH

Howell (1930) stated that many aquatic mammals tend to have relatively broad muzzles. He believed that an increase in muzzle breadth was related to development of a nasal closure mechanism, which "crowded" the narial opening by a large fibro-muscular pad (see for example phocids and otters). Mitchell and Tedford (1973) also argued that a broad muzzle was an aquatic adaptation in *Enaliarctos* believing that it provided additional space for warming inspired air.

Metamynodontines have the largest muzzles in the family, but they are also relatively more brachycephalic than other amynodontids. Muzzle width is probably correlated with dietary habits (see Mead and Wall, 1998, for a review of this character). We do not believe this character provides useful information on the question of aquatic versus terrestrial mode of life in amynodontids.

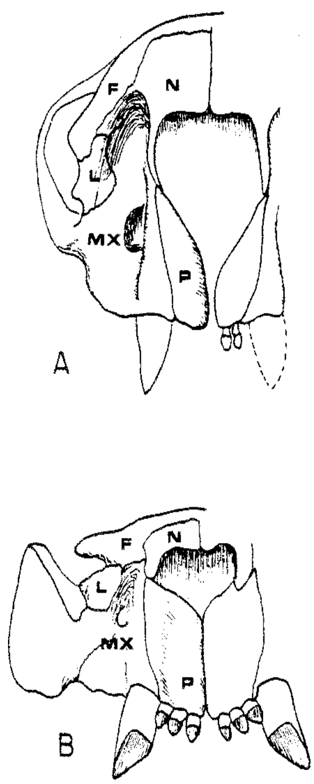

FIGURE 3— Lacrimal development in A, *Amynodontopsis*; and B, *Metamynodon*. Abbreviations: F, frontal; L, lacrimal; MX, maxilla; N, nasal; P, premaxilla.

ORBITAL POSITION

High placement of the orbit on the skull is a likely adaptation to a semi-aquatic mode of life. *Rostriamynodon* (Figure 1D) and *Amynodon* show no significant change in orbital position from other primitive perissodactyls (like *Hyrachyus*), and it is likely that both of these early amynodontids were terrestrial. Derived amynodontids exhibit two strikingly different orbital patterns. *Cadurcodon* (Figure 1C) represents one extreme in which the orbit is located low on the skull. Expansion of the frontal sinuses in cadurcodontines has elevated the nasals and skull roof far above their position in *Rostriamynodon*. Such unusual skull proportions in cadurcodontines can best be explained as proboscis modifications in this group (Wall, 1980). *Metamynodon* (Figure 1B) typifies the opposite pattern. In this genus the orbit is located high on the skull, practically even with the anterior skull roof, a position consistent with an amphibious mode of life.

SUMMARY OF CRANIAL CHARACTERS

There is no single skull pattern that can be defined as typically amynodontid. Since there are several different skull configurations it is likely that different amynodontids were adapted to different modes of life. Amynodontid cranial anatomy indicates a dichotomous evolutionary pattern stemming from a common ancestral skull form. This dichotomy is illustrated in Figure 4 using distorted coordinates to depict evolutionary change from the primitive amynodontid, *Rostriamynodon*. Cadurcodontines remained terrestrial but modified the skull for a proboscis. Only metamynodontines, shifted to an aquatic mode of life, and cranial anatomy in this group converged toward a *Hippopotamus*-like pattern.

POST-CRANIAL CHARACTERS

It is easy to differentiate a cursorial terrestrial mammal from a permanently aquatic one on the basis of skeletal anatomy. Most of the difference between these extremes can be attributed to two major factors. First, there are differences in mode of locomotion, appendicular in the terrestrial mammal and axial in the aquatic mammal. Second, is the differing effect of gravity on the two body forms. All land mammals must constantly support their own body weight. A column of water, however, passively supports aquatic mammals. The majority of mammals fall somewhere between extremes of cursoriality and permanently aquatic. Less specialized terrestrial and aquatic mammals are more difficult to differentiate. For example, can the life habits of *Ceratotherium simum* (white rhinoceros) and *Hippopotamus amphibius* be accurately determined solely from a study of postcranial anatomy? Both the rhino and the hippo move entirely by appendicular locomotion and, since the hippo feeds on land, each is subjected to gravitational force, but the two animals lead very different lives. Scott (1937) stated that "Short of the development of flippers, there seems to be no general character of skeleton which distinguishes aquatic from terrestrial mammals." We disagree with Scott's statement. Although skeletal differences may be subtle, they must exist if terrestrial and amphibious animals are optimally adapted to their different environments.

STRENGTH OF THORACIC SPINES

Scott (1941) commented that the neural spines in *Metamynodon* were "remarkably short and weak, another indication of aquatic habits." Scott (1937) also interpreted the unusually weak neural spines of *Astrapotherium* as an aquatic adaptation in this extinct South American ungulate. In neither paper did Scott explain why he thought weakness of neural spines was an aquatic adaptation. We assume, however, that Scott believed that head weight was partially supported by the surrounding water. The neural spines of large terrestrial ungulates are enlarged in the withers to serve as attachment sites for a powerful nuchal ligament supporting the neck and head. Two factors influence the size of the nuchal ligament, neck length, and head weight. The strong nuchal ligament in *Equus* is primarily due to its elongate neck. The nuchal ligament is better developed in oxen (Sisson and Grossman, 1953) where enlargement is primarily due to the larger skull size and addition of horns.

Figure 5 illustrates the skeletons of several modern and fossil ungulates. The six animals pictured are arranged in decreasing relative size of thoracic neural spines from top to bottom and left to right. *Brontops* (an extinct titanothere) and *Rhinoceros*, the Indian rhinoceros, exhibit the greatest development of neural spines. Both of these animals had relatively large heads requiring a well-developed nuchal ligament for weight support. *Amynodon* and *Hippopotamus* have neural spines intermediate in size between *Rhinoceros* and the next size group below. Although the hippo skull is much larger than the skull of *Amynodon*, its neural spines are

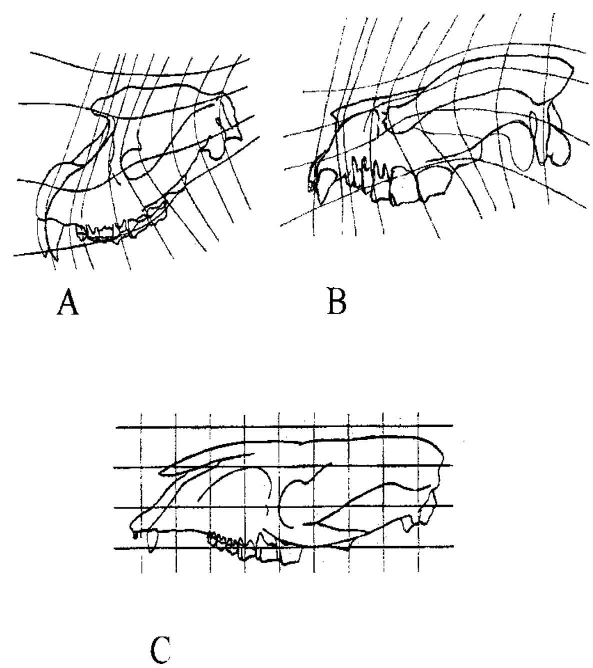

Figure 4— Distortion grid showing cranial modifications in A, *Cadurcodon* and B, *Metamynodon* based on the primitive amynodontid C, *Rostriamynodon*.

only slightly better developed than in this primitive amynodontid. Based solely on the large size of its skull, the hippo should have neural spines larger than the rhino and roughly equal to that of the titanothere. Since it does not, the hippo probably depends on periodic support from water to relieve stress on neck musculature and the nuchal ligament.

The neural spines of *Metamynodon* are even more weakly developed than in *Hippopotamus* and show a clear size reduction from the condition seen in *Amynodon.* As pointed out by Scott (1937), *Astrapotherium* shows an extreme reduction in neural spine size. Part of this weakness could be due to the small size of the skull, but even the lightly built tapir has better neural spine development than *Astrapotherium*.

There is a clear association between well-developed thoracic neural spines and terrestrial habits in large ungulates. A reduction in neural spine size could be related to acquisition of amphibious habits. Based on this character, *Amynodon* and *Sharamynodon* (a basal cadurcodontine whose complete skeleton is illustrated in Osborn, 1936) fall into a medium-sized terrestrial ungulate range, whereas *Metamynodon* neural spine development indicates an aquatic mode of life for this taxon.

RIB CAGE DIAMETER

The broad, expansive rib cage of *Metamynodon* has been compared to that of *Hippopotamus* as additional evidence for aquatic habits in amynodontids (see for example, O'Harra, 1920; Troxell, 1921; and Scott, 1941). However, Howell (1930) did not believe there was any relationship between aquatic habits and development of a barrel-like chest cavity in *Hippopotamus*. Instead, Howell suggested that the food habits of hippos required an enormous gut, which expanded the rib cage.

Although increased space for an enlarged digestive tract may be the proximal cause for ribcage expansion, the ultimate factor allowing such a modification to occur may still have been a shift to aquatic habits. Coombs (1975) presented a mechanical analysis of weight forces acting on a round-bodied tetrapod and a narrow-bodied sauropod. His analysis showed that weight is supported by serratus musculature originating along the ribcage and inserting on the scapula. Contraction of the serratus musculature creates a force pulling the rib cage outward. This force is resisted by ligaments spanning the articular surfaces between the ribs and vertebral column and by ventral rib attachment to the sternum (Coombs, 1975). Rotational force or moment is the product of

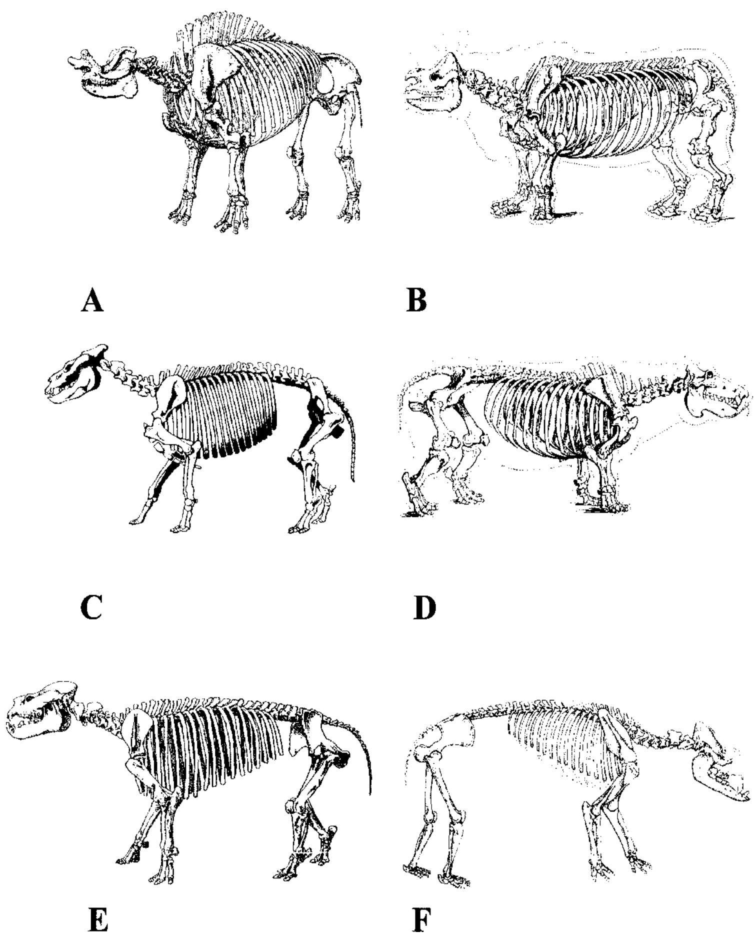

FIGURE 5—Skeletons of various ungulates illustrated in order of decreasing size of thoracic neural spines (a good indicator of nuchal ligament size) relative to skull size and neck length. A, *Brontops* (Scott, 1941); B, *Rhinoceros* (Young, 1962); C, *Amynodon* (Wall, 1998); D, *Hippopotamus* (Young, 1962); E, *Metamynodon* (Scott, 1941); and F, *Astrapotherium* (Scott, 1937). Not to scale.

a force times its lever arm. Rotational force for a given body weight will be greater in a round-bodied animal than in a narrow-bodied one. Therefore a round-bodied animal must either develop stronger resistance forces to compensate for its rib cage mechanical disadvantage or find some other method of reducing rotational force on the ribs (or both). Coombs pointed out that resistance force at the ribs can be increased by enlarging the lever arm of Rp (this is accomplished by increasing the distance between rib tuberculum and capitulum). Since the transverse processes (capitulum attachment site) on thoracic vertebrae in *Metamynodon* are relatively large (Scott, 1941), this animal has shown some selection for increase in resistance force acting on the ribs. If *Metamynodon* were aquatic however, additional relief from rotational stress at the ribcage would result from water buoyancy. It is conceivable that the ability to at least temporarily relieve the ribcage from body load stress by entering water made body cavity expansion mechanically feasible in both *Metamynodon* and *Hippopotamus.*

Ribcage evidence implies that *Metamynodon* could have been semi-aquatic. *Amynodon* and *Sharamynodon* have considerably narrower bodies than *Metamynodon*, and the ribs themselves were more like the characteristic t-shape of terrestrial mammals. It seems likely therefore that at least primitive amynodontids were terrestrial.

Limb proportions

The relative lengths of appendicular skeletal elements provide useful insights into the locomotor adaptations of mammals (see discussion in Wall and Hickerson, 1995). Locomotor differences between large terrestrial and aquatic ungulates should be discernable. The large size of both rhinos and hippos requires a significant locomotor out force to overcome inertia during changes in motion. There can be differences, however, in the amount of outward force that is actually used in propulsion and the amount that is "wasted." The nature of the substrate the animal is traveling on is an important factor. A hard, packed substrate, as on dry land, provides firmer footing, and relatively little energy is lost in moving across it. A muddy river or marsh bottom, however, will give when the animal tries to push off, decreasing propulsive force. In addition deep mud requires additional force to slog through it. Another factor influencing the amount of force required for locomotion is the medium through which the animal is moving. A terrestrial rhino meets little resistance from surrounding air compared to the water resistance faced by a submerged aquatic mammal.

Although the mode of locomotion is the same in the rhino and hippo the amount of force required to produce movement will be different, therefore modifications of the skeleton should be visible in the hippo to provide greater force. The magnitude of the propulsive force produced by the limbs pushing off the ground is related to the amount of input force and the lever arm lengths of these two forces. This relationship can be formulated as: $F_o = F_i I_i / I_o$ where F_o is force output, or as in this case propulsive force; F_i is force input (which for the front limb comes primarily from contraction of the triceps muscle); I_i is the input lever arm, or the perpendicular distance from the fulcrum (elbow joint) to the line of action of the muscle; and I_o. is the output lever arm, or distance from the fulcrum to ground contact. The formula indicates that output or propulsive force can be increased either by increasing input force or input lever arm, decreasing the output lever arm (for example *Teleoceras*), or a combination of these factors. To simplify analysis, manus length and triceps force have not been included in this study. Table 1 gives the length of the olecranon process (proportional to I_i) and total radius length (proportional to I_o) for a series of ungulates. The index presented in Table 1 shows the relative size of the input lever arm compared to the majority of output lever arm. Two groups can be distinguished from the index values presented. Animals with a high index are *Metamynodon*, *Teleoceras*, *Choeropsis* (pygmy hippopotamus), and *Hippopotamus*. All other mammals listed in Table 1 have small indices but some increase is visible based on overall body size and probably reduced cursorial habits. Thus *Rangifer* (caribou) has the lowest index measured in this study while the most ponderous animal measured, *Brontops*, has the highest index for a terrestrial mammal.

Based on evidence from limb proportions it appears that both *Metamynodon* and *Teleoceras* were aquatic and that *Aphelops* was terrestrial. The relatively low index of *Amynodon* places it not only with terrestrial mammals but also suggests that it was relatively cursorial. *Paramynodon* is interesting in that although it falls within the terrestrial group it is intermediate in proportions between *Amynodon* and *Metamynodon* (an idea first recognized by Colbert, 1938). Since *Paramynodon* is a primitive metamynodontine its limbs may have been only marginally adapted for aquatic life. Continued selection for aquatic adaptations therefore probably resulted in the condition seen in *Metamynodon*.

Muscle reconstruction

A thorough reconstruction of body musculature in amynodontids is beyond the scope of this paper, but relative development of certain muscles may be useful in differentiating between terrestrial and aquatic life habits. Of particular

Table 1 — Comparative forelimb proportions in some aquatic and terrestrial ungulates.

Taxon	Olecranon (mm)	Radius (mm)	Index (O/Rx100)
Rangifer (AMNH 24206)	62	288	21.53
Tapirus (UMA 24)	60	194	30.9
Ceratotherium (GCM 575)	122	367	33.3
Aphelops (UF 26043)	112	346	32.37
Brontops (SDSM 523)	190	476	39.9
Amynodon (AMNH 1961)	73	286	25.52
Paramynodon (AMNH 20013)	95	298	31.9
Metamynodon (MCZ 11968)	138	281	49.11
Teleoceras (UF 26038)	110	230	47.8
Choeropsis (AMNH 148452)	87	163	53.3
Hippopotamus (AMNH 15898)	137	282	48.58

interest are several muscles in the hind limb: Mm. popliteus, gastrocnemius, soleus, extensor digitalis longus, and peroneus tertius.

The same selection factors bringing about proportional changes in limb elements of aquatic and terrestrial mammals will also have an affect on the musculature operating the limbs. Relative muscle development can be determined by examination of the muscle's site of origin and insertion.

The popliteus originates in a pit on the lateral epicondyle of the femur. In *Hippopotamus*, *Teleoceras*, and *Metamynodon*, this pit is large and distinct. In *Ceratotherium* and *Aphelops* the popliteus pit is shallower and not as distinct. Difference in pit size between these two groups implies that Mm. popliteus is performing differently in these two groups of animals. The popliteus inserts high on the tibia, functionally it can act as a synergist, aiding the Mm. gastrocnemius/soleus complex (which inserts on the calcaneum) in plantar flexion of the foot. Enlargement of the gastrocnemius/soleus musculature in *Hippopotamus*, *Teleoceras*, and *Metamynodon* is also indicated by increased roughness of the femoral supracondyloid crests and head of the calcaneum (the calcaneal tuber in *Metamynodon* is also relatively longer than in terrestrial rhinos). The reason for the differences cited above becomes apparent from a study of hind limb mechanics. The ankle joint is functionally analogous to the elbow joint (they can both act as Class I levers) and the same relationship between in forces and out forces described above holds true for the ankle as well. The amount of propulsive force applied to the ground (F_o) is proportional to the input force and lever arm. For plantar flexion at the ankle joint the input force is provided by Mm. popliteus, gastrocnemius, and soleus. The input lever arm is the length of the calcaneum tuber. Since both of these components are enlarged in *Hippopotamus*, *Teleoceras*, and *Metamynodon*, these animals could produce greater propulsive force than is possible in the relatively equal-sized terrestrial rhinos. As mentioned above, an aquatic animal meets more resistance while walking than a terrestrial mammal. This evidence supports an amphibious mode of life for *Metamynodon* and *Teleoceras*.

Mm. extensor digitalis longus and peroneus tertius are important in maintaining the stifle joint which locks the hind limb in place while the animal is standing (as in horses). Both of these muscles originate from the extensor fossa on the distal end of the femur just posterior to the lateral ridge of the trochlea. *Ceratotherium* and *Aphelops* have an expanded, distinct extensor fossa. *Hippopotamus*, *Metamynodon* and *Teleoceras*, however, have a reduced extensor fossa. As mentioned above, Mm. extensor digitalis longus and peroneus tertius help maintain the stifle-joint, an important weight bearing adaptation in terrestrial ungulates. The relatively poor development of this mechanism in *Hippopotamus*, *Metamynodon* and *Teleoceras* could be due to acquisition of aquatic habits, which provided weight support from surrounding water.

The only amynodontid available for comparison with *Metamynodon* is the primitive genus, *Amynodon*. In *Amynodon* the popliteus pit is distinct, but the crests along the supracondyloid fossa are not enlarged, the fossa itself is shallow and the calcaneum tuber is relatively smaller than in *Metamynodon*. These skeletal characters suggest that *Amynodon* had a large popliteus but that its gastrocnemius/soleus complex was not enlarged. Most cursorial ungulates, including *Equus*, have a large popliteus. Terrestrial mediportal mammals generally show a reduction in size of M. popliteus, whereas large amphibious ungulates increase the size of the popliteus. Apparently the popliteus is serving a different purpose in all three groups (cursorial, mediportal, and semi-aquatic). In cursorial mammals M. popliteus increases spring in the leg, particularly in saltators like *Gazella*. Heavy terrestrial mammals do not rely on speed to as great an extent and therefore M. popliteus is reduced. In semi-aquatic mammals M. popliteus adds to plantar flexion force (acting with the gastrocnemius and soleus), and therefore would be large in these mammals. *Amynodon* also has a well-developed extensor fossa indicating this animal probably had an efficient stifle joint.

Summarizing characters of hind limb musculature, *Metamynodon* and *Teleoceras* show aquatic adaptations similar to those of *Hippopotamus*. *Amynodon*, however, does not; this animal shows characters more typical of a cursorial or subcursorial mammal. It seems evident therefore that primitively amynodontids were subcursorial, terrestrial mammals and that metamynodontines shifted to a semi-aquatic mode of life.

ADAPTIVE RADIATION OF METAMYNODONTINES

Intermediate evolutionary stages between *Amynodon* and *Metamynodon* are seen in two Asiatic amynodontids, *Paramynodon* and *Zaisanamynodon* and one North American genus, *Megalamynodon*. These genera show a clear trend toward increasing adaptation for an amphibious mode of life. *Zaisanamynodon* in particular comes close to (but does not equal) *Metamynodon* in a number of these characters. The initial radiation of metamynodontines occurred during the middle Eocene. *Megalamynodon* and *Paramynodon* exhibit roughly equivalent adaptive stages in North America and Asia. Unfortunately, the relatively poor fossil record for both of these primitive metamynodontines does not allow for a definitive systematic review of the relationship between these two taxa.

Historically, *Megalamynodon* is viewed as the ancestor of *Metamynodon* (Scott, 1945), however, the Asiatic *Zaisanamynodon* shares more derived characters with *Metamynodon* (Wall, 1989). Migration between Asia and North America was a significant factor in amynodontid evolution from the middle Eocene to the middle Oligocene (Wall, 1998). Hanson (1996) has assigned the amynodontid specimens from Hancock Quarry (upper Clarno Formation, Duchesnean) to the Asiatic taxon *Procadurcodon*. Hanson suggested that *Procadurcodon* could be a sister taxon to *Zaisanamynodon*. This scenario would open up the possibility that *Metamynodon* is derived from an Asiatic source rather than descending from *Megalamynodon*.

Metamynodon is a rare component of the late Eocene mammal fauna of North America. Fossils of *Metamynodon* are significantly more abundant from early Oligocene (Orellan) strata. This apparent increase in *Metamynodon* population size might be an artifact of the extensive channel sandstones from this time period exposed in the southern unit of Badlands National Park (in fact these beds are extensively referred to in the literature as *Metamynodon* channel sandstones). A decline in *Metamynodon* numbers probably occurred during the Whitneyan since this taxon is not evident in the *Protoceras* channel sandstones (Poleslide Member of the Brule, well exposed in the southern unit and Palmer Creek areas of Badlands National Park). *Metamynodon* specimens are reported from Whitneyan deposits in North Dakota, making for a more complicated evolutionary scenario than previously thought.

The taxonomic relationship of the enigmatic "*Cadurcotherium*" *indicum* from the Miocene of India is open to question. Wall (1989) placed this taxon in the Metamynodontini based primarily on dental characters. Until recently the skull and skeleton of this genus was unknown. The dentition in this rhino is the most highly derived of any amynodontid, but is most like *Cadurcotherium cayluxi*. Bonis (1995) described a skull and partial skeleton of *Cadurcotherium cayluxi* from the European Oligocene. This animal is clearly more like cadurcodontines than metamynodontines. If the amynodontid from the Miocene of India is not a metamynodontine, then *Metamynodon* may be the most derived member of the tribe.

In summary, anatomical evidence supports the taphonomic association of *Metamynodon* with a riparian habitat. The front cover illustration for this volume presents the likely appearance of this amphibious rhino in a streamside swale habitat with herbaceous vegetation (the habitat reconstruction is based on Retallack, 1983).

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A PRELIMINARY ASSESSMENT OF PALEONTOLOGICAL RESOURCES AT BIGHORN CANYON NATIONAL RECREATION AREA, MONTANA AND WYOMING

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Abstract—Paleontological resources occur throughout the Paleozoic and Mesozoic formations exposed in Bighorn Canyon National Recreation Area. Isolated research on specific geologic units within Bighorn Canyon has yielded data on a wide diversity of fossil forms. A comprehensive paleonotological survey has not been previously undertaken at Bighorn Canyon. Preliminary paleontologic resource data is presented in this report as an effort to establish baseline data.

INTRODUCTION

Bighorn Canyon National Recreation Area (BICA) consists of approximately 120,000 acres within the Bighorn Mountains of north-central Wyoming and south-central Montana (Figure 1). The northwestern trending Bighorn Mountains consist of over 9,000 feet of sedimentary rock. The predominantly marine and near shore sedimentary units range from the Cambrian through the Lower Cretaceous. Many of these formations are extremely fossiliferous. The Bighorn Mountains were uplifted during the Laramide Orogeny beginning approximately 70 million years ago. Large volumes of sediments, rich in early Tertiary paleontological resources, were deposited in the adjoining basins.

This report provides a preliminary assessment of paleontological resources identified at Bighorn Canyon National Recreation Area.

STRATIGRAPHY

The stratigraphic record at Bighorn Canyon National Recreation Area extends from the Cambrian through the Cretaceous (Figure 2). The only time period during this interval that is not represented is the Silurian. Brief descriptions of the stratigraphic units exposed in Bighorn Canyon are provided below.

Gros Ventre Formation & Gallatin Limestone (Cambrian)
Cambrian strata are poorly exposed in the deepest cuts into Bighorn Canyon. The lack of paleontological specimens has led to the Gros Ventre and Gallatin Formations being mapped as one unit. The Gallatin is a gray limestone unit with a mud-cracked gray-green shale and beds of flat-pebble limestone conglomerate. Identification of these units is based upon lithologic correlation with similar strata exposed in the Bighorn Basin.

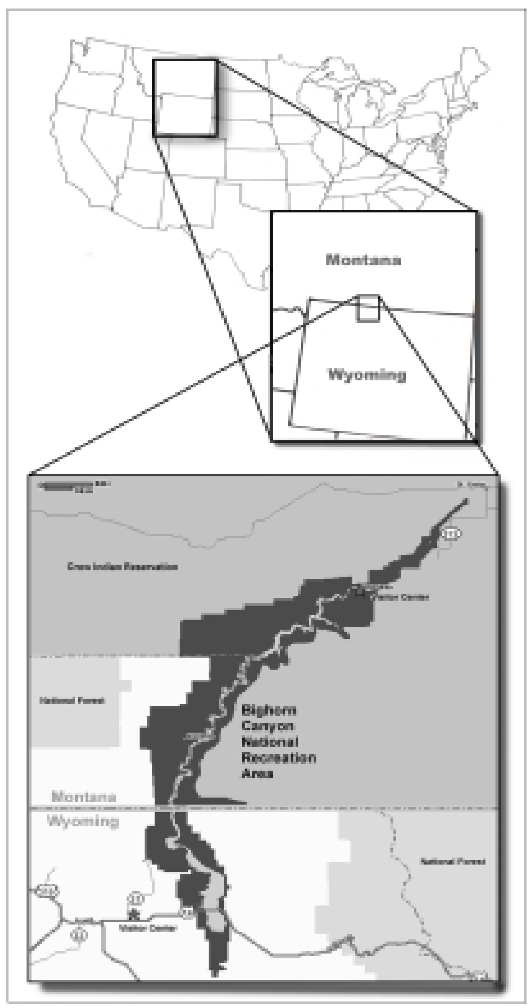

Figure 1— Map showing the location of Bighorn Canyon National Recreation Area, Montana and Wyoming.

BIGHORN DOLOMITE (Upper Ordovician)
The Ordovician Bighorn Dolomite is appoximately 400 feet thick in Bighorn Canyon. The unit consists of a lower massive dolomitic limestone member and an upper thin-bedded dolomite and limestone member. The lower member forms a distinct continuous cliff through the Bull Elk Basin section of the canyon. Darton (1906) reported the Bighorn Dolomite to be Upper Ordovician in age. An archaeogastropoda is reported from the Bighorn Dolomite in Bighorn Canyon.

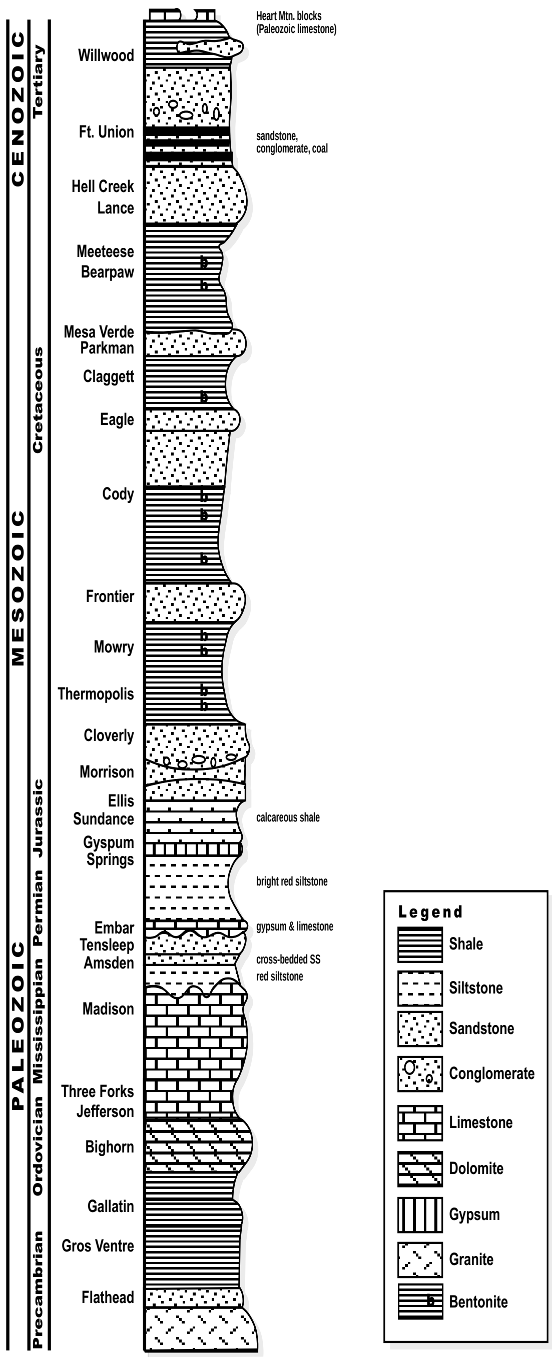

FIGURE 2— Stratigraphic column for Bighorn Canyon National Recreation Area, Montana and Wyoming.

THREE FORKS SHALE & JEFFERSON LIMESTONE (Devonian)
Devonian age rocks, believed to correlate to the Three Forks Shale and the Jefferson Limestone, are exposed in Bighorn Canyon along Big Bull Elk Creek and in Devils Canyon. The Big Bull Elk Creek section is approximately 220 feet thick and the Devils Canyon section is approximately 180 feet thick. Brachiopods of the genus *Atrypa* sp. were collected from this unit at about 60 feet below the contact with the Madison Limestone in Devils Canyon. *Atrypa* sp. and the coral *Amplexiphyllum* sp. were collected from the limestones between 40 to 60 feet below the contact with the Madison Limestone in the Big Bull Elk Creek area (Richards, 1955).

MADISON LIMESTONE (Mississippian)
The Madison Limestone consists of approximately 700 feet of limestone and dolomite and forms the rim of Bighorn Canyon for its entire length. An abundance of marine invertebrates, including bryozoans, corals, brachiopods, and crinoids are preserved in the Madison Limestone. Crushing teeth of the cochliodont *Hybodus* also occur in this unit.

AMSDEN FORMATION (Pennsylvanian)
The Amsden Formation consists of interbedded sandstone, limestone, siltstone and shale. The unit ranges from 230 to 280 feet in the Bighorn Mountains. Marine invertebrate fossils were collected from the Amsden Formation by L.G. Henbest of the U.S. Geological Survey (Richards, 1955). The following fossils are reported from the Amsden: *Bradyina sp., Climacammina sp., Profusulinella sp., Pseudostaffella sp., Tetrataxis sp.,* and sponge spicules.

TENSLEEP SANDSTONE (Pennsylvanian)
The Tensleep Sandstone is a light-gray to yellow-gray, cross-bedded sandstone. This unit ranges between 75 and 110 feet thick in the Bighorn Mountains. L.G. Henbest of the U.S. Geological Survey collected *Bradyina sp., Climacammina sp., Fusulina rockymontana, Pseudostaffella sp., Wedekindellina euthysepta,* and *W. excentrica* from the Tensleep Sandstone (Richards, 1955).

EMBAR FORMATION (Permian)
The Embar Formation consists of a series of limestones, dolomites, shales, siltstones and sandstones. The unit is up to 100 feet thick in the Bighorn Mountains. No fossils are reported from the Embar Formation (Richards, 1955).

CHUGWATER FORMATION (Permian/Triassic)
The Chugwater Formation forms red bluffs around the Bighorn and Pryor Moutains. This fine-grained red sandstone unit ranges from 450 to 650 feet thick. The only fossils from this unit occur in the gray chert pebbles within the basal conglomerate. These are reported to be Pennsylvanian fauna eroded from the Tensleep Sandstone or Amsden Formation (Richards, 1955).

PIPER FORMATION (Jurassic)
The Piper Formation is a red sandstone and siltstone unit

with beds of gray limestone and gypsum. This unit is between 150 and 200 feet thick in the Bighorn Mountains. No fossils are reported from the Piper Formation.

SUNDANCE FORMATION (Jurassic)
The Sundance Formation, previously referred to as the Rierdon and Swift Formations, is a series of fossiliferous marine sandstones and shales. The total thickness of this unit is about 500 feet on the eastern flank of the Bighorn Mountains. The lower section contains numerous *Belemnites sp., Gryphaea sp.*, and the star-shaped crinoid columnals *Pentacrinus* sp.. The upper section contains a lenticular fossiliferous sandstone bed at the top of the unit (Richards, 1955).

MORRISON FORMATION (Jurassic)
The Morrison Formation is a gray-green siltstone and sandstone unit that ranges in thickness between 140 to 280 feet in the Bighorn Mountains. Fragmentary dinosaur bones are preserved in the non-marine Morrison Formation. A sauropod track locality was identified on the west side of Sykes Mountain in the upper portion of the Salt Wash Member (Engelmann and Hasiotis, 1999).

CLOVERLY FORMATION (Early Cretaceous)
The Early Cretaceous Cloverly Formation was first described by Darton for exposures on the east flank of the Bighorn Mountains (Darton, 1904). The formation is exposed in the northern and eastern portions of the Bighorn Mountains and ranges between 300 to 400 feet thick. This formation consists of a basal conglomeratic sandstone member, a middle variegated shale member, and upper shale, siltstone, and sandstone member. Fossils have not been reported from this formation in the Bighorn Mountains.

THERMOPOLIS SHALE (Early Cretaceous)
A section of the Thermopolis Shale was measured in the Bighorn Mountains on the east side of Soap Creek dome (Rogers, et al., 1948). This unit consists of approximately 425 feet of dark-gray shale with many bentonite beds and ironstone concretions. The unit is crosscut by fine-grained sandstone dikes. Fossils are not reported from this unit in the Bighorn Mountains.

MOWRY SHALE (Early Cretaceous)
The Mowry Shale lies conformably over the Thermopolis Shale in the Bighorn Mountains. This unit is exposed on the eastern edge of the Bighorns and ranges in thickness between 350 and 400 feet. The Mowry consists of dark-gray shale and light-gray siltstone and sandstone. Fish scale impressions are abundant in the Mowry Shale (Richards, 1955).

FRONTIER FORMATION (Late Cretaceous)
The Late Cretaceous Frontier Formation consists about 260 feet of dark-gray concretionary, sandy shale with interbedded bentonite (Richards, 1955). This unit contains a few lenses of cherty sandstone in the Bighorn Mountains and in the Bighorn Basin. Fossils are not reported from this unit in the Bighorn Mountains.

CODY SHALE (Late Cretaceous)
The Cody Shale is approximately 2000 feet thick and is composed of seven members (Thom, et al., 1935). All of the members are fossiliferous except for the lowest member of the Cody Shale. Identification of the fossil material was made by W.A. Cobban (Richards, 1955).

Greenhorn Calcareous Member: *Allocrioceras annulatum, Mytiloides labiatus, Ostrea sp., Plicatula sp., Pseudaspidoceras sp., Quitmaniceras sp., Scaphites delicatulus, Vascoceras catinus, Watinoceras reesidei*, and fish bones.

Carlile Shale Member: *Baculites besairiei, Crassatellites reesidei, Inoceramus altus, I. flaccidus, Membraniporina sp., Nucula sp., Ostrea congesta, Placenticeras stantoni, Prionocyclus wyomingensis, Scaphites corvensis, S. nigricollensis, Tritonium kanabense*, and *Veniella goniophora*.

Niobrara Shale Member: *Anomia sp., Baculites codyensis, B. mariasensis, B. sweetgrassensis, Clioscaphites vermiformis, Inoceramus deformis, Ostrea congesta, Pteria nebrascana, Scaphites impendicostatus, Veniella sp.* and indeterminant nautiloids, gastropods, pelecypods, echinoid spines, and fish scales.

Telegraph Creek Member: *Baculites sp., Ostrea sp.*, and *Scaphites hippocrepis.*

Shale Member equivalent to the Eagle Sandstone: This unit is considered equivalent to the Eagle Sandstone based upon the fossil assemblage including: *Anomia sp., Baculites aquilaensis, B. haresi, B. minerensis, B. thomi, Callista pellucida, Capulus microstriatus, Cardium whitei, Corbulamella gregaria, Crenella elegantula, Cymbophora sp., Cymella montanensis, Drepanochilus evansi, Glyptoxoceras novimexicanus, G. rubeyi, Goniochasma crockfordi, Inoceramus barabini, I. saskatchewanensis, I. subdepressus, Leptosolen conradi, Lima sp., Lithophaga sp., Pholadomya subventricosa, Pinna dolosoniensis, Placenticeras meeki, P. planum, Scaphites aquilaensis, S. hippocrepis, S. stantoni, Spironema tenuilineata, Syncyclonema halli, Tellina scitula, Volsella meeki*, crustacean remains, fish scales and reptilian bones.

Claggett Shale Member: *Baculites aquilaensis, B. asperiformis, B. haresi, Caprinella coraloidea, Inoceramus barabini, I. sagensis, I. saskatchewanensis, I. vanuxemi, Jeletzkytes brevis, Pteria notukeuensis*, and *Yoldia sp.*

PARKMAN SANDSTONE (Late Cretaceous)
The Parkman Sandstone is a sandy shale and sandstone approximately 250 feet thick in Bighorn Canyon. Darton, who

first described this unit, made a small collection of fossils from the Parkman Sandstone (Darton, 1906). These fossils were identified by T.W. Stanton as being Late Cretaceous marine organisms. The beds above the basal sandstone of the Parkman Sandstone, that occur northwest of Hardin, have been suggested to be a continuation of the fresh-water and brackish-water beds of the Judith River Formation (Hancock, 1920; Thom et al., 1935).

BEARPAW SHALE (Late Cretaceous)
The Bearpaw Shale is a fossiliferous, dark-gray marine shale that is exposed in the Ninemile area. The unit is approximately 850 feet thick. Richards (1955) divides the Bearpaw Shale into three members.

Upper Member: *Baculites compressus, B. grandis, Cymbophora cf. gracilis, Chlamys nebrascensis, Discoscaphites nicolletti, Inoceramus altus, I. barabini, Jeletzkytes nodosus, Lucina occidentalis, L. subundata, Nucula planimarginata, Ostrea sp., Placenticeras meeki, P. planum, Polinices concinna, Protocardia subquadrata, Pteria linguaeformais*, and *Yoldia evansi.*

Bentonitic Member: *Acmaea? occidentalis, Baculites compressus, Cuspidaria moreauensis, C. ventricosa, Cymbophora gracilis, Cymella meeki, Dentalium pauperculum, Drepanochilus evansi, D. nebrascensis, Ellipsoscapha occidentalis, E. subcylindrica, Fasciolaria gracilenta, Gervillia recta, Inoceramus vanuxemi, I. tenuilineatus, Jeletzkytes brevis, J. nodosus, J. quadrangularis, Lucina subundata, Ostrea subalata, Placenticeras intercalare, P. meeki, Polinices concinna, Pteria parkensis, Syncyclonema halli, Yoldia evansi,* and *Y. ventricosa.*

Lower Member: *Baculites compressus, Didymoceras nebrascense, Inoceramus barabibi, I. cf. palliseri, I. sagensis, I. saskatchewanensis, I. tenuilineatus, Lucina sp., Ostrea sp., Placenticeras meeki,* and *Yoldia sp.*

Tertiary and Quaternary gravels and alluvium are present on the flanks of the Bighorn Mountains. Six principal terraces are associated with the Bighorn River and its tributaries. No fossils have been reported from the terraces.

PALEONTOLOGICAL RESOURCE PROTECTION

Two case incident reports related to the unauthorized collecting of paleontological resources were produced in 1994. Both incidents documented park visitors involved with the illegal collection of invertebrate fossils from Mesozoic rock units, possibly the Sundance Formation, within BICA. In both cases, the unauthorized fossil collecting occurred in the Sykes Mountain area.

PALEONTOLOGICAL RESOURCE INTERPRETATION

The Bighorn Canyon Visitor Center in Lovell has paleontological displays titled “Rocks Reveal the Past”. The following specimens are included in this interpretive exhibit.

CAMBRIAN
- algal stromatolite
- trilobite

ORDOVICIAN
- sponge
- coral (honeycomb and large vesicles)
- mollusk

MISSISSIPPIAN
- brachiopod casts and molds
- coral

TRIASSIC
- coral

JURASSIC
- dinosaur bone fragments
- gastroliths
- oysters (*Gryphea*)
- pelecypods
- belemnites

CRETACEOUS
- ammonites, baculites, and scaphites
- bivalves – pelecypods
- shark’s teeth
- crocodile teeth

PALEONTOLOGICAL RESOURCES NEAR BIGHORN CANYON

The remains of an *Allosaurus* were collected from Morrison Formation on BLM land about 20 miles south of Bighorn Canyon National Recreation area.

Bighorn Basin: A thick sequence of fossiliferous Paleocene and Eocene strata, including the Polecat Bench, Fort Union, and Willwood Formations, occurs in the Bighorn Basin. The fossil-bearing strata have been divided into thirteen different mammal zones including: two Torrejonian zones, five Tiffanian zones, one Clarkforkian zone, and 5 Wasatchian zones (Woodburne, 1987).

Natural Trap Cave: Natural Trap Cave is a karst sinkhole feature developed within the Mississippian Madison Limestone on the western slope of the Bighorn Mountains in north-central Wyoming. Late Pleistocene paleontological resources have been excavated from stratified sediments within Natural Trap Cave (Anderson, 1974).

ACKNOWLEDGEMENTS

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AN AETOSAUR (REPTILIA:ARCHOSAURIA) FROM THE UPPER TRIASSIC CHINLE GROUP, CANYONLANDS NATIONAL PARK, UTAH

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Abstract—A partial skeleton of the aetosaur *Stagonolepis* sp. is the first tetrapod body fossil recovered from Upper Triassic strata in Canyonlands National Park. The specimen consists of a partial tooth and numerous disarticulated vertebrae, ribs, and scutes found in the Blue Mesa Member of the Petrified Forest Formation (Chinle Group) near Upheaval Dome. *Stagonolepis* is an index taxon of the Adamanian land-vertebrate faunachron, and indicates a late Carnian (228-218 Ma) age for the Blue Mesa Member in Canyonlands National Park, an age supported by lithostratigraphic and biostratigraphic correlations to other Stagonolepis-bearing strata.

INTRODUCTION

The Chinle Group, as defined by Lucas (1993), consists of all nonmarine Upper Triassic strata in the western United States. These deposits were laid down in a vast depositional system that spanned at least 2.5 million km^2. Despite more than 120 years of vertebrate paleontological research on the Chinle, we are not aware of any Upper Triassic tetrapod body fossils from Canyonlands National Park (CANY), even though there are extensive, well-exposed Chinle outcrops throughout the park. Recently Hasiotis (1995) described Upper Triassic crayfish burrows from CANY, and Lucas et al. (1995) described an Upper Triassic dinosaur footprint from CANY. Here we provide a description of the first Chinle body fossil reported from CANY, a partial skeleton of the aetosaur *Stagonolepis* sp., and discuss its biochronological significance. In this paper NMMNH = New Mexico Museum of Natural History and Science, Albuquerque.

STRATIGRAPHY

Previous studies of the Chinle Group in the vicinity of CANY include Stewart et al. (1972) and O'Sullivan and MacLachlan (1975). Here, we follow the lithostratigraphy of Stewart et al., (1972), with some subsequent modification as advocated by Lucas (1993).

The stratigraphic section we use here was measured near Upheaval Dome, where Chinle strata disconformably overlie the Lower-Middle Triassic Moenkopi Group and are overlain disconformably by the Upper Triassic-Lower Jurassic Wingate Sandstone. Due to stratigraphic disruption caused by the salt diapir that forms Upheaval Dome (Jackson et al., 1998), the section dips 20 degrees to N60 degrees east. The Chinle Group at this section consists of the following named units (ascending): Shinarump Formation, Cameron Formation, Petrified Forest Formation, Owl Rock Formation, and Rock Point Formation (Fig. 1). The Petrified Forest Formation is readily subdivided into the lower Blue Mesa Member, medial Moss Back Member, and upper Painted Desert Member. The complete Chinle Group section is approximately 138 m thick (Fig. 1).

The partial skeleton we describe here was found in a grayish-green, pisolitic calcrete ledge 11.5 m above the base of the Blue Mesa Member of the Petrified Forest Formation (Fig. 1). The fossiliferous horizon, designated NMMNH locality 3279, consists of an 0.7-m-thick, slightly sandy, very well-indurated pisolitic calcrete to calcarenite. The matrix is grayish yellow-green, unweathered, with some grayish red mottling, and locally weathers to yellowish gray. We interpret this deposit as representing a fluvial deposit that was subsequently subjected to extensive pedogenic modification. The tetrapod bones are jumbled and occur throughout this massive, non-stratified unit.

PALEONTOLOGY

The specimen we describe here is housed at the NMMNH, where it is catalogued as NMMNH P-26938. It consists of a nearly complete and prepared dorsal paramedian scute (Figs. 2-3), a partial tooth, and 14 matrix blocks with scattered vertebrae, ribs, and scutes (Tab. 1).

At least four groups of tetrapods known from the Chinle possess armor or armored elements that have a sculptured texture of pits and ridges—metoposaurid amphibians, phytosaurs, sphenosuchians, and aetosaurs. The scutes of NMMNH P-26938 are rectangular osteoderms and clearly not skull fragments, clavicles, or interclavicles of metoposaurid amphibians. Furthermore, the vertebrae associated with the

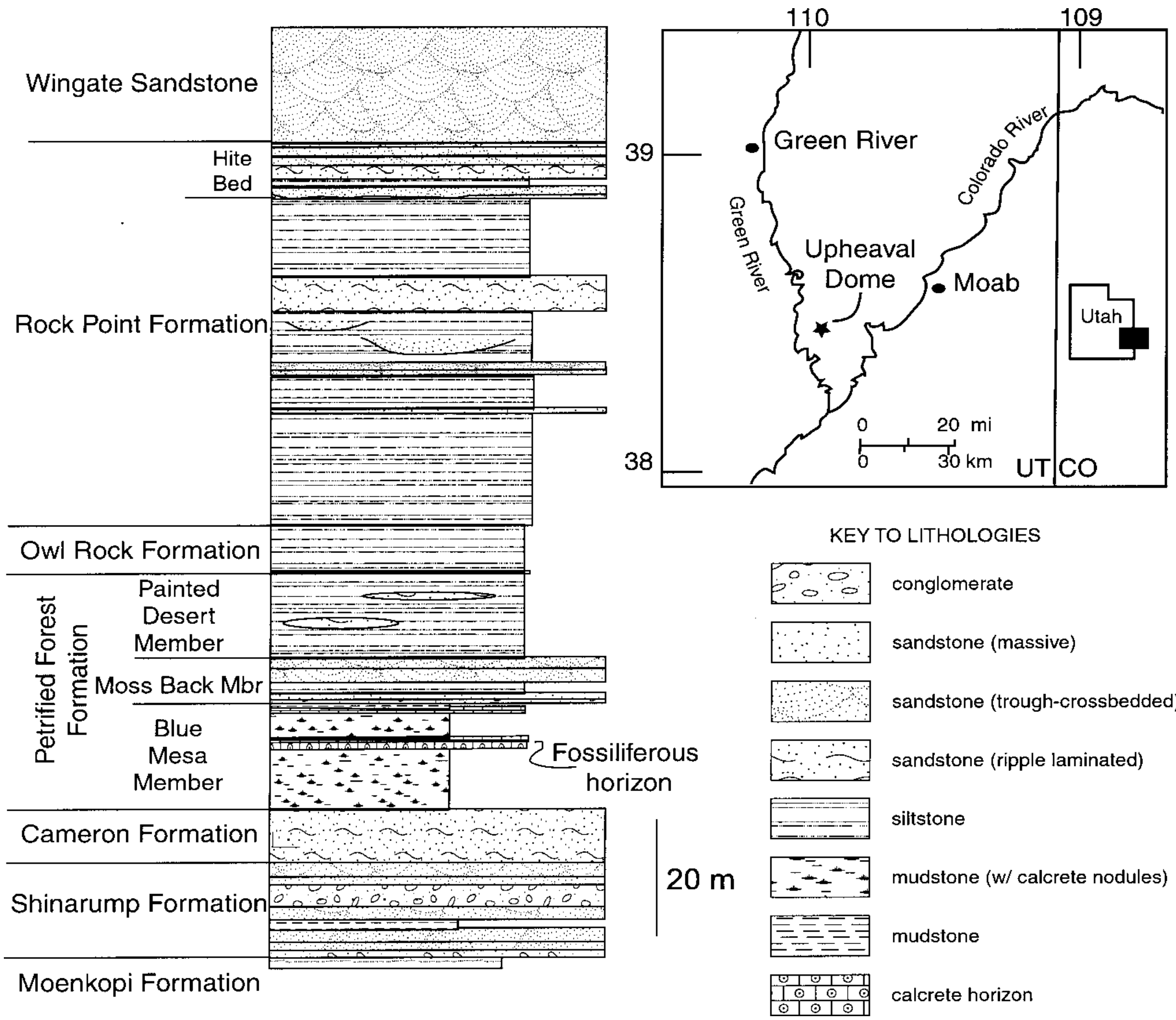

FIGURE 1— Location map and stratigraphic section showing the location and stratigraphic position of the fossil described here. Index map modified from Jackson et al. (1998).

specimen are taller than wide, and medially constricted, as are those of many archosaurs, and thus cannot represent metoposaurs. The flat, rectangular shape, presence of an anterior articulating surface, and lack of anteriorly- or posteriorly- projecting lappets on scutes assigned to NMMNH P-26938 preclude their assignment to any of the other armored archosaur groups. Phytosaur scutes are typically keeled and oblate to circular, and lack an articular surface. Sphenosuchian scutes (including those of rauisuchians) are flat, but generally either rhomboidal and/or possess anteriorly or posteriorly projecting lappets. Therefore, NMMNH P-26938 clearly pertains to an aetosaur.

The most diagnostic element of P-26938 is the incomplete dorsal paramedian scute (Fig. 2). Heckert and Lucas (1999) recently reviewed the phylogenetic significance of aetosaur scutes, and our taxonomy follows their conclusions. Diagnostic features of this scute include the lack of a ventral keel, its low width:length (W:L) ratio, the presence of an anterior bar (Figs. 2A, 3), the generally radial pattern of the shallow pits on the dorsal surface (Fig. 3), and the transverse arching (Fig. 2C,D). The lack of a ventral keel precludes assignment to the aetosaurs *Redondasuchus* and *Typothorax*.

As preserved, this scute is 35 mm long and 57 mm wide, yielding a low (1.6) W:L ratio. This size and low W:L ratio preclude assignment to the aetosaurs *Typothorax*, *Paratypothorax*, and *Aetosaurus ferratus*. The presence of an anterior bar precludes assignment to *Desmatosuchus*. The presence of pitting precludes assignment to *Coahomasuchus*. The scute is exceedingly fragile, and a block of matrix obscures details regarding the presence, position, and size of the dorsal boss. Normally, this structure is quite pronounced and contacts the dorsal margin of the scute in *Stagonolepis* (Case, 1932: pl. 1; Long and Ballew, 1985: figs. 13-14; Long and Murry, 1995: figs. 69-72). In this specimen the boss clearly does not extend anteriorly past the middle of the scute as a longitudinal keel, which precludes assignment to *Aetosaurus crassicauda*. The scute is gently arched transversely (Fig. 2C), as is typical in caudal paramedian scutes of *Stagonolepis* (Long and Ballew, 1985). Therefore, we assign this scute, and the associated partial skeleton, to *Stagonolepis* sp.

Of the other material assigned to P-26938, the tooth consists of a partial crown. The crown is short and bulbous, and conforms well to an aetosaur tooth (Walker, 1961), but is otherwise undiagnostic. The remaining material consists primarily of incompletely exposed vertebrae and ribs. Some of the vertebrae appear to have extensive transverse processes, a characteristic of *Stagonolepis* (Long and Murry, 1995), but are not well enough exposed to measure. The few other scutes that can be discerned are only exposed ventrally. A large, fragmentary phytosaur tooth is also exposed on one block, but is otherwise undiagnostic.

FIGURE 2— Photographs of NMMNH P-26938, a partial dorsal paramedian scute of *Stagonolepis* sp. from the Blue Mesa Member of the Petrified Forest Formation in CANY. (A) dorsal view; (B) ventral view; (C) anterior view; and (D) posterior view.

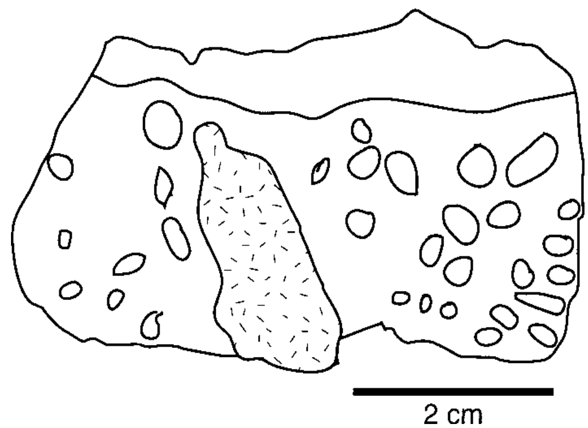

FIGURE 3— Interpretative sketch of NMMNH P-26938, a partial dorsal paramedian scute of *Stagonolepis* sp. from the Blue Mesa Member of the Petrified Forest Formation in CANY, based on the photograph in FIGURE 2A.

AGE

The aetosaur *Stagonolepis* is an index taxon of the Adamanian land-vertebrate faunachron (lvf) of Lucas and Hunt (1993). The type Adamanian fauna is from the general vicinity of "Dying Grounds" in the Blue Mesa Member at Petrified Forest National Park (PEFO). The Adamanian is of well-constrained latest Carnian age, and spans the time interval of 228-218 Ma (Lucas, 1997, 1998). The presence of *Stagonolepis* in the Blue Mesa Member of CANY indicates an Adamanian age for that unit. *Stagonolepis* was widely distributed during this time interval and can be used to correlate strata in North America, South America, and the United Kingdom (Lucas and Heckert, 1996).

CONCLUSIONS

An incomplete scute facilitates identification of a partial aetosaur skeleton as *Stagonolepis* sp. This aetosaur is an age-diagnostic fossil, and confirms lithostratigraphic correlation of the Blue Mesa Member in CANY to the Blue Mesa Member in PEFO. The presence of *Stagonolepis* indicates an Adamanian (latest Carnian) age for these strata.

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K. Kietzke discovered the specimen described here and brought it to our attention. Personnel in CANY facilitated research there by SGL, and provided a permit to allow the NMMNH to collect this specimen. T. Goodspeed and A.P. Hunt assisted in the field. J. Estep coated and photographed the specimen. Two reviewers offered helpful suggestions.

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GIANT ISLAND/PYGMY MAMMOTHS: THE LATE PLEISTOCENE PREHISTORY OF CHANNEL ISLANDS NATIONAL PARK

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ABSTRACT—The northern Channel Islands of California are included in Channel Islands National Park (CHIS). These modern islands are the remnant high ground of a late Pleistocene island named Santarosae. At some time during the Rancholabrean land mammal age Santarosae was colonized by mainland mammoths (*Mammuthus columbi*). With eustatic sea level rise due to the end of the Ice Age meltoff, as much as 76% of Santarosae was submerged. Mammoths met the challenge of diminished range and decreasing resources by size reduction, to less than 50% of the stature of *Mammuthus columbi*. The pygmy form (*Mammuthus exilis*) is known from San Miguel, Santa Rosa, and Santa Cruz islands. The Channel Islands contain the remains of the only island dwelling pygmy mammoths in the world.

INTRODUCTION

The California Channel Islands (Figure 1) have been known to produce remains of small mammoths since a Coast and Geodetic survey in 1856. These remains were first reported in scientific literature by Stearns (1873). Fifty-five years passed until the first paleontological report (Stock and Furlong, 1928) was published, giving the new species designation *(Elephas) Mammuthus exilis*.

Post-1928 published research of these island mammoths was essentially non-existent until investigations by Phil Orr of the Santa Barbara Museum of Natural History (SBMNH) were published (Orr 1956a, b, c; 1959; 1960; 1967; 1968). Even then, the mammoths were of secondary importance to Orr, who concentrated on island archaeology. His collection of mammoth remains was in support of his interpretation that early island people ate the last of the island mammoths.

Louise Roth (1982; 1984; 1990; 1992; 1993; 1996) conducted a series of zoological studies on the island mammoths. It should be noted here that those studies were based primarily on museum collections housed at the Santa Barbara Museum of Natural History (Orr's collections) and the Los Angeles County Museum (collected by Stock, Furlong, and others). Access to Santa Rosa Island was restricted by the Vail and Vickers Cattle Company.

During the 1970's a large collection of *M. exilis* remains was accumulated by Boris Woolley, a member of the ranch family. This collection was donated to the Santa Barbara Museum of Natural History in 1995, by his widow, Margaret.

The National Park Service acquired San Miguel, Santa Rosa, Las Anacapas, and a portion of Santa Cruz in 1987. The establishment of Channel Islands National Park (CHIS) led to increased access to the islands, with concurrent research and researchers.

THE 1994 DISCOVERY

In June 1994 Tom Rockwell and a graduate student, Kevin Colson, from San Diego State University (SDSU) were examining elevated marine terraces and structural geology of Santa Rosa Island. At one locality on Carrington Point, Tom saw what appeared to be bones protruding from a steep, sandy, ice plant covered slope. Kevin examined the objects and verified they were bones, apparently representing the axial skeleton of a large (for Santa Rosa Island) land vertebrate. The location excluded large pinnipeds such as elephant seals.

Don Morris, CHIS archaeologist, contacted Agenbroad via telephone, asking if he would come confirm the tentative identification as an island mammoth. Jim Mead and Agenbroad flew to Oxnard from Hot Springs, South Dakota, and were transported to the island site. Examination of the exposed skeletal elements confirmed it was an articulated skeleton of *Mammuthus exilis*, and that it held the promise of being essentially complete.

My (Agenbroad) recommendation was that the specimen should be salvaged prior to the winter rains, as its location and exposure made it extremely vulnerable to loss by erosion. It was decided to excavate and salvage the skeleton in August 1994. Joined by Don Morris (CHIS), Tom Rockwell (SDSU), Louise Roth (Duke University), and my son Brett, we exposed, mapped, prepared and recovered more than 90% of a pygmy mammoth skeleton. There had been some pre-discovery erosional damage and loss.

The skeleton lay extended, on its left side, with the limbs extended toward the south (into the steep sand slope). Removal of the overburden exposed a nearly complete skeleton (Figure 2) of a mature, male, pygmy mammoth. Small bones were preserved, in life position. This indicated the specimen was in primary context (where the animal had died) rather

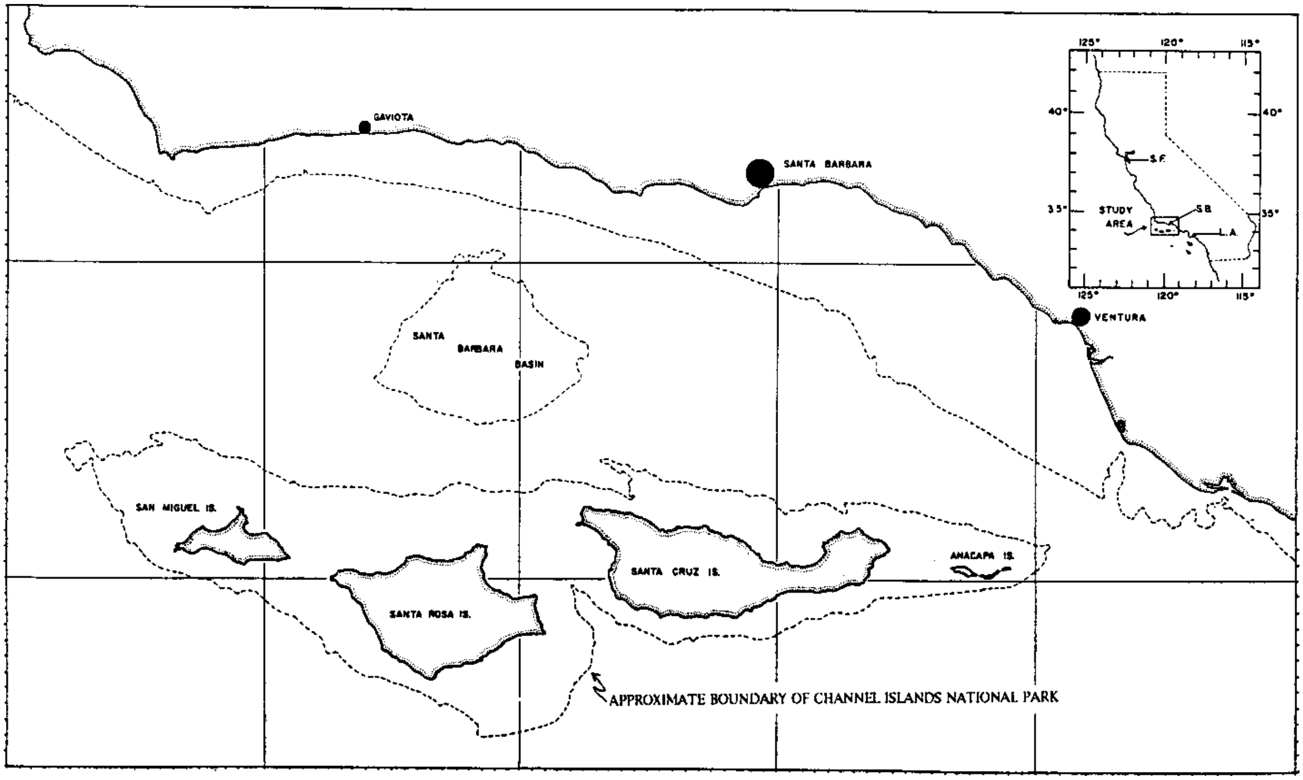

FIGURE 1— A location map of Channel Islands National Park. The approximate boundary coincides with the shoreline of Pleistocene island, Santarosae.

than decomposing, disarticulating, and being scattered or redeposited. It appears that the mammoth lay down on the surface of the terrace, in the lee of a sand dune, and was buried by that dune, shortly after death.

The remains were air-lifted by helicopter to the ranch headquarters where they were put in containers and placed on a Park Service boat for transport to Ventura.

From Ventura, the skeleton was transported to the Mammoth Site of Hot Springs, South Dakota, for cleaning, preparation, preservation, and replication. A fiberglass replica can be viewed at the Channel Islands National Park visitor center, and also at the Santa Barbara Museum of Natural History. The original bones were returned to the Santa Barbara Museum of Natural History, the CHIS repository for paleontological remains.

PLEISTOCENE MAMMOTHS AND THE "SUPER" ISLAND

Eustatic sea level lowering of ± 100 m, due to water tied up and stored as glacial ice and snow packs, changed the coast of Southern California. In particular, there was a seaward extension of the coastline and the presence of a large island offshore of the modern Santa Barbara–Ventura coast. That "super" island (Figure 1) was christened Santarosae by Phil Orr (1968).

Most researchers considered Santarosae to be the extension of the Santa Monica mountains into the Pacific ocean, creating a land bridge (Fairbanks, 1897; Stock and Furlong, 1928; Chaney and Mason, 1930; Stock, 1935, 1943; Valentine and Lipps, 1967; von Bloeker, 1967; Weaver and Doerner, 1967; Hooijer, 1976; Madden, 1977; Azzaroli, 1981). Mammoths were postulated to have crossed this land bridge from the mainland, to ultimately be marooned on the island, with the rise in sea level from melt water of the terminating Pleistocene glaciation.

If such a land bridge ever existed, it was submerged by late Pleistocene time (pre-mammoth). The presence of a deep water strait of 4–6 km width has been demonstrated by Johnson (1978) and Wenner and Johnson (1980). Late Pleistocene mainland mammoths (*Mammuthus columbi*) were the original island mammoths (Johnson, 1981; Madden, 1977, 1981; Roth, 1992; Agenbroad, 1998). This meant the island colonization by mammoths was accomplished by Columbian mammoths swimming to Santarosae. The sea breezes carrying the scent of vegetation from the island to the mainland was the apparent impetus for such a venture. This would be greatly enhanced by environmental stress of the coastal mainland pasturage, due to wild fires, or severe drought.

Once established on Santarosae, the mammoth population faced selective pressures which resulted in body size reduction. These pressures included shrinking territory (island submergence by eustatic sea level rise; reducing Santarosae by as much as 76%); overcrowding by increased population and decreased territory; resource stress caused by overcrowding and shrinking land mass; and by natural stresses such as lightning-strike fires and/or drought intervals. These forces became selective for smaller individuals, ultimately producing *Mammuthus exilis*, and the phylogenetic elimination of *Mammuthus columbi* from the islands. It is possible there were several colonizations of the island (islands) by Columbian mammoths, however there is no fossil evidence of pygmy mammoths on the coastal mainland (i.e. no reverse migration(s).

With sea level rise, there was an increasing width of deep-water strait which, in effect marooned the island mammoths.

DISCUSSION

The 1994 skeleton is the most complete *Mammuthus exilis* skeleton ever discovered. Recent information regarding the Wrangel Island mammoths (*Mammuthus primigenius*) (Vartanyan et al., 1993) as no longer considered to be dwarf forms (Tikhonov, 1997), places the distinction of the only pygmy, island dwelling mammoths as *Mammuthus exilis*.

Mammoth elements collected since CHIS became established, plus an intensive pedestrian survey and selective collection initiated in 1996 has nearly doubled the mammoth material in the SBMNH. That, with the Boris Woolley collection, has greatly increased the osteological collection. Preliminary comparisons of the pygmy mammoth bones and Columbian mammoth bones from the Mammoth Site of Hot Springs, South Dakota have been initiated.

The post-1994 survey of the islands has produced more than 150 localities (a locality being defined as mammoth remains not associated with the last locality). Erosion during winter storms exposes new remains while destroying others. We have observed material being destroyed within six months of exposure. Our procedure has been to collect those specimens threatened by erosion, while leaving more stable specimens in situ.

Chronology of the islands and their mammoth deposits is depauperate. Prior to 1994, there were only 15 published radiocarbon dates pertaining to island mammoths. Eleven of those dates were branded “equivocal” by Wenner et al. (1991). Their contention was two fold: 1) there is (was) no fire-produced charcoal on the islands, that the dated “charcoal” was due to groundwater carbonization; and 2) all mammoth remains were secondary (i.e. redeposited) so any dates of associated material were of no value.

Interior bone derived from the right femur of the 1994 skeleton was dated, using the accelerator-mass spectrometer method. Tom Stafford, then of the University of Colorado, derived collagen from the sample, which produced an AMS ^{14}C date of 12,840 ± 410 (CAMS-24429). That date, derived from an in situ skeleton in primary deposition refutes many of the objections proposed by Wenner et al. (1991). In addition,

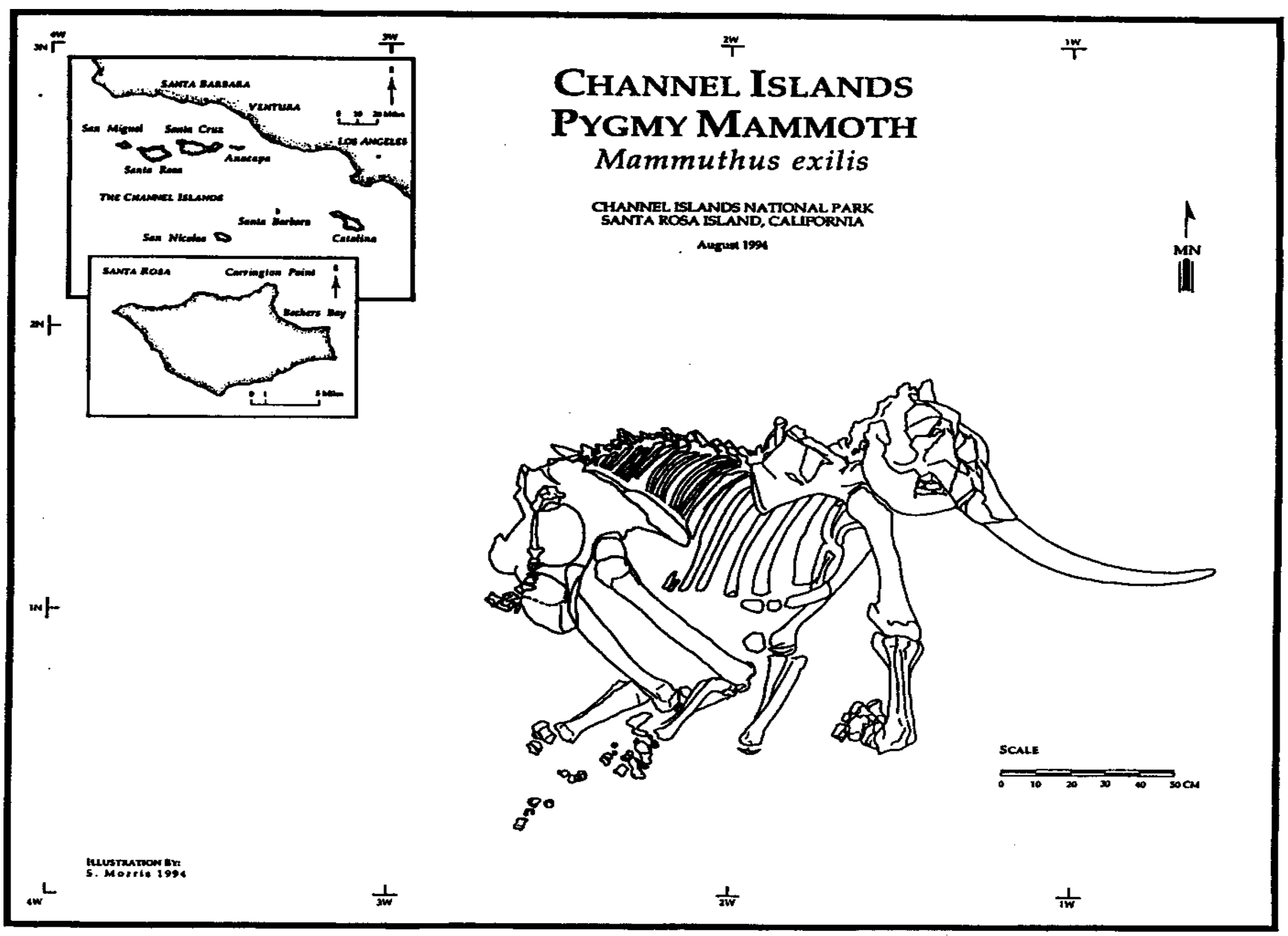

FIGURE 2— The articulated 1994 skeleton of *Mammuthus exilis* from Santa Rosa Island. (Drawn by Susan Morris)

five more dates for CHIS mammoth remains have been produced on associated material (Agenbroad 1999).

Additional radiocarbon dates are essential to understand the time of extinction, rate of dwarfing, possible environmental stresses and the potential for contemporaneity with the earliest humans on the islands. Recent archaeological investigations (Erlandson et al. 1996; 1997) have increased the antiquity of humans on the islands to greater than 11,000 years. Perhaps Orr (1968) was correct; maybe the last mammoths met the first people to arrive on the islands. A tight chronologic framework of the most recent mammoth remains will be crucial to evaluate that possibility.

ACKNOWLEDGMENTS

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STRATIGRAPHIC AND PALEONTOLOGIC RECORD OF THE SAUK III REGRESSION IN THE CENTRAL APPALACHIANS

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ABSTRACT—The Beekmantown and St. Paul Groups in western Maryland, including the mostly complete section exposed along the Chesapeake & Ohio Canal National Historic Park, preserve the best record available of deposition during the Early and Middle Ordovician in the central Appalachian basin. Conodonts and trilobites from this area can be used, not only to document the age and correlations of the formations and their members, but also to test and constrain the sequence/cycle stratigraphy and depositional history for this time interval in this part of eastern Laurentia.

INTRODUCTION

Early Paleozoic strata in the central Appalachian basin record a prolonged deepening and shallowing event (first-order cycle of Vail and others, 1977) that began in the latest Precambrian and continued into the early Middle Ordovician. Sloss (1963) termed the unconformity-bounded package created by this cycle the Sauk Sequence. Vail and others (1977) concluded that the transgressive apex of this first-order cycle coincided with shorter term second- and third-order transgressive episodes that all reached their maxima sometime in the early Ordovician. Although the stratigraphic position of this transgressive peak is evident throughout the cratonic interior of the United States, it is not as well constrained within the marginal orogenic belts, in part owing to regional tectonic signals. In the central Appalachians, this major deepening maximum resulted in the deposition of the Lower Ordovician Stonehenge Limestone, which Hardie (1989) and Taylor and others (1992) interpreted as a third-order cycle. If these interpretations are correct, the Stonehenge Limestone represents the time of maximum deepening for the Sauk Sequence, or at least for the highest of three subsequences (Sauk III) delineated by Palmer (1981) and subsequently recognized by Read (1989) as his Sequence 5. Rock exposures in and near C & O Canal National Historic Park in western Maryland provide one of the most complete stratigraphic sections to preserve a record for this interval of time anywhere in the Appalachian region. [As with all artifacts, plants, and animals, the fossils from this and other National Parks can be collected only with formal permission from the appropriate Park Superintendent.] The section described in this paper occurs along the Potomac River in Washington County, Maryland, approximately from mile-markers 101 to 103.5. It begins in the upper member of the Lower Ordovician Stonehenge Limestone and continues upward through the remainder of the Lower Ordovician and the entire Middle Ordovician. This paper reports on work in progress toward refining the cyclostratigraphy and biostratigraphy of the Beekmantown Group, which represents the apex and regressive phase of Sauk III in the central Appalachians. Brezinski provided the cyclostratigraphic interpretations. Repetski and Taylor contributed the sections on conodont and trilobite faunas, respectively.

LITHOSTRATIGRAPHY

The stratigraphic section along the canal was first described by Sando (1957), who measured (up-section from west to east) 3852 feet (1174 m) of the Beekmantown Group (Stonehenge Limestone through Pinesburg Station Dolomite), 370 feet (113 m) of the St. Paul Group (Neuman, 1951), and 300 feet (91 m) of the Chambersburg Limestone. While this spectacular stratigraphic section spans most of the Lower and all of the Middle Ordovician, we will concentrate in this paper on the Lower Ordovician part of the section, i.e., the Beekmantown Group. The lowest formation in the group is the Stonehenge Limestone, a regionally-extensive limestone-dominated unit in the central Appalachians that is approximately 300 m thick in the study area. It is divisible into three members: the Stoufferstown Member at the base, overlain by unnamed middle and upper members (Sando, 1958). The Stoufferstown Member consists of ribbon-bedded, siliceous limestone and is up to 70 m thick. It is best developed in Pennsylvania and Maryland, north of the Potomac, and is not as easily recognized in northern Virginia. The middle member is composed of approximately 100 m of thick-bedded, locally cyclic microbial boundstone and associated grainstones that Taylor and others (1992) interpreted as representing a barrier reef complex. The upper member comprises 150 m of thin-bedded limestone with abundant

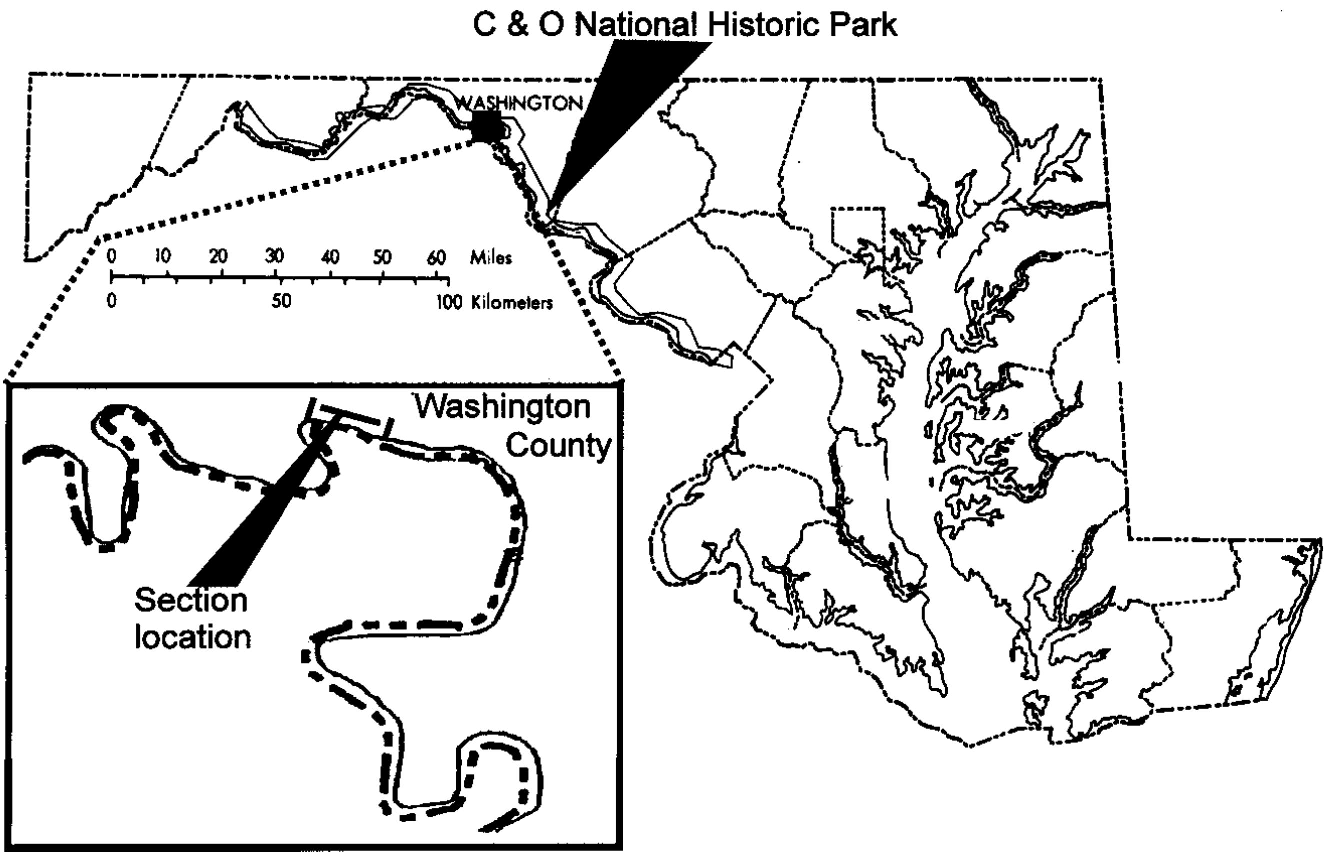

FIGURE 1— Generalized location map of the C&O National Historic Park and location of study section (inset).

grainstone beds that locally are oolitic.

The contact between the Stonehenge and overlying Rockdale Run Formation generally is placed at the lowest tan, laminated dolomite or dolomitic limestone. The appearance of such dolomites reflects a change in depositional mode from accumulation of non-cyclic subtidal limestone in the Stonehenge, to deposition of peritidal cycles comprising shallow subtidal limestone and intertidal and supratidal dolomites in the Rockdale Run. The Rockdale Run Formation is more than 850 m thick and is dominated by fourth- or fifth-order cycles that range from 1-5 m in thickness. Subtidal lithologies at the base of a typical cycle include thin- to medium-bedded packstone to grainstone, burrow-mottled lime wackestone, and thrombolitic boundstone. These grade upsection into ribbony limestone, which is overlain by a laminated dolomite or dolomitic limestone that caps the cycle. The relative thickness of the limestone and dolomite portions of the cycles varies with their position within the formation. Low in the formation, cycles comprise thicker limestone intervals capped by thin (0.3 m) dolomites. Near the top of the formation, dolomite dominates the cycles and the limestone portions are thin (<1m) or absent.

Sando (1957) identified three lithologically distinct intervals within the Rockdale Run Formation in this area. He recognized that silicified algal masses are common in the basal 100-200 feet (30-60 m) of the formation, allowing this interval to be mapped as a chert-rich zone. About 200 feet (61 m) higher in the formation is an interval of similar thickness characterized by abundant oolitic grainstone that Sando (1957) informally termed the oolitic member. An abundance of dolomite in the upper third of the formation defined a third member, although the thickness of this upper dolomite member is highly variable. Overlying the Rockdale Run Formation is the Pinesburg Station Dolomite, the top formation of the Beekmantown Group. The Pinesburg Station is approximately 400-500 feet (120-160 m) thick and consists of cherty, laminated dolomite and burrow-mottled dolomite. Except for stromatolites, the Pinesburg Station lacks macrofossils. Conodonts are the only microfossils reported from the Pinesburg Station in this area (Boger, 1976; Harris and Repetski, 1982a).

The Pinesburg Station Dolomite is overlain by a sequence of interbedded limestone and dolomite, termed the St. Paul Group by Neuman (1951). Neuman subdivided the St. Paul Group into a lower formation, the Row Park Limestone, and an upper unit, the New Market Limestone. The Row Park consists of massive lime mudstone with thin interbeds of laminated dolomitic limestone. It is approximately 280 feet (85 m) thick. Characteristic lithologies of the New Market Limestone include: 1) medium-bedded, burrow-mottled limestone, 2) stromatolitic limestone, and 3) gray to tan, laminated dolomite and dolomitic limestone. It is capped by a light to medium gray, micritic limestone. The New Market Limestone is approximately 220 feet (67 m) thick. Fossils are not common in either formation, but some fossiliferous horizons do occur in the upper part of the New Market Limestone. Macluritid gastropods (snails) dominate the fauna. Overlying the St. Paul Group is the Chambersburg Limestone, which comprises medium- to dark-gray, medium- to wavy-bedded and even nodular-bedded, shaly, fossiliferous limestone.

CYCLE STRATIGRAPHY

Three different scales of cyclicity are represented by sedimentary cycles within the Beekmantown Group. Hardie (1989), Taylor and others (1992), and Cecil and others (1998) interpreted the Stonehenge as a single third-order transgressive-regressive cycle, with maximum deepening occurring during depostion of the middle member. The Stoufferstown Member appears to represent the transgressive phase, and the upper member the regressive phase of the cycle. The Rockdale Run Formation was deposited in shallow to very shallow waters during deposition of hundreds of fifth-order cycles, which are superimposed on larger (fourth- and third-order) cycles. Hardie (1989) and Cecil and others (1998) have argued that three (or more) third- or perhaps fourth-order sea level cycles are evident in this formation (Figure 2). These larger scale cycles become increasingly dolomitic toward the top of the Rockdale Run, suggesting that the deepening accomplished at the apex of each cycle was somewhat less than that achieved at the transgressive peak of the preceeding cycle. This led Cecil and others (1998) to speculate that these third- to fourth-order cycles in the Rockdale Run Formation were superimposed on an even larger scale cycle. In that context, Cecil and others (1998, fig. 13) also suggested that the faunas recognized by Sando (1957, 1958) may reflect ecological responses to deepening episodes during deposition of the Rockdale Run. Consequently, the major transgression manifested in the Stonehenge Limestone is interpreted here as apex of the Sauk III subsequence. The upper member of the Stonehenge and overlying Rockdale Run Formation are treated here as the physical record of the following regression.

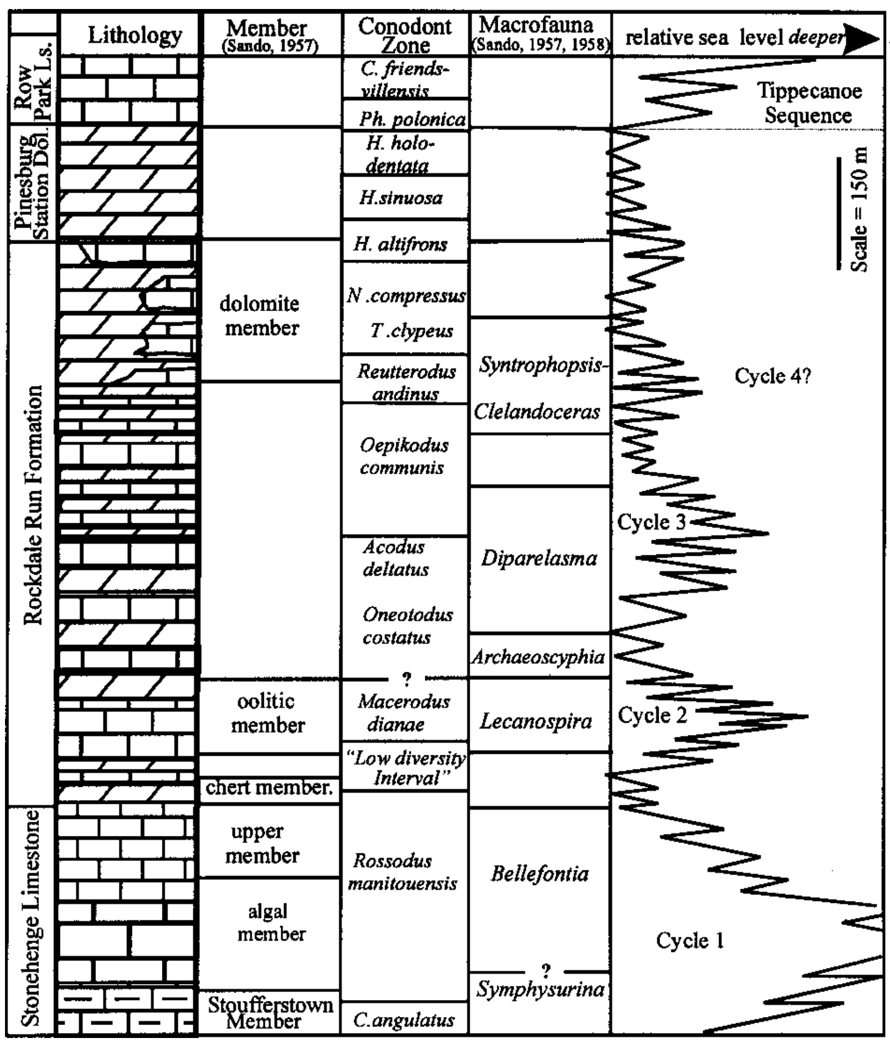

FIGURE 2— Relationship between lithostratigraphy, fauna and cycle stratigraphy of the Stonehenge through lower St. Paul Group along the C&O Canal at the study locality (modified from Cecil and others (1998). Conodont zonation follows that of Ross and others (1997) for the Lower Ordovician, i.e., through *R. andinus* Zone, and that developed by Harris and Repetski (1982b) for eastern North America/ Laurentia for the lower Middle Ordovician.

The vertical arrangement of lithologies within the Pinesburg Station Dolomite and St. Paul Group led Mitchell (1982) and Brezinski (1996) to interpret these units as separate transgressive and regressive pairs. In most areas of North America, a lowstand in sea level in the early Middle Ordovician produced a major unconformity that separates the Lower and Middle Ordovician Series. Based on conodont data from scores of sections spanning the Lower to Middle Ordovician boundary interval along the U.S. Appalachians from Alabama to Vermont, Harris and Repetski (1982a, b; Repetski and Harris, 1982; 1986) demonstrated that the major unconformity, known in the central Appalachians as the Knox/Beekmantown unconformity, was pre-Blackriveran, with the maximum lowstand most likely occurring during the late Whiterockian or Chazyan. Derby and others (1991), using numerous fossil groups, as well as physical stratigraphy, applied to the thick Ordovician succession of southern Oklahoma, concluded that the maximum regional regression marking the Sauk III-Tippecanoe mega-sequence boundary occurred during the middle Whiterockian. Placed thusly, this event boundary falls within the middle to upper part of the Pinesburg Station Dolomite in the central Appalachian basin depocenter, that is, in the area including the C & O Canal section. The subsequent Ordovician deepening event in the central Appalachians produced the Chambersburg Limestone and likewise was the result of the onset of downwarping that occurred during the Taconic orogeny. This deepening produced the graptolitic black shales of the overlying Martinsburg (Brezinski, 1996).

BIOSTRATIGRAPHY

Conodonts

The conodont succession of the Lower and Middle Ordovician of the central Appalachians is known only in the broad sense, as very few of the details of that succession are published. However, it is clear that they are among the most useful guides for the correlation of these strata. Conodonts are present in nearly all of the lithologies of the Beekmantown and St. Paul Groups sampled thus far, even though rather large samples (ca. 6 kg) often are needed in the dolomites of the intertidal to supratidal facies to extract useful faunas.

Conodonts identified by Wilbert Hass, of the U.S. Geological Survey, were the first published from the Sauk III succession of the eastern U.S. (*in* Sando, 1958). These small collections were extracted from limestone chips remaining from Sando's splitting for crack-out trilobites, brachiopods, and mollusks in the latter's study of the Beekmantown in western Maryland, south-central Pennsylvania, and northwestern Virginia. Hass had available only two previous publications on Lower Ordovician conodonts from North America on which to base his identifications, so most of his taxa are in open nomenclature. However, he was able to characterize correctly, if somewhat broadly, the stratigraphic position of nearly all of Sando's faunas in terms of the Missouri (Branson & Mehl, 1933) and upper Mississippi Valley (Furnish, 1938) successions that were the subjects of those previous studies.

Since 1958, J. Boger (1976; Boger and Bergström, 1976) examined the conodonts of the upper part of the Rockdale Run Formation, Pinesburg Station Dolomite, and St. Paul Group from several localities in western Maryland, and Repetski and A.G. Harris collected the C & O Canal section, largely as part of their larger study of the Lower/Middle Ordovician boundary interval in the U.S. Appalachians (Harris & Repetski, 1982a, b; Repetski & Harris, 1982, 1986). These collections, as well as others collected recently in the course of our study of the Stonehenge interval (e.g., Taylor and others, 1992; Taylor and others, 1996) contributed to this study as well. Because of these previous studies, most of our data are from these two intervals; currently we are filling in the database for the lower through middle parts of the Rockdale Run Formation.

From our work elsewhere in the central Appalachians, we know that the base of the Stonehenge, representing the onset of a broad regional transgression, falls at or near the base of the *Cordylodus angulatus* Zone (following the North American Lower Ordovician conodont zonation as used in Ross and others, 1997). The succeeding *Rossodus manitouensis* Zone begins well into the Stoufferstown Member of the Stonehenge. As elsewhere, this zone extends through a thick stratigraphic interval, and, while distinctive and widespread, its resistance to reliable subdivision thus far has hampered somewhat its utility for more precise correlation. The *R. manitouensis* Zone extends a short way, a few feet to a few tens of feet, depending on one's specific choice of contact horizon, into the basal part of the Rockdale Run Formation, where a major faunal turnover occurs (Ethington & Clark, 1971; Ethington and others, 1987). The succeeding "Low Diversity Interval" spans part of Sando's (1957) lower chert member of the Rockdale Run, thus also largely coinciding with the shallowing episode of depositional Cycle 2 as used herein.

Our preliminary work on the lower and middle parts of the Rockdale Run Formation indicates that the *Macerodus dianae* Zone ranges from low in the oolitic member through some part of the overlying *Lecanospira* local macrofaunal zone at the C & O Canal section. Thus, the temporal range of the *M. dianae* Zone approximates much of the transgressive-regressive depositional Cycle 2 in this area. Details of the boundaries of this zone, and of the overlying *Acodus deltatus—Oneotodus costatus* Zone are not yet precisely known. However, the appearance of *Oepikodus communis* and *Diaphorodus delicatus* at at least 435 ft below the top of the Rockdale Run indicates that the base of the *O. communis* Zone falls within the transgressive part of depositional Cycle 3.

The upper part of the Rockdale Run and all of the Pinesburg Station Dolomite represent chiefly very shallow environments (Cycle 4 herein). Macrofossils are extremely scarce (Rockdale Run) to lacking entirely (Pinesburg Station) through this interval, suggesting stressed conditions most likely involving elevated salinities. Thus, dating and correlation using shelly fossils is difficult to impossible. The conodonts are present in this interval but are scarce at many levels. Enough diagnostic taxa have been obtained to enable identification of all of the recognized biozones of the early and middle Whiterockian for warm shallow-water carbonate facies of eastern North America (Harris and Repetski, 1982b). The Sauk III-Tippecanoe sequence boundary, which most likely occurs in the upper part of the *Histiodella holodentata* or lower part of the *Phragmodus polonica* Zone, thus falls within the middle or upper part of the Pinesburg Station. Physical evidence for unconformity has not been demonstrated in the western Maryland area, and all of the zones are represented. Thus, any hiatus in this interval would be of minor magnitude. Strata of the overlying St. Paul Group are limestones, reflective of more normal marine conditions accompanying the initial transgressive phase of the Tippecanoe sequence. They contain more eurytopic conodont taxa and also show the return and upward increase of macrofaunas.

TRILOBITES

Trilobites collected from the lowest and highest beds of the Stonehenge Limestone establish the position of the transgressive and regressive phases of the Stonehenge depositional cycle within a finely resolved framework of zones and subzones developed for basal Ordovician strata in Oklahoma (Stitt, 1983). Collections from the basal few meters of the Stonehenge in northern Virginia (Orndorff and others, 1988) and central Pennsylvania (Taylor and others, 1992) include *Clelandia texana* Winston and Nicholls, and *Hystricurus millardensis* Hintze. These species are restricted to the *Symphysurina* Zone and occur only in the middle (*Symphysurina bulbosa* Subzone) to upper (*Symphysurina woosteri* Subzone) part of that zone. No trilobites have been recovered yet from the basal beds of the Stonehenge Limestone along the C & O canal. Identifiable specimens have been found at two horizons within the basal Stoufferstown Member in a pasture exposure near St. Pauls Church, approximately two miles north of the canal. Both collections, one (Sample SP4) from the basal bed of the Stonehenge and another (Sample SP5.9) from 47 feet (14.3m) above the base of the formation, are dominated by several species of *Symphysurina*. Sample SP4 includes two cranidia (central portion of the head) and one pygidium (tail). The cranidium (Figure 4A-B) differs from that of all previously described species of *Symphysurina* in possessing a deep, trough-like border furrow at the front. The same bed yielded one pygidium (Figure 4C), but too few specimens were recovered from that horizon to evaluate whether it represents the same species as the new cranidium. While discovery of a new species is always welcome, it obviously has little immediate utility for correlation to other areas.

Sample SP5.9, collected from a thin, normally-graded bed, provided a much larger collection. The dominant species (Figure 4D) exhibits a typical, non-furrowed cranidium with a small, shelf-like anterior border. The associated pygidium is more distinctive, with a posterior margin that is flared outward slightly, particularly near the axis, producing a distinctly triangular shape. This species has not been identified yet, but a systematic search of the literature is under way to evaluate the more than 25 species of *Symphysurina* that have been named in previous studies. Sample SP5.9 also provided a second *Symphysurina* pygidium (Figure 4F), which resembles that of *Symphysurina woosteri*, the eponymous species of the highest of three subzones recognized by Stitt (1983) in the *Symphysurina* Zone in Oklahoma. However, no cranidium or librigena ("free cheek") was recovered to allow confident assignment to this species.

Sample 5.9 also provided a few specimens of *Clelandia*, another genus whose species are useful for determining position within the *Symphysurina* and *Bellefontia-Xenostegium* Zones. Although the material is fragmentary, some specimens (Figure 4E) were complete enough to display distinct lateral glabellar furrows like those that characterize *C. texana* and *C. albertensis*, the two species that occur in the lower to middle part of the *Symphysurina* Zone throughout North America. Collectively, therefore, species recovered from the Stoufferstown Member of the Stonehenge Limestone near St. Paul's Church support earlier studies that attributed the transgression at the base of this formation to sea-level rise during deposition of the middle subzone (*Symphysurina bulbosa* Subzone) of the *Symphysurina* Zone. Additional study of the collections already in hand, and supplemental sampling of the upper half of the Stoufferstown Member in and near the C&O Canal, should allow refinement of correlation between the Appalachians and the Oklahoma standard succession.

Additional sampling is needed to establish the position of the base of the *Bellefontia-Xenostegium* Zone within the Stonehenge Limestone. Neither of the collections from the St. Pauls Church section includes species of *Bellefontia* and *Xenostegium*, indicating that the base of the *Bellefontia-Xenostegium* Zone lies higher within the formation. Recent discovery of *Clelandia parabola* and *Xenostegium franklinense*, two species characteristic of the lower part of the *Bellefontia-Xenostegium* Zone, in the upper half of the Stoufferstown Member in central Pennsylvania (Taylor, in press) assigns the highest beds of that member and all of the overlying reef-dominated middle member to the *Bellefontia-Xenostegium* Zone in that area. No diagnostic trilobite species have yet been identified from the upper Stoufferstown or the middle member in Maryland to establish whether that zonal boundary lies at approximately the same level within the Stonehenge in the Great Valley. For that reason, we align that zonal boundary with the member boundary in Figure 2, adding a question mark to express the uncertainty as to its position within the formation.

The scarcity of trilobite collections within the middle member also poses a problem in establishing the position of subzonal boundaries within the *Bellefontia-Xenostegium* Zone. The abundant occurrence of *Bellefontia collieana* in grainstones of the upper member in Pennsylvania and Maryland assigns those beds to the middle subzone, the *Bellefontia collieana* Subzone. Whether the apex of the Sauk Sequence, represented by the middle member of the Stonehenge, lies within that subzone or the underlying *Xenostegium franklinense* Subzone, cannot be established in the absence of trilobite data from that member. Additional sampling in the middle member is planned to resolve that issue.

Trilobites from the upper member of the Stonehenge constrain the timing of the regression recorded by a return to cyclic peritidal deposition at the contact with the overlying Rockdale Run Formation. This culmination of the "Stonehenge Regression" apparently occurred during deposition of the *Bellefontia collieana* Subzone of the *Bellefontia-Xenostegium* Zone because the highest collections from the upper member of the Stonehenge in Maryland and Pennsylvania contain *Bellefontia collieana* (Figure 4G-K), which is restricted to the subzone that bears its name. The recovery of *Xenostegium franklinense* (Figure 4L) from beds near the top of the upper member in the C&O Canal section provides additional support for that subzonal assignment. This species occurs only in the lower two subzones of the *Bellefontia-Xenostegium* Zone in Oklahoma; it is not known to occur as high as the *Bellefontia chamberlaini* Subzone. Collections from the upper member of the Stonehenge lack *Bellefontia chamberlaini*, whose lowest occurrence defines the base of the *B. chamberlaini* Subzone in Oklahoma. Similarly, *Hystricurus missouriensis*, which is also characteristic of the highest subzone, has not been found despite the recovery of large collections that include at least three other species of *Hystricurus* from the upper member in central Pennsylvania. Little information on faunas younger than the *Bellefontia collieana* Subzone is likely to emerge from the central Pennsylvania succession because the Stonehenge is overlain in that area by the Nittany Dolomite, which provides very few macrofossils, especially from low within the formation. The less pervasively dolomitized facies of the Rockdale Run Formation, exceptionally well-exposed along the C&O Canal, offers much greater potential for advancing our knowledge of trilobite faunas and conditions through the Early Ordovician as additional sampling is conducted in the Beekmantown Group in the central Appalachian region.

CONCLUSIONS

Our preliminary work demonstrates the importance of integrating biostratigraphic and physical stratigraphic data in interpreting the depositional history of the Beekmantown Group. Improved biostratigraphic control provides greater accuracy and precision in identifying and correlating specific depositional cycles within the thick Lower Ordovician carbonate succession of this region. For example, by better constraining the limits of the *Macerodus dianae* conodont Zone, we can determine whether the oolitic member of the Rockdale Run Formation (Cycle 2 in this paper) correlates with an interval of off-platform carbonates at the top of the Grove Limestone in the shelfbreak succession in the Frederick Valley of Maryland (Taylor and others, 1996). Work in progress in both these areas is aimed at increasing our level of biostratigraphic control at the C & O Canal section and surrounding areas.

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FIGURE 3— (next page) Scanning electron photomicrographs of some Lower and Middle Ordovician conodonts from the C & O Canal section, Washington Co., MD, and related units in the central Appalachians. Specimens are reposited in the type collections of the Department of Paleobiology, U.S. National Museum of Natural History (USNM), Washington, D.C. 20560. *A, Phragmodus flexuosus* Moskalenko. Lateral view of ramiform (S) element, X 70; 48 feet below top of Pinesburg Station Dolomite, section near Marion, Franklin Co., PA, USGS fossil locality no. 9302-CO, USNM 506993. *B, Paraprioniodus costatus* (Mound). Upper anterolateral view of P(?) element, X 105; 520 ft below top of Bellefonte Dolomite (largely correlative with upper Rockdale Run through Pinesburg Station formations), section near Tyrone, PA, USGS loc. no. 11568-CO, USNM 506994. *C, Leptochirognathus quadratus* Branson & Mehl. Inner lateral view of quadratiform element, X 70; Pinesburg Station Dol., same sample as fig. A, USGS loc. no. 9302-CO, USNM 506995. *D, Appalachignathus delicatulus* Bergström and others. Inner lateral view of S element, X 105; 435 ft above base of St. Paul Goup at its type section, Clear Spring 7-1/2 minute quadrangle, MD, USGS loc. no. 9320-CO, USNM 506996. *E, Pteracontiodus* cf. *Pt. gracilis* Ethington & Clark. Posterolateral view of quadracostate (Sd) element, X 105; 260 ft below top of Rockdale Run Formation, C & O Canal section; USGS loc. no. 11569-CO, USNM 506997. *F, Histiodella altifrons* Harris. Lateral view of blade-like element, X 210; top foot of Rockdale Run Formation, C & O Canal section; USGS loc. no. 11570-CO, USNM 506998. *G, Chosonodina rigbyi* Ethington & Clark. Posterior view, X 140; Beekmantown Group, 154 ft above base of upper limestone and dolomite member of Gathright and others (1978), Grottoes section, Rockingham Co., VA, USGS loc. no. 11571-CO, USNM 506999. *H, Dischidognathus* n. sp. Posterolateral view, X 140; 360 ft below top of Rockdale Run Fm., C & O Canal section; USGS loc. no. 11572-CO, USNM 507000. *I, Neomultioistodus compressus* (Harris & Harris). Outer lateral view of Sc element, X 70; 560 ft below top of Bellefonte Dol., section near Tyrone, PA, USGS loc. no. 11573-CO, USNM 507001. *J, Plectodina* n. sp. Anterior view of Sa element, X 70; same sample as Fig. E, Rockdale Run Formation, C & O Canal section, USGS loc. no. 11569-CO, USNM 507002. *K, Tricladiodus clypeus* Mound. Posterior view of Sa element, X 105; 85 ft above base of upper limestone and dolomite unit of Gathright and others (1978), Beekmantown Group, Grottoes, VA section, USGS loc. no. 11574-CO, USNM 507003. *L, Diaphorodus delicatus* (Branson & Mehl). Lateral view of P element, X 90; Beekmantown Gp., 55 ft below top of upper dolomite member of Gathright and others (1978), Grottoes, VA, section, USGS loc. no. 9248-CO, USNM 507004. *M, Oepikodus communis* (Ethington & Clark). Lateral view of ramiform (S) element, X 90; Rockdale Run Formation, Unit 161 of Sando (1957) at C & O Canal section, USGS loc, no. 11575-CO, USNM 507005. *N, Reutterodus andinus* Serpagli. Inner lateral view, X 140; Beekmantown Gp., 98 ft above base of upper dolomite member of Gathright and others (1978), Grottoes, VA, section, USGS loc, no. 11576-CO, USNM 507006. *O, Eucharodus toomeyi* (Ethington & Clark). Inner lateral view, X 55; same sample as Fig. M, approx. 810 feet below top of Rockdale Run Formation, C & O Canal section, USGS loc. no. 11575-CO, USNM 507007. *P, Tropodus comptus* (Branson & Mehl). Posterobasal view, X 60; same sample as Fig. M and O, USGS loc, no. 11575-CO, USNM 507008. *Q, Toxotodus carlae* (Repetski). Lateral view, X 140; approx. 6 ft below Knox unconformity, section near Lexington, VA, USGS loc. no. 11577-CO, USNM 507009. *R., Colaptoconus quadraplicatus* (Branson & Mehl). Lateral view, X 90; Rockdale Run Formation, same sample as Fig. M, O, and P, Unit 161 of Sando (1957), C & O Canal section, USGS loc. no. 11575-CO, USNM 507010. *S, Drepanodus* cf. *D. concavus* (Branson & Mehl). Lateral view of oistodontiform (M) element, X 55; Rockdale Run Formation, same sample as Fig. M, USGS loc, no. 11575-CO, USNM 507011. *T, Cordylodus angulatus* Pander. Lateral view, X 70; one foot below top of Stonehenge Limestone, C & O Canal section, USGS loc. no. 11578-CO, USNM 507012. *U, Variabiloconus bassleri* (Furnish). Inner lateral view, X 70; one foot above base of Rockdale Run Formation, C & O Canal section, USGS loc. no. 11579-CO, USNM 507013. *V, Loxodus bransoni* Furnish. Inner lateral view, X 100; same sample as Fig. U, C & O Canal section, USGS loc. no. 11579-CO, USNM 507014. *W, Rossodus manitouensis* Repetski & Ethington. Inner lateral view of oistodontiform (M) element, X 70; same sample as Fig. T, USGS loc. no. 11578-CO, USNM 507015. *X, Rossodus manitouensis* Repetski & Ethington. Posterolateral view of coniform (S?) element, X 100; same sample as Fig. U, USGS loc. no. 11579-CO, USNM 507016. *Y, Scolopodus sulcatus* Furnish. Outer lateral view, X 70; same sample as Fig. U and X, USGS loc. no. 11579-CO, USNM 507017.

FIGURE 3

FIGURE 4—Stereophotographs of trilobite species from the Stonehenge Limestone in Maryland and central Pennsylvania. Views are dorsal unless labelled otherwise. All specimens are housed in the invertebrate collections at Carnegie Museum of Natural History (CM). *A-B, Symphysurina* n. sp. 1 – cranidium, CM 45797, X3.2; sample SP4, from basal bed of Stonehenge Limestone in St. Paul's Church section. *A,* dorsal view; *B,* anterior oblique view showing anterior border and deep border furrow. *C, Symphysurina* sp. – pygidium, CM 45798, X4.5; sample SP4. *D, Symphysurina* sp. 2 – CM 45799, X3.9; sample SP5.9, from Stoufferstown Member, 47 feet (14m) above base of Stonehenge in St. Paul's Church section. Medium-sized pygidium in upper left of photo; small cranidium, anterior end down, in lower right. *E, Clelandia* sp. – cranidium, CM45800, X6.1; sample SP5.9. *F, Symphysurina woosteri?* – pygidium, CM45801, X4.4; sample SP5.9. *G-H, Bellefontia collieana* (Raymond) –slightly deformed, small cranidium, CM45802, X2.9; from upper member of Stonehenge Limestone in C&O canal section, horizon 137 feet (41.8 m) below contact with Rockdale Run Formation. *G,* dorsal view; *H,* anterior oblique view. *I-J, Bellefontia collieana* (Raymond) – partially exfoliated, medium-sized cranidium, CM45803, X3.2; from horizon 64 feet (19.5 m) above base of upper member of Stonehenge Limestone in central Pennsylvania, Bellefonte North section of J.F. Taylor (unpublished). *I,* dorsal view; *J,* anterior oblique view. *K, Bellefontia collieana* (Raymond) – small pygidium, CM45804, X2.9; C&O Canal section, same horizon as figures *G-H. L, Xenostegium franklinense* Hintze – small pygidium, CM45805, X4.5; from upper member of Stonehenge Limestone in C&O canal section, horizon 34 feet (10.4 m) below contact with Rockdale Run Formation.

NON-MARINE TRACE FOSSILS FROM THE MORRISON FORMATION (JURASSIC) OF CURECANTI NATIONAL RECREATION AREA, COLORADO

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Abstract—The Morrison Formation (Jurassic) of Curecanti National Recreation Area has proven vertebrate paleontological resources. In addition to the vertebrate fossil record in the Park, there are several types of non-marine invertebrate trace fossils. There are at least four types of invertebrate trace fossils present in the Park. Of these types, three (unionid burrows, crayfish burrows, and termite nests in rhizolith traces) are highlighted here. The presence of these trace fossils in the Park illustrates the mosaic nature of the ecosystem preserved within the Morrison Formation.

INTRODUCTION

Continental trace fossils have proven value as indicators of past environments and biodiversity (Bown and Kraus, 1983; Hasiotis, 1998; Hasiotis and Dubiel, 1995; Hasiotis and Demko, 1998; Hasiotis et al., 1998; Ratcliffe and Fagerstrom, 1980; Retallack, 1984). As in-place fossils, they provide direct evidence of the details of an ancient depositional environment, or they can indicate ecological interactions, such as burrows on wood or bone. Additionally, since body fossils of terrestrial invertebrates are quite rare, trace fossils provide evidence of biodiversity that is not otherwise readily available.

The purpose of this report is to briefly highlight three of the types of non-marine trace fossils found in the Morrison Formation (Late Jurassic) of Curecanti National Recreation Area (CURE) that have been mentioned elsewhere (Fiorillo and McCarty, 1996). A fourth type of trace fossil, simple vertical tubes approximately 1 cm in diameter and up to 35 cm long, is also present, but given the decided ambiguity of its taxonomic origin, it will not be discussed further here. All but the crayfish burrows discussed below were found in the Red Creek section in CURE that is described elsewhere (Fiorillo and McCarty, 1996).

In addition to the traces discussed in this report, CURE has produced the remains of at least two taxa of dinosaurs (Fiorillo and May, 1996, Fiorillo et al., 1996) and conchostracans (Fiorillo and May, 1996) from the Morrison Formation. These non-marine trace fossils, combined with the dinosaur data, indicate that the Morrison ecosystem in this park is much more complex than had been previously recognized.

CURECANTI NATIONAL RECREATION AREA BACKGROUND

Curecanti National Recreation Area encompasses the eastern portion of the Black Canyon of the Gunnison, and shares a common boundary with the Black Canyon of the Gunnison National Monument, with both parks being managed as one unit. CURE is arguably one of the lesser-known parks in the National Park Service. The park contains three dams that comprise the Wayne N. Aspinall Unit of the Upper Colorado River Storage Project, where the largest reservoir created by the dams, Blue Mesa Reservoir, serves as a major recreational resource for fishermen and boating enthusiasts.

The park is recognized for having exposures of rocks that date to over 1.7 billion years, making these rocks among the oldest in western North America. In addition, fossil resources that have significant scientific and educational value have been recently recognized at CURE. The most important of these fossil finds is in the Upper Jurassic Morrison Formation in the park (Figure 1).

FIGURE 1—View of the best exposure of the Morrison Formation in Curecanti National Recreation Area. From the highest point on this ridge, the Morrison Formation comprises approximately the lower half of the exposure.

The remains of two dinosaur taxa have been found at a quarry in CURE: an articulated partial sauropod skeleton consisting of several posterior cervical and anterior thoracic vertebrae, ribs, and fragmentary limb materials; and isolated theropod teeth. The sauropod has been referred to the genus *Apatosaurus* and the theropod teeth assigned to the genus *Allosaurus* (Fiorillo and May, 1996; Fiorillo, et al., 1996).

MORRISON FORMATION BACKGROUND

The Morrison Formation of the western United States has produced the vast majority of the Jurassic dinosaurs from North America. This important fossil-unit, composed largely of ancient stream, floodplain, and lake deposits, is found at the surface or in the subsurface from Montana to New Mexico and from Oklahoma to Utah (Dodson et al., 1980). Recent work has shown the Morrison Formation to contain a diverse flora and fauna (Carpenter et al., 1998a; 1998b). However, most of these remains have been derived from only a few major localities. The Morrison Formation can be subdivided into several members (Peterson and Turner-Peterson, 1987; Peterson, 1988a). The youngest is the Brushy Basin Member, which is the source of most of the Morrison vertebrate remains (Lawton, 1977; Dodson et al., 1980, Carpenter et al., 1998a; 1998b, and others).

The age of this rock unit has traditionally been considered to be Late Jurassic. The age of the Morrison Formation had been under debate, with dates ranging from pre-Kimmeridgian (Hotton, 1986) to Neocomian (Bowman et al., 1986; Kowallis, 1986). More recent Ar/Ar dates have established that the majority of the Brushy Basin Member is firmly in the late Kimmeridgian and Tithonian. It had been suggested that the uppermost part of the member may extend into the Early Cretaceous (Kowallis et al., 1991), but it now appears that the entire formation is within the Jurassic (Kowallis et al., 1998).

Several members of the Morrison Formation are considered to be fluvial in origin and to represent alluvial fan complexes, while the Brushy Basin Member also incorporates a playa-lake complex in the eastern part of the Colorado Plateau (Peterson and Turner-Peterson, 1987). Structural and sedimentological relationships indicate that the Morrison Formation is a clastic wedge thinning from the ancestral Rocky Mountains to the retreating Late Jurassic interior sea (Dodson et al., 1980; Peterson, 1988a; Peterson and Turner-Peterson, 1987; Peterson and Tyler, 1985). The Morrison Formation is unconformably overlain by several time-equivalent continental units such as the Cloverly Formation in the Bighorn Basin of Wyoming and Montana, the Cedar Mountain Formation in the San Rafael Swell of Utah, and the Burro Canyon Formation in the San Juan Basin of Colorado and New Mexico.

Historically, climatic interpretations for Morrison Formation deposition range from wet to dry (see Dodson et al.,1980 and Demko and Parrish, 1998 for review). The presence of aquatic vertebrates, such as crocodiles, turtles, and fishes has suggested to some that the Morrison Formation represents, at least in part, a humid environment (Mook, 1916; Moberly, 1960). In contrast, playa lake deposits in the Brushy Basin Member (Peterson and Turner-Peterson, 1987; Turner and Fishman, 1991), eolian deposits in the Bluff Sandstone Member (Peterson, 1988b) and lake deposits in the Morrison Formation of southeastern Colorado (Prince, 1988) attest to drier conditions. To account for these two conflicting sets of environmental indicators, some workers have invoked a strong seasonality during Morrison times (Moberly, 1960; Dodson et al., 1980; Prince, 1988), or a mosaic of physical conditions during deposition (Demko and Parrish, 1998).

UNIONID BURROWS

Burrows attributed to unionid clams (Figure 2) are an uncommon component of the trace fossil assemblage found in the Morrison Formation of Curecanti National Recreation Area. This identification is based on comparison with published photographs of Cretaceous unionids from the Judith River Group of Dinosaur Provincial Park, Alberta, Canada (Koster et al., 1987), and personal observations of similar burrowed beds in the Judith River Formation of south-central Montana. These traces in the Morrison Formation were only found in one location in CURE, near Red Creek, and occurred as a dense cluster of preferentially aligned, bulbous burrows. The generally symmetrical form of the burrows indicates that both valves were present during the formation of these traces, which were made by living clams in an upright orientation. Evanoff et al. (1998) report six taxa of unionids in the Morrison Formation. However, based on the available data from CURE, no further taxonomic identification is offered for these unionid burrows.

The preferred orientation and clear outline of the burrows indicates little to no reworking of this horizon. The presence of these burrows also indicates no transport of clams at the site. Further, modern unionids inhabit free flowing, well-oxygenated, non-ephemeral waters (Hanley, 1976). Given the preferred orientation of these burrows, flow appears to have been from the upper left to the lower right (or vice versa) of Figure 2. Following Koster et al. (1987) and Hanley (1976), the bulbous burrows are interpreted as dwelling structures (domichnia) for these Jurassic clams in a free flowing channel.

FIGURE 2—Unionid burrows in a sandstone matrix. These are interpreted as dwelling structures (domichnia) of clams in a free-flowing channel. Camera lens cap is approximately 5 cm in diameter.

CRAYFISH BURROWS

Roughly tubular traces, approximately 4 to 5 cm in diameter that are attributed to crayfish, were present but as with the unionid burrows, were also uncommon at CURE. Figure 3 is a photo of an overturned block with the filled in, or negative of a burrow attributed to a crayfish. Hasiotis et al. (1998) have documented similar burrows elsewhere in the Morrison Formation. In their study, they were able to differentiate various burrow surface textures as resulting from the various moving parts of crayfish. Such an analysis is not offered here.

Of more interest however is the discussion by Hasiotis et al. (1998) regarding the relationship between burrow depth and water table height, where the longer the burrow, the deeper the water table. Whereas they were able to document burrows up to 100 cm long, the burrows at Curecanti National Recreation Area are only up to 15 cm long, indicating a relatively high mean (or dry season) water table.

FIGURE 3—Negative impression of a crayfish burrow. This block is overturned from its original position. Camera lens cap is approximately 5 cm in diameter.

TERMITE NESTS IN RHIZOLITH TRACES

One sandstone in the Park contains an abundance of chambered vertical, or near vertical, sharply delineated structures believed to be termite nests (Figure 4). These structures have diameters up to 6 cm and are roughly cylindrical. There are multiple levels with individual rooms. No spiral ramps are evident. The longest traceable structure was 65 cm in length. These structures tend to have a slight downward taper with rare, secondary lateral branches.

These structures compare favorably with those described by Hasiotis and Dubiel (1995) for traces in the Chinle Formation of Petrified Forest National Park and Hasiotis and Demko (1998) for traces found elsewhere in the Morrison Formation. All of these structures have been attributed to termites. Hasiotis and Demko (1998) assign their Morrison Formation termite traces to Isoptera (Kalotermitidae?).

Elsewhere in the Morrison Formation these structures are interpreted as being associated with rhizoliths (Hasiotis and Demko, 1998). Rhizoliths have been defined as being tubular and vertical with diameters that range to over 100 cm with a downward taper, and with lateral branches of lesser diameter (Hasiotis and Demko, 1996). In contrast to the crayfish burrows that are primarily dependent on soil moisture levels, termite nests such as those described elsewhere in the Morrison Formation are primarily dependent on organic matter (i.e., tree roots) and secondarily dependent on soil moisture needed for the termite colony.

FIGURE 4—Termite nest in a rhizolith trace. Notice the chambers within the nest. Camera lens cap is approximately 5 cm in diameter.

The sharp delineation of the chambered, downward tapering traces with lateral branches at Curecanti National Recreation Area indicates that these termites were similarly following rhizoliths. Following Hasiotis and Demko (1998), because the nests fill the rhizoliths at CURE, the woody plants being utilized must have been intact and the destruction of the woody material probably occurred near or after the death of the plants.

DISCUSSION AND CONCLUSIONS

Based on field data and clay mineralogical analysis, the lower part of the Brushy Basin Member of the Morrison Formation in Curecanti National Recreation Area has been interpreted as being deposited under humid conditions (Fiorillo and McCarty, 1996). Further, the clay mineralogy profile of this local section is suggestive of periods of non-deposition.

The trace fossils described here are all found in sandstones that are dispersed through this paleopedological section (Fiorillo and McCarty, 1996). The presence of these traces (including the mentioned vertical tubes) in this interval indicates that during periods of non-deposition, in addition to the dinosaurs roaming the landscape, there was also an abundance of smaller life forms in the ecosystem preserved in the Morrison Formation.

On a larger scale, mentioned earlier in this report, the Morrison Formation clearly was a complex mosaic of depositional environments. Predictably, this discussion highlights the complexity that is also observable at much finer scales of resolution.

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ALL IS NOT QUIET ON THE PALEONTOLOGICAL FRONT IN DENALI NATIONAL PARK

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Abstract—Recent paleontological investigations of Paleozoic and Mesozoic fossil faunas from Denali National Park are challenging much of the previous stratigraphic and paleotectonic interpretations of the area. Faunas from two tectonostratigraphic terranes, heretofore considered to have had origins in southerly latitudes, suggest that at least some of their early depositional histories took place in higher, cooler paleolatitudes. A few faunas demonstrate a close association, if not a direct tie, to the Siberian continent in early Paleozoic time. These findings suggest that the current tectonic model of the accretionary history of Alaska may need re-examination.

SUMMARY

It has long been generally accepted that most of Alaska is composed of accreted "tectonostratigraphic terranes", representing bits and pieces of island arcs, ocean crust, and rifted continental margins that have been swept across the vast reaches of the Pacific Ocean and smashed onto the western margin of the North American continent. In Denali, previous investigators have identified up to eight different terranes, found either wholly or partially within the Park or Preserve. These include the Pingston (turbidite apron), McKinley (island arc), Mystic and Dillinger (continental shelf and slope), and Chulitna (oceanic crust and continental margin), which were originally described during the 1980's (Jones and others 1981, 1982, 1983, 1984, 1987), and were, for the most part, interpreted to have origins in more southerly latitudes. In most cases, these terranes or stratigraphic packages have only been reconnaissance mapped, and little detail is known about their origins or displacement histories.

A mapping investigation, conducted by the Alaska Division of Geological & Geophysical Surveys along the southeastern margin of the Park in rocks of the Healy A-6 quadrangle, has brought a number of paleontologists into the challenge of unravelling the relative ages of a number of geological units in the infamous "Chulitna Terrane". A number of faunal groups are under investigation by the following specialists: Paleozoic radiolarians, Mun-zu Won (Natural Science College, Pusan, Korea); Permian brachiopods and other megafauna, Robert B. Blodgett (Oregon State Univ.); Paleozoic-Triassic conodonts, Norman M. Savage (Univ. of Oregon); Triassic brachiopods, Michael R. Sandy and Monica Stefanoff (Univ. Dayton, OH); Triassic scleractinian corals and hydrozoans, George D. Stanley, Jr. (Univ. of Montana); and Triassic bivalves, Christopher McRoberts (SUNY at Cortland, NY). Several papers and abstracts are currently in press or preparation on the radiolarian and brachiopod faunas of this terrane (Won and others, in press; Stefanoff and others, 1999)

The Triassic faunas are especially noted for their exotic character in relation to North American cratonal faunas, and indicate that this terrane was then situated near or at the paleoequator (Nichols and Silberling, 1979; Blodgett and Clautice, 1998). Additionally, the warm water, transgressive Upper Triassic carbonate lithologies suggest either a low paleolatitude, or a sheltered embayment or inland sea (Whalen and others, 1999). In contrast, Permian faunas from the same terrane indicate that previously it was probably situated at much higher, cooler paleolatitudes in the Northern Hemisphere, as it contains many elements of the well-known "Arctic Permian" fauna (Blodgett and Clautice, 1998).

Much attention is now also being focused on rocks of another separate tectonic entity, the Mystic terrane (now ranked as a subterrane of the Farewell terrane) which is broadly exposed across much of the northern and western parts of the Park. Conodonts from early Late Devonian (Frasnian) age rocks in the Healy C-6 quadrangle, near the West Fork of the Toklat River, are being described in an article by Savage and others (in press). Rocks of the Mystic terrane are especially well-exposed in the area of Shellabarger Pass in the Talkeetna C-6 quadrangle, and fossils in the immediate area rank amongst the best in terms of preservation anywhere within the Park. Fossil calcareous sponges of Silurian age were described several years back by J. Keith Rigby (Brigham Young Univ., Provo, UT) and others from atoll-like algal reefs (Rigby and others, 1994). Several manuscripts are submitted or nearing completion on Devonian brachiopods by Blodgett, A.J. Boucot (Oregon State Univ.), and Brease and on Early Jurassic spiriferid brachiopods (the first ever recognized in North America) by Sandy and Blodgett (submitted). Fossils from Emsian (late Early Devonian) strata at the base of the Mystic "terrane", along with the aforementioned Silurian sponges are of Siberian and/or Uralian affinities, and suggest that the Mystic terrane most probably represents a rifted sliver of the Siberian continent (Blodgett, 1998; Blodgett and Brease, 1997).

The recent explosive growth of paleontological investigations within Denali National Park and Preserve indicate that we are now entering a "Golden Age" for the understanding of the park's geology and fossils. At this time, we eagerly anticipate many new exciting results on the fossil faunas of the park, as well as for the modelling of the accretionary growth of interior Alaska.

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FOSSIL BIRDS OF FLORISSANT, COLORADO: WITH A DESCRIPTION OF A NEW GENUS AND SPECIES OF CUCKOO

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Abstract—Specimens of fossil birds, both skeletons and feathers, have been known from deposits near Florissant, Colorado since the late 1870s. Three species of birds have been named from this area. One specimen is tentatively identified as belonging in the Coraciiformes (rollers and their relatives). The phylogenetic relationships of the other two species are unclear and they have been placed into Aves: incertae sedis. A recently collected fossil with an almost complete skeleton, except for the skull, is a very important find. Herein this specimen is described as a new genus and species with affinities to the arboreal cuckoos (Cucuiformes, Cuculidae, Cuculinae) of the Old World.

INTRODUCTION

The fossil birds from Florissant, Colorado are few but extremely interesting for several reasons. The two best preserved and prepared specimens have affinities with two Old World groups of birds: rollers (Coraciiformes: Coraciidae; Olson, 1985:139) and cuckoos (Cuculiformes: Cuculidae, Cuculinae; described herein). Modern rollers and cuckoos (subfamily Cuculinae) are found in Europe, Africa, and southern Asia to Australia. Rollers get their common name from their acrobatic flight. They are medium-sized birds that do not walk well, but have a labored hop when on the ground. In trees they fly from perch to perch and seldom climb. The Old World "typical" cuckoos (Cuculinae) are best know because they all are parasitic breeders, laying their eggs in other birds nests. These medium-sized birds are good fliers, some migrating long distances.

The first fossil bird described from the Florissant Lake Beds was a new genus and species of small oscine perching bird (Passeriformes), *Palaeospiza bella* (Allen, 1878:443). Wetmore (1925:190) felt that though *P. bella* was "handsome to look upon" it lacked sufficient characters to show a relationship with any known group of birds. Therefore, he placed it in its own family, Palaeospizidae. In his "Catalogue of fossil birds, Part 5 (Passeriformes)" Brodkorb (1978:216) listed *P. bella* under Aves Incertae Sedis and mentioned that "even the ordinal assignment may be incorrect." Olson (1985:139) stated that he had examined the specimen and "Because it is anisodactyl it is most likely some sort of coraciiform."

The next fossil bird to be described was in 1880 when Edward Drinker Cope described a plover, *Charadrius sheppardianus*, from the "Amyzon Shales" near Florissant. Olson (1985:175) examined the holotype and found it "impossible even to assign the specimen to order, much less to genus." Therefore, he assigns the specimen to Aves incertae sedis. Another avian species from Florissant is *Fontinalis pristina*, which was originally identified by Lesquereux (1883) as a moss, but this was later rectified by Knowlton (1916) who recognized it as a feather.

METHODS AND MATERIALS

The Florissant fossil cuckoo was identified and described using the skeletons of modern species of birds in the comparative osteology collection in the Ornithology Division, Florida Museum of Natural History (UF); the Division of Birds, the Field Museum of Natural History (FMNH); and Georgia College Ornithology Collection (GCOC). After comparing and eliminating all other orders and most of the living families of birds the following specimens were used for comparison and detailed descriptive osteology. Cuculidae: *Centropus superciliosus* (UF 33856), *Clamator cafer* (FMNH 319965), *Clamator glandarius* (UF 38176, 38731), *Coccyzus erythropthalmus* (GCOC 579), *Crotophaga ani* (UF 38970), *Cuculus canorus* (UF 38175), *Cuculus saturatus* (FMNH 357422), *Geococcyx californiana* (FMNH 317279); Musophagidae: *Corythaixoides leucogaster* (UF 21422), *Musophaga rossae* (UF 38727), *Tauraco corythaix* (UF 38726); Opisthocomidae: *Opisthocomus hoazin* (UF 33314); Bucconidae: *Bucco teetus* (UF 33259), *Chelidoptera teuebrosa* (UF 33263), *Monasa atra* (UF 33260), *Monasa morphoeus* (UF 33261).

The osteological terminology used is from Howard (1929) and *Nomina Anatomica Avium* (Baumel, 1979). The Latin terms are replaced by the English equivalents. All measurements are in millimeters and were taken with dial calipers.

SYSTEMATIC PALEONTOLOGY

Order Cuculiformes
Family Cuculidae
Subfamily Cuculinae
Genus *Eocuculus* new genus

Diagnosis—Tarsometatarsus cuculiform obligate zygodactyl, which differs from types found in Psittaciformes, Piciformes, and Sandcoleiformes; postcranial skeleton like that of a small, arboreal cuculid approximately the size of *Coccyzus erythropthalmus* except that the skeleton is robust and the tarsometatarsus is short like that of *Cuculus saturatus* and *C. canorus*; *Eocuculus* differs from all other known fossil cuckoos by its small size and robust skeleton.

Eocuculus cherpinae new species
Figs. 1-3.

Holotype—DM 10682 slab and counter slab DM 10683 consisting of a partial associated skeleton (missing the head) with feather impressions. Collected by Colette Cherpin and Jeffery Carpenter and donated to the Denver Museum of Natural History on 24 May 1993.

Plastotypes—Silicone molds made from DM 10682 and DM 10683 are stored with the holotype at the Denver Museum of Natural History.

Formation and age—Florissant Formation, late Eocene, early Chadronian North American Land Mammal Age, approximately 32.0-34.0 Ma.

Locality—Clare Ranch in Teller County, Colorado. Lake George map T13S, R71W, Sec. 11.

Diagnosis—Same as for genus.

Etymology—Genus derived from the latin for *eo* meaning early plus *cuculus* meaning a cuckoo. Trivial name *cherpinae* feminine for the surname Cherpine. This new species is named in honor of Colette Cherpin, one of the collectors of the holotype, who died tragically in an automobile accident in 1994 at age 25. Colette was an enthusiastic amateur paleontologist who made a significant contribution to the science of paleo-ornithology.

Measurements (mm)—Left humerus: length - 27.0, distal width - 5.4; Left ulna: length - 27.0; Right ulna, length - 27.7; Left radius, length - 24.7; Left carpometacarpus, length - 15.2, proximal depth through MCI - 4.9; Left Digit II, phalanx 1, length - 6.9, greatest depth - 3.1; Left Digit II, phalanx 2, length - 6.0; Synsacrum, length - 23.1; Left tibiotarsus, length - 33.7; Right tibiotarsus, length - 32.5; Left tarsometatarsus, length - 17.0, proximal depth - 3.7; Right tarsometatarsus, length -17.0, proximal width - 4.0, distal width - 4.2.

GEOLOGIC SETTING

Florissant Fossil Beds National Monument is located at the geographical center of Colorado, about 40 miles west of Colorado Springs. Geographically the area is referred to as the Rocky Mountain Peneplain with an average elevation of 2800 m. Geologically the Monument and the surrounding area were formed by several episodes of uplift and erosion during the late Cretaceous, continuing into the late Eocene (70 to 35 mybp). Uplift exposed a large intrusive batholith, which today is the Pike's Peak Granite. The Florissant valley drainage system was impounded by pyroclastic flow from a nearby volcano, which formed Lake Florissant. Fine-grained mud, silt, and volcanic ash were deposited in the lake, entombing elements of the surrounding areas biota. Although vertebrate fossils are rare (MacGinitie, 1953; Meyer and Weber, 1995), the compacted lacustrine sediments preserved many plants and insects in wonderful detail. The extraordinary quality of the preservation is shown by the presence of feather impressions on the slab and counter slab of *Eocuculus* (Fig. 2).

DESCRIPTION AND COMPARISONS

Eocuculus cherpinae is a small arboreal cuckoo (Cuculiformes: Cuculidae) based on the apomorphic condition of an accessory articulating process, or sehnenhalter, on the trochlea of Digit IV of the tarsometatarsus, which has Digit IV permanently reversed for obligatory zygodactyly. Obligate zygodactyly also occurs in parrots (Psittaciformes: Psittacidae), toucans and jacamars (Piciformes: Ramphastidae and Galbulidae, respectively), and the Eocene zygodactyl birds (Sandcoleiformes: Sandcoleidae), but each of these has its own unique apomorphic condition of the sehnenhalter (Olson, 1983; Houde and Olson, 1992) for their arboreal life styles.

Osteological characteristics of the post-cranial skeleton of *Eocuculus* are more similar to species in the genus *Cuculus* (Cuculinae), e.g., the Common (*C. canorus*) and Oriental (*C. saturatus*) cuckoos of the Old World. These cuckoos have shorter but more robust wing and leg bones as compared to the Great Spotted Cuckoo, *Clamator glandarius* (Cuculinae), New World cuckoos (Cocccyzinae), ground-cuckoos (Neomorphinae), and the anis (Crotophaginae). The coccyzine, neomorphine, and crotophagine cuckoos and *Clamator* all have a gracile skeleton with the shaft of the humerus bowed in along the internal surface, ulna with prominent secondary papillae, posteriorly bowed femur, and proportionately longer tibiotarsus and tarsometatarsus. *Eocuculus* and *Cuculus* have a straighter humerus, no prominent secondary papillae, straight femur, and a shorter leg. The ground-cuckoos have much longer legs, especially the tarsometatarsus, for being cursorial.

Eutreptodactylus itaboraiensis Baird and Vickers-Rich 1997 from the late Paleocene is the earliest known fossil cuckoo in the family Cuculidae. The characteristic cuculiform sehnenhalter is not as well developed as in extant cuculids and therefore differs from *Eocuculus*, which has completed the rotation of the accessory articulating process of Digit IV.

Primitive ground birds blend avian bony characteristics from three families of birds: Musophagidae (turacos), Opisthocomidae (hoatzin), and Cuculidae (cuckoos). *Foro panarium* (Foratidae) Olson 1992 first appears in the fossil record in the Lower Eocene Green River Formation, Wyoming. Because of the mosaic nature of this bird Olson (1992) "by default" placed it into the Cuculiformes. *Foro panarium* has long legs like the ground-cuckoos and therefore is unlike *Eocuculus*.

FIGURE 1— *Eocuculus cherpinae*, new species, holotype slab (DMNH 10682, above) and counter slab (DMNH 10683, below).

FIGURE 2— *Eocuculus cherpinae,* plastotype of slab (DMNH 10682, above). Feather impressions on holotype slab (DMNH 10682, below).

Also of note from the early Eocene are fossils of cuckoos tentatively identified only to order from the Naze, London Clay, Essex, England (Feduccia, 1996:167; pers. obs. 1998). The diverse flora and fauna of the Naze are represented in the private collection of Michael Daniels, but have not yet undergone rigorous taxonomic study.

The only named European fossil cuckoo is *Dynamopterus velox* (Milne-Edwards, 1892) from the Eo-Oligocene Phosphorites du Quercy, France. This purported cuckoo is at least three times larger than *Eocuculus* but of uncertain affinities.

The earliest North American record for a typical cuckoo in the family Cuculidae is *Neococcyx maccorquodalei* (Weigel, 1963) from the early Oligocene, Cypress Hills Formation, southwestern Saskatchewan. The holotype of *N. maccorquodalei* is the distal end of the right humerus (SMNH 1420). *Neococcyx maccorquodalei* is slightly larger (greatest distal width, 6.2 mm) than *Eocuculus cherpinae* (5.4 mm). Also, *Eocuculus* is more like *Cuculus* and differs from *Neococcyx* by having a larger entepicondyle, a deeper intercondylar furrow, and a straighter humeral shaft. Weigel based his comparisons on the Yellow-billed Cuckoo, *Coccyzus americanus*, which is closest in size and osteological features.

The only other North American fossil cuckoo is *Cursoricoccyx geraldinae* (Martin and Mengel, 1984) from the early Miocene, Martin Canyon A Local Fauna of Logan County, Colorado. *Cursoricoccyx* is a ground-cuckoo (Cuculidae, Neomorphinae) and therefore differs from *Eocuculus* by its larger size and longer legs.

DISCUSSION

Eocuculus cherpinae is the earliest record of an arboreal cuckoo (Cuculidae, Cuculinae) from the middle Tertiary

FIGURE 3— *Eocuculus cherpinae,* outline drawing of holotype slab (DMNH 10682).

of North America. It shares certain osteological similarities with species in the Old World genus *Cuculus*. *Eocuculus cherpinae* is yet another example of a member of the Paleocene global avifauna (Olson, 1989). It was during the Paleogene when the global climate decay began and there was a transition from a tropical and more equitable climate to a more seasonal climate with broader daily temperate range and distinctive seasons (Wolfe, 1980). Eventually this climate decay led to the Great Ice Age of the Quaternary and the fragmentation of the global avifauna into the relictual distribution for birds we have today (Olson, 1989). The global avifauna has been preserved for us at such important fossil localities as the Naze, London Clay, Essex, England; Green River and Willwood formations, Wyoming; Messel oil shales, Germany; and from the Phosphorites du Quercy, France (Feduccia, 1996:167-169).

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PALEOECOLOGY AND PALEOENVIRONMENTS DURING THE INITIAL STAGES OF EOCENE FOSSIL LAKE, SW WYOMING

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ABSTRACT—Initial development of Fossil Lake resulted from ponding of freshwater in the southern half of Fossil Basin. Detailed stratigraphic analysis of the lower unit of the Fossil Butte Member (Green River Formation) revealed a well-developed lacustrine sequence south of Fossil Butte, and indicates four major depositional facies: (1) open lacustrine, (2) marginal lacustrine, (3) carbonate mudflat, and (4) marginal fluvio-deltaic. The open lacustrine facies is characterized by kerogen-rich to kerogen-poor finely laminated micrites that consist of calcite and very little dolomite. These carbonates contain well- preserved fossil fish, ostracods, mollusks and amorphous kerogen (produced mainly by algae). These rocks grade laterally into bioturbated micrites, and ostracodal and gastropodal limestones. Nearshore carbonates consist mostly of calcite and are typically well bioturbated. Common fossils include mollusks and ostracods. In some localized areas limestones can be oolitic, contain some typical nearshore plant remains and occasionally lag deposits of vertebrate bones. The carbonate mudflat facies is mainly restricted to the eastern margin where sediments were subaerially exposed and conditions favored precipitation of dolomite as indicated by several dolomitic units with mudcracks. Sheet-wash events along the margins during lowstands ripped up carbonates on the mudflats and redeposited them over scoured surfaces. Although fluvial events occurred throughout the life of the lake, towards the end of lower unit time fluvial activity increased. At this time a Gilbert-type delta developed from the southwest, prograded into the lake, virtually filled the whole lake, and culminated lower unit deposition.

INTRODUCTION

The Green River Formation of southwestern Wyoming, northwestern Colorado, and northeastern Utah was deposited in a system of three lakes that existed in intermontane basins during the Early and Middle Eocene (Bradley, 1963). Fossil Lake, the smallest, and adjacent to the much larger Lake Gosiute (Greater Green River Basin), occupied the Fossil Syncline, now called Fossil Basin (Figure 1). Fossil Butte National Monument is near the geographical center of Fossil Basin.

Sediments and fossils of the lower unit (informal term coined by Buchheim, 1994a) of the Fossil Butte Member, Green River Formation, were studied to reconstruct the paleogeography and paleoenvironments of a sedimentary basin that records a complete sequence of lacustrine facies and contains an abundant fossil fauna and flora, as well as the history of the initial stages of Fossil Lake.

This study is significant because the lower unit is probably the least studied and least understood of the Fossil Butte Member units. Its nature, extent and total thickness were not known until this study. Because the entire depositional sequence occurs in a comparatively small area (1,500 km^2, versus 17,000 km^2 in the adjacent Green River Basin) a detailed basin analysis is possible in relatively short distances and stratigraphic thicknesses.

PREVIOUS WORK

Pioneering studies in Fossil Basin started in the mid-1800s. Under the auspices of the U. S. Department of the Interior, Geological and Geographical Survey of the Territories, several workers produced extensive reports, including the first geological and paleontological descriptions from Fossil Basin.

The structure and geology of Fossil Basin were mapped in the early 1900s, whereas the geologic units were formally described by Oriel and Tracey (1970) who subdivided the Green River Formation in the basin into the Fossil Butte and Angelo members. Other mapping and geology were done by Rubey et al. (1975), Vietti (1977) and M'Gonigle and Dover (1992). Buchheim (personal communication) informally subdivided the Fossil Butte Member into the lower, middle and upper units, and recognized that the lower unit thickened considerably in the southern half of the basin. This led Biaggi (1989) to his documentation of an early previously unknown lacustrine phase. Petersen (1987) described the occurrence and geologic history of a "Gilbert-type" delta system in the sandstone tongue of the Wasatch Formation, especially prominent in the southern half of Fossil Basin. Buchheim (1994a, b) discussed the lithofacies, paleoenvironments and the history of saline fluctuations, and proposed a detailed depositional model for the Fossil Butte Member. Buchheim

FIGURE 1—Maps showing the location of Fossil Basin within the overthrust belt of southwestern Wyoming, the study localities, and location of other ponded basins in the foreland province. Important structural features are indicated. Study location abbreviations: AR, Angelo Ranch; BD, Bear Divide; CC, Clear Creek; CaC, Carter Creek; ChC, Chicken Creek; FB, Fossil Butte; FR, Fossil Ridge; HC, Hill Creek; LMC, Little Muddy Creek; MC, Muddy Creek; ShC, Sheep Creek; S/LMC, Sheep/Little Muddy Creek; WC, Warfield Creek (After Lamerson, 1982 and Dickinson et.al., 1988).

and Biaggi (1988) in their study of a time-synchronous unit at the base of the middle unit discovered significant variation in the number, thickness and organic content of laminae within the bed and questioned the varve interpretation for that horizon. Trivino (1996) studied the mineralogy and isotopic composition of the laminae of this bed and concluded that the deposition of these lamina were primarily a result of fresh-water inflow events. Loewen and Buchheim (1997) described fresh-water to saline transitions in the later stages of Fossil Lake.

McGrew (1975), McGrew and Casilliano (1975), Buchheim (1986), Elder and Smith (1988), Grande and Buchheim (1994) and Ferber and Wells (1995) discuss aspects of the paleoecology and taphonomy of the fossil fishes. Grande (1984) provided a rather complete catalogue and description of the fossils of the basin as well as other Green River Formation basins in Wyoming, Colorado, and Utah. Leggitt (1996) and Leggitt and Buchheim (1997) described fossil bird mass mortality beds both in the Angelo and Fossil Butte members. Cushman (1983) interpreted the palynoflora of the Fossil Butte member in his study of the depositional environments, paleoecology and paleoclimatology of these sediments in Fossil Basin. For a comprehensive bibliography of the geology of the Green River Formation in the region see Smith (1990).

This study proposes to complement these investigations and provide a more complete picture of the depositional environments and paleoecology of the lower unit of the Fossil Butte Member, which contains a well-preserved fauna and flora. The lower unit represents a lake that existed earlier, and had a depocenter further to the south, than the main body of the Green River Formation sediments in Fossil Basin.

GEOLOGIC STRUCTURE

Ponded basins (e.g., Green River Basin and others, Figure 1) in the core of the Laramide province occur adjacent to the overthrust belt and formed large freshwater and saline lakes that became regional sediment traps (Dickinson et al., 1988). Within the overthrust belt itself, Fossil Basin is a small, linear and structurally controlled basin.

Fossil Basin was formed during the Late Cretaceous-Early Tertiary on the hanging wall of the Absaroka thrust system as a result of both structural and depositional influences. The basin was divided into a northern basin and a southern basin by a cross-basinal, northwest-southeast-trending Little Muddy Creek transverse ramp (Lamerson, 1982; Hurst and Steidtmann, 1986). This might have implications for accumulation of lacustrine sediments in the southern half of Fossil Basin. As thrust reactivation and continuous uplift of the basin margins took place, fluvial and lacustrine sedimentation occurred in a symmetrical basin with a stable depocenter (Coogan, 1992).

STRATIGRAPHY

In Fossil Basin the Green River Formation was divided by Oriel and Tracey (1970) into two members: the Fossil Butte Member and the overlying Angelo Member. The Fossil Butte Member was named for excellent exposures along the southern edge of Fossil Butte (where the type section is) in what is now Fossil Butte National Monument, and along the north and east ridges of Fossil Ridge, just south of the monument, where the most extensive fossil fish quarries are found (Oriel and Tracey, 1970). The Fossil Butte Member consists of laminated micrite, siltstone, mudstone and claystone with some thin tuff beds. These rocks grade laterally toward the margin of ancient Fossil Lake into algal, ostracodal and gastropodal limestone. Siliciclastic, deltaic deposits interfinger with the lacustrine sediments at the margin of the basin (Rubey et.al., 1975).

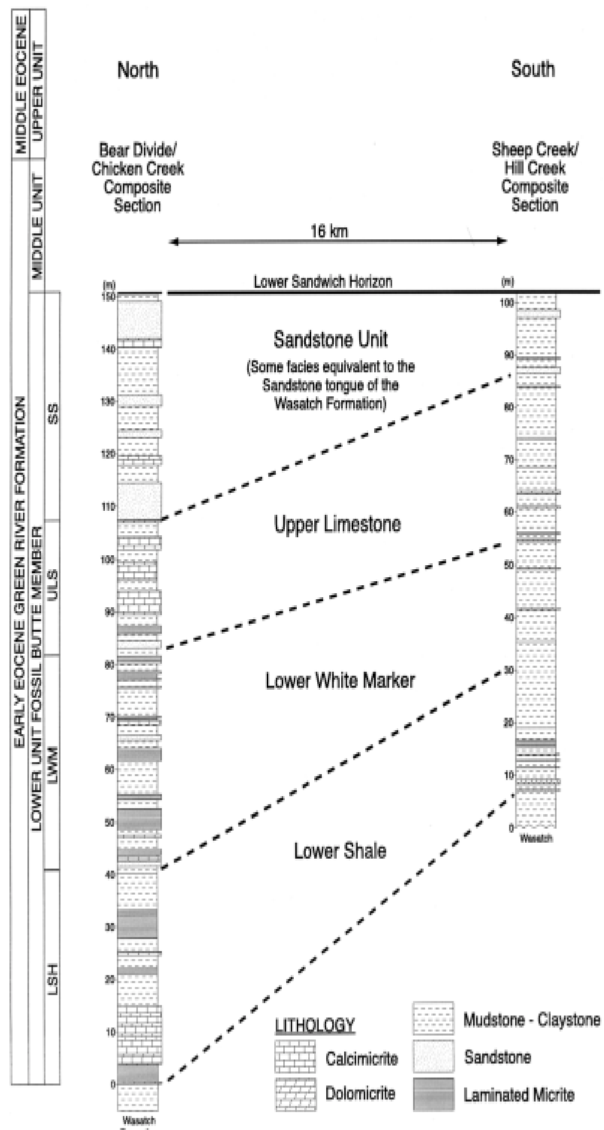

FIGURE 2—Stratigraphic correlation of lower unit composite sections in southern Fossil Basin. Informal subunits within the lower unit of the Fossil Butte Member are used to correlate sections in the depocenter to the north (Bear Divide/Chicken Creek) with sections at more marginal locations to the south (Sheep Creek/Hill Creek).

Buchheim (1994a) followed a natural lithologic breakdown and divided the Fossil Butte Member into three major units, the lower, middle and upper (Figure 2), which can be correlated with distinct depositional environments. The lower unit represents the first stage of Fossil Lake and consists of siliciclastic mudstone and sandstone, ostracodal and gastropodal limestone, bioturbated calci- and dolomicrite, and laminated micrite. In the southern half of Fossil Lake the uppermost part of the lower unit equivalent to the sandstone tongue of the Wasatch Formation and forms a wedge below the middle unit. This is a deltaic facies exhibiting foreset, topset and bottomset beds (Petersen, 1987).

The middle unit is a well-developed lacustrine sequence which is best exposed at the Fossil Butte Member type section. It consists primarily of kerogen-rich laminated micrite (oil shale), with abundant fossil fish, insects and plants. The upper unit is characterized by the presence of calcite pseudomorphs after saline minerals in the laminated dolomicrites, some of which are petroliferous.

Buchheim (1994a, b) and Buchheim and Eugster (1998) studied in detail the lithofacies and depositional environments of kerogen-rich laminated micrites, especially abundant in the middle unit of the Fossil Butte Member.

Field studies in Fossil Basin uncovered a much more well-developed lacustrine sequence than previously thought for the lower unit time period. Kerogen-rich laminated micrite with abundant fish remains discovered south of Fossil Butte suggest a more southerly lake depocenter for the lower unit deposition (Biaggi, 1989).

FOSSILS AND AGE

The Fossil Butte Member has yielded such a variety of fossil invertebrates, vertebrates, and plants that this Konservat-Lagerstätten (a term meaning a bonanza horizon or mother lode, used for fossil biotas which show superb preservation) is one of the most extensive known in North America. Nevertheless, the precise age of the member has remained uncertain due to the lack of comparable reference material (Oriel and Tracey, 1970). Because of this problem, dating has been restricted to the intertonguing Wasatch sediments, which have yielded an abundant mammalian fauna (Gazin, 1959). Interestingly the Green River Formation of Fossil Basin was assigned a Lostcabinian age even though no mammals of that age were known from the basin (Gazin, 1959; Schaeffer and Mangus, 1965). Breithaupt (1990) questioned this assignment after reports of the discovery of *Orohippus* in the middle unit of the Fossil Butte Member.

In his study of the palynoflora Cushman (1983) and Cushman et al. (1984) concluded an early to middle Eocene age for the Fossil Butte Member (i.e., late Lostcabinian to early Bridgerian). He correlated the majority of the Fossil Butte Member sediments with those of the Wilkins Peak Member in the Green River Basin. Based on sedimentological evidence he predicted that the lower boundary of the Fossil Butte Member would be equivalent to some portion of the Tipton Shale Member (Cushman, 1983). See Cushman (1998) for a discussion of the palynostratigraphy and age of the Fossil Butte Member. Buchheim (1994a) reported a K-Ar age date on a sample of feldspar from the "K-spar tuff" near the top of the middle unit of the member, that yielded an age of 50.2±1.9 Ma, close to the start of Bridgerian time. More recently Froelich and Breithaupt (1997) reported the occurrence of the mammal *Lambdotherium* from the middle unit (F2 of Grande and Buchheim, 1994). This fossil is typically Lostcabinian in age.

MATERIALS AND METHODS

Nine stratigraphic sections of the lower unit (Fossil Butte Member, Green River Formation) were measured in the southern half of Fossil Basin, and several additional sections were studied especially in the southernmost reaches of the basin to determine the extent of the lake during lower unit time (Figure 1). Over 200 samples of the lacustrine carbonates and carbonate-bearing sedimentary rocks were collected. Fossil occurrences were recorded and significant specimens collected. The lithologic character, sedimentary structures, and paleontology of the individual sedimentary units were noted. Detailed stratigraphic and sample data, as well as stratigraphic correlation diagrams of the measured sections were recorded by Biaggi (1989).

Standard sedimentologic and petrographic techniques were used (including X-Ray diffraction analysis on 51 samples), and data analysis included Markov Chain Analysis (to establish lithofacies assemblage and cyclic relationships) and basin analysis mapping techniques (i.e., isopachs, facies maps).

RESULTS AND DISCUSSION

Results from this study indicate an extensive and well-developed lacustrine sequence for the lower unit in the southern half of Fossil Basin, south of Fossil Butte. The Fossil Butte Member at its type locality (Fossil Butte) consists mainly of the middle and upper units and only a few meters of the lower unit (a total of 70 to 90m). It is not representative for the well-developed lower unit south of there, which itself measures more than 120 meters. The lower unit is characterized by a dominance of siliciclastic sedimentary rocks, which in the central part of the basin average twice the amount of carbonates and in the southern region dominate the sections. Laminated rocks are less abundant, and interbedding of carbonates with siliciclastics is more common on a small scale. The lithofacies nomenclature and classification followed in this report is that of Buchheim (1994a), which better describes the nature of the Fossil Basin carbonate rocks. It is based on mineralogy, kerogen content, grain size and sedimentary structures.

LITHOFACIES AND FACIES RELATIONSHIPS

The most common lithofacies in the lower unit (Figure 3) are kerogen-poor laminated micrite (KPLM), kerogen-rich laminated micrite ("oil shale", KRLM), bioturbated or massive micrite, ostracodal and gastropodal limestone, and siliciclastic sandstone, siltstone and mudstone. Minor lithofacies include burrowed laminated micrite, alternating kerogen-poor laminated calcimicrite and siliciclastics (KPLMSil), dolomicrite, and volcanic tuff (Figure 3). Laminated micrites constitute about 50 percent of the carbonates, and appear as a wide spectrum of carbonates ranging from buff to brown, friable slope-forming sediments to dark brown to black, well-indurated ledge-forming rocks. The reader is referred to Buchheim (1994a, table 1) for a detailed description of the individual lithofacies, and Biaggi (1989) for a series of Markov analyses, which confirmed the cyclic succession of lithofacies in the lower unit into a well-defined lithofacies assemblage. This lithofacies succession, a lacustrine transgressive sequence (or from margin to basin center), is Sandstone-Siltstone-Mudstone-Micrite-KPLM-KRLM.

In contrast to the middle and upper units, the lower unit reflects a paucity of dolomite deposits with some isolated dolomicrite beds at localities CC, ChC, BD (see Figure 1 for locality abbreviations), and some ostracodal dolomicrites at the AR locality in the eastern margin of the basin.

Figure 2 shows the stratigraphic correlation of two composite sections in the lower unit, and a further subdivision of the lower unit into four major subunits. The northern BD/ChC/CC composite section is typical of the sections near the depositional center of lower unit time Fossil Lake, and the ShC/HC composite section is representative of the more marginal/nearshore localities. North of Fossil Butte, lower unit sediments thin rapidly, whereas in the vicinity of Fossil Butte-Fossil Ridge the best-developed middle and upper unit sequences occur. This indicates a shift of the basin depositional center to the north.

Subdivision of the lower unit (Figure 2) allowed better correlation throughout the basin, and reflects general environmental trends. The major subunits are: 1) a lowermost "Lower Shale"(LSH) subunit, consisting of alternating mudstone, calcimicrite and siliceous calcimicrite, and oil shale and organic rich mudstone at the basin center (ChC, RH, CC). Towards the basin margins this subunit grades into siliciclastics with a few alternating thin limestones. 2) "Lower White Marker"(LWM) subunit, very noticeable in outcrop due to weathering of oil shale and calcimicrite, contains few siliciclastics, and denotes a time of maximum transgression during lower unit time evident from thin but extensive oil shale (KRLM) beds. These oil shales are thickest at locality CC, extend as far as ShC in the south and marginal localities (AR and BD), and contain abundant fossils. 3) "Upper Lime-

FIGURE 3—Lithofacies of the lower unit. 1-2. Kerogen-rich laminated micrite (KRLM), CC-07. Dark kerogen laminae (klm) alternate with lighter calcite laminae (clm). 1, small divisions on scale - 1mm; 2, scale bar = 0.1mm. 3. Kerogen-poor laminated micrite (KPLM), from ChC-14. 4. Peculiar type of quartz-rich kerogen-poor laminated micrite (KPLMSil) showing siliceous (sil) alternating laminae, from FB-46. 5. Bioturbated micrite showing burrows (b), from HC-22. 6. Bioturbated kerogen-poor laminated micrite showing disrupted kerogen (klm) and calcite (clm) laminae, from ChC-87; scale bar = 0.5mm. 7. Analcimic tuff from CC-04. 8. Abundant ostracods (os) one mm in length dominate this ostracodal limestone, S/LMC-40.

TABLE 1—Summary of useful criteria for distinguishing paleoenvironments of the lower unit, Fossil Butte Member, Green River Formation. KRLM=kerogen-rich laminated micrite; KPLM=kerogen-poor laminated micrite; BM=bioturbated micrite; LS=limestone.

	Open Lacustrine	Marginal Lacustrine	Carbonate Mudflat	Marginal Fluvio/Deltaic
Lithofacies	KRLM (oil shale) KPLM Fossiliferous LS Calcareous mudstone	BM Ostracodal LS Gastropodal LS Oolite Tufa	Dolomicrite Ostracodal dolostone	Fluvio-lacustrine siliciclastic sandstone, siltstone Deltaic siliciclastics Prodelta mudstone Fluvial-floodplain clastics
Mineralogy	Calcite &/or dolomite Anoxic sediments?	Calcite Oxygenated bottoms	Dolomite/Calcite Highly alkaline & saline	Quartz, feldspar, mica, calcite
Sedimentary structures	Laminites	Bioturbation Thin to massive bedding	Mudcracks Lenticular lamination Carbonate rip-ups Scour structures	Trough cross bedding Ripple marks Deltaic foresets, bottomsets and topsets
Fossils	Fish (whole, bones, scales, coprolites) Gastropods, bivalves Ostracods Insects Plant fragments Algae: kerogen	Fish bones, coprolites Bivalves, Gastropods Ostracods Burrows Beach "lag" deposits Vertebrate bones Bird nesting sites *Equisetum* & *Typha* stems	Ostracods Bird bones	Reptiles Mammals Fish bones & scales Gastropods, bivalves Ostracods

stone" (ULS), is characterized by several limestone beds that alternate with siltstone and mudstone and a unit of KRLM occurring at the bottom of the unit. Most of the limestones are rich in gastropods and ostracods, and typify a more littoral environment. Capping the lower unit in most of the southern half of Fossil Basin is the 4) "Sandstone Unit" (SS), which forms major sandstone cliffs in this region. Part of this unit forms the sandstone tongue of the Wasatch Formation, and was studied in detail by Petersen (1987) who described it as part of a "Gilbert-type" delta that brought great influxes of siliciclastics from the S-SW into Fossil Lake.

The total carbonates isopach map (Figure 4-1) and the total thickness isopach map (Figure 4-2) suggest that Fossil Lake might have extended farther west than Bear Divide (BD). Faulting and erosion have produced an extensive topographical depression to the west with no lacustrine deposits. The occurrence of nearshore carbonates 32km to the west hints at a possible explanation for the thick lower unit deposits near Bear Divide.

Figure 4-1 shows that the KRLM ("oil shale") is located more centrally in the lake (CC, FR), whereas both the total section thickness isopach and the siliciclastic/carbonate ratio isopach map (Figure 4-2) show a marked high towards the west and southwest. This relationship suggests that greater siliciclastic influx from the west/southwest was accompanied by calcium-rich waters, which when mixing with the saline-alkaline waters of the lake, resulted in a greater precipitation of calcium carbonate in those areas. This supports the conclusions of Buchheim and Eugster (1986) and Buchheim (1994a).

In the southern part of Fossil Basin sections become increasingly siliciclastic, and eventually are replaced by the Wasatch Formation in the vicinity of Hill Creek. At the southernmost locality studied, HC, the general lithofacies relationships are dominated by alternating siltstones and limestones with only one thin occurrence of KPLM containing ostracods. In the northern part of the basin, the lower unit thins rapidly and is characterized by bioturbated rocks and only a few thin beds of laminated micrite.

A few primarily analcime-rich tuffs occur in the lower unit sedimentary sequence and are not as abundant as in the middle and upper units.

The KPLMSil is evidence of cyclicity and vertical variability. These well-developed sequences of alternating KPLM and organic rich mudstones (some with abundant plant fragments) are typical in the lower part of the sections at BD and ChC.

From the basin depocenter KRLM laterally grades toward the margins into less organic-rich but much thicker laminated carbonates (KPLM) and subsequently into bedded or massive micrite. This facies change can be directly related to organic dilution towards the margins (as also suggested by Moncure and Surdam, 1980, Piceance Creek Basin; Sullivan, 1985, Wilkins Peak Member; Buchheim and Biaggi, 1988, Fossil Basin; and Buchheim, 1994a, b, Fossil Basin). Due to the influx of siliciclastics and calcium-rich waters at the margins of the lake, sedimentation was greater at the marginal environments, interrupting an otherwise continuous deposition of carbonate and organic matter. This accounts for the noted shoreward increase in laminae number as well as laminae thickness (Buchheim and Biaggi, 1988).

This is in agreement with the idea of periodic sheet floods bringing in plant remains and other organics from floodplains thus leading to an increase in productivity and precipitation of carbonates. In addition, increased inflow probably resulted in higher precipitation of carbonates at the lake margins as the fresher calcium-rich fluvial waters came in contact with more saline and alkaline waters of the lake. This increased carbonate precipitation at the margins resulted in dilution of organics in those areas.

PALEOECOLOGY AND PALEOENVIRONMENTS

Fischer and Roberts (1991) equated the changing interpretations proposed for the Green River Formation oil shales with a pendulum swinging from a meromictic open-drainage lake model (first suggested by Bradley, 1929, 1931, 1948, 1964, and later supported by many), to a closed drainage playa-lake model (first proposed by Eugster and Surdam, 1973; Eugster and Hardie, 1975, and later supported by others), to a more intermediate position that combined aspects of both (Surdam and Stanley, 1979). See discussions of these interpretations by Surdam and Stanley (1979), Picard (1985), Sullivan (1985), Biaggi (1989), Fisher and Roberts (1991), and Grande (1994). Surdam and Stanley (1979), Buchheim and Surdam (1981), Grande (1989), Buchheim (1994a), and Grande and Buchheim (1994) recognized that the lake system was dynamic and capable of changing depositional environments over relatively short intervals of time. Nevertheless, the fact that investigators have studied paleoenvironments at specific disconnected intervals of time and space has resulted in seemingly conflicting models that need not be in conflict at all (Grande, 1994).

Much of the recent discussions have revolved around the water chemistry of Fossil Lake. On the one hand sedimentologists have proposed that both Fossil Lake and Lake Gosiute were saline, whereas paleontological evidence suggests these lakes were fresh. After a detailed analysis of the horizons on which different authors had based their conclusions, Grande (1994) concluded that at different times and in different areas of the lake, water chemistry varied and included saline cycles.

The model presented here resembles those of Buchheim (1994a) for Fossil Basin, and Ryder et al. (1976) and Fouch and Dean (1982) for the Uinta Basin. The model is illustrated in Figure 5, and shows the occurrence and distribution of four major depositional environments: (1) open-lacustrine, (2) marginal-lacustrine, (3) carbonate mudflat, and (4) fluvio-deltaic. The figure represents the depositional settings in Fossil Lake at the end of lower unit time. Useful criteria that characterize each depositional facies are shown in Table 1. Criteria are grouped according to lithofacies, mineralogy, sedimentary structures and paleontology.

The open-lacustrine facies developed in the central part of the lake to form an elongated (north to south) body of sediments that extend from Fossil Ridge to Chicken Creek. KRLM formed at the depocenter and grades laterally into

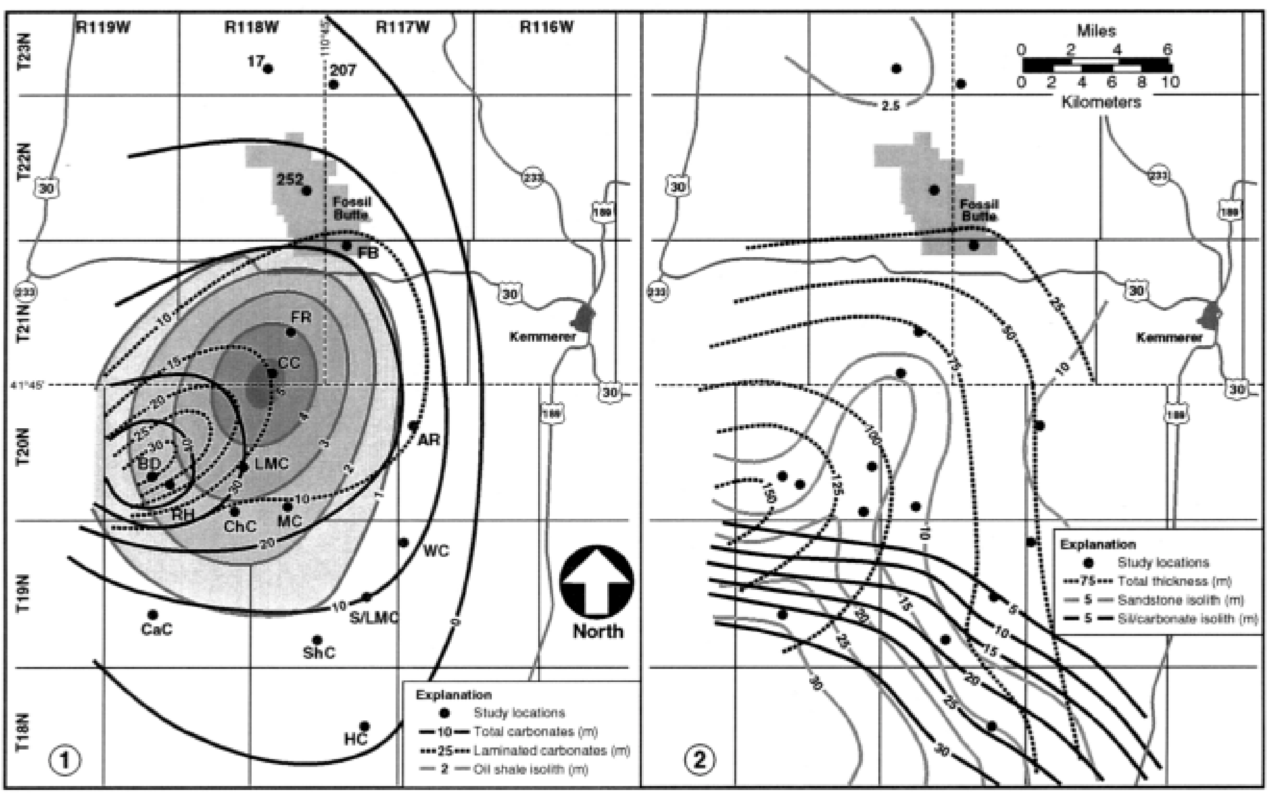

FIGURE 4—Isopach maps. 1. Isopachs illustrating three types of carbonate distribution in the lower unit, Fossil Butte Member. Total carbonate thickness (solid lines), laminated carbonate thickness (dashed lines), and KRLM thickness (oil shale) in the screened patterns. 2. Isopachs illustrating the total thickness of sediments (dashed lines), siliciclastic/carbonate ratio (solid lines), and sandstone thickness (screened lines).

KPLM. This gradation involves the dilution of kerogen by calcite from depocenter to margin and an increase in laminae thickness and number (Buchheim and Biaggi, 1988; Buchheim, 1994b; Trivino, 1996). Fossils are most abundant and diverse in this facies (Table 1). The most common fish in the open-lacustrine facies is the herring *Knightia* (Figure 6-1), with minor occurrences of *Phareodus* and *Priscacara*. Buchheim and Surdam (1981) report this association from the Laney Member of the Green River Formation in the Green River Basin. The gastropods (Figure 6-3,4) are all indicators of fresh shallow water with very low salinities (Hanley 1974, 1976). Algae was probably responsible for the origin of the kerogen that forms the organic lamination of the calcimicrites as well as for the precipitation (through their photosynthetic processes) of low-Mg calcite, both of which alternate to form the laminated KRLM and KPLM (Dean and Fouch, 1983).

This facies is surrounded shoreward by the marginal-lacustrine facies. Rocks consist of thinly bedded to massive micrite, bioturbated micrite, ostracodal and gastropodal limestone (grain-supported), and oolite. These are dominated by calcite and toward the margins become greatly diluted by siliciclastics and eventually are replaced by mudstone and siltstone of the fluvio-deltaic facies. Also, micrite with gastropods and ostracods (Figure 6-5) is replaced at the margins by ostracodal and gastropodal limestone (Figure 3-8). In addition this facies contains fossil fish bones and coprolites, and few bivalves. In some localized marginal areas particular "bone beds" of terrestrial vertebrates (birds, Figure 6-2) suggest the formation of beach strandline deposits. Leggitt and Buchheim (1997) found evidence for *Presbyornis* nesting in these sites near the ancient shoreline (see Leggitt et al., 1998). This environment is similar to the 'littoral paleoenvironment' of Buchheim and Surdam (1981).

A localized carbonate mudflat developed along the eastern margin (near locality AR, Figure 5). This mudflat environment underwent periods of subaerial exposure that produced dolomitization, mudcracks and other desiccation features. With increased energy conditions (scour structures), laminated dolomicrite and dolomitic mudcracked sediments were ripped-up and redeposited as dolomitic clasts in other calcitic carbonates. The repeated cycles of dolomitic carbonates, calcitic carbonates and siliciclastics in the AR section indicate the rapidly changing nature of the environments in Fossil Lake. In an otherwise freshwater (low salinity) Fossil Lake, this locality (AR) was subjected to several periods of hypersalinity and very high alkalinity levels.

The fluvio-deltaic facies is the dominant facies in the western, southwestern, and southern margins of Fossil Lake. Fluvial events dominate the southern margins throughout the life of the lake. At the southwestern margin a major "Gil-

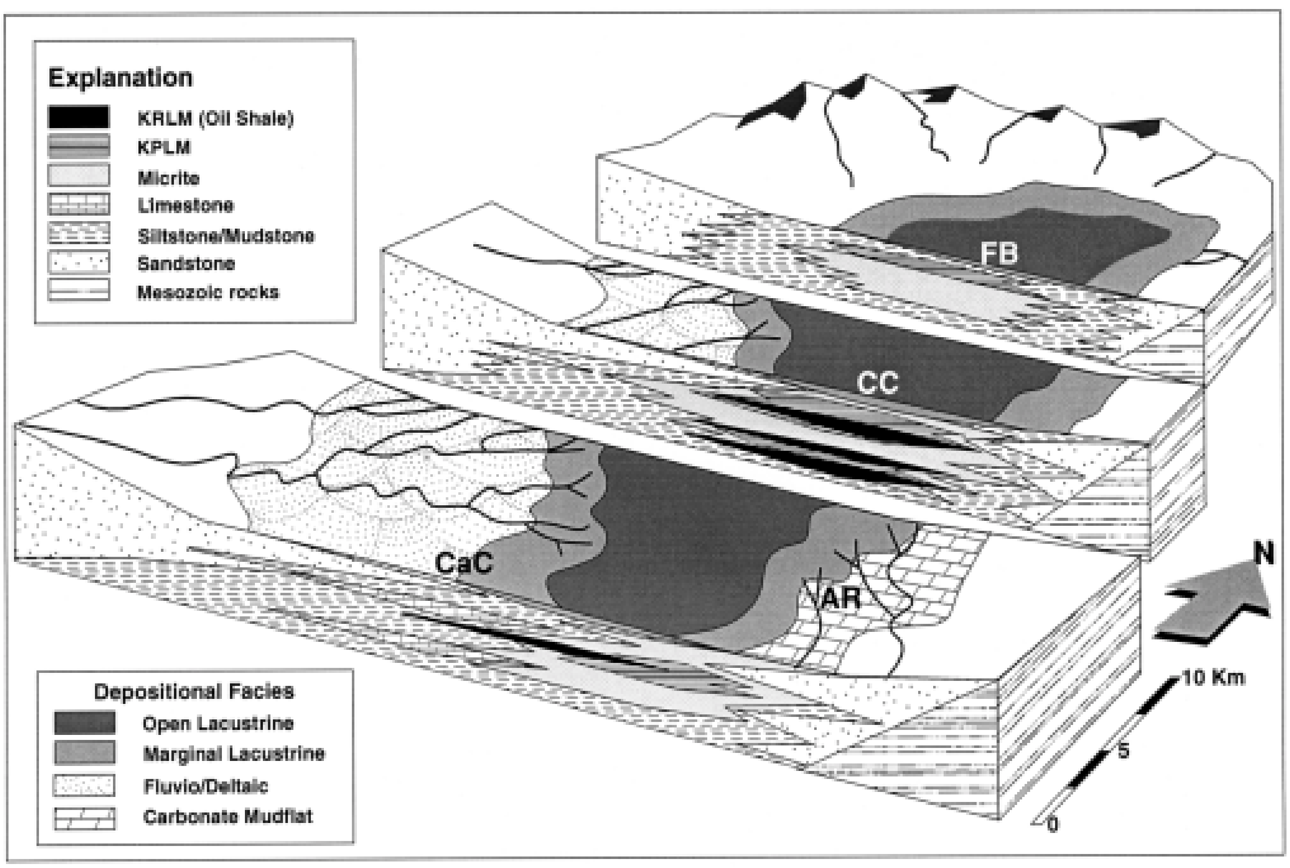

FIGURE 5—Block diagram illustrating the depositional model for the lower unit, Fossil Butte Member. The model depicts the distribution of interpreted depositional environments: open-lacustrine, marginal lacustrine, fluvio/deltaic and carbonate mudflat facies in Fossil Lake as it existed in the Early Eocene.

FIGURE 6—Fossils of the lower unit. 1. *Knightia* (herring). 2. Vertebrate bones (possibly *Presbyornis*), ShC. 3. Gastropods from CC and ShC include *Omalodiscus* (o) and more common *Physa*. 4. Juvenile gastropods, *Goniobasis* (g) 2mm long from ShC-06, with unidentified larger gastropod. 5. Ostracods (os) in laminae plane of a KRLM, length = 1.3mm, CC-11. 6. Insect, 1 cm long, CC-11. 7. *Equisetum* (horsetail). 8. Flower from CC-11.

bert-type" delta at the end of lower unit time gradually covered most of the southern half of Fossil Lake with deltaic sandstone and related siliciclastics, which graded laterally into claystone at Fossil Butte. The deltaic environment developed when a modified "Gilbert-type" and Catatumbo River-type delta prograded into Fossil Lake from the southwest to the northeast. Petersen (1987) identified typical deltaic subenvironments. Prodelta mudstone extended as far north as Fossil Butte where it alternates with carbonate laminae in a four meter sequence at the top of the lower unit.

FOSSIL LAKE HISTORY, 'THE BEGINNINGS'

During the Late Cretaceous-Early Eocene tectonic development of Fossil Basin fluviatile infilling was the dominant mode of deposition. Since Campanian-Maastrichtian time, the basin was divided by a paleotopographic ridge, the Little Muddy Creek transverse ramp. Because of this tectonic setting, the lower unit accumulated primarily in southern Fossil Basin, whereas the northern half was characterized by fluvial deposition. The initial filling of Fossil Lake, during the Late Early Eocene (lower unit time) resulted in an extensive freshwater lake with a well-established shoreline. Close to the shore *Presbyornis* colonies became established along the western (Bear Divide) and eastern (Warfield Creek) margins. The lake had its center of deposition (from distribution of oil shales in the lower unit) in the vicinity of the Clear Creek locality, around which an open lacustrine depositional facies developed. Here, KRLM (oil shale) and KPLM were deposited from the depocenter towards the margin respectively, alternating with calcareous mudstone. A rich community flourished in this environment and is characterized by high productivity, as seen from the abundance of kerogen and fossils preserved in the sediments. Surrounding this open-lacustrine environment was a marginal-lacustrine setting, which sustained a variety of organisms and facilitated the deposition of micrite, fossiliferous limestone and siliciclastics. These conditions fluctuated during most of the life of Fossil Lake, when climatic and or tectonic events (including a few volcanic events that deposited ash layers over the bottom of the lake) caused regressions and transgressions, as well as sudden increased input of siliciclastics in the lake by sheet floods or storm processes. After sediment infilling of the southern end of Fossil Basin by lacustrine and deltaic processes, Fossil Lake expanded to its maximum, resulting in deposition of the oil shale- and fossil-rich middle unit.

CONCLUSIONS

1. The lower unit of the Fossil Butte Member is a well-developed lacustrine sequence in Fossil Basin. Because of tectonic basinal features it was deposited mostly in the southern half of Fossil Basin, but extends from the vicinity of Loc. 17 to near Hill Creek where it grades into the intertonguing Wasatch Formation. The eastern shoreline of Fossil Lake ran north to south just east of Angelo Ranch. Additional studies are needed to determine the western extent of Fossil Lake, but there is good evidence that it might have extended much further west (even during lower unit time), possibly up to the vicinity of Bear Lake (Utah).

2. Lithofacies include laminated and non-laminated micrites: KRLM (kerogen-rich laminated micrite), KPLM (kerogen-poor laminated micrite), bedded to massive micrite (with varying degrees of bioturbation), ostracodal and gastropodal limestone, dolomicrite, and KPLMSil (kerogen-poor laminated micrite with high alternating clay lamina); siliciclastics: fluvial and deltaic sandstone, siltstone and mudstone; occasional tuff and chert. The absence of saline minerals and the analcime-rich nature of the tuffs attest to the fresh (low salinity) nature of the water and the carbonates indicate the alkaline nature of Fossil Lake.

3. Lithofacies of the lower unit of the Fossil Butte Member change laterally and vertically; variety and cyclicity indicate a dynamic system. These lithofacies were deposited in four major depositional environments: 1) open-lacustrine, 2) marginal-lacustrine, 3) carbonate mudflat, and 4) fluvio-deltaic. The open-lacustrine facies is characterized by KRLM, KPLM and associated calcareous mudstone, and was conducive to the preservation of abundant fossils, probably by rapid sedimentation and by anoxic conditions below the sediment-water interface. Lamination indicates a low-energy environment, whereas the varied fossil fauna suggest shallow freshwater conditions. Lithofacies grade into each other from depocenter to margin, in relationships that are dependent on calcareous precipitation and siliciclastic sediment inflow from the margins, and factors such as distance from depocenter to margins, changes in depth, oxygenation and water chemistry. At the depocenter of the lake KRLM grades towards the margin into KPLM and subsequently into bedded to massive micrite, and/or fossiliferous limestone (grainstone). Laminae thickness and number increase towards the margins, as organic matter (kerogen) is diluted by increased calcite precipitation and siliciclastic sedimentation in the marginal areas. The marginal-lacustrine facies occurs in these areas, where micrite is dominant as well as ostracodal and gastropodal limestone. This facies also sustained a varied fauna but preservation is not as good, probably due to the action of bioturbators. Another type of marginal facies is the carbonate mudflat, restricted to the Angelo Ranch area where significant subaerial exposure and evaporation was conducive to precipitation of dolomite. The fourth depositional facies is the fluvio-deltaic paleoenvironment, characterized by deposition of sandstone, siltstone and mudstone, with some associated limestone. This deltaic depositional event culminated lower unit lake sedimentation and set the stage for deposition of middle unit sediments throughout Fossil Basin.

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VEGETATIONAL HISTORY AND CLIMATIC TRANSITION IN AN EOCENE INTERMONTANE BASIN: PLANT MICROFOSSIL EVIDENCE FROM THE GREEN RIVER FORMATION, FOSSIL BASIN, WYOMING

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Abstract—The palynoflora of the Green River Formation in Fossil Basin, Wyoming, provides an excellent opportunity to study the vegetational history of an Eocene intermontane basin. Outcrop samples were collected and processed for plant microfossils from three measured sections representing the center and marginal areas of Fossil Lake.

The abundance of hardwood, riparian and conifer taxa suggests that moist lowlands and floodplains existed around Fossil Lake with upland forests on the surrounding ridges and mountains. Streams originating in the highlands supplied water for Fossil Lake and the surrounding vegetation. The palynofloral assemblage of the Fossil Butte Member and the lower part of the Angelo Member indicate that a mixed mesophytic forest grew near Fossil Lake.

A mixture of subtropical and warm temperate floral elements in the Fossil Butte Member suggests the climate was transitional between humid, subtropical and drier, warm temperate with fluctuations during various episodes of deposition.

INTRODUCTION

The purpose of this study was to use plant microfossils to interpret the vegetational history and paleoclimate of an intermontane basin during deposition of the lacustrine Eocene Green River Formation in Fossil Basin, Wyoming. Fossil Lake was one of three major Eocene lakes whose sediments form the Green River Formation (Figure 1). Fossil Lake lay to the west of the much larger Lake Gosiute, which covered most of southern and central Wyoming. Fossil Lake formed along the eastern edge of the Idaho-Wyoming thrust belt in a small, structurally controlled basin. The Crawford Mountains and Tunp Range form the western boundary, Oyster Ridge the eastern boundary, and the Uinta Mountains the southern boundary. The lacustrine Green River Formation consists of buff colored, laminated calci- and dolomicrite, brown to black, kerogen-rich, laminated calci- and dolomicrite, siltstone, mudstone, and claystone with several thin tuff beds. Laterally, these lithologies grade into algal, ostracodal, gastropodal, and bioturbated calcimicrites deposited in shallow water near the shore of ancient Fossil Lake (Rubey, Oriel, and Tracey, 1975; Buchheim, 1994).

Buchheim (1994) divided the Green River Formation in Fossil Basin into three informal units (Figure 2). Each of these units represents a distinct depositional phase of Fossil Lake. Briefly, the lower unit is a lacustrine sequence characterized by siliciclastic mudstone and sandstone, bioturbated calci- and dolomicrite, and kerogen-rich and kerogen-poor laminated micrite. Some fossil fish and gastropods occur in the lower unit. Toward the margin of the lake the Sandstone Tongue of the Wasatch Formation separates the lower unit from the middle unit. The middle unit is a well-developed lacustrine sequence characterized by laminated calci- and dolomicrite with high kerogen content. Toward the margin the laminated micrite becomes bioturbated. The middle unit contains most of the fossils that occur in the basin. The upper unit represents the waning stages of the lake. It is characterized by poorly laminated dolomite-rich carbonates, many of which contain calcite pseudomorphs after saline minerals, and some kerogen-rich, laminated dolomicrite. Fossils are rare in the upper unit. The lower, middle, and lower part of the upper units form the Fossil Butte Member and the upper part of the upper unit forms the Angelo Member (Buchheim, 1994).

PREVIOUS PALEOBOTANICAL STUDIES

Lesquereux (1873 to 1883) first described fossil plants from the Green River Formation in a series of papers published as part of the U.S. Geological Survey of the Territories. Newberry (1883, 1898) followed with more descriptions of fossil plants from the same area as Lesquereux. Although the exact location(s) from which these floras were collected are not known, it is thought that the fossil plants of Lesquereux and Newberry were collected from the western part of the Green River Basin, i.e., Lake Gosiute (MacGinitie, 1969). Knowlton (1923) later revised the taxonomy of the Green River flora and published lists of earlier collections. Knowlton also

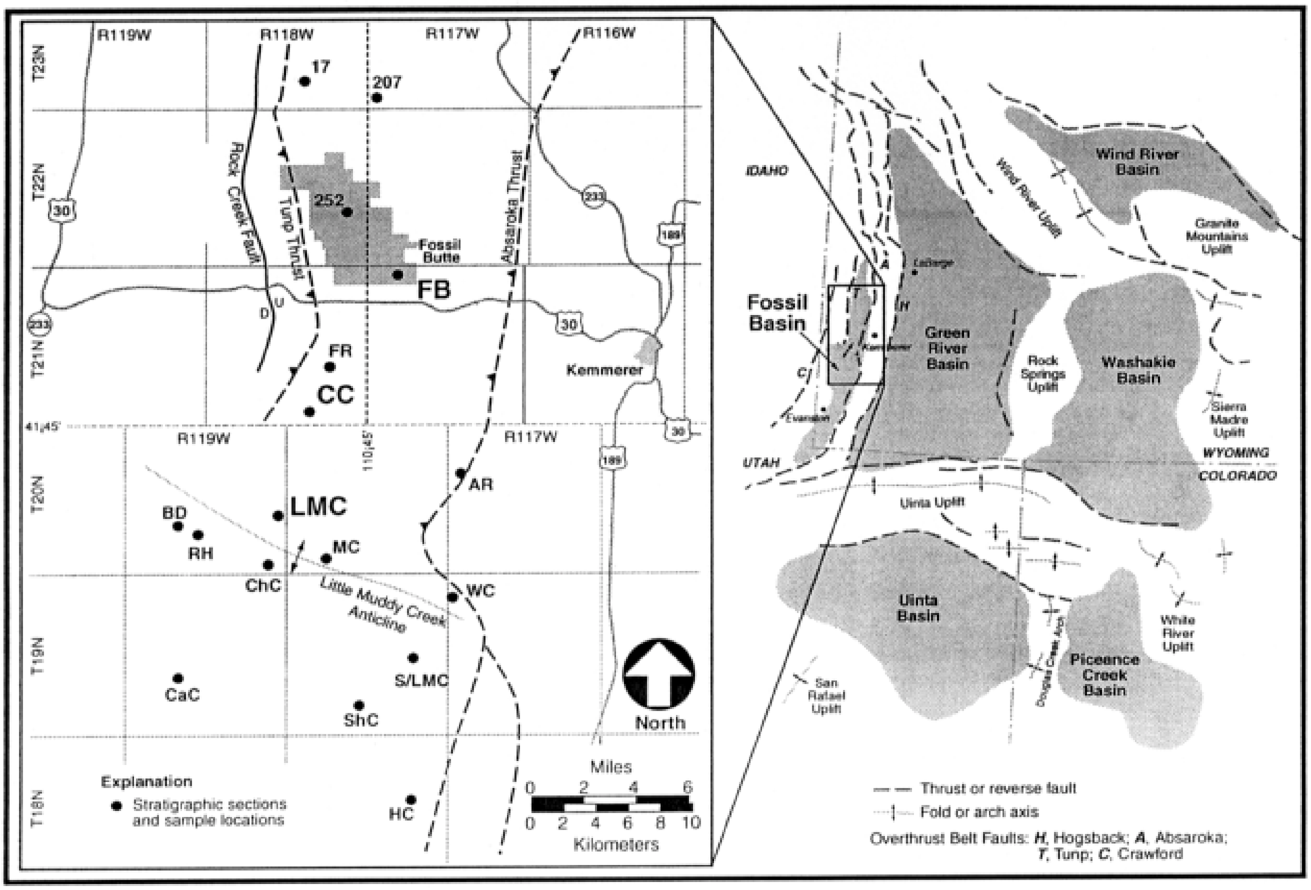

FIGURE 1—Geographic and geologic features in the vicinity of Fossil Basin, Wyoming. Study localities are FB, CC, and LM in the left-hand figure. Modified from Buchheim and Eugster (1998) and Biaggi and Buchheim (this volume). Shaded areas represent areal extent of the Eocene Green River lake system.

included descriptions of fossil plants from the Green River Formation of northwestern Colorado (Lake Uinta). Knowlton's collections were probably from a higher stratigraphic horizon than those from Lake Gosiute (MacGinitie, 1969). In other studies, Cockerell (1909, 1925, 1927) contributed several new species to Knowlton's list of Uinta Basin taxa. Consequently, the described Green River Flora was a composite of assemblages from numerous stratigraphic horizons deposited in separate lake basins.

As more of the Green River Flora was described, later paleobotanical studies became more interpretive. Brown (1929, 1934) believed the Green River Flora was an assemblage of plants from warm, wet lowlands with plants transported from surrounding cool, dry uplands. MacGinitie (1969) similarly interpreted the Green River Flora of the Uinta Basin to represent warm temperate to tropical floras similar to those that now exist in Mexico and some parts of Central and South America.

Bradley (1931) published the earliest study of the Green River palynoflora. His work on the pollen and spores laid the foundation for the more extensive research by Wodehouse (1933). Based on his study of the palynoflora, Wodehouse believed that Lake Uinta existed in a hot, desert valley and was fed by streams originating in surrounding highlands where there was greater precipitation. Wodehouse also suggested that Lake Uinta was shallow and muddy with extensive marshy areas along the margins. In addition, the presence of conifer pollen provided evidence for the existence of a flourishing "mesophytic forest" in the neighboring highlands (Wodehouse, 1933). Later studies by Newman (1974, 1980) in the Uinta and Piceance Creek basins led to the development of a palynostratigraphy for the Green River Formation in these basins.

In Fossil Basin, Brown (1929, 1934) studied the megaflora and concluded that Fossil Lake existed in an intermontane basin. Unfortunately, Brown did not provide specific locality or stratigraphic information and it is difficult to draw specific conclusions regarding the vegetational history from his research. However, McGrew and Casilliano (1975) used Brown's overall interpretation of the megaflora and pictured swamps and floodplains surrounding Fossil Lake with nearby ridges and highlands providing the elevational changes reflected in the plant assemblages. Lacking from all of the previous paleobotanical research is a study on the plant microfossils of the Green River Formation in Fossil Basin. This study begins to fill that void and utilizes plant microfossils to understand the vegetational history of the Green River Formation in Fossil Basin.

METHODS

Forty-nine outcrop samples of the Green River Formation in Fossil Basin were collected and processed for plant microfossils. The samples were collected from three measured stratigraphic sections corresponding to localities 217, 122 and 740 of Buchheim (1994) and illustrated in Figure 2. The three stratigraphic sections were measured at localities FB, CC, and LM in Figure 1. The Fossil Butte section (FB, locality 217 [SW ¼ NW ¼ sec. 5, T. 21 N., R. 117 W.]) represents an intermediate area of the lake, just north of the lake depocenter. The Clear Creek section (CCS, locality 122 [NW ¼ SE ¼ sec. 35 and NE ¼ SE ¼ sec. 34, T. 21 N., R. 117 W.]) represents the depocenter of Fossil Lake. The Little Muddy Creek section (LM, locality 740 [SE ¼ SE ¼ sec. 24, T. 20 N., R. 118 W.]) represents an environment more proximal to the lake margin. Rock samples were collected from each of the major lithologies at each section. Phillips Petroleum Company processed the samples using standard palynological techniques. Twelve of the 49 samples produced palynomorphs. Analysis of the palynoflora included pollen counts of all 12 samples. Ten of the 12 productive samples contain statistically adequate numbers of palynomorphs. Two hundred or more palynomorphs were counted from each of the 10 statistically adequate samples.

THE PALYNOFLORAL ASSEMBLAGE

The outcrop samples from the Fossil Butte Member and lower Angelo Member of the Green River Formation yielded a diverse palynoflora. The assemblage consists of 176 forms representing 38 families, 54 genera, and 7 identifiable species. Approximately 2270 pollen, spores, dinoflagellates, and acritarchs were identified from the 12 productive samples. Of the 2270 plant microfossils, 1.5% represent non-bladdered conifers, 23% bladdered conifers, 37.5% angiosperms, 14% ferns and lower plants, 1% dinoflagellates, 22.5% acritarchs, and 0.5% of unknown affinity. The stratigraphic variation in relative abundance of the representative palynomorphs is shown in Figure 3.

The alga *Pediastrum* constitutes 8% of the total plant microfossils identified. However, its primary occurrence is in one sample from the lower part of the middle unit (FB-4) where it composes 91% of the entire assemblage (Figure 3). The most common member of the fern group is *Laevigatosporites*, which makes up 3.5% of the total. However, unlike *Pediastrum*, *Laevigatosporites* is distributed throughout the stratigraphic sequence. Other fern spores (e.g., *Cyathidites* and *Deltoidospora*) are restricted to the middle and upper units.

Among the gymnosperms, *Pinus* (9%) is the most abun-

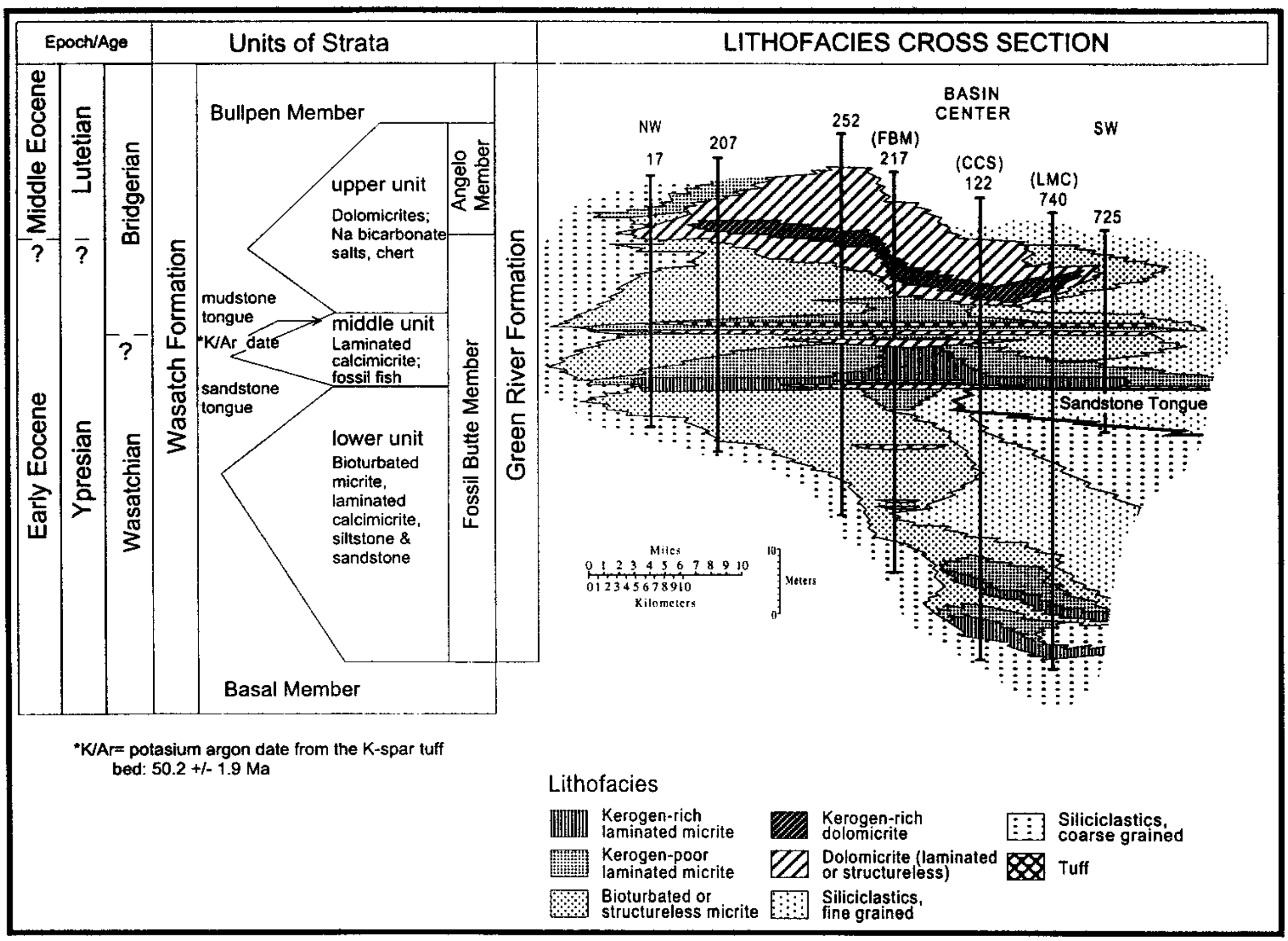

FIGURE 2—Generalized plant microfossil diagram illustrating relative abundance of various plant types, including aquatic palynomorphs. The light gray shading indicates < 5% abundance.

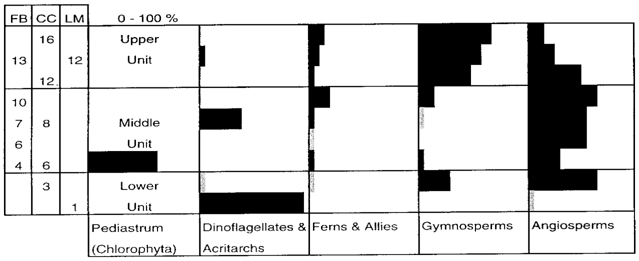

FIGURE 3— Stratigraphic chart illustrating stratigraphic units, facies relationships and relationships of measured sections. Locality 217 = FB, 122 = CC, and 740 = LM. Modified from Buchheim and Eugster (1998).

dant taxon with *Picea* (2.5%) the next most common type. Other gymnosperms present are *Podocarpus* (2%), *Abies* (0.5%), *Taxodium* (0.5%), *Tsuga* (0.5%), and *Juniperus* (0.5%). Gymnosperm pollen occurs in all three units of the Green River Formation (Figure 3). More specifically, gymnosperm pollen is fairly abundant in the lower unit, less abundant in the middle unit, then becomes very abundant in the upper unit.

Among the angiosperms present, the most common taxa are *Carya* (5.5%), *Ulmus* (3%), Compositae (2.5%), Chenopodiaceae (2.5%), *Momipites* (2%), *Salix* (1.5%), *Platycarya* (1.5%), and *Quercus* (0.5%). Of the most common angiosperm taxa, *Carya*, *Ulmus*, *Momipites*, *Salix*, *Platycarya*, and *Quercus* occur in all three units. Asteraceae, Chenopodiaceae, and Poaceae occur only in the middle and upper units. Overall, the angiosperms are more abundant in the lower and middle units (Figure 3).

In summary, both angiosperm pollen and gymnosperm pollen occur in the lower unit, but the angiosperm pollen are more abundant (Figure 3). In the middle unit, the angiosperm pollen dramatically increases in abundance (among the terrestrial taxa) and the gymnosperm pollen decreases. In the upper unit, the gymnosperm pollen become more abundant and the angiosperm pollen decrease.

Dinoflagellates and acritarchs occur primarily in the lower and middle units, although there are a few in the upper unit (Figure 3). In two samples, (CC-8 from the middle unit and LM-1 from the base of the lower unit) the dinoflagellates and acritarchs are the only taxa present with the exception of one unidentified triporate pollen in LM-1. In sample FB-6 (from the middle unit) a large number of acritarchs and a few dinoflagellates occur with a diverse angiosperm pollen assemblage.

PALEOCLIMATE

The overall climatic range of plant microfossil taxa in the Fossil Basin palynoflora is tropical to boreal. However, the majority of taxa have climatic ranges that overlap in the subtropical to warm temperate climate zones.

The palynomorph assemblage of the lower unit includes several important climatic indicators. *Abies*, *Picea*, *Alnus*, *Corylus*, and *Pterocarya* are all elements of warm temperate or cooler climates. The other dominant taxa in the lower unit such as *Pinus*, *Podocarpus*, *Carya*, and *Platycarya* have wider climatic ranges. This palynofloral assemblage suggests that the climate during deposition of the lower unit was warm temperate.

In the middle unit, pollen of *Ulmus*, *Carya*, and the Chenopodiaceae are dominant. Along with these taxa, the majority of the plants represented by pollen in the middle unit have broad climatic ranges. However, the Bombacaceae range from tropical to subtropical and occur in low numbers in the middle unit. Based on the presence of the Bombacaceae and the scarcity of forms found in cooler climates (i.e., *Abies*, *Picea*, *Alnus*, *Corylus*, and *Pterocarya*) the climate during deposition of the middle unit was probably more subtropical than the lower unit.

The plant microfossil assemblage of the upper unit yielded a mixture of the forms that occur in the lower and middle units. From the lower part of the upper unit, *Picea*, *Tsuga*, *Castanea*, and *Pterocarya* indicate that the climate may have become cooler. However, the occurrence of the Bombacaceae in the lower part of the upper unit suggests that the transition was gradual. The cooler climate indicators, such as *Abies*, *Picea*, and *Tsuga*, become more abundant higher in the upper unit. However, the occurrence of *Reevesia* (a tropical to subtropical element) in the uppermost sample of the upper unit suggests that the climate was transitional between subtropical and warm temperate.

Overall, the mixture of elements from subtropical to warm temperate climates in the middle and upper units suggests that the climate may have fluctuated from the warm temperate climate in the lower unit, to more subtropical in the middle unit, and then back to a warmer temperate climate in the middle of the upper unit. Alternatively, the assemblage may simply represent a transitional flora characterized by mixed subtropical and warm temperate elements. As a whole, the palynoflora is well represented by plants that occur in subtropical climates (83%) and those that occur in warm temperate climates (93%). The palynomorph data suggest that the climate of Fossil Basin was in transition between subtropical and warm temperate with slight fluctuations during the life of Fossil Lake.

PALEOECOLOGY

In the lower unit, the dominant plant microfossil taxa are *Pinus*, *Picea*, *Carya*, *Platycarya*, and *Corylus*. The predominance of these taxa suggests that the areas around the lake were heavily wooded. The occurrence of *Platycarya* (in all three units) suggests that there were also open, ephemeral habitats where this early successional plant could thrive (Wing and Hickey, 1984). However, the occurrence of *Pinus*, *Picea*, *Alnus*, *Carpinus*, and *Tilia* represent vegetation similar to that which MacGinitie (1969) concluded occurred 900 meters above Lake Uinta. It is likely that streams carried palynomorphs from the surrounding highland floras into Fossil Lake. The presence of these streams is supported by the occurrence of riparian taxa such as *Platanus*, *Salix*, and *Populus*. At lower elevations, vegetation composed of *Alnus*, *Carya*, *Corylus*, *Myrica*, *Platycarya*, *Podocarpus*, *Tilia*, and

Ulmus grew. Around Fossil Lake itself, forests of *Populus*, *Pterocarya*, and *Salix* grew on the floodplains, while in the moist lowlands, cattails, ferns, and horsetails thrived.

During deposition of the middle unit the vegetation adjacent to Fossil Lake remained much the same as in the lower unit. However, the vegetation at the lower elevations became better developed and taxonomically more diverse, perhaps due to increased rainfall and a more subtropical climate. During this time, the upland vegetation was partially displaced upward by elements from the warmer, lowland vegetation. The sedimentological data suggest that during deposition of the middle unit the lake reached its peak development (see Buchheim and related papers, this volume).

During deposition of the upper unit the dominant vegetation around Fossil Lake was once again the upland flora. *Carya*, *Myrica*, *Platycarya*, *Populus*, *Quercus*, *Tilia*, and *Ulmus* are still well represented. However, rainfall was probably more restricted to the highlands where *Abies*, *Picea*, *Pinus*, *Podocarpus*, and a variety of ferns flourished. The shallowing of the lake is indicated by the increased abundance of *Taxodium*-type pollen in the upper unit and would also corroborate with the deposition of evaporite sequences that occur in the upper unit. The changes in the flora and the shallowing of the lake during deposition of the upper unit probably resulted from the onset of a cooler, drier climate.

CONCLUSIONS

Overall, the vegetation that existed around Fossil Lake during deposition of the lower, middle, and upper units of the Green River Formation in Fossil Basin indicates that the lake existed in an intermontane basin and was affected by slight fluctuations in climate and rainfall.

The abundance of hardwood, riparian, and conifer taxa suggests that moist lowlands and floodplains existed around Fossil Lake with upland forests on the surrounding ridges and mountains. The occurrence of *Platycarya* throughout the section suggests that there were also open, ephemeral habitats where this early successional plant thrived. These ephemeral habitats were a result of fluctuating lake levels throughout the life of Fossil Lake (see Buchheim and related papers, this volume). Streams originating in the highlands supplied water for Fossil Lake and the surrounding vegetation. The palynoflora assemblages of the Fossil Butte Member and the lower part of the Angelo Member indicate a mixed mesophytic forest grew near Fossil Lake.

The mixture of subtropical and warm temperate floral elements in the Fossil Butte Member suggests the climate was transitional between humid, subtropical and drier, warm temperate with fluctuations during various episodes of deposition.

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CADDISFLY (TRICHOPTERA) LARVAL CASES FROM EOCENE FOSSIL LAKE, FOSSIL BUTTE NATIONAL MONUMENT

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Abstract—The Caddisfly (Trichoptera) larval cases from two sites in the Green River Formation of Eocene Fossil Basin are predominantly preserved as aggregates of calcareous tubes. The cases are tube shaped, slightly curved and generally lack sand grains or other particles in their case wall structure. Rare caddisfly larval cases from both sites show carbonate particles incorporated into the case structure. We believe that these caddisfly larval cases were constructed primarily of silk. The caddisfly larval cases are associated with lake-margin tufa, stromatolites and tufa-encrusted logs. This association illustrates the influence of metazoans in shaping the internal fabric of these Eocene lacustrine tufas.

INTRODUCTION

Extant caddisflies are small insects closely related to moths and butterflies. Their unique larval stages are almost all aquatic. Caddisfly larvae can be divided into three categories of lifestyle related to their use of silk (Williams, 1989). The first category consists of those that are free living larvae that use silk strands to maintain position in flowing water. The second category consists of caddisflies that spin nets to catch food. The third group construct diverse portable cases made of silk, plant and/or mineral particles. These case-building caddisflies build either asymmetrical purse cases, bilateral tortoise cases, or tube cases (Wiggins, 1996).

Caddisfly larval cases have been recognized in several ancient lacustrine settings since Charles Lyell (1854) first reported fossilized cases from the Eocene of Auvergne, France. A. C. Peale first reported caddisfly larval cases from the Eocene Green River Formation during the Hayden expedition of 1877. Scudder (1878) believed these belonged to "some genus of Limnephilidae near *Anabolia*". Bradley (1924) described two additional types of caddisfly larval cases from the Green River Formation. All three types of caddisfly cases occur in rocks preserved from Lake Gosiute, east of Fossil Lake.

Since 1924, no new occurrences of caddisfly larval cases have been reported from the Green River Formation, despite intense paleontologic research. Researchers reported small tubes from two other sites in Lake Gosiute and interpreted them as "*Oocardium* tufa" (Bradley, 1974; Jensen and Buchheim, 1983). We have reinterpreted this "*Oocardium* tufa" as tufa that contains caddisfly larval cases (Leggitt et al., 1999).

Two new sites within Fossil Basin, adjacent to Fossil Butte National Monument (Figure 1), exhibit similar tubes to those previously interpreted as caddisfly larval cases from Lake Gosiute. These new sites represent the first reported occurrence of caddisfly larval cases from Eocene Fossil Lake.

GEOLOGIC SETTING AND STRATIGRAPHIC CONTEXT

Fossil Lake formed within Fossil Basin during the early Eocene (Figure 1). The Green River Formation of Fossil Basin is a lens of lacustrine limestone within the fluvial siliciclastics of the contemporaneous Wasatch Formation (Oriel and Tracey, 1970). Oriel and Tracey (1970) divided the Green River Formation of Fossil Basin into the Fossil Butte and Angelo members. Detailed stratigraphic correlation suggests that the assigned contacts between the two members occur at different stratigraphic horizons throughout the basin. Buchheim (1994) informally divided the Green River Formation in Fossil Basin into lower, middle and upper units of the Fossil Butte Member, based on lithologic characteristics. Due to ambiguity in Oriel and Tracey's divisions, we use the informal classification of Buchheim (Figure 1). The fossils in this report occur in the upper unit of the Fossil Butte Member of the Green River Formation.

The two sites with small tubes also contain stromatolites and tufa. They are located at the extreme edges of the Green River Formation in Fossil Basin (Figure 1) in rocks interpreted as nearshore-lacustrine facies (Leggitt, 1996; Loewen, 1999).

The first site (south shore) is located on a hill in the SW ¼ SW ¼ section 4, T. 19 N, R. 117 W near Warfield Springs. It is stratigraphically lower than the east shore site. The sample was found as float from a regionally extensive bed of tufa-coated tree branches and logs (Figure 2). This bed consists of massive limey mudstone that grades basinward into facies with calcite pseudomorphs after saline minerals. The tufa-coated log unit at this locality is interpreted as the southern

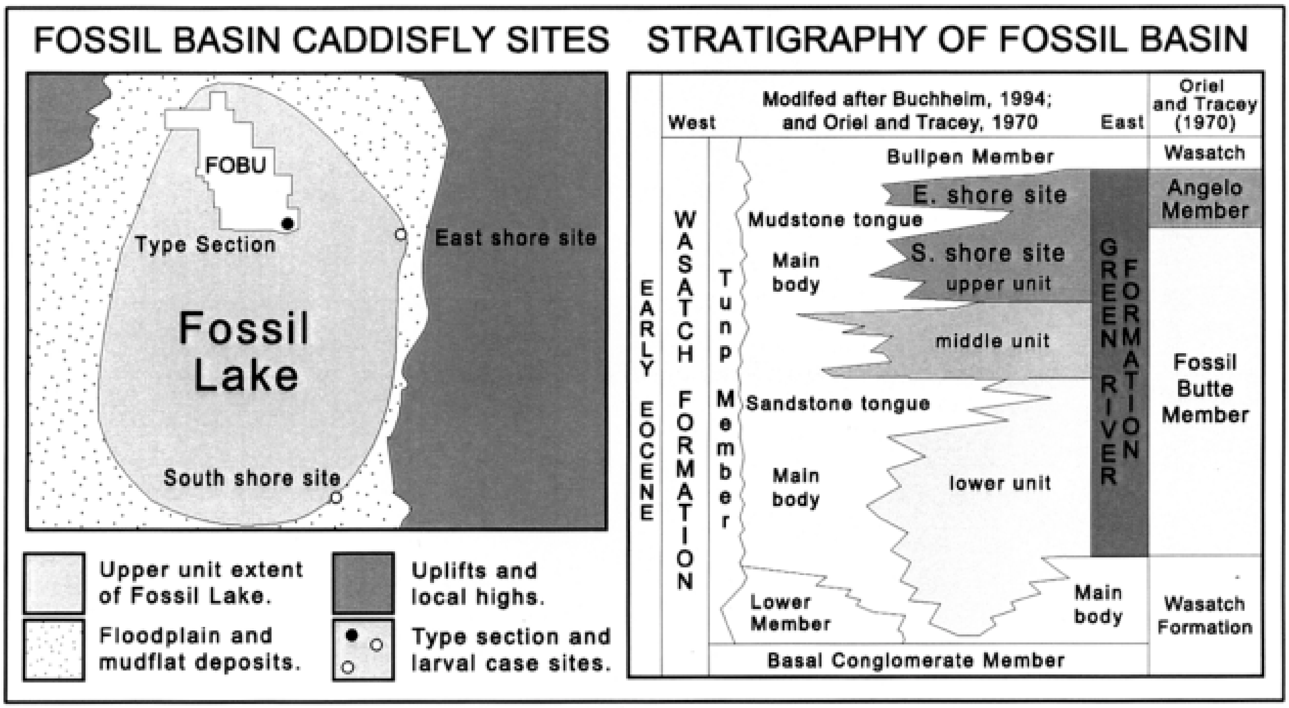
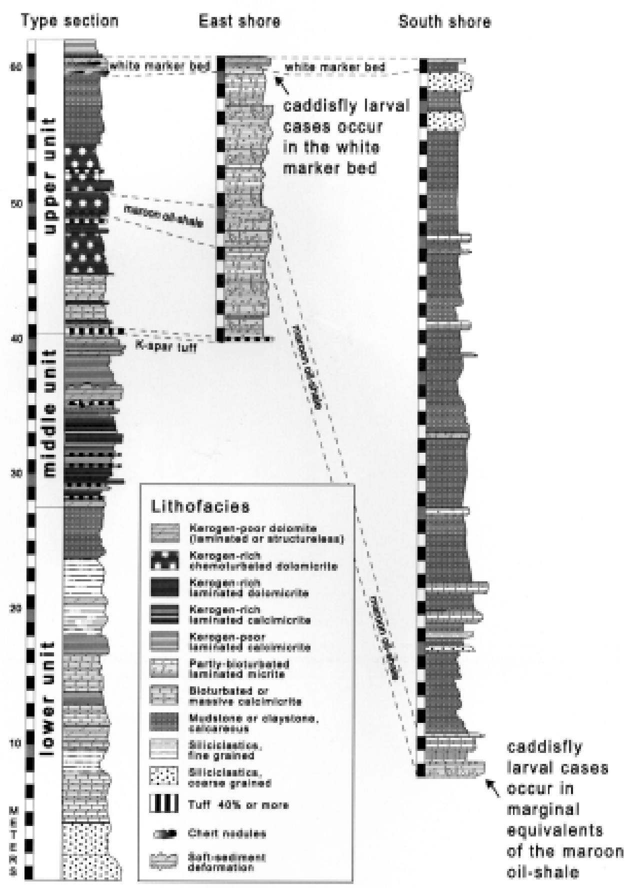


FIGURE 1—Two sites with tubes interpreted as caddisfly larval sites are located in Fossil Basin (left). The stratigraphic relationships of the two sites to the Green River (stippled) and Wasatch formations (white) are depicted on the right (modified after Buchheim, 1994 and Oriel and Tracey, 1970).



shoreline of Fossil Lake during deposition of the “maroon oil shale” unit of Loewen and Buchheim (1998).

The south shore site is interpreted as a freshwater margin of a saline alkaline lake (Loewen and Buchheim, 1998; Loewen, 1999). This freshwater margin in the south may have existed as an embayment fed by freshwater streams. This first site represents the extreme southeastern end of the lake during deposition of the maroon oil shale.

The second site (east shore) is located near the top of the south facing bluff in the NW ¼ NE ¼ section 12, T. 21 N, R. 117 W just north of westbound Highway 30 where it enters Fossil Basin. At this location, the unit is a kerogen-poor, completely bioturbated micrite with abundant ostracods and gastropods including *Goniobasis*. At the center of the basin this layer contains Magadi-type chert and evaporites (Loewen, 1999).

The east shore site is interpreted as a paleoshoreline where Fossil Lake lapped up onto the Eocene highs of the Oyster Ridge thrust belts (Loewen, 1999). This site represents the extreme eastern extent of the white marker bed. It pinches out a few meters to the east.

FIGURE 2—The stratigraphic position and lateral correlation of the two caddisfly larvae sites in marginal facies and their relationship to the basinal Type Section of the Fossil Butte Member.

FIGURE 3—*A,* Porous tufa with bark impressions forms the base of the south shore specimen. This is covered by a stromatolite layer (black arrows). Larval cases are located on top of the stromatolite layer. *B,* The forked end of the east shore specimen is covered with a finely laminated stromatolite coating and larval cases. Dashed lines indicate the surface on which the entire structure was deposited. Arrows indicate the finely laminated stromatolite layers.

FIGURE 4— *A–D,* Caddisfly larval cases from the south shore site. *E–H,* Caddisfly larval cases from the east site. *A,* Tufa-coated log with stromatolite layer and larval cases coating it from the south shore site. *B,* Stromatolite lamination and cross-section of the larval cases . *C,* Cross-section of a single larval case. *D,* Close-up of the curled particles coating a case. *E,* Caddisfly larval cases and the forked end of the log from the east shore site. *F,* Close-up of the stromatolite laminae coating the log. *G,* Close-up of the larval cases. *H,* Close-up of the curled particles coating an individual case.

DESCRIPTION OF THE TUBES AND TUFA FROM BOTH SIDES

The south shore specimen has bark impressions on its basal surface. The bark impression is coated with a 43 mm thick layer of porous carbonate interpreted as tufa (Figure 3A, 4A). This tufa includes ostracods and pockets of finely laminated stromatolitic material (Figure 4B). The tufa is succeeded by a layer of finely-laminated columnar stromatolite 12 mm thick. This stromatolite layer is covered with small tubes (Figure 4C, 4D). The entire structure is coated with a 2 mm thick layer of finely-laminated stromatolite.

The specimen from the east shore consists of a roughly cylindrical, elongate shape resembling a log resting horizontally sub-parallel to the paleoshoreline. It is coated with finely laminated carbonate and surrounded by small tubes (Figure 3B, 4E). The cylindrical shape is interpreted as originally consisting of a log or tree branch. The wood later rotted and was replaced by bioturbated micrite. The log is 60 cm long with one end that is 24 cm wide and 11 cm high. The other end forks into two branches about 9 cm in diameter (Figures 3B and 4E), and is coated with a 3 – 4 mm thick layer of finely-laminated stromatolite material (Figure 4F). The stromatolite surface is covered with small tubes (Figure 4G). Carbonate detritus and ostracods form the matrix around the cases. The entire structure is coated on the top surface with a 3 mm thick layer of finely-laminated stromatolite.

The small tubes at both sites consist of cylindrical, slightly curved elongate structures. The tubes are slightly tapered. They range from about 15 to 20 mm long and 1.7 to 2.0 mm in internal diameter. External diameter ranges from 1.9 to 2.2 mm. In cross section the tube walls exhibit rare angular and curved carbonate fragments from 0.1 to 0.2 mm in diameter comprising the tube wall (Figure 3D, 3H). The tube walls also contain rare, angular quartz grains about 0.1 mm in diameter. The tubes are coated inside and out by finely laminated carbonate.

DISCUSSION

The slightly curved tubes from both sites are interpreted as caddisfly larval cases. They are similar to other reported caddisfly larval cases from the Green River Formation (Scudder, 1878; Bradley, 1924). The larval cases from Fossil Basin may have been primarily constructed from silk because case-building particles are rarely observed. Some of the cases contain small carbonate grains, which have been incorporated into the case structure. These curved carbonate grains may be small clastic fragments or pieces of stromatolites and tufa that the larvae harvested from their surroundings. Similar quarrying behavior has been noted in modern caddisflies (Drysdale, 1999). The finely laminated carbonate coating the tubes inside and out was probably deposited after the cases were abandoned.

The logs with tubes coating them from both sites are coated with either porous tufa or a layer of finely laminated stromatolite material. This suggests that the log was submerged in place for a period of time. Caddisfly larvae subsequently colonized this surface. The aggregation of cases formed a chaotic, rigid latticework that may have acted as a baffle that collected small carbonate particles between the cases. Ostracods occur in the matrix surrounding the cases in both specimens.

Today, caddisfly larvae are associated with shallow, well-lighted, well-oxygenated, nearshore-lacustrine and fluvial environments (Mackay and Williams, 1979). They have been used as indicators of nearshore-lacustrine paleoenvironments in the Green River Formation (Bradley, 1928). The tubes interpreted as caddisfly larval cases from the two sites in Fossil Basin are consistent with the marginal lacustrine interpretation of these two sites (Loewen, 1999).

The co-occurrence of caddisflies with tufa at these sites suggests a link between metazoan insect larvae and the tufa- and stromatolite-building processes. It is likely that the caddisfly populations directly contributed to megascopic tufa fabric formation and were strongly involved in reshaping the micro- and macroscopic fabric of this tufa. Recent studies have shown the importance of aquatic insect larvae, including Trichoptera larvae, in the development and alteration of some modern tufa fabrics (Humphreys et al., 1995; Drysdale, 1999).

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INCISED VALLEY FILLS IN THE LOWER PART OF THE CHINLE FORMATION, PETRIFIED FOREST NATIONAL PARK, ARIZONA: COMPLETE MEASURED SECTIONS AND REGIONAL STRATIGRAPHIC IMPLICATIONS OF UPPER TRIASSIC ROCKS

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ABSTRACT—Sedimentologic analysis and complete measured stratigraphic sections of the entire Upper Triassic Chinle Formation exposed in Petrified Forest National Park, Arizona have identified a succession of incised paleovalley cut-and-fill complexes in the lower part of the Chinle. These paleovalley complexes are similar in aspect and process of formation to the sediment-filled scours in the Petrified Forest Member of the Chinle Formation in the Park that were described by earlier workers. In addition, this research highlights the first recognition of exposures of the Moenkopi Formation and Shinarump Member of the Chinle Formation within Petrified Forest National Park.. The uppermost part of the Moenkopi has been incised by a paleovalley cut prior to deposition of the Shinarump, and the Moenkopi that was exposed on interfluves between Shinarump paleovalleys was peodogenically modified into "mottled strata" typical of similar Moenkopi exposures elsewhere on the Colorado Plateau. Outcrops of the Shinarump, Monitor Butte, and Mesa Redondo Members of the Chinle Formation in Petrified Forest National Park are similar to other exposures in this region of northeastern Arizona in that they successively fill paleovalleys cut into underlying older units. Recognition of the paleovalley cuts and their subsequent fill elucidates the stratigraphic complexity of the lower Chinle and the relative ages of the units.

INTRODUCTION

The Upper Triassic Chinle Formation has long been known to have been deposited in a fully continental basin (Stewart et al., 1972, and references therein). Based on detailed mapping and measurement of stratigraphic sections by various workers over the past forty years, the lower part of the Chinle (Shinarump, Mesa Redondo, and Monitor Butte Members and their stratigraphic equivalents) was previously described as a complexly interfingered succession of strata (Witkind, 1956, 1961; Cooley, 1959; Phoenix, 1963; Witkind and Thaden, 1963; Davidson, 1967; Stewart et al., 1972). More recently, however, sedimentologic analyses and application of concepts from other continental case studies have led to reinterpretations of much of the "complex interfingering" as a succession of incised paleovalley cut-and-fill complexes (Blakey and Gubitosa, 1983, 1984; Pierson, 1984; Kraus and Bown, 1986; Dubiel, 1987, 1992, 1994; Haney, 1987; Kraus and Middleton, 1987; Blakey, 1989; Demko, 1995a,b; Demko et al., 1998). These paleovalley erosional systems and their subsequent stratal fill are replete with valley walls, interfluve areas with superposed paleosols, and tributary drainage systems. Petrified Forest National Park (PEFO) is located near the interfluve (drainage divide) between two major Shinarump Member paleodrainages (Figure 1): the Painted Desert and the Vermillion Cliffs paleovalleys of Blakey (1989). In addition, Petrified Forest National Park's position is also on the margin of a younger Monitor Butte paleovalley system (Demko et al., 1998), compounding the complexity of stratal relations in the lower part of the Chinle. Because of its position in this paleogeographic setting, the stratigraphy of the lower part of the Chinle Formation within Petrified Forest National Park is characterized by thinner stratal packages and more evidence of pedogenesis than is typical of some of the Chinle Formation in areas to the east or west of the Park that are within the axes of the Shinarump paleovalleys (Figure 2). Although even younger paleovalley erosional surfaces and their fills are present in the upper part of the Chinle Formation in and around Petrified Forest National Park (Kraus and Bown, 1986; Kraus and Middleton, 1987) and elsewhere in the Chinle on the Colorado Plateau (Stewart et al., 1972; Dubiel, 1994), they are not described here.

STRATIGRAPHIC SETTING

Mapping and stratigraphic section measurement for sedimentologic research on the Chinle Formation throughout the Colorado Plateau (Dubiel, 1987, 1994; Demko, 1995a; Hasiotis,

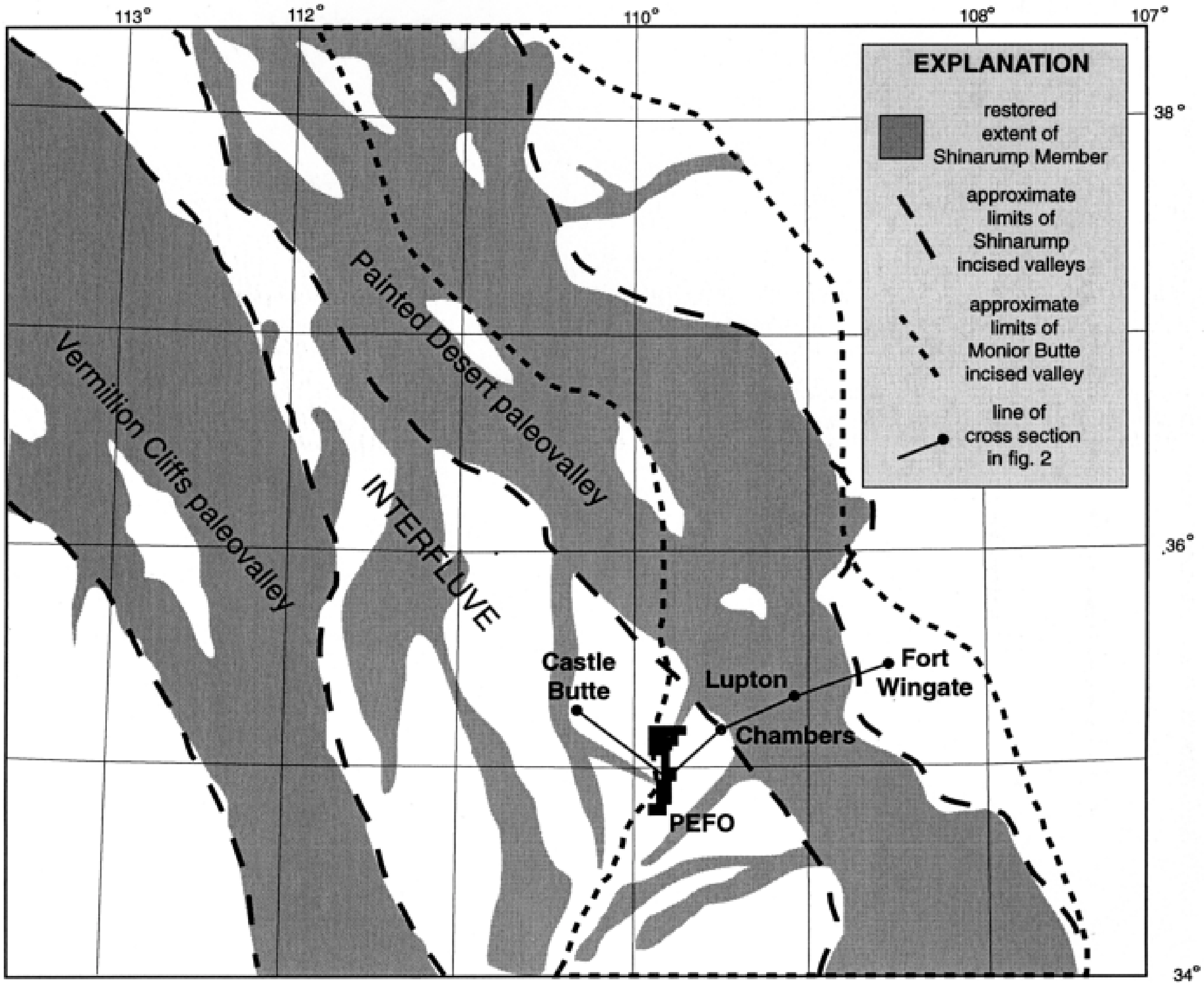

FIGURE 1—Map showing location of Petrified Forest National Park in northern Arizona and its position relative to paleovalleys within the Chinle Formation. Also shown is line of cross section depicted in Figure 2

1996) and for construction of a complete stratigraphic section of the Chinle specifically for Petrified Forest National Park (Dubiel, 1993; Hasiotis and Dubiel, 1993a,b; Demko, 1995b; Dubiel et al., 1995; Hasiotis and Dubiel, 1995a,b; Demko et al., 1998; Hasiotis et al. 1998) highlighted several sedimentologic features and concepts impacting the interpretation of the stratigraphy of the lower part of the Chinle Formation. First, the oldest stratigraphic interval exposed within the Park is the pedogenically-modified uppermost exposures of the Lower and Middle Triassic Moenkopi Formation. This pedogenically modified strata at the top of the Moenkopi exhibits the typical blue and white mottled coloration and large diameter burrows characteristic of the unit elsewhere on the Colorado Plateau. Elsewhere on the Colorado Plateau the unit has been referred to by earlier workers (e.g., Stewart et al., 1972; Dubiel, 1987, 1994) as the "mottled strata" and was formed under subaerial pedogenic weathering processes similar to those that formed the mottled strata in the Chinle (Stewart et al., 1972; Dubiel, 1987, 1994). This interval of Moenkopi exposed, in Petrified Forest National Park, pedogenically modified while it formed part of the interfluve concommitant with cutting and filling of the adjacent lowest Shinarump paleovalleys in the Chinle, is exposed in low-relief hills in and along the wash between The Haystacks and Newspaper Rock Mesa south of the Teepees in Petrified Forest National Park. Second, there are patchy outcrops of coarse to very-coarse grained, quartz-overgrowth-cemented sandstone (0-1.75 m thick), similar lithologically, petrographically, and sedimentologically to the Shinarump Member elsewhere, that occur in small scours cut into the underlying mottled strata of the Moenkopi. Finally, the stratal package that includes the Newspaper Sandstone (sensu Billingsley, 1985) and the olive-green to greenish-gray "leaf shale" beds of the Tepees area (see Stagner, 1941) is a genetic package of facies that fills an incised valley cut into underlying red and purple-red mudstones and gray tuffaceous sandstones (the cut and fill was noted by Kraus and Bown, 1986, although they did not use the term paleovalley), which, in turn, rest upon the coarse-grained sandstones of the Shinarump and the mottled strata at the top of the Moenkopi (Demko, 1995a,b; Dubiel et al., 1995). This entire package is capped by a thick, well-developed, red calcareous vertisol that forms a distinctive, easily correlatable red band around the Tepees area and east to Blue Mesa (Demko, 1995a,b).

INTERPRETATION

We have interpreted the succession of facies described above, from "mottled strata" developed on the Moenkopi Formation through the distinctive red vertisol, to be time-equivalent, in ascending order, to the pedogenically modified uppermost exposures of the Moenkopi Formation, and to the Shinarump, Mesa Redondo, and Monitor Butte Members of the Chinle Formation (Dubiel et al., 1995) as they are recognized and described farther to the east of Petrifed Forest National Park where they were deposited within the axes of the aforementioned paleovalleys. The mottled unit at the base of our measured sections in Petrified Forest National Park is identical to pedogenically modified Moenkopi observed elsewhere on the Colorado Plateau (Stewart et al., 1972; Dubiel 1987; 1994), whereas the coarse-grained, quartz-cemented sandstones that overlie this unit are petrographically and sedimentologically identical to thicker and better exposed Shinarump Member sandstones within the Painted Desert paleovalley trend and to other Shinarump outcrops throughout the Colorado Plateau (Witkind, 1956; Phoenix, 1963; Witkind and Thaden, 1963; Davidson, 1967; Stewart et al., 1972; Blakey and Gubitosa, 1983, 1984; Pierson, 1984; Dubiel, 1987, 1994; Haney, 1987). The thin and patchy nature of the coarse-grained sandstones are interpreted to reflect the relative position of Petrifed Forest National Park on an interfluve of the main Shinarump paleovalley systems. Furthermore, because these small Shinarump outcrops are topographically higher than exposures of the Shinarump adjacent to the Park, we interpret the coarse sandstones as deposits of stratigraphically higher, and thus slightly younger, small fluvial deposits relative to the main trunk paleodrainage system within the major Shinarump paleovalley.

The succession of red and purple-red mudstones and tuffaceous sandstones that overlie the pedogenically modified mottled strata of the Moenkopi and the coarse Shinarump sandstones is equivalent to the Mesa Redondo Member of Cooley (1958; 1959) and to the "lower red member" of Stewart et al. (1972). These strata were the youngest to be deposited within the Shinarump-age paleovalleys, and at their latest stages, they were deposited in a position such that the Mesa Redondo units overtopped the interfluves. They are characterized by gleyed, well-drained paleosols and trough cross-bedded sandstones. This succession was then incised again due to degradation of the drainage system (see Figure 7 in Stewart et al., 1972), which cut a subsequent paleovalley almost paleogeographically coincident with the underlying Shinarump paleovalley (Figure 1). This second paleovalley was subsequently filled by the greenish-gray and olive shales and fine-grained, ripple-laminated sandstones of the Monitor Butte Member. The correlation of these strata with the thicker sections of the Monitor Butte Member to the east and northeast of Petrifed Forest National Park is supported by both sedimentology (Stewart et al., 1972a; Dubiel, 1994; Demko, 1995a) and by plant microfossil (Litwin et al., 1991) and macrofossil zonations (Ash, 1970, 1972a,b, 1975, 1989). Within this and other Monitor Butte paleovalley axes, there is evidence of a series of cutting and filling episodes marked by well-developed paleosols and mass-movement slumps of the paleovalley walls (previously described by Green, 1956; Ash, 1978; and Dubiel et al., 1993). However, at Petrifed Forest National Park, on the edge of the paleovalley, only the last cut-and-fill episode is recorded by the preserved strata, which includes the comparatively thin "leaf shale" and Newspaper sandstone on the edge of this paleovalley system (see Ash, 1978; Billingsley, 1985; and Demko, 1995a for terminology). The well-developed red calcareous vertisol at the top of Monitor Butte-equivalent strata represents pedogenic modification of the final stages of aggradation of the paleovalley system; above this stratigraphic level there was a change in Chinle fluvial style from the paleovalley-wall confined systems of the Shinarump through Monitor Butte, to the more unconfined rivers (that is, not confined within paleovalley walls) of the overlying Petrified Forest Member (Blakey and Gubitosa, 1984; Dubiel, 1994; Demko, 1995).

DISCUSSION

Heckert and Lucas (1998) suggested that the oldest strata in PEFO were their "Blue Mesa Member of the Petrified Forest Formation" and that Dubiel et al. (1995) misidentified and miscorrelated certain strata within Petrifed Forest National Park. The basis of their assignment rests on the general composition and coloration of the mudstones and sandstones that commonly occur below the Sonsela Sandstone and on their interpretation of tetrapod biostratigraphy (Lucas, 1993, 1997). Their "Blue Mesa Member of the Petrified Forest Formation", as well as many other units they describe, is purported to be present and laterally continuous from west-central New Mexico to southeastern Nevada (Lucas, 1993; 1997).

Based on our interpretation, summarized above in this paper, we submit that Heckert and Lucas (1998) misidentified the Mesa Redondo and Shinarump Members of Cooley (1958, 1959) and Repenning et al. (1969) and included it within their "Petrified Forest Formation" (Lucas, 1993) and that they miscorrelated these and other lithostratigraphic units. We also note that Heckert and Lucas (1998) misquoted and incorrectly restated lithologic descriptions and interpretations from Dubiel et al. (1995). Part of their figure 4 (Heckert and Lucas, 1998, p. 133) in which they attributed a Chinle stratigraphic column and interpretation to "Dubiel et al., 1995" could not have been constructed from the information in that report. The report by Dubiel et al. (1995) is an abstract with no illustrations and with insufficient verbal information to reconstruct a section and attribute it to those authors. Thus, Hechert and Lucas (1998) erroneously attributed a diagrammatic interpretation to us that does not represent what our actual published data and interpretations state. Heckert and Lucas' (1998, p. 133) figure 4 was soley based on their stratigraphic interpretation and their misunderstanding of the stratigraphic designations and descriptions presented in Dubiel et al. 1995. In fact, our complete measured section of the entire Chinle Formation in Petrified Forest National Park was available in Demko (1995a,b) and Hasiotis et al. (1998) and is reproduced here as Fig. 2. It extends downward about 30 m farther than the section attributed to us by Heckert and Lucas' (1998) and it is this additional 30 m of our measured section that includes those rocks of the Shinarump and Monitor Butte Members of the Chinle Formation that Heckert and

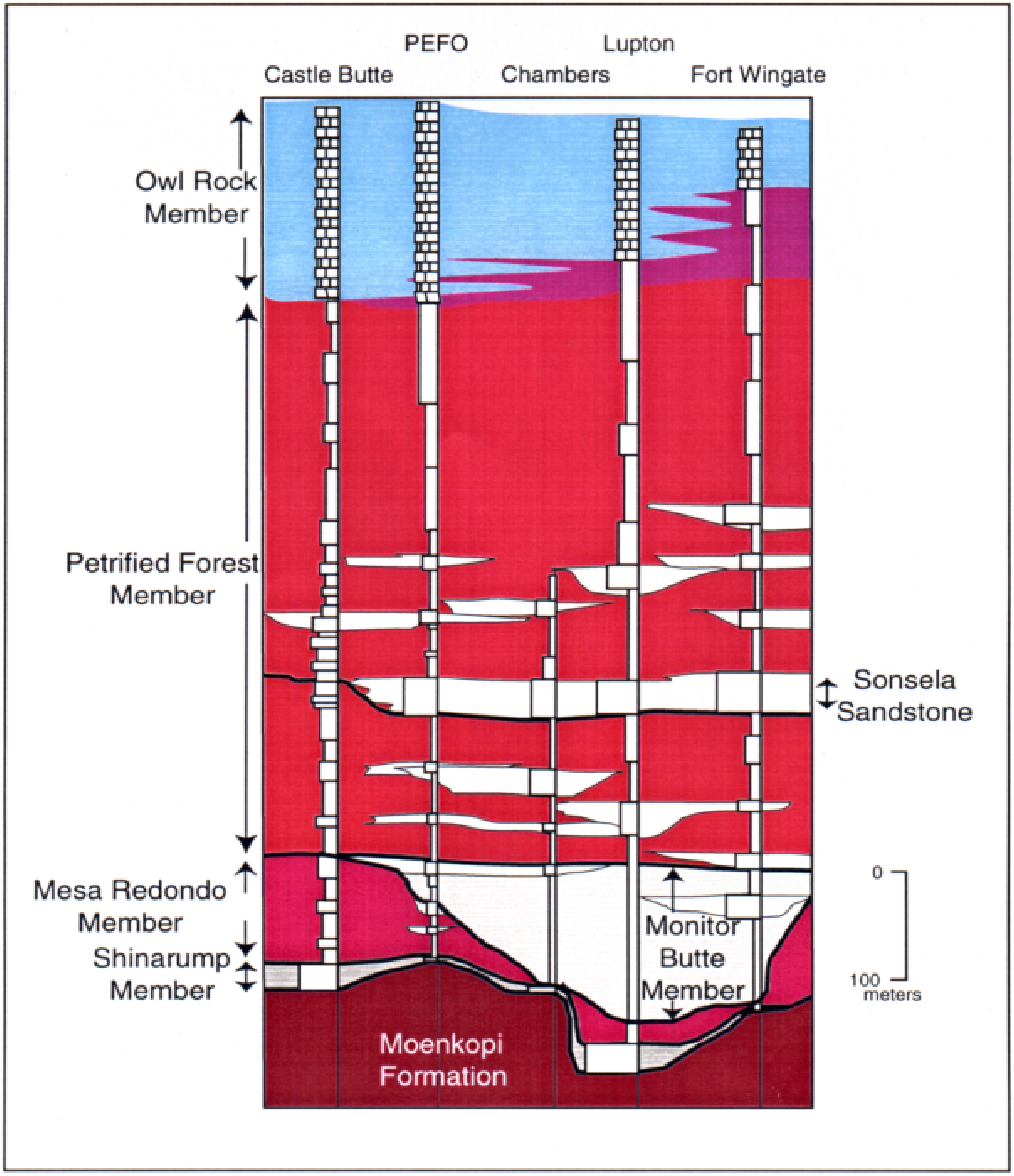

FIGURE 2—Stratigraphic cross section of measured sections of the Chinle Formation in and near Petrified Forest National Park, showing stratigraphy and nomenclature of units and their related paleovalley systems (shown by heavy lines). The figure is not meant to show individual unit lithology, but the relative width of the individual stratigraphic column denotes sandstone (thick) and mudstone (thin) units. The Owl Rock Member is only shown schematically to contain carbonate and calcareous siltstone units. Sections at PEFO, Lupton, and Ft. Wingate are by the authors, and sections at Castle Butte and Chambers are from Repenning et al., (1969).

Lucas (1998) did not attribute to our section in their illustration and that they contend are not present in Petrified Forest National Park. Thus, the arguments in Heckert and Lucas (1998) that "Dubiel et al., 1995" misidentified or miscorrelated strata at the base of the Chinle in Petrifed Forest National Park are deprived of practical significance because those arguments are based on their misunderstanding of our work and their failure to identify or recognize the critical outcrops under discussion. It is possible that Heckert and Lucas (1998) simply made an error in referencing "Dubiel et al. (1995)" rather than Demko (1995a or 1995b) or Hasiotis et al. (1998), each of which do contain our published measured section, but if that is the case, then they incorrectly reproduced the actual stratigraphic units and measured stratigraphic thicknesses that we reported in our measured section. The entire discussion by Heckert and Lucas (1998) that outcrops of Moenkopi and Shinarump strata can not occur in Petrified Forest National Park based on their assumed lithostratigraphy is obviated by the fact that they failed to observe or note the critical outcrops of these units in Petrifed Forest National Park and their lack of recognition of the sedimentologic position of these strata within paleovalleys.

The recognition of paleovalley systems, and successive cut and fill events, is of signal importance to the relative stratigraphy of the strata and the biostratigraphy interpreted from those rocks. Facies that might first appear to be laterally adjacent, and thus correlative, may in fact be separated by scoured surfaces; their subsequent fill by younger rocks places strata of different ages in an apparent laterally adjacent position, a relation previously described for the both the Petrified Forest Member of the Chinle Formation higher in the section in Petrifed Forest National Park and for the Willwood Formation of the Bighorn Basin (Bown and Kraus, 1981a,b; Bown, 1984; Kraus and Middleton, 1984; Kraus and Bown, 1986). In the lower part of the Chinle Formation in Petrified Forest National Park (and in the Petrified Forest Member as noted by earlier workers), recognition and documentation of these paleovalley fills, their relative ages, and their relative paleogeography, are crucial for defining stratigraphic and biostratigraphic relations.

In addition to the signal importance of the identification of the Moenkopi Formation and Shinarump Member of the Chinle Formation in Petrified Forest National Park for stratigraphic and biostratigraphic correlation and sedimentologic analyses of depositional systems, there are other major ramifications for the application of old and new nomenclature to these Triassic rocks, especially over large areas. Such a situation exists in the attempt to raise the Chinle Formation to group-status. Discussions describing the utility of established Chinle Formation nomenclature have already been well presented by Dubiel (1994). The accepted member designations within the Chinle Formation (e.g., Stewart et al., 1972a; Dubiel, 1994) are well-defined and of local significance because they represent several disparate facies and successions of strata (Dubiel, 1994). Many of the deposits belong to specific incised paleovalley-fill systems (e.g., Blakey, 1989; Dubiel, 1994). The well-established formal and informal names also represent rocks that were deposited under distinct subsidence rate, base-level, and climatic settings. These major controls manifest themselves as alluvial, lacustrine, and eolian sequences with unique internal geometries that cannot be randomly correlated lithostratigraphically across large regions of a fully-continental basin, especially when large-scale incised paleovalleys are present. An attempt to do so (Lucas, 1993, 1997) illustrates major flaws using simple layer-cake lithostratigraphic correlations to reproduce stratigraphic relations within Upper Triassic rocks in the western United States. Continued usage of group-designation and superfluous formation names associated with it (sensu Lucas, 1993) will mislead subsequent workers with regard to the local and regional correlation of Upper Triassic rocks, and it also creates confusion by adding previously discarded and extraneous new names into the literature.

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PROBABLE REPTILE NESTS FROM THE UPPER TRIASSIC CHINLE FORMATION, PETRIFIED FOREST NATIONAL PARK, ARIZONA

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Abstract—We report evidence for the earliest known reptilian nests in alluvial deposits from the Petrified Forest Member of the Upper Triassic Chinle Formation (Early Norian), Petrified Forest National Park, Arizona. The Triassic nest ichnofossils are nearly 120 million years older than nests previously described from the Late Cretaceous of the Western Interior of the United States. These structures are found in the first "flattop sandstone #1" above the Sonsela Sandstone/Rainbow Forest Sandstone complex at the south end of the park. The hollow, bowl-shaped pits are present in relatively large numbers and occur in two small areas. The pit openings are sometimes constricted with an expansion below. Inside, the shape is circular to elliptical and forms spherical to elongate pits. Rarely, scratch marks are found across the walls. Internal, partial layering is found at the bottom and along the sides. Some pits are rimmed by elliptical depressions with irregular surfaces that contain a few poorly defined vertebrate footprints.

The bowl-shaped pits are interpreted as nest-holes constructed by vertebrates, possibly phytosaurs, aetosaurs, rauisuchians, or dinosaurs. The nests are very similar to those constructed by Late Cretaceous dinosaurs and sea turtles, extant turtles (Reptilia: Cheloniidae), crocodiles, and alligators (Repitilia: Crocodylidae). Females that congregated in specific areas, which are interpreted as nesting sites, most likely excavated the Chinle nests. The patches of irregular ground around the nests represent trample ground and body pits created by the adult. The layering within the nests may represent active modification of the internal walls and floors and backfilling after eggs were deposited. Possible impressions in the basal portion may represent unhatched or partial eggshells.

These ichnofossils appear to represent the earliest known evidence of vertebrate reproductive behavior. If so, they would also represent one of the earliest forms of parental care such that eggs were placed in specialized structures. This is a major step toward the rearing of offspring. Nesting has likely evolved several times in different groups of primitive vertebrates, but basic nest-hole architecture in extant reptiles with Early Mesozoic ancestry has changed very little in nearly 220 million years.

INTRODUCTION

The fossil record of amniotes begins in the Pennsylvanian Period based on reptilian body fossils and foot prints (Carroll, 1964, 1969; Lockley, 1989). Body and trace fossil evidence for reptilian nesting behavior is exceedingly rare in the geologic record. Late Cretaceous groundnest excavations of non-avian dinosaurs (Horner and Makela, 1979; Horner, 1992; Novell *et al.*, 1995; Varrichio *et al.*, 1997) and sea turtle nests (Bishop *et al.*, 1997) represent *in situ* evidence of nesting. Fossil eggshell fragments, complete egg clutches, and groups of juvenile remains also provide evidence of nesting (Andrews, 1932; Lapparent and Zybyszewski, 1957; Hirsch *et al.*, 1989; Hirsch, 1994; Kirkland, 1994).

Possible Late Triassic dinosaur eggs (Kitching, 1979; Grine and Kitching, 1987) and Permian eggshell (Hirsch, 1979) have also been reported, but not in nests. Smith (1987) documented the helical burrows of mammal-like reptiles in Upper Permian rocks of South Africa, but made no inferences to brood rearing. No specialized nest structures have been reported from rocks older than the Cretaceous.

We report on evidence for the earliest known reptile nests from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona (Fig. 1). Hollow, bowl-shaped pits present in large numbers within limited areas exhibit pronounced similarities to hole-nests excavated by extant turtles (Reptilia: Cheloniidae), crocodiles, and alligators (Repitilia: Crocodylidae). Although no fossil material was found within the nests, the size and location of the nests suggests that the constructors may have been reptiles such as aetosaurs, phytosaurs, rauisuchians, or dinosaurs.

GEOLOGIC SETTING

The study area is at the south end of Petrified Forest National Park (PEFO), Arizona (Fig. 1), where the lower part of the Upper Triassic Chinle Formation is exposed in badlands, buttes, and mesas (Fig. 2). The lower part of the Chinle was deposited in a succession of valley-fill sequences (Cooley, 1958, 1959; Repenning *et al.*, 1969; Stewart *et al*, 1972; Demko, 1995; Demko *et al.* 1998). The upper part of the Chinle, of which only the lower part of the Owl Rock Member is preserved within park boundaries, was deposited in a re-

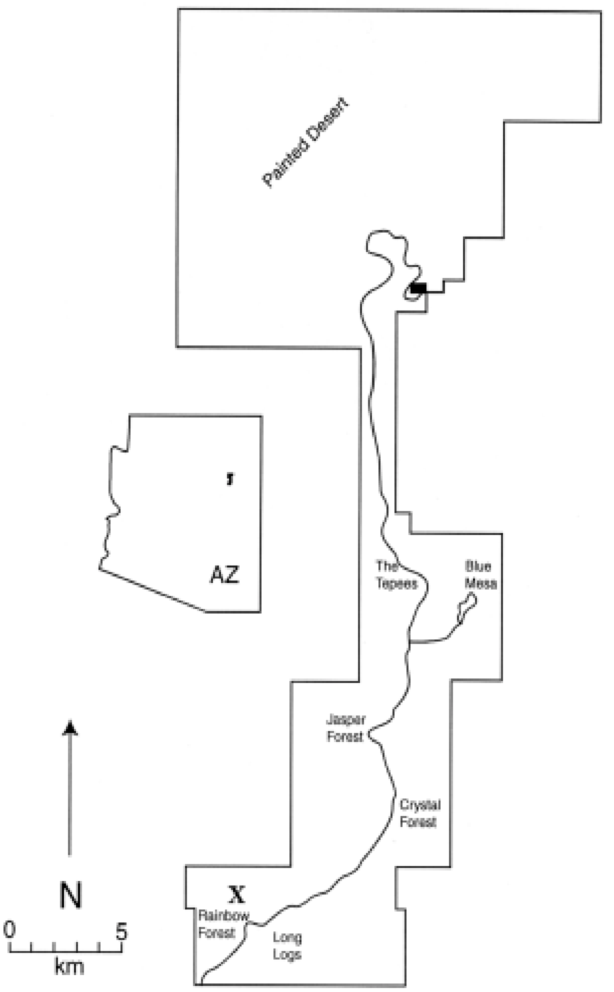

FIGURE 1—Locality map of Petrified Forest National Park (PEFO), Arizona, and the ichnofossil study area (**X**).

gionally dynamic basin complex of alluvial-lacustrine systems (Stewart *et al*, 1972; Dubiel, 1989, 1994).

Bowl-shaped pits are present locally in the flattop sandstone #1 (Billingsley 1985) above the Sonsela/Rainbow Forest Sandstone complex in the upper part of the Petrified Forest Member in the Chinle Formation (Norian) (Fig. 2). These ichnofossils are found in the uppermost part of a 1.5-m-thick upper fine- to medium-grained, trough cross-stratified sandstone. At this locality, the unit has a relatively planar base and a slightly undulatory top representative of an exposure surface with pedogenic features. Further north, this unit contains inclined, heterolithic, accreted strata composed of trough cross-bedded and ripple-bedded sandstones interbedded with mudstone and siltstone. Also in this interval are small, silicified trunks with lateral roots, rhizoliths, small-diameter backfilled meniscate burrows, crayfish crawling trails, wasp cocoons, coleopteran or lepidopteran cocoons, and termite nests assigned to *Archeoentomichnus isp*.

The ichnofossil-bearing rocks are interpreted as deposits from a medium- to high-sinuosity meandering river. The floodplain contained immature cumulative paleosols capped by a simple, mature paleosol. Based on the sedimentary structures and the degree of pedogenesis, the bowl-shaped pits are interpreted to have been in areas close to the active channel where paleosols were weakly developed.

DESCRIPTION OF THE ICHNOFOSSILS

Two distinct localities with a combined total of over 100 pits are found along first flattops sandstone #1 (sensu Billingsley, 1985). Many of the pits at the first locality occur in large float blocks weathered from the outcrop. The pits at the second locality are found *in situ* along the top of the outcrop. The density of pits is approximately 1/m^2 based on measurements for blocks with more than one pit. Proximity of pits averaged 64 +/- 38 cm (N=19), although at least one pair of pits show overlap and another pair had a distance of 150 cm between them.

Discrete hollow, bowl-shaped pits characterize over 100 ichnofossils (Fig. 3). The circular to elliptical openings range from 10-20 cm in diameter and average between 15-16 cm. Occasionally they are associated with a constriction at or just below the paleosurface. Below the opening the internal part of the structures range from 11-44 cm in diameter, averaging 30-35 cm. The walls and floors appear compacted with

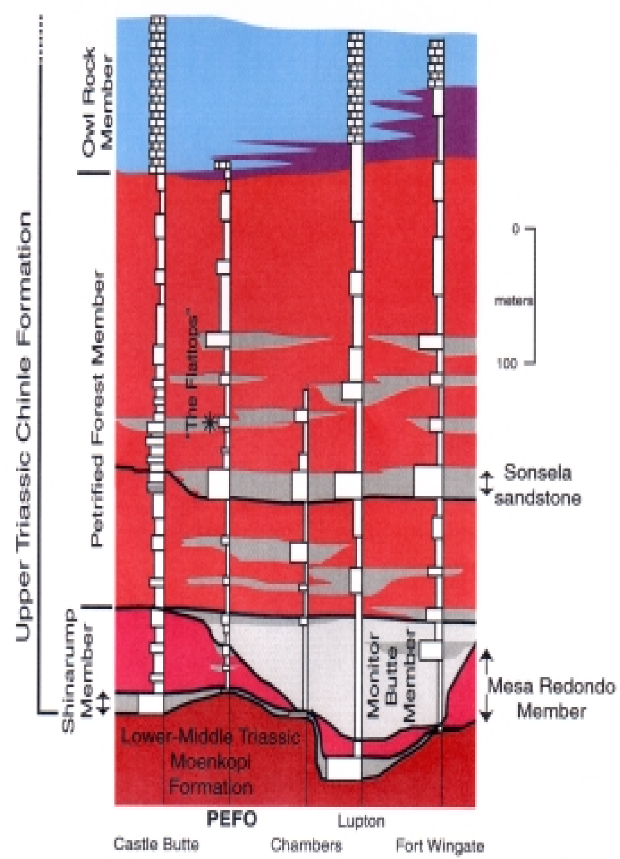

FIGURE 2—Composite measured section of the Upper Triassic Chinle Formation in Petrified Forest National Park, the stratigraphic position of the ichnofossils (asterisk), and relationship of these units to the regional geology. Modified from Dubiel *et al.* (this volume).

several layers of sediment. Narrow, elongate, shallow furrows, 7-15 cm in length, are rare and preserved in the walls. The bottoms of a few of the structures contain crescentic to oval indentations around 4-5 cm long and 2-4 cm wide. In some cases, shallow, broad depressions from 63-65 cm long and 35-40 cm wide are present above the deeper, larger pits. The surfaces of these depressions are highly irregular with bumpy protrusions and multidirectional elongate furrows found clustered with one another (Fig. 4). Rare individual vertebrate tracks are found with the irregular surfaces.

INTERPRETATION

The pits and depressions are interpreted as vertebrate nest-holes based on our comparisons of the Triassic ichnofossils to modern burrows and nests constructed by invertebrates and vertebrates. The pits represent the nest proper, most likely excavated by females, in which the eggs were laid. These ichnofossils are very similar to the nest-holes excavated by extant sea and terrestrial turtles (Reptilia: Cheloniidae), crocodiles, and alligators (Repitilia: Crocodylidae) (Brannen and Bishop, 1993; Bishop *et al.*, 1997). In the Triassic nests, the elongate furrows and the compacted thin layers of sediment along the walls and floors reflect the excavation and completion of the nest prior to egg-laying. The crescentic to oval patterns seen in one of the nests grossly resemble impressions of eggshells or eggs. Modern turtle and crocodile eggs have a leathery texture and are not highly calcified. Egg characteristics cannot be determined from the Triassic impressions at this time. The large shallow depressions associated with some of the nests are interpreted as body pits made by the female excavating her nest and laying her eggs. The highly irregular bumpy protrusions and multidirectional elongate furrows within these shallow depressions represent trampled ground that sometimes preserve

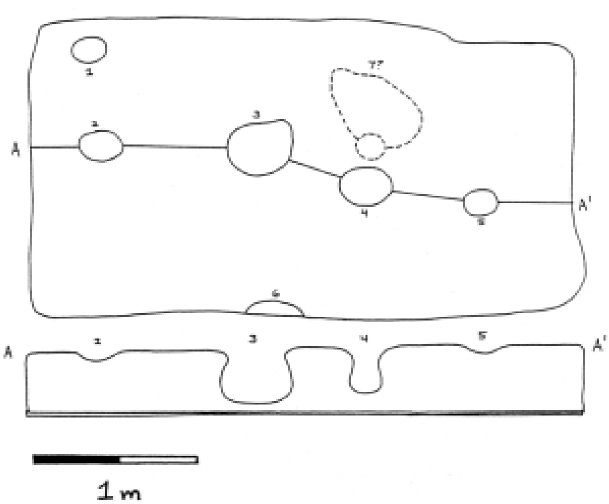

FIGURE 3—An example of a block of sandstone with the nest ichnofossils, with a schematic diagram of the block.

FIGURE 4— A. Example of trampled ground around some of the nest ichnofossils. B. Close-up of a partial footprint within the trampled area.

partial footprints of the nest-maker. Smaller, incomplete pits associated with the nests are interpreted as test pits made by females testing the substrate conditions (e.g., texture, consistency, moisture), as observed in extant turtles (Hailman and Elowson, 1992; Brannen and Bishop, 1993). Thus, several incomplete or much smaller pits adjacent to completed pits and other pits and depressions show various stages of completion as compared to those that appear to be completely constructed nests.

The distribution of the Chinle nest-holes are also similar to the nest distribution of extant sea and terrestrial turtles (Reptilia: Cheloniidae), hole-nesting crocodiles, and hole-nesting alligators (Repitilia: Crocodylidae), as opposed to mound-nesters (Cott, 1961; Webb *et al.*, 1983; Woodward *et al.*, 1984; Thorbjarnarson, 1996). Today, the females of these reptiles congregate along rivers, swamps, and beaches to construct their nests and lay their eggs. The females and their offspring return to the same areas to nest for many consecutive years, reflecting nesting site-fidelity (Cott, 1961; Carr, 1967; Mazzotti, 1989; Leslie, 1997). Similar patterns of nest site-fidelity have also been observed with nests constructed by Late Cretaceous dinosaurs (Horner, 1982). Nests interpreted as having been constructed during the same reproductive season are separated by a mean distance analogous to the body-length of adult hadrosaurs. For the Chinle, the spacing between the nests is similar to the length of the interpreted body pits. A few examples of nest construction overlap likely reflect recolonization of the nesting site. This interpretation is supported by observed nest-site reuse by extant crocodilians and alligatorids (Cott, 1961; Webb *et al.*, 1983; Thorbjarnson and Hernandez, 1993). However, in some cases, nesting sites can be also occupied by more than one species of reptile, such as crocodilians and iguanas (Dugan *et al.*, 1981; Bock and Rand, 1989). This implies that the nests may not necessarily be indicative of monospecific nest makers. At this point, the morphology of the Chinle nests suggests only one type of nest-maker.

DISCUSSION

Based on the size, spacing, and distribution of the nest ichnofossils, the constructors could have been aetosaurs, small phytosaurs, rauisuchians, or dinosaurs. Within 1500 m of the nesting sites is fossil evidence of reptilians that lived within the same stratigraphic interval, which include a partial skull, teeth, and armor plates of phytosaurs, armor plates of aetosaurs, and tracks and trackways of swimming reptiles (Martin and Hasiotis, 1998). Evidence of theropod dinosaurs are also found in both the lower and higher stratigraphic levels (Padian, 1986; Hunt, 1995; Long and Murray, 1995; Hunt *et al.*, 1996; Martin and Hasiotis, 1998). The Triassic nest ichnofossils are nearly 120 million years older than nests previously described from the Late Cretaceous of the Western Interior of the United States. Whoever the nest-makers were, their ichnofossils suggest that they were gregarious, lived and bred along or in perennial watercourses, and exhibited basic parental instincts. There is no way to tell if these reptiles tended to their nests, eggs, or young after hatching. However, the pattern of nests is analogous to that observed for dinosaurs in the Late Cretaceous purported to have cared for their eggs/offspring (Horner and Makela, 1979; Horner 1982; Varricchio *et al.*, 1997) and hole-nesting crocodilians and alligatorids (e.g., Kushlan and Simon, 1981; Mazzotti, 1989; Thorbjarnson, 1996).

The morphology of the Triassic nest ichnofossils and the pattern of their occurrence suggest that basic nest construction and architecture has remained relatively unchanged for over 200 million years. The ichnofossils imply that eggs were cared for through their deposition in excavated nests, rather then simply laid on the ground or in vegetation. This observation indicates that rudimentary parental care may have begun at least in the Triassic and may be even older, and is a major step toward the rearing of offspring and advanced parental care.

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OCCURRENCES OF *ZAMITES POWELLII* IN OLDEST NORIAN STRATA IN PETRIFIED FOREST NATIONAL PARK, ARIZONA

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Abstract—*Zamites powellii* is one of the most common fossil leaves found in Carnian sediments of the Upper Triassic Chinle Formation and Dockum Group. It is rarely found in Norian sediments. Here, however, we report a Norian occurrence in Petrified Forest National Park, Arizona. *Z. powellii* was found in channel-fill deposits up to 5 m above the Sonsela Sandstone, generally considered to be the Carnian/Norian boundary in the Park. The geology of this locality highlights the reasons why plant assemblages are rarely found in Norian deposits: preservational biases limit the abundance of the fossils and a lack of stratigraphic control across the Carnian/Norian boundary makes age identification uncertain.

INTRODUCTION

Zamites powellii provides one of the most common fossil leaves, if not the most common fossil leaf, found in the lower part (Carnian) of the Upper Triassic Chinle Formation and Dockum Group in the southwestern United States (Daugherty, 1941; Ash, 1967, 1972a, 1974, 1975, 1978). The fossil is found in the *Eoginkigites* and *Dinophyton* floral zones (Litwin et al., 1991) which, in Petrified Forest National Park (PEFO), Arizona, occur in and below the Sonsela Sandstone (Ash, 1967, 1980). The Sonsela Sandstone is a widely recognized marker bed throughout the Park, and is believed to approximate the Carnian/Norian boundary (Litwin, 1986; Litwin et. al., 1991). With few exceptions, *Z. powellii* only occurs below it (Ash, 1975). The absence of *Z. powellii* in Norian sediments may be attributed to preservational biases that have limited the abundance of the fossils and/or a lack of stratigraphic control across the Carnian/Norian boundary resulting in localities with an uncertain age affiliation. It is these few exceptional localities that are discussed here.

KNOWN LOCALITIES

Carnian localities of *Z. powellii* in the western United States are known from the lower part of the Chinle Formation in western New Mexico, Arizona, Utah and the Dockum Group of eastern New Mexico, western Texas and western Oklahoma (Daugherty, 1941; Ash, 1975, 1988). In the Carnian sediments of the Chinle Formation fossils have come from the Sonsela and Poleo Sandstones, and the Lower Petrified Forest, Monitor Butte, Mesa Redondo, and Shinarump Members (Ash, 1972b, 1974, 1980). In the Carnian sediments of the Dockum Group, fossils are known from the Santa Rosa Sandstone (referred to as the Santa Rosa Formation, Ash, 1972a, 1988), as well as the Trujillo and Tecovas Formations (Ash, 1980).

A few possible Norian localities of *Z. powellii* have been documented by Ash (1970, 1972b, 1975). One locality is reported to be in the Upper Petrified Forest Member (Norian) of the Chinle Formation in the southern end of PEFO at a locality called “Walker’s Stump” (Ash, 1970; Ash and Hevly, 1974; Walker, 1974). Two other potentially Norian localities, both in the Dockum Group, were described by Ash (1975). Near Santa Rosa, New Mexico, *Z. powellii* is in the base of the Chinle Shale Formation, and at Boys Ranch in Texas, it is found in the Trujillo Sandstone (Ash, 1972a, 1975).

Z. POWELLII AT GATESY’S PLUNGE IN PEFO

Z. powellii (identified by S. Ash, personal commun., August 1998; Fig. 1) was found during the summer of 1998 in the Gatesy’s Plunge area (near Jasper Forest) in PEFO (Fig. 2) in sediments that lie up to 5 m above the Sonsela Sandstone (Fig. 3). Because the Sonsela Sandstone is considered to be the marker bed for the Carnian/Norian transition in PEFO, the locality may be placed confidently within the Norian.

Within PEFO, the Sonsela Sandstone is a highly recognizable and traceable unit averaging between 10 and 12 m thick and is characterized as light gray-to-tan, fine- to medium-grained, moderately sorted, subangular-to-subrounded, quartz arenite and conglomerate with horizontal bedding, and tablular and trough cross-bedding (Elzea, 1983; Billingsley, 1985; Ash, 1987; Murry and Long, 1989). Typically, the sandstone forms cliffs, but it is known to thin out and intertongue with sediments above and below it (Billingsley, 1985; Murry and Long, 1989). This is the case with the *Z. powellii* locality. The Sonsela Sandstone can be seen in its “typical” form as a

FIGURE 1—Photograph of *Z. powellii* from Gatesy's Plunge, PEFO. Penny is 1.8 cm.

prominent cliff, capping mesas in the Jasper Forest area of PEFO. It can be physically traced from these cliffs to a more modest sand body at the base of hills in the Gatesy's Plunge area. In the region where stratigraphic section 4 was measured (Figs. 3 and 4) the Sonsela Sandstone is a fine to very-fine grained reddish lithic arenite as described by Dott (1964). This is one of the more inconspicuous manifestations of this sandstone in the Park.

The plant material was found in an approximately 4 m thick unit of gray, silty mudstone and siltstone interlayered with fine- to medium-grained, moderately to poorly sorted lithic wacke (Fig. 3; stratigraphic section 1). Most of the carbonaceous material found was disseminated fragments, but whole leaf impressions of *Z. powellii* were also obtained (Fig. 1). The plant-bearing stratum can be traced laterally about 0.75 km, (see stratigraphic section 2; Fig. 3), but no whole leaf impressions were found elsewhere in it, only carbonaceous fragments and dark stained (presumably from carbon) rock.

The plant locality is in channel-fill sediments at the base of a +15 m deep paleochannel (Herrick, in prep.). Preliminary work done on reconstructing the paleoenvironment of the Gatesy's Plunge area indicates that deposition took place in a meandering fluvial system (Herrick, in prep.). Taphonomic settings like those at the *Z. powellii* locality are reported to favor plant preservation in the Chinle Formation (Demko et al., 1998).

DISCUSSION AND CONCLUSIONS

"Carnian" plant fossils have been found in younger sediments (Daugherty, 1941; Ash, 1972b, Ash, 1992) and one might expect in the future to find *Z. powellii* among them. However, there are relatively few localities of leaf compressions reported above Carnian sediments, and the age of these is only questionably referred to the Norian. These two issues will be briefly examined.

Though the leaf assemblages that are found in the Norian are very similar to those in the Carnian, they are considerably more rare (Ash, 1972b). This may be attributed to preservational biases. Plant assemblages are concentrated in lower Chinle members where they were preserved within incised valleys that were cut into the underlying Triassic rock (Demko et al., 1998). In contrast, the upper Chinle members were deposited across the fluvial plain that formed once the incised valleys were filled in (Demko et al., 1998). Accordingly, as Ash (1972b) has noted, the apparent difference

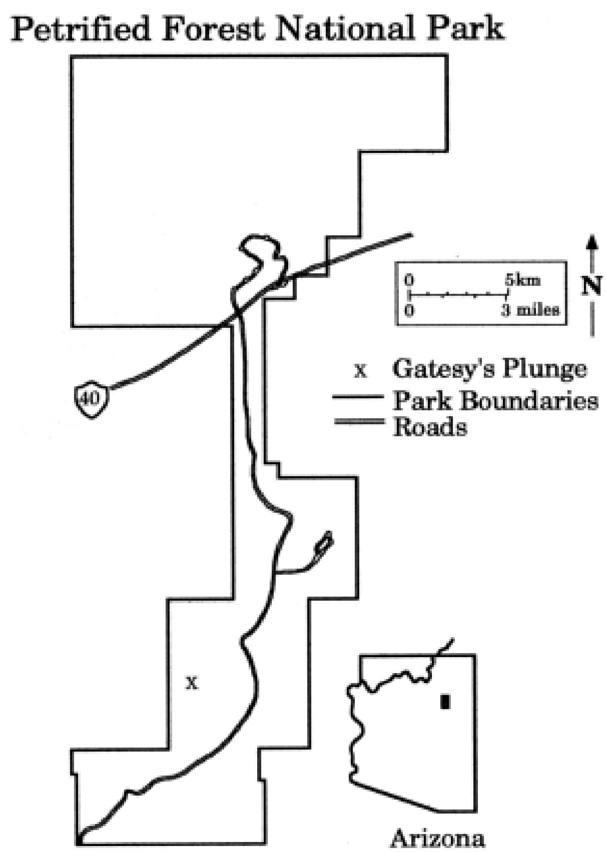

FIGURE 2—PEFO indicating Gatesy's Plunge. Inset: Arizona. Modified from Billingsley (1985).

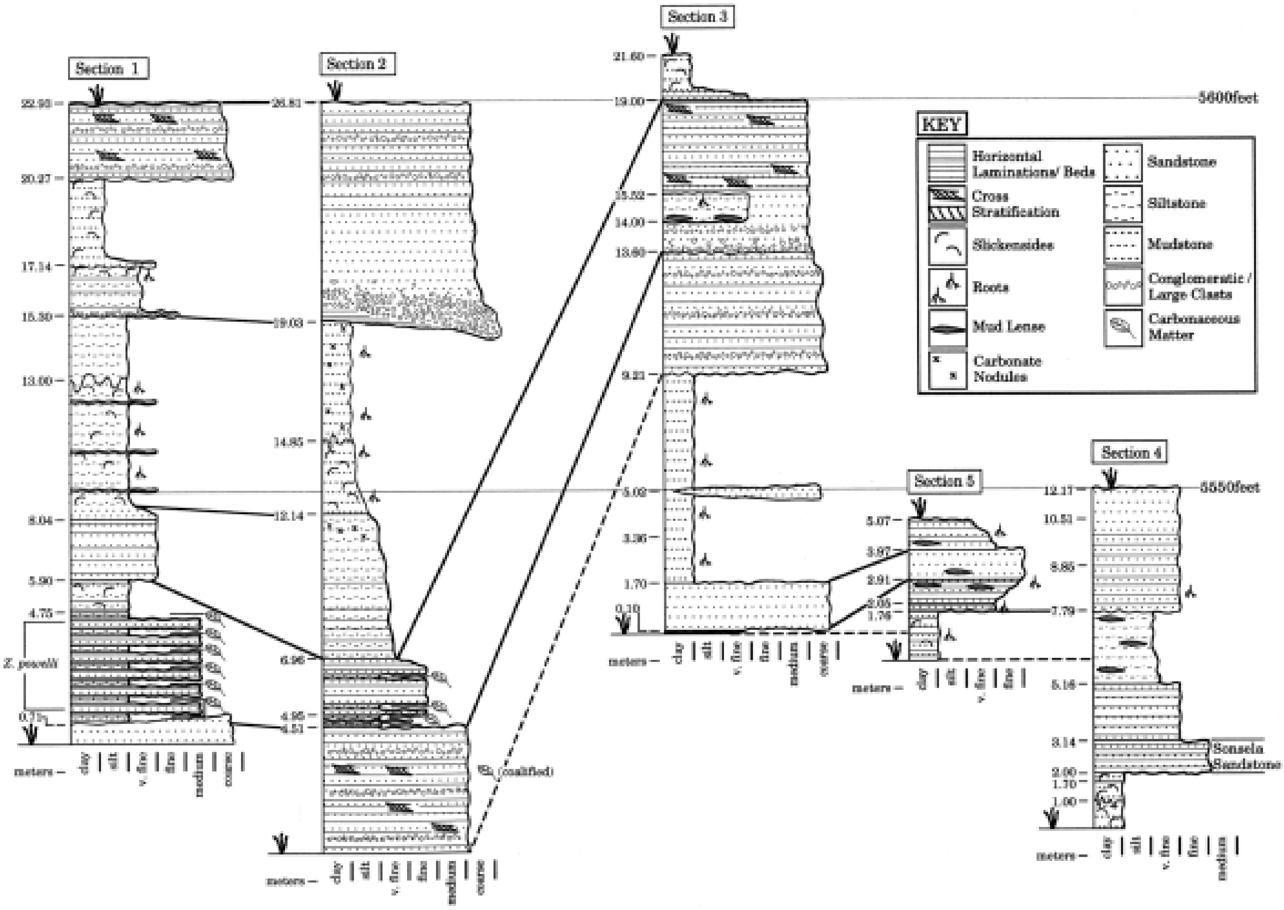

FIGURE 3—Stratigraphic sections of Gatesy's Plunge showing lithostratigraphic correlation between the Sonsela Sandstone (Section 4) and the *Z. powellii* locality (Section 1). Horizontal spacing not to scale.

between the abundance of plant assemblages in Carnian and Norian sediments may not be real. This may simply be an artifact of different depositional systems and associated preservation, as has been shown to occur elsewhere on the Colorado Plateau (Demko, et al., 1998). It follows that if we look in Norian valley-fill and channel-fill sequences, we may indeed find more floral assemblages.

A lack of stratigraphic control across the Carnian/Norian boundary has resulted in uncertainty in assigning a Norian age to some localities. Two *Z. powellii* localities, the Chinle Shale Formation locality near Santa Rosa New Mexico, and the Trujillo Sandstone locality at Boy's Ranch in Texas, are questionably referred to the Norian (Ash 1972a, 1975).

Recent stratigraphic work does not shed light on the Chinle Shale Formation locality. We have not found further reference to a "Chinle Shale Formation" of the Dockum other than by Ash (1972a, 1975). Reeside et al. (1957) and Chatterjee (1986) cite an unnamed shale member of the "Chinle" (quotations their's) Formation of the Dockum Group. Lucas and Hunt (1989) recognized and renamed a lower (Carnian) and an upper (Norian) shale member of the Chinle Formation of the Dockum Group, but it is uncertain to which shale member Ash (1972a, 1975) refers. Therefore, the Chinle Shale locality cannot unequivocally be considered Norian.

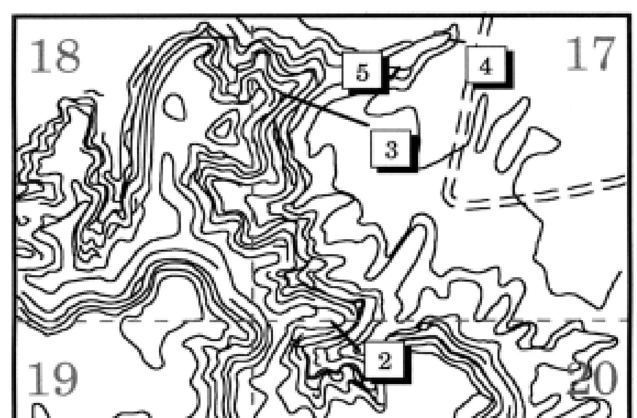

FIGURE 4—Topographic map of Gatesy's Plunge area in Jasper Forest with locations of stratigraphic sections indicated. Specimen found in NE1/4 NW1/4 NW1/4 Section 20 T17N R24E. Contour interval 10 feet. Taken from USGS, Arizona, Agate House 7.5 min. quadrangle.

With respect to the Trujillo Sandstone, recent stratigraphic work (Ash, 1980, Dubiel, 1994) correlates this unit with sediments just under the Sonsela Sandstone. These studies suggest a late Carnian age for Ash's (1972a, 1975) Trujillo Sandstone locality.

As for the third possible Norian occurrence of *Z. powellii*, the Walker's Stump locality in PEFO, more work needs to be done to clarify the stratigraphic position of these fossils. The Walker's Stump locality is discussed by Ash (1972b) who only states that "*Otozamites powellii*" is "in or above Sonsela Sandstone" (p. 27, table 1). This locality has not been discussed since Ash's (1975) reassignment of the fossils found there from *Otozamites* to *Zamites*. Ash maintains that the fossils are correctly assigned to *Zamites* (S. Ash, personal communication, May 1999).

We were fortunate to find the PEFO locality at Gatesy's Plunge, because we can place the PEFO *Z. powellii* locality within the context of an unambiguous local stratigraphy. Based upon that stratigraphic position, *Z. powellii* from Gatesy's Plunge in PEFO is undoubtedly of Norian age.

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NEW DISCOVERIES OF LATE TRIASSIC DINOSAURS FROM PETRIFIED FOREST NATIONAL PARK, ARIZONA

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ABSTRACT—The Mesalands Dinosaur Museum has been conducting research during the last four years at Petrified Forest National Park under the auspices of the Dawn of the Dinosaurs Project. Twelve new dinosaur localities have been discovered to add to the three previously known. This success is due to use of the taphofacies approach to exploration. All of the dinosaur localities occur in two narrow stratigraphic intervals above and below the Sonsela Member in the Petrified Forest Formation in calcareous paleosols. Blue Mesa Member (Carnian) localities yield small and large theropods, whereas Painted Desert Member (Norian) localities include both theropods and the ornithischian *Revueltosaurus*. Associated faunas are dominated by small, terrestrial tetrapods.

INTRODUCTION

Petrified Forest National Park is famous for exquisitely preserved petrified wood that is abundant in the Upper Triassic strata of the area (Heckert and Lucas, 1998a). However, these rocks also contain a significant record of fossil vertebrates that elucidate one of the most important turnovers in terrestrial tetrapods.

The Late Triassic saw the replacement of archaic faunas dominated by dicynodonts, rhynchosaurs and temnospondyls by the archosaurian faunas that were to dominate the remainder of the Mesozoic (e. g., dinosaurs, pterosaurs) as well as the advent of many other significant clades (e. g., mammals, turtles). The most critical time period in this transition is the late Carnian through the early Norian when all the major clades emerged and archaic groups such as the dicynodonts and rhynchosaurs became extinct (Hunt, 1991). The area in and around Petrified Forest National Park has long yielded significant specimens of fossil vertebrates from this time interval (e. g., Camp, 1930, Long et al., 1989). However, until 1982 no dinosaur specimens had been recovered from the Park (Hunt et al., 1998). In the early 1980's field parties from the University of California Museum of Paleontology collected from three dinosaur localities (Padian, 1986; Long and Murry, 1995). In 1996, field parties from the Mesalands Dinosaur Museum started the Dawn of the Dinosaurs Project to study early dinosaur evolution in the Park and elsewhere (Hunt et al., 1996; Hunt, 1998). This project has resulted in the discovery of an additional 12 dinosaur localities, an increase of 400% (Figure 1). The purpose of this paper is to present initial findings from the 1998 and 1999 field seasons and to relate them to previous work. MDM refers to Mesalands Dinosaur Museum, PEFO to Petrified Forest National Park and UCMP to University of California Museum of Paleontology.

GEOLOGIC SETTING

All Upper Triassic strata preserved in Petrified Forest National Park pertain to the Petrified Forest, Owl Rock and Bluewater Creek formations of the Chinle Group (Lucas, 1993, 1995; Heckert and Lucas, 1998b). Significant vertebrate fossils are restricted to the Blue Mesa and Painted Desert Members of the Petrified Forest Formation that are respectively late Carnian and early-middle Norian in age (Hunt and Lucas, 1995). The majority of vertebrate fossils from these units, and all the dinosaur fossils reported herein, are from narrow stratigraphic intervals above and below the Sonsela Member which divides the Blue Mesa and Painted Desert members (Figure 1).

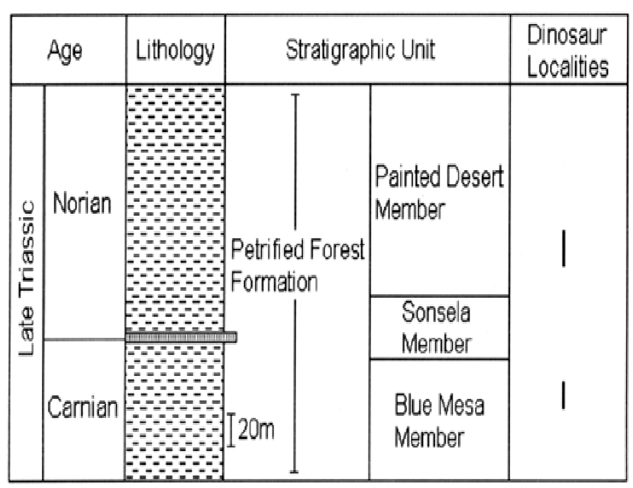

FIGURE 1—Stratigraphic distribution of dinosaur localities within the Upper Triassic Petrified Forest Formation, Petrified Forest National Park.

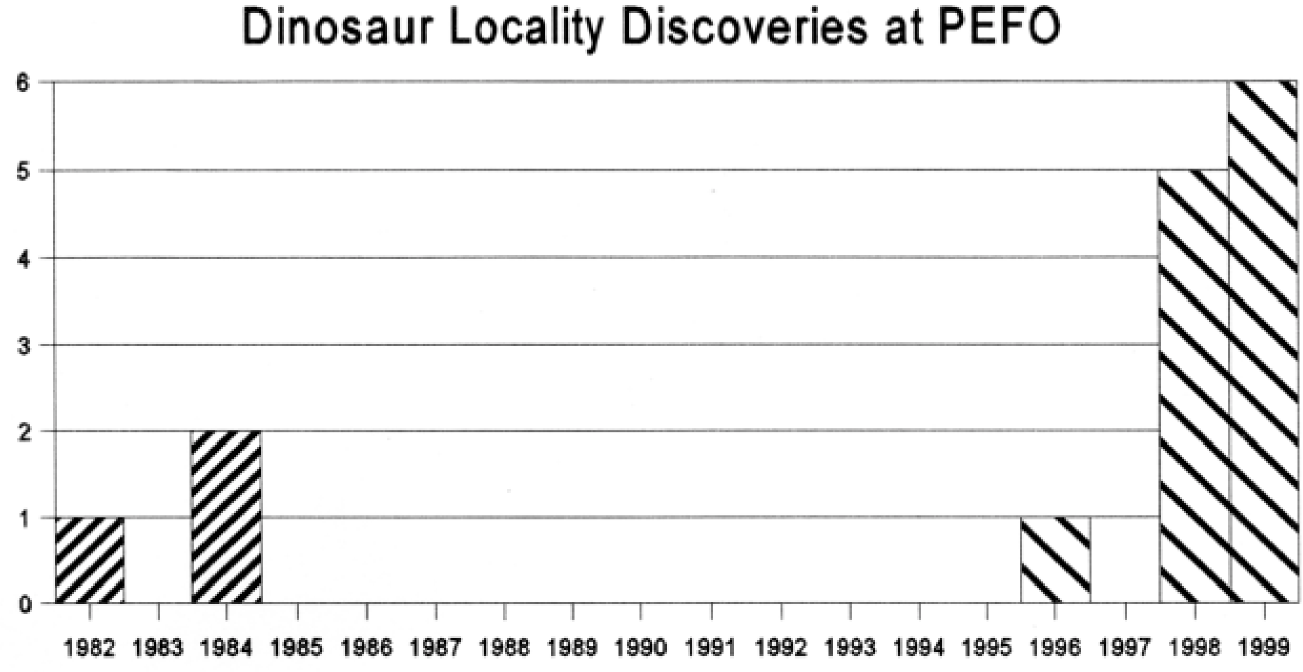

FIGURE 2—Chronology of discovery of dinosaur localities at Petrified Forest National Park. Left slanted shading indicates discovery by University of California Museum of Paleontology and right slanted shading by Mesalands Dinosaur Museum. See Table 1 for supporting data.

NEW DINOSAUR LOCALITIES

During the last two years an additional 11 dinosaur localities have been discovered at Petrified Forest National Park (Figure 2). The success of this fieldwork has been the result of the development of a taphofacies search model for Late Triassic vertebrate localities. Andrew Newell and Adrian Hunt developed a taphofacies model for fossil vertebrate localities from the Norian Bull Canyon Formation of eastern New Mexico and recognized three principal taphofacies: channel-hosted, proximal floodplain-hosted and paleosol-hosted taphofacies (Newell, 1992; Hunt, 1994; Hunt and Newell, 1996). Subsequently, this model, with minor revisions, has been found to be applicable to other Late Triassic vertebrate localities in the western United States including those at Petrified Forest National Park (Hunt and Santucci, 1993, 1994; Hunt, 1995; Hunt et al., 1995; Watts et al., 1996). Dinosaur fossils are restricted to the paleosol-hosted taphofacies both within Petrified Forest National Park and at almost all other dinosaur localities in the western United States. The principal exceptions to this model are the *Coelophysis* quarry at Ghost Ranch and a nearby quarry currently being excavated by Andrew Heckert of the New Mexico Museum of Natural History and Science. Host paleosols are characterized by color mottling, calcareous concretions and root casts.

The majority of prior investigators at Petrified Forest National Park had been indiscriminately sampling all taphofacies that they encountered. Since the majority of the paleoenvironments preserved in the Petrified Forest Formation represent proximal floodplains, the phytosaur-metoposaur communities dominate most prior collections of fossil vertebrates from the Park. Even with intensive exploration for dinosaur-bearing paleosols, only 15 dinosaur sites have been found at Petrified Forest National Park. This contrasts with over two hundred other localities that yield fossil tetrapods within the Park. A similar disparity between the frequency of dinosaur-bearing paleosols as opposed to other vertebrate-fossil localities is found in the Bull Canyon Formation of eastern New Mexico (Hunt, 1994).

Prior to 1996, there were no known dinosaur localities in the Carnian Blue Mesa Member of the Petrified Forest Formation within the Park. Dinosaur Ridge was discovered in 1996 by Tom Olson, an intern working for the Mesalands Dinosaur Museum. This site produces a diverse fauna that includes postcranial and cranial fragments of a small theropod and a lesser number of postcranial elements of a larger theropod. Other faunal elements include small, terrestrial tetrapods including the diminutive aetosaur *Acaenosuchus* which we consider to be a valid taxon (*contra* Heckert and Lucas, 1999). Mesalands interns Howard Beuhler and Jack Rogers found two other Blue Mesa localities in 1998. Dinosaur Wash yields diverse small reptile specimens including abundant postcrania and teeth of a small theropod. Dinosaur Wash East yielded one saurischian cervical vertebra which appears to represent a prosauropod.

The remainder of the other nine new dinosaur localities occur in the Painted Desert Member of the Petrified Forest Formation. With the exception of a hollow, theropod limb shaft from Flattops, all these localities occur in a restricted area within the Painted Desert portion of the Park. The area between Dinosaur Hill and Zuni Well Mound contains several abandoned channels filled with pedogenically-modified mudstones that yield abundant terrestrial vertebrate fossils, including dinosaurs. These facies are genetically related in an area that was initially heavily scoured and was subsequently subject to repeated flooding. The sequence of events was: (a) the area was incised by channelized flow; (b) the area was subject to periodic flooding that filled scours with mudstone and siltstone - during this time period no streams traversed the area; and (c) there was pedogenic modification of the overbank deposits between flood events. During the second and third stages vertebrate remains were incorporated into the strata. The sedimentologic context of the Painted Desert localities is thus analogous to that of dinosaur-bearing localities in the Revuelto Creek area of eastern New Mexico in the contemporaneous Bull Canyon Formation (Hunt, 1994). These data underscore the conceptual validity of the Early Revueltian (early Norian) acme zone for terrestrial tetrapods proposed by Hunt and Lucas (1993).

The most common dinosaur in Painted Desert localities is *Revueltosaurus callenderi* which is known from tens of teeth. No other specimens of this early ornithischian have yet been identified. The second most common dinosaur is a small theropod that is represented at most localities by vertebrae and limb fragments. The most significant individual specimen is a partial skeleton of the larger theropod that Padian (1986) erroneously referred to *Coelophysis bauri*. This specimen was found in 1999 at Jeremiah's Perch and is currently only partially excavated, but it includes at least femora, tibiae, cervical vertebrae, teeth as well as many other elements.

The most common member of the associated fauna is the diminutive metoposaurid *Apachesaurus gregorii* that had a much more terrestrial habit than other members of its family (Hunt et al., 1993). This taxon is known from abundant intercentra, several partial skeletons, partial skulls, clavicles and interclavicles. Small terrestrial reptiles are also common at these localities including *Hesperosuchus*, a *Vancleavea*-like animal, a new armored crurotarsan described by Hunt (1994) from New Mexico and other taxa. Lungfish toothplates and a partial skull are also present as are abundant coprolites and rarer gastropods. Phytosaur specimens are ubiquitous in the Park, but most dinosaur localities yield only a small number of fragments of these crurotarsans and a disproportionate number of specimens represent juveniles.

CONCLUSIONS

There are two distinctive features of the Late Triassic dinosaur localities at Petrified Forest National Park: (1) all localities occur in pedogenically modified fills of scours; and (2) all localities occur in two narrow stratigraphic intervals (Figure 1). The restriction of dinosaur fossils to calcretes strongly suggests that Late Triassic dinosaurs were living in well-drained, open country in contrast to the phytosaur-metoposaur communities that are found in wetter, proximal-floodplain settings and which represent channel-margin ecosystems (cf. Hunt, 1991). The restriction of dinosaur specimens to narrow stratigraphic intervals is probably related to the developmental stage of transgressive systems tracts, but needs further study (Hunt and Lucas, 1993).

It is clear that the taphofacies approach to fossil exploration has been highly successful in the last few years and we are confident that additional dinosaur-bearing localities will be found in the future utilizing this methodology. Much additional work needs to be done to analyze the taxonomy and faunal associations of the dinosaurs from the Park. This analysis will greater increase our understanding of the early evolutionary ecology and diversification of the dinosaurs in the context of the major faunal changes of the Late Triassic.

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Locality Name (in PEFO records)	**Stratigraphy**	**Dinosaur Taxa**	**Associated Fauna**	**Year Discovered**	Institution
Dinosaur Hill	Painted Desert Member	"*Coelophysis bauri*", *Revueltosaurus callenderi*	Diverse small reptiles including a sphenosuchian, *Apachesaurus gregorii*, *Arganodus* sp., phytosaurs, and coprolites	1982	UCMP
Dinosaur Hollow	Painted Desert Member	Chindesaurus bryansmalli	Small reptiles and phytosaurs	1984	UCMP
Chinde Point North 2	Painted Desert Member	?Chindesaurus bryansmalli	None	1984	UCMP
Dinosaur Ridge	Blue Mesa Member	Small theropod Large theropod	Diverse small reptiles including *Acaenosuchus*, phytosaurs, and coprolites	1996	MDM
Zuni Well Mound	Painted Desert Member	Small theropod *Revueltosaurus callenderi*	Diverse small reptiles including a sphenosuchian, *Typothorax coccinarum*, *Vancleavea campi*, phytosaurs, *Apachesaurus gregorii*, *Arganodus* sp., Gastropoda, and coprolites	1998	MDM
Dinosaur Wash	Blue Mesa Member	Small theropod	Small reptiles, phytosaurs, and coprolites	1998	MDM
Dinosaur Wash East	Blue Mesa Member	?Prosauropod	Small reptile and phytosaurs	1998	MDM
RAP Hill	Painted Desert Member	Small theropod *Revueltosaurus callenderi*	Small reptiles, juvenile and other phytosaur, *Apachesaurus gregorii*, *Vancleavea campi*, and coprolites	1998	MDM
Flattops	Painted Desert Member	Small theropod	*Typothorax coccinarum*, *Paratypothorax*, and phytosaurs	1998	MDM
Katie's Draw	Painted Desert Member	Large theropod *Revueltosaurus callenderi*	Juvenile and other phytosaur, Gastropoda, and coprolites	1999	MDM
Mesa Mound	Painted Desert Member	*Revueltosaurus callenderi*	Juvenile and other phytosaur, *Apachesaurus gregorii*, *Arganodus* sp., and coprolites	1999	MDM
Jeremiah's Perch	Painted Desert Member	"*Coelophysis bauri*", *Revueltosaurus callenderi*	None	1999	MDM
RAP Hill North	Painted Desert Member	Small theropod *Revueltosaurus callenderi*	Diverse small reptiles including a sphenosuchian and *Aetosaurus*, *Apachesaurus gregorii*, *Arganodus* sp., and coprolites	1999	MDM
RAP Hill South	Painted Desert Member	*Revueltosaurus callenderi*	*Apachesaurus gregorii* and coprolites	1999	MDM
RAP Hill West	Painted Desert Member	Small theropod *Revueltosaurus callenderi*	*Apachesaurus gregorii* and coprolites	1999	MDM

TABLE 1—Stratigraphic, taxonomic and discovery date data for Late Triassic dinosaur localities from the Petrified Forest Formation, Petrified Forest National Park (data from Padian, 1986; Long and Murry, 1995; Hunt et al., 1996; Hunt, 1998; Hunt et al., 1988; and unpublished data).

THE OLDEST TRIASSIC STRATA EXPOSED IN PETRIFIED FOREST NATIONAL PARK REVISITED

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ABSTRACT—The measured sections show that the oldest strata in Petrified Forest National Park are present in the vicinity of the Haystacks. Controversial units are exposed in this vicinity; these include sandstones, siltstones, mudstones and a purple mottled horizon, whose characteristics are reminiscent of strata of the Moenkopi Formation (Early to Middle Triassic) and "mottled strata" respectively. Recently, some authors questioned the affinity of these units to the Moenkopi Formation and have correlated them instead to the Bluewater Creek Formation present at Fort Wingate (NM) on the basis of similar lithologies. A detailed investigation of the area reveals that the stratigraphy does not rule out the possibility of finding Moenkopi strata in PEFO. Correlation of the PEFO units with the New Mexico strata seems unlikely as they are shown to be of limited lateral extent and highly variable over short distances.

INTRODUCTION

Petrified Forest National Park (PEFO) is one of the best places in the American Southwest to study the Late Triassic Chinle Formation due to the extent and the quality of its exposures. Although extensive sedimentological and stratigraphical work has been done in the vicinity of PEFO (Gregory 1917; Cooley, 1958, 1959; Roadifer, 1966; Stewart et al., 1972a; Billingsley, 1985a,b; Kraus and Middleton, 1984, 1987; Kraus et al. 1984; Middleton et al., 1984; Ash, 1987, 1992; Murry, 1990; Demko, 1994, 1995a,b; Demko et al., 1998; Hasiotis and Dubiel, 1993a,b; Dubiel, 1993; Dubiel and Hasiotis, 1994a,b; Dubiel et al., 1995; Lucas, 1993a, 1995; Lucas and Heckert, 1996; Heckert, 1997; see also Hasiotis et al., 1993), there has been some ambiguity over the identity of the basal strata. Previous researchers (Dubiel et al., 1995; Dubiel, personal communication, 1998; Demko, personal communication, 1998; Demko, 1995a; Lucas, 1993a; Heckert, 1997) have recognized that the stratigraphically lowest Chinle exposures in PEFO are in the western part of the Tepees, near the Haystacks (Fig. 1). Dubiel et al. (1995) identify these strata as basal Chinle with local exposure of the Early to Middle Triassic Moenkopi Formation. However, Heckert and Lucas (1998) disagree with this interpretation and assign the strata to the Bluewater Creek Formation of the Late Triassic Chinle Group (*sensu* Lucas, 1993a), as described in the vicinity of Fort Wingate, New Mexico.

In the summer of 1998, we constructed a detailed, centimeter-by-centimeter, composite stratigraphic section of the PEFO by measuring 33 columnar sections throughout the Park (Fig. 2). Although several researchers have published composite sections of the PEFO (Dubiel et al., 1995; Demko, 1995a; Murry, 1990; Lucas, 1993a; Lucas and Heckert, 1996; Heckert, 1997), the extreme lateral variability of the Chinle strata have hindered the development of a robust stratigraphy; thus, we physically traced beds from outcrop to outcrop to establish correlations. The measured sections described in this paper (Fig. 3) represent the basal portion of our composite stratigraphic section. The sections document the presence of the controversial exposures, although their relationship to the Moenkopi Formation remains uncertain.

As noted above, in a complex fluvial system like the one represented by the Chinle Formation, the high lateral variability of facies can hinder correlation of lithostratigraphic units over long distances. Therefore, we refrain from using any stratigraphic nomenclature for "members" or "formations" to correlate localities as too often they resemble facies rather than correlatable lithostratigraphic units.

MOENKOPI/CHINLE CONTACT IN NORTHEASTERN ARIZONA

MOENKOPI FORMATION—The uppermost unit of the Moenkopi Formation (the Holbrook Member first named by Hager [1922]), consists of interstratified and interfingering beds of sandstone and siltstone, although a significant mudstone component may be present (McKee, 1954; Stewart et al., 1972b, Lucas, 1993b). The sandstone beds in the uppermost Moenkopi vary greatly in thickness and are discontinuous or irregularly interfingering with the siltstone beds (Stewart et al., 1972b). These sediments have been interpreted as representing deposition in a fluvial system with associated floodplain deposits (McKee, 1954; Stewart et al., 1972b; Blakey, 1974; Dubiel, 1994).

MOENKOPI/CHINLE UNCONFORMITY—A regional unconformity present between the Moenkopi Formation and the overlying Chinle Formation was first recognized by Gilbert (1875). A pre-Chinle-aged degradational fluvial system apparently eroded the Moenkopi Formation and formed an irregular to-

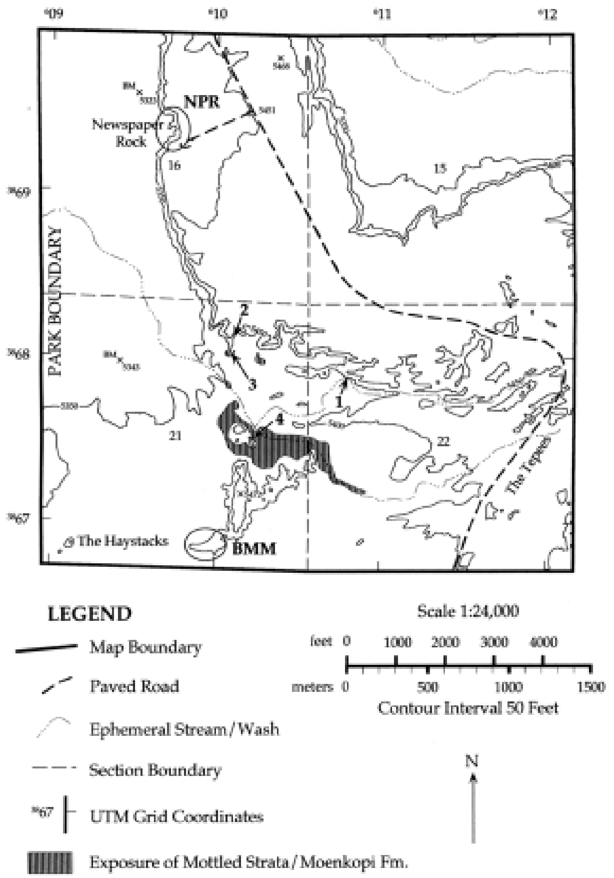

FIGURE 1—Locality map of the area studied in T18N R24E, including observed outcrops of strata interpreted as the "mottled strata"/ Moenkopi Formation. Also shown are the locations of Sections 1-4 and the approximate location of the sections measured by Lucas (1993a) (BMM) and Heckert and Lucas (1998) (NPR). (Modified from USGS topographic map, Adamana Quadrangle, 7.5 minute, 1982).

pography with an intricate complex of westward- and northwestward-trending paleovalleys and large channels (Cooley, 1959; Repenning et al. 1969; Blakey, 1974; Blakey and Gubitosa, 1983, 1984). The average relief carved into the Moenkopi is approximately 15 to 45 meters, but the largest depression reaches a depth of 90 meters and a width of 8 kilometers (Repenning et al. 1969; Blakey, 1974).

A period of nondeposition and/or episodic deposition, represented by pedogenic "mottled strata" (Stewart et al.,1972a, 1972b), occurred between the incision of paleovalleys into the Moenkopi and the deposition of the Chinle Formation. The "mottled strata" exhibit distinctive reddish purple, pale reddish brown, and light greenish gray mottles, and have developed in the first few feet of the Chinle and/or underlying Moenkopi Formation. Dubiel (1987) reports its occurrence tens of meters into basal Chinle units above the unconformity in southeastern Utah. The variability in the stratigraphic levels at which the "mottled strata" developed suggests that at least episodic deposition was occurring locally as it formed. Other than the presence of the "mottled strata" paleosol, several observations made by Blakey and Gubitosa (1984, their Table II) support an indeterminately long hiatus between the incision of the paleovalley topography into the Moenkopi Formation and the deposition of the basal Chinle units.

CHINLE FORMATION—In the Late Triassic, a change in fluvial regime allowed the rivers to start filling the paleovalleys with sediments thought to be derived from the Uncompaghre and Mogollon Highlands (Stewart et al. 1972a; Blakey and Gubitosa, 1983; Dubiel, 1987, 1994). The basal Chinle sediments filling the topography, known as the Shinarump Member, consist of tabular, trough cross-stratified sandstones and conglomerates containing lenses of mudstones and siltstones (Cooley, 1959; Repenning et al. 1969; Stewart et al. 1972a). The conglomerates, generally gray in color, contain pebbles and cobbles of quartz, quartzite, jasper, chert and petrified wood. Shinarump deposits are not continuous, but rather are found locally as lenticular, channel-like deposits (Gregory, 1917; Holyoak, 1956; Cooley, 1959; Repenning et al., 1969, Stewart et al. 1972a; Blakey and Gubitosa, 1983, 1984; Dubiel, 1983, 1987).

Because of the highly localized nature of the Shinarump deposits, another unit, the Mesa Redondo Member, represents the basal deposits of the Chinle Formation when the Shinarump Member is absent (Cooley, 1958, 1959; Repenning et al., 1969, Stewart et al. 1972a). According to Cooley (1958, p.9), the Mesa Redondo "either lies unconformably on the Moenkopi Formation or overlies and intertongues laterally with the Shinarump member". At the type locality approximately 10 miles southeast of the PEFO (near Hunt, AZ), the Mesa Redondo Member can be subdivided into three subunits: 1) a lower brownish-gray to grayish-red-purple mudstone-siltstone lenticular thinly-to-thickly-bedded unit; 2) a medial trough cross-stratified conglomerate and sandstone unit containing pebbles and cobbles of limestone, chert, jasper and quartz, grading into; 3) an upper mudstone-siltstone unit lithologically similar to the lower unit. The medial conglomeratic unit probably represents a channel deposit, as in some localities this unit is absent and the unit is then composed only of mudstones and siltstones (Cooley, 1958).

The close association of the Shinarump and Mesa Redondo Members suggests that they together form a facies complex of channel and overbank deposits. This could explain the close association and interfingering of these two units and why the Mesa Redondo lithologies overlie the Moenkopi Formation when Shinarump lithologies are absent.

STRATIGRAPHY

Four sections were measured (Fig. 3) using a Topcon GTS-211D electronic total station. Correlation between sections was accomplished by physically tracing two marker beds (referred to as SS and SP) from the southern face of the mesa capped by the Newspaper Rock sandstone (hereafter referred to as the Newspaper Rock Mesa) to buttes farther south (Fig. 1).

Unit SS (Fig. 3) is easily traceable from outcrop to out-

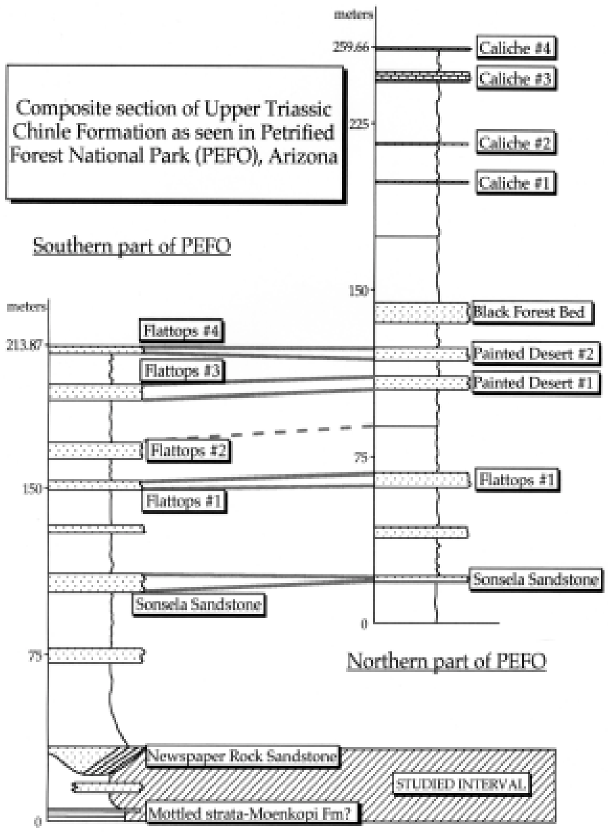

FIGURE 2—Composite stratigraphic section of the Upper Triassic Chinle Formation as constructed in Petrified Forest National Park, Arizona. Correlation between the northern and southern ends of the Park were made by tracing the Sonsela Sandstone and the distinct dark purple and blue paleosol sequence situated at the base of Blue Mesa toward the north in outcrops outside PEFO. Lithological features observed in strata situated above Flattops #2 are reminiscent of the red strata of the Painted Desert in the north.

crop. In the area of Section 1, SS is a white, very coarse, poorly sorted, conglomeratic sandstone with angular grains. It is composed of quartz and biotite and contains lenses of mudstone. The size of the particles composing this unit decreases toward section 3, where SS turns into a well sorted, coarse lithic wacke, composed of quartz, biotite and lithic fragments, and containing lenses of mudclasts. Bed SS unconformably overlies two distinct pedogenically-altered siltstones in the vicinity of Section 1. A deep red, gray-mottled unit is present at the base of this section; a densely mottled purple paleosol occurs in the uppermost part of this unit.

A second marker bed, SP (Fig. 3), typifies the lateral facies variability in a fluvial system. In the area of Section 1, SP is a well-developed paleosol, but it is present in the area of Section 2 as a sandstone. The gradual transition from the paleosol facies to the sandstone facies can be seen in the outcrops between Sections 1 and 2. The paleosol can be divided into two distinct sub-units: a thick purplish-red muddy siltstone with abundant grey mottles, underlying a thin, blue, fissile siltstone exhibiting mottling and slickensides. The sandstone facies is a white, lithic wacke with fine to medium sand-sized particles being mostly quartz, biotite, mudclasts, and lithic fragments. In the vicinity of Sections 2 and 3, SP is easily identifiable as a channel due to its arcuate, erosional lower contact.

Pedogenically-altered strata are observed at the base of Section 2 and 3 and in washes. (Fig. 3 and 4). Gray-mottled, red mudstones, siltstones, and sandstones are present at the base of buttes, and a purple- and yellow-mottled paleosol is developed in the uppermost part of those rocks. Dubiel et al. (1995) interpreted these lithostratigraphic units respectively as the Moenkopi Formation and the "mottled strata" that formed on it (*sensu* Stewart et al. [1972a]). These units are particularly well-exposed in very small outcrops present in washes and can also be recognized at the base of buttes (Fig. 1).

A highly weathered purple-mottled paleosol has been recognized at the base of Section 3. The upper part of this paleosol has been partially eroded by a channel that deposited a poorly sorted, conglomeratic sandstone unit containing chert pebbles and mudclasts (Fig. 3, Section 3, unit B). The distinctive dark red lithostratigraphic unit is not present at the base of Section 3; however, its presence close to the base of the section can be inferred from the fact that it can be seen outcropping in a nearby wash. Trough cross-stratification is observed in the red sandstone at this small outcrop and a mottled unit identical to the one described by Stewart et al. (1972a, their fig. 4) is also present (Fig. 4).

THE STRATIGRAPHICALLY LOWEST ROCKS IN PEFO

Numerous authors (most recently Lucas, 1993a; Heckert and Lucas, 1998; Dubiel et al., 1995; Murry, 1990; Demko, 1995) have measured and described sections in the western Tepees-Haystacks area, the stratigraphically lowest area of the Park. Correlation among these measured sections has often been made on the basis of the Newspaper Rock sandstone body. A series of inclined heterolithic strata (IHS), inferred to represent lateral accretion deposits, are laterally associated with the Newspaper Rock sandstone. These are considered to be a part of the Newspaper Rock sandstone body for correlation purposes.

CORRELATION WITH PREVIOUSLY DESCRIBED SECTIONS—Measured sections from previous work were situated on a topographic map of the Park (Adamana Quadrangle, 7.5 minute series, USGS, 1982) and their topographic position was taken into account to correlate them with the work presented here (Fig. 1). Lucas (1993a) built a composite section for the Blue Mesa Member in the Tepees-Haystacks area. The relevant section for this paper, the type Blue Mesa Member segment A (hereafter referred to as BMM) was measured in the vicinity of the Haystacks, approximately 1 km south-southeast of Section 3. He assigned these strata to the basal Blue Mesa Member (Fig. 5). As reported graphically in Heckert and Lucas (1998), BMM is capped by a sandstone unit situated at the base of the Newspaper Rock sandstone. This sandstone (unit 8 of BMM; Fig. 5) caps the buttes in the Hay-

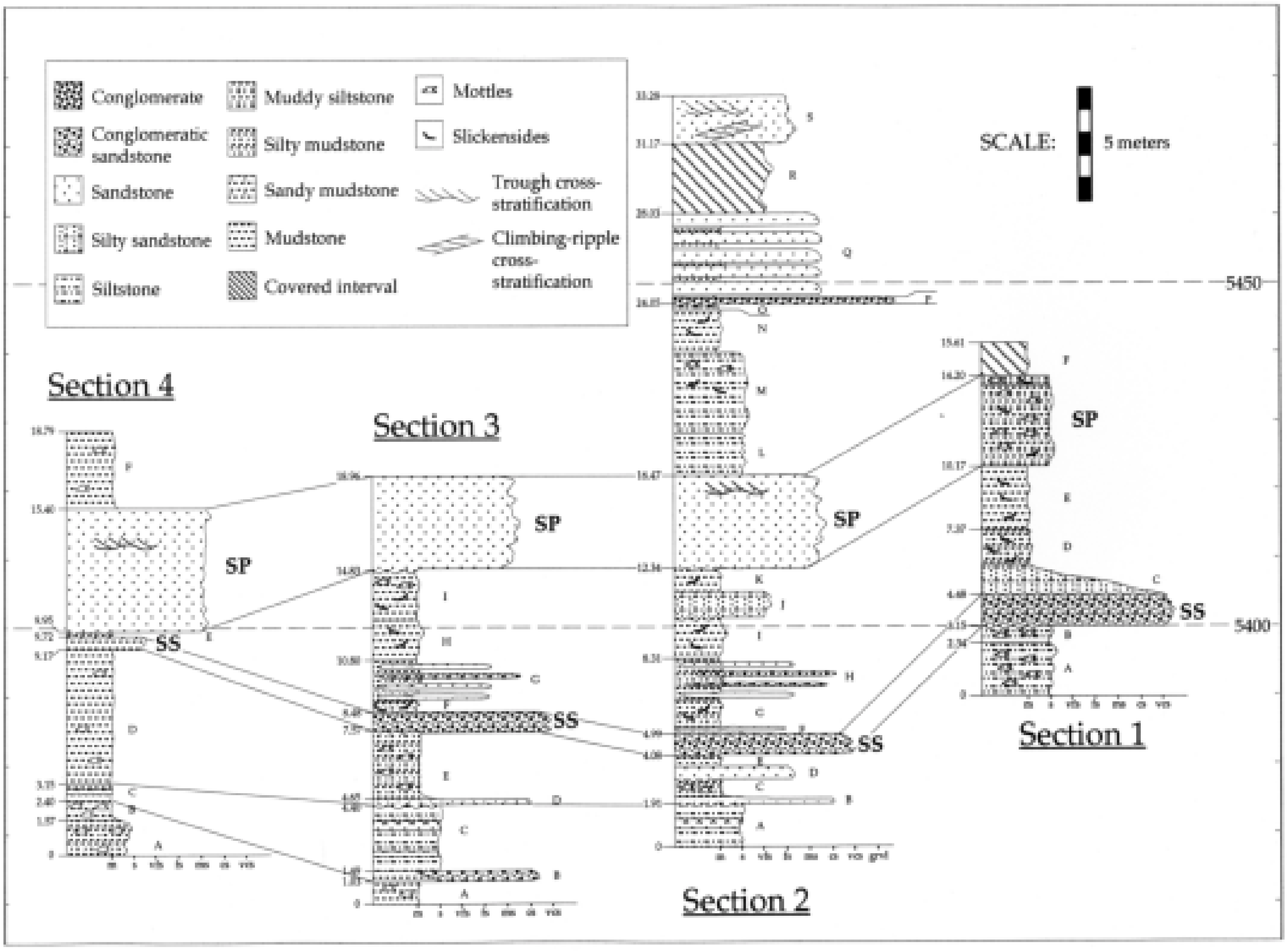

FIGURE 3—Correlations among measured sections in the vicinity of the Haystacks. Notice the lateral variability of unit C of Section 3. The relative distance between the sections is not to scale. The sections are located as follows: SECTION 1 - SE 1/4 NW 1/4 NW 1/4 Sec 22 T18N R24E; SECTION 2 - NE 1/4 NW 1/4 NE 1/4 Sec 21 T18N R24E; SECTION 3 - NE 1/4 NW 1/4 NE 1/4 Sec 21 T18N R24E; SECTION 4 - SW 1/4 SE 1/4 NE 1/4 Sec 21 T18N R24 E.

stacks area and is situated at approximately the same topographic elevation as the covered interval (unit R) of our Section 2 (Fig. 1). Heckert and Lucas (1998) established a correlation between the Newspaper Rock section (NPR), reported to contain the oldest rocks in the Park, and BMM on the basis of the Newspaper Rock sandstone (see Fig. 5).

We investigated their correlation by physically tracing the Newspaper Rock sandstone in the field, and following beds SS and SP between the localities (Fig. 5). The Newspaper Rock sandstone downcuts into the underlying strata north of Section 3, resulting in its direct superposition over SP in NPR. Bed SP turns into a paleosol both toward NPR and BMM and can be followed accordingly into these sections. SS is absent in NPR; it merges with SP in proximity to Section 3. Unit 3 of NPR correlates horizontally with the chert-bearing unit (unit C) in Section 2. Toward BMM, SP downcuts and comes close to merging with SS. In BMM, SP is represented by a paleosol situated in mid-section (units 4 and 5). Bed SS almost merges completely with SP (Section 4) but is still distinct in BMM. The red silty mudstone (unit 1) at the base of BMM is the red paleosol situated between the chert-bearing unit and SS in Section 3 (unit E) and the same paleosol seen underlying SS in Section 1 (unit 1, Fig. 3).

IDENTITY OF THE STRATA—The correlation between NPR and BMM proposed by Heckert and Lucas (1998) is incorrect. The basal sandstone of BMM (unit 2) is stratigraphically much higher (approximately 6 meters between SS and the chert-bearing unit in Section 4) than the basal sandstone of NPR (unit 3) (Fig. 5). This precludes the possibility of having any Moenkopi exposures in the vicinity of BMM.

At NPR, on the other hand, Heckert and Lucas (1998) have recognized rocks situated approximately at the same stratigraphic level as the rocks thought to represent the "mottled strata" developed on Moenkopi units in Section 3; they assigned these red mudstones to the Bluewater Creek Formation (*sensu* Lucas and Hayden, 1989). At NPR, we did not observe any strata similar to the one described from Section 3 (Fig. 5) or from the several wash outcrops thought to contain the Moenkopi Formation. Their absence at NPR could be related to the uneven nature of the Moenkopi/Chinle contact due to the development of paleovalleys into the Moenkopi Formation prior to Chinle deposition, or simply because they were too weathered to be easily recognized.

DISCUSSION

Heckert and Lucas (1998) argue for a Bluewater Creek Formation affinity for the lowermost strata present in PEFO instead of the Moenkopi Formation by: 1) using data obtained from cores to identify the depth of the Moenkopi/Chinle contact, and 2) correlating strata in PEFO with lithostratigraphic units present near Fort Wingate, NM.

Cores.—Subsurface data were obtained from the water-well logs published by Harrell and Eckel (1939). The logs describe an artesian well and cores obtained when drilling two water wells near the rail lines at Adamana, 2.6 km northwest of the Newspaper Rock outlook in PEFO (approximately 3.85 km north-northwest of Section 3).

A Moenkopi/Chinle contact has been identified 15 meters below the surface in the artesian well at Adamana (Harrell and Eckel, 1939). Heckert and Lucas (1998) estimate that approximately 25-30 meters of rock must be present below the base of NPR to reach the stratigraphic level of the Moenkopi/Chinle contact seen in Adamana and use this argument to reject the possibility of finding Moenkopi strata in PEFO.

As previously noted, the Chinle was deposited in paleovalleys incised into the Moenkopi; these depressions have an average depth of 15 to 45 meters (Cooley, 1959; Repenning et al. 1969; Blakey, 1974; Blakey and Gubitosa, 1983, 1984). The subsurface data of Harrell and Eckel (1939) do not obviate the possibility of finding a Moenkopi/Chinle contact within PEFO. A contact slope of 0.9 percent would be enough to explain the presence of Moenkopi strata at Section 3 and a Moenkopi/Chinle contact 30 meters below the level of NPR at Adamana.

Stratigraphic nomenclature—To identify the member affinity of the lowermost PEFO strata, Heckert and Lucas (1998) correlated the tuffaceous, micaceous sandstone present near the base of NPR and BMM (units 3 and 2 respectively, Fig. 5) with the basal ashy sandstone of their Blue Mesa member in the vicinity of Fort Wingate, NM. In this locality, the ashy sandstone overlies red mudstones of the Bluewater Creek Formation described by Lucas and Hayden (1989). Thus Heckert and Lucas (1998) assigned the stratigraphically lowest rocks they observed in PEFO to the Bluewater Creek Formation.

The credibility of such a correlation is diminished when we observe that NPR's basal sandstone and BMM's basal sandstone are situated at different stratigraphic levels and, because they represent two distinct sandstone bodies, cannot be correlated (Fig. 5). Moreover, NPR's unit 3 can be traced laterally into a chert-bearing siltstone unit (unit C of Section 3, Fig. 5). The correlation proposed by Heckert and Lucas (1998) was established purely on the basis of the similarity of lithologies: a tuffaceous sandstone overlying red strata situated near the base of a section.

Careful investigation in the field shows that direct correlation between similar lithologies cannot be made in the context of a fluvial system with lateral facies variability. The changing nature of NPR's basal sandstone (unit 3) within 1.5 km reflects this (Fig. 1). Indeed, it is hard to conceive of a fluvial sedimentary process that can explain the deposition of a continuous sandstone layer over the 125 km separating the PEFO (Arizona) from Fort Wingate (New Mexico). The similarity of Fort Wingate's and NPR's sandstones is fortuitous (as are the similarities of many non-correlatable lithofacies exposed throughout PEFO), but in no case implies lateral correlability. It is unlikely that the strata described in PEFO by Heckert and Lucas (1998) are genetically related to the outcrops in western-central New Mexico, and they should not be assigned to the Bluewater Creek Formation on the basis of these arguments.

Moenkopi/Chinle contact—The presence of a Moenkopi/

Figure 4—Small outcrop situated in wash at SW 1/4 NE 1/4 NE 1/4 Sec 21 T18N R24E (N34°57.00 w109°47.593) showing stratigraphically lowest units present in the vicinity of the Haystacks: 4.1) red, large scale trough cross-stratified sandstone with greenish gray reduction haloes (paleocurrent measurements: 39°, 46°, 53°); 4.2) purple-mottled unit, thought to represent a paleosol developed on Moenkopi rocks prior to Chinle deposition. Scale is 50 centimeters.

Chinle contact within PEFO cannot be rejected. Even though a typical Shinarump conglomerate (Cooley, 1959; Repenning et al., 1969; Stewart et al., 1972a) was not identified at any of our localities in PEFO, that should not deter us from considering the possibility of having reached the Moenkopi Formation since Shinarump lithologies are highly discontinuous in nature. Some fine material described in Sections 1 through 4, especially the pedogenically-modified red and purple siltstones well exposed in Section 1 (units A and B), are reminiscent of the Mesa Redondo Member lithologies (Cooley, 1958; Stewart et al., 1972a). Overbank deposits of the Mesa Redondo Member, laterally interfingering with Shinarump channel deposits not outcropping in the studied area as described, could very well be overlying Moenkopi strata in PEFO. Further investigation is needed to resolve this question with certainty. Clay mineral analysis of the paleosols developed on the basal siltstones (Sections 2 and 4) might shed light on their relationship to either formation. A high bentonite content would suggest a Chinle origin, while a non-bentonitic composition would be a Moenkopi indicator (Stewart et al. 1972a). Preliminary results clearly indicate a low smectite content for NPR's basal red mudstone (unit 1) (Heckert, 1997), although the relationship of that lithostratigraphic unit to the exposures at the base of Sections 3 and 4 and in the washes remains unclear.

CONCLUSION

The stratigraphy in the studied area does not rule out the interpretation made by Dubiel et al. (1995) that the lowest units present in PEFO pertain to the Moenkopi Formation. Lithologic and stratigraphic descriptions of the strata present at the Moenkopi/Chinle contact throughout northeastern Arizona resemble those of the units found in the studied area. This interpretation does not contradict subsurface stratigraphy obtained from cores (Harrell and Eckel [1939] as discussed by Heckert and Lucas [1998]) because of the un-

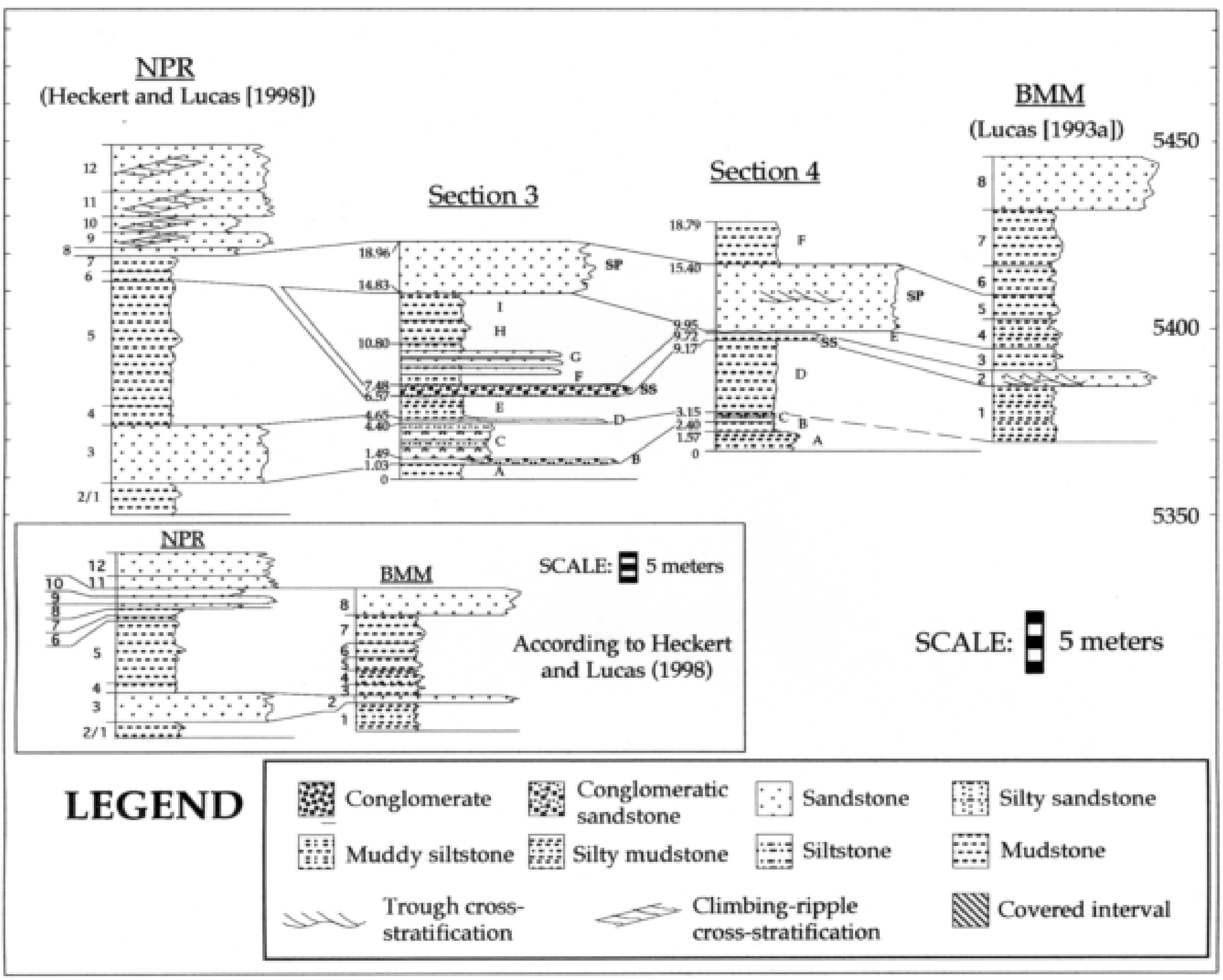

FIGURE 5—Correlation of Newspaper Rock section (*NPR*, Heckert and Lucas[1998]) and type Blue Mesa "Member" segment A (*BMM*, Lucas [1993a]) with Sections 3 and 4. Although the base of NPR is at a stratigraphic level similar to the base of Sections 3 and 4, no good exposure of Moenkopi was found there. The additional sections are located as follows: *NPR* SE 1/4 SE 1/4 NW 1/4 Sec 16 T18N R24E; *BMM* SW 1/4 SW 1/4 SE 1/4 Sec 21 T18N R24E.

even nature of the Moenkopi/Chinle contact.

Our work challenges the feasibility of correlating distant localities using descriptive lithostratigraphic units, as suggested by Lucas (1993a) and Heckert and Lucas (1998), in the context of a fluvial system with extreme lateral variation. In a fluvial system, facies are highly lenticular and the imposition of a simple, layered, sequential stratigraphy serves more to cloud issues than to elucidate them. The use of "members" nomenclature appears inappropriate, because these more closely resemble facies than lithostratigraphic units of time significance. For this reason, "members" cannot be used to correlate distant localities.

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A SYSTEMATIC STUDY AND TAPHONOMIC ANALYSIS OF THE MAMMAL REMAINS FROM THE PACKRAT MIDDENS OF TIMPANOGOS CAVE NATIONAL MONUMENT, UTAH

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ABSTRACT—An excavation of the fossil bearing packrat middens of Timpanogos Cave National Monument was undertaken to gain insight into the prehistoric fauna of the American Fork Canyon. The fauna found in this cave have not previously received any systematic study. The primary excavations were of abandoned packrat middens found near the entrances to the caves. Identification of the remains was limited to the mammals, which form the majority of the collection. These proved to be extant species that are still living in the canyon. Of primary taphonomic interest is that the packrats collected a broad range of species and the specimens were very well preserved.

INTRODUTION

This paper describes the fauna excavated from various locations within Timpanogos Cave in May 1998. Excavation sites were originally identified by the park Cave Resource Manager, Rod Horrocks, during cave surveying and a project in which fill was removed from the Entrance Room of Hansen Cave (Horrocks 1994 and 1995). As an experienced caver, Horrocks recognized the importance of these fossils and proposed that they be excavated. However, he lacked the necessary funding and the time. In searching for a senior independent research project I contacted Vincent Santucci, at Fossil Butte National Monument, who suggested this project to me. This study represents the first attempt to categorize the fossil deposits of this park.

The only related research done in this canyon was an excavation of American Fork Cave in 1938 by George Hansen and William Lee Stokes for its archeological remains. This cave is within Timpanogos Cave National Monument, but lies only 140 feet above the river bed. The faunal assemblage was created by human activity when it was occupied by Native Americans. The authors identified 13 species of mammals, all of them similar to these found in this investigation (Hansen and Stokes 1941).

During this excavation fossil birds, reptiles and mammals were found, but this study is limited to the identification and analysis of the mammal fossils. Specimens were identified to species level or to the most specific taxonomic category that could be reached with confidence. Eleven mammal species were identified, all of which still live in the canyon today. This makes it probable that the fauna are Holocene in age. However, without absolute dating this cannot be determined.

GEOGRAPHIC AND GEOLOGIC SETTING

LOCAL GEOLOGY—Timpanogos Cave National Monument is in the American Fork Canyon, which cuts into the Wasatch Front near Salt Lake City, Utah. The cave is situated below tree-line, approximately 366 m (1200 ft.) above the floor of the canyon. It is accessible only by a footpath that winds its way up the mountain side. The terrain is rugged with steep cliff faces.

The Wasatch Front is a north-south block fault that forms the eastern boundary of the Salt Lake and Utah basins and on a larger scale, the eastern edge of the Great Basin. The Great Basin is an area of north-south trending horst and graben mountain ranges formed by extension. Throughout this area, fault blocks form ranges that are separated by down-faulted alluvial basins. The western fault scarp of the Wasatch mountains rises sharply out of the Salt Lake and Utah basins. This fault block is dissected by a series of parallel streams that have cut east-west canyons through the block. The American Fork Canyon formed near the intersection of the Uinta fold axis and the Wasatch Fault. The block faulting in this area is still active (White and Van Gundy 1974).

The rocks that make up the Wasatch Front illustrate the Pre-Cambrian and Paleozoic history of the area. The oldest geologic formation within the American Fork Canyon is the Mutual Formation. This unit is a Proterozoic conglomerate with quartz sandstone and shale members. The Mutual Formation is overlain by a clastic and conglomerate transgressive Cambrian sequence 600 m thick (Baker and Crittenden 1961).

Above the Cambrian there is an unconformity, associated with uplift and subsequent erosion that lasted until the middle Paleozoic. The Fitchville Formation begins a transgressive sequence of Mississipian carbonates. At the base of this formation is a dolomitic sandstone and on top of that are two thick layers of massive dolomite. The next formation is the Gardison. This has 3-6 m of dark gray coarse grained and crossbedded dolomite. The next 24-30 m are banded layers of limestone and siltstone. The top of the formation is 120 m of massive limestone and dolomite.

Above this is a cliff-forming unit called the Deseret. It is composed of light to dark gray limestone and dolomite, 130 m, thick with lenticular cherts. There is a limited amount of fossil material in this formation, but it has been identified as being of Middle Mississipian age. Timpanogos Cave lies within this formation.

During the Miocene, extension caused the normal faulting that raised the Wasatch. This has continued to the present, but much of the Pleistocene and Holocene geologic activity has been carving of the terrain by frost, streams and glaciers (Baker and Crittenden, 1961).

The American Fork Canyon is a very deep and narrow v-shaped stream valley. Though there is evidence of Pleistocene glaciation at higher elevations in this area, there is no evidence that the canyon was created by glacial activity. The even slope of the walls and the sharp v-shape of the canyon suggest that it was the American Fork River and frost action that did the work (White and Van Gundy 1974). The steep slope of the canyon begins where the valley floor is at 1,700 m in elevation and rises to 2,400 m at the Sagebrush Flats, the top of the canyon. The cave lies at 2,000 m, cut almost straight into the side of Mount Timpanogos.

Mt. Timpanogos is one of the most prominent peaks in the Wasatch Front, rising to an elevation of 3,600 m. Like most of the high peaks in this area it records past glacial modification. There are large cirques on the north and east slopes as well as glacial moraine sediments (White and Van Gundy, 1974). Today there are no glaciers in this area. The Timpanogos ôglacierö is a misnomer. It is a snowfield that often melts completely in the summer (Baker and Crittenden, 1961).

CAVE DESCRIPTION—Timpanogos Cave National Monument was established to protect three caves, Hansen, Middle and Timpanogos Caves. They are collectively referred to as Timpanogos Cave. These caves have been connected by tunnels to allow easier access for tourists. The first cave discovered was Hansen Cave. The first area excavated was the Entrance Room of Hansen Cave. The room is 9 m across and 21 m long. Small alcoves in the walls of this room that contain packrat middens were excavated.

Middle Cave consists of a single high and narrow passage. This cave contains some of the most spectacular formations, including aragonite needles and helictites. Nothing was excavated from this cave during the project. The entrance to this cave may contain Pleistocene-Holocene deposits. However it is difficult to access. There were several places of difficult access throughout the cave system that we speculated to be fossil bearing localities. We did not excavate these so that a maximum amount of time could be spent on known fossil bearing localities.

Timpanogos Cave may be somewhat independent from the other two. It is the longest cave of the three at 180 m. What makes it independent is that the length of the cave is oriented at a slightly different bearing than the other two. Near the entrance to this cave we conducted limited excavation of a small area known as the Boneyard.

CLIMATE—The general climate of the western United States is characterized by the western mountains blocking moisture from the Pacific Ocean making it drier (Petersen, 1994). In addition to this the elevation makes it cooler. This creates a pattern across the region where high mountains are moist and cool, alternating with warm dry lowlands.

Mountains also produce major effects on the local climate, and may have a separate climate themselves. Maximum precipitation occurs between 1200-2400m. Thus a mountain can become a moisture island and develop good vegetative cover. There is often a large climate difference over short distances. This depends on the slope and aspect of a mountain. Mountain flora and fauna are strongly influenced by temperature and precipitation because there are often many changes in climate there are often very different ecological communities along a mountain slope (Petersen, 1994).

PACKRAT BIOLOGY

Packrats or woodrats, as they are also known, are members of the family Muridae. This is the largest mammalian family and includes rats and mice. The packrats of North America are all members of the genus *Neotoma*, of which there are 21 living species. The earliest known *Neotoma* species is 6.6 million years old. The extant species of packrats in the southwestern United States are known from middens at least 50,000 years old (Vaughan 1990).

Packrats are compact long tailed rodents that weigh between 100-400g. They have strong feet for grasping and climbing. Their molars are flat-crowned with prismatic ridges. This is typical of animals adapted to eating low nutrition fibrous plants, like grasses. Their diet is opportunistic, controlled by the plants found in the environment they are inhabiting.

The distribution of packrats covers most of North America, from 2¦ south of the Arctic circle to Nicaragua. Some species have restricted ranges and may only occur in one mountain range. In contrast *N. cinerea* ranges from the District of Mackenzie in Canada to Arizona. This species is most often boreal, and is the best candidate to be the packrat responsible for the middens in Timpanogos Cave.

All packrat species build more or less substantial middens. This provides shelter and they will often improve a natural shelter with a midden of sticks, plant material, bones and mammal dung. This material is collected from a 30-50 m radius area. Inside the midden is the nest. It is 20-30 cm in diameter and made of soft shredded plant fibers. It can be found in the center of the midden, in burrow beneath it or in rock crevice below it. Middens are occupied by one packrat at a time except during breeding (Vaughan 1990).

Middens serve several functions. They are primarily built as predator defense, but they also protect the packrat from the environment. The insulating properties of the midden provide a temperature buffer. In the desert they cool the packrat, and in winter the midden insulates against cold weather. This is very important since packrats do not hibernate. The midden also serves as a food cache during the winter. The packrats low energy diet necessitates a den for protection and thermal regulation. Additionally they have relatively low reproductive rates and slow growth rates so it is necessary for them to effectively protect their young (Vaughan 1990).

MATERIALS AND METHODS

Bones were excavated from three areas: the Entrance Room of Hansen Cave, the Boneyard, and Hidden Mine Cave. All the excavations were made from abandoned packrat middens or their detritus (which may be the case in Hidden Mine). These are most likely Holocene in age. In general bones were collected first from the surface, and when a midden was identified it was excavated. All the sediments were shoveled into buckets by trowels and then taken outside of the cave to be screened. The material was then dry screened through $^{1}/_{8}$ inch mesh screen. This may have biased the collection to material greater than $^{1}/_{8}$ inch, but a smaller screen

TABLE 1—List of mammal species collected from Timpanogos Cave National Monument.

SPECIES	COMMON NAME	MODERN	ENTRANCE ROOM	HIDDEN MINE	BONEYARD
Sorex vagrans	Vagrant Shrew	x			
Myotis evotis	Plainnose Bat	x			
Myotis sublatus	Long-eared Bat	x			
Corynorhinus rafinesqui	Small-footed Bat	x			
Antrozous pallidus	Pallid Bat	x			
Ochotona princeps	Pika	x			
Lepus americanus	Snowshoe Hare	x	1		
Lepus townsendi	Whitetail Jackrabbit	x			
Sylvilagus nuttalli	Mountain Cottontail	x			
Marmota flaviventris	Yellowbellied Marmot	x	2	3	
Spermophilus sp.	Ground Squirrel	x	2	1	1
Spermophilus armatus	Uinta Ground Squirrel	x			
Spermophilus varigatus	Rock Squirrel	x			
Spermophilus lateralis	Golden-Mantled Squirrel	x			
Eutamius dorsalis	Cliff Chipmunk	x			
Eutamius quadrivittatus	Colorado Chipmunk	x			
Tamiasciurus hudsonicus	Red Squirrel	x			
Glaucomys sabrinus	Northern Flying Squirrel	x			
Castor canadensis	Beaver	x			
Peromyscus c.f. *maniculatus*	Deer Mouse	x	2	13	
Neotoma c.f. *cinerea*	Bushytail Woodrat	x	7	21	2
Microtus sp.	Vole	x	3	2	
Ondatra zibethica	Muskrat	x			
Erithezon dorsatum	Porcupine	x			
Canis latrans	Coyote	x			
Urocyon cinereoagenteus	Gray Fox	x			
Vulpes fulva	Red Fox	x			
Ursus americana	Black Bear	x		2	
Bassariscus astutus	Ringtail	x			
Martes americana	Pine Marten	x		2	
Mustela vison	Mink	x		1	
Mustela erminea	Ermine	x			
Mustela frenata	Longtail Weasel	x			
Mephitis mephitis	Stripped Skunk	x			
Spilogale putorius	Spotted Skunk	x			
Taxidae taxus	Badger	x			
Procyon lotor	Raccoon	x		1	
Felis concolor	Mountain Lion	x			
Lynx rufus	Bobcat	x			
Cervus canadensis	Elk	x			
Odocoilius hemionus	Mule Deer	x			
Alces americana	Moose	x			
Ovis canadensis	Bighorn Sheep	-	3	3	

size was not used because of the moisture content in the cave sediments. In most cases the sediment was so muddy that it clumped in the screen. Wet screening was not used because there was no water source near the cave and it was not practical to move a large amount of material up and down the mountain.

FOSSIL LOCALITIES

ENTRANCE ROOM OF HANSEN CAVE—Excavations were made in seven different areas within the Entrance Room to Hansen Cave (will be referred to as the Entrance Room). The areas excavated were somewhat disturbed since they lie along the cave trail and most of the floor was covered with rock debris from the tunnel connecting this cave to middle cave. The sediment from these areas was dark red-brown and about 80-90% organic material. It consisted of a great deal of plant remains: twigs, pine needles, pine cones, leaves, and rodent feces.

HIDDEN MINE CAVE—Hidden Mine was a completely different type of excavation. Hidden Mine is a drift mine that was excavated near the turn of the century. Miners staked a claim in this area because of iron oxide staining found near a fissure in the limestone. The miners blasted an adit into the side of the canyon to reach the narrow fissure more easily. Upon reaching the fissure they expanded it and continued tunneling. The expansion of the fissure by the miners provided access to sediments in the side of the lower fissure. We rappelled down the fissure and excavated the deposit while hanging from a rope. We collected the sediment in buckets and hauled it out to be screened.

BONEYARD—Located near the outside entrance to Timpanogos cave, the Boneyard is a small area only accessible by crawling into a small alcove (Figures 2 and 7). This area contained an abandoned packrat midden, but produced so little bone that it was not included in some analyses. The sediment was very similar to the Organ Pipe Room.

IDENTIFICATION AND ANALYSIS

All identifications were made by comparing the recenly collected material with the mammal collections at the Academy of Natural Sciences, Philadelphia, Pennsylvania. All species identifications were based on cranial material. Post-cranial elements in rodents are treated differently than cranial elements because it is nearly impossible to identify rodent species from post-cranial elements. For this analysis I divided post-cranial elements into two subsets by size. The large rodent group represents rodents the size of packrats and larger. The small rodent group represents rodents smaller than packrats. Of the identified rodent species *Neotoma*, *Marmota*, *Lepus* and *Spermophilus* are large rodents and *Peromyscus* and *Microtus* are small rodents. It is likely that other species that were not identified from cranial elements are represented by post-cranial elements. This is another reason for classifying post-cranial elements by size only.

The large and small rodent classification was qualitative rather than quantitative. This will add error to the counting, but facilitates a quick division of the sample. The division was done through visual comparison to packrat post-cranial material. Larger bones were considered large rodents and smaller bones were classified as small rodents.

RESULTS

FAUNAL ANALYSIS—Eleven species of mammals were identified from these deposits. Table 1 lists the mammal species that have been identified as living in the American Fork Canyon today. This is list was given to me by Natural Resource management of Timpanogos Cave National Monument. Also included are the minimum number of individuals (MNI) of each species for the three excavation areas. *Ovis canadensis*, the Bighorn sheep, is the only species not now living in the canyon. The Bighorn sheep did occupy the canyon during historical times, but it was hunted to extinction in this area (Rod Horrocks, personal conversation, 1998).

Listed below is a description of each taxon recovered from the excavation. A general description of the remains of each species is given. In addition to this the present and fossil biogeography is given.

REPTILIA

One mandible from an unknown species of snake was recovered from Hidden Mine. It is 2.5 cm long and remarkably well preserved. The full dentition is preserved, but no other reptile elements were recovered from any site. This is not surprising given the high elevation and typically cool temperatures of the canyon.

AVES

There is a small number of bird bones in the collection. They represent a minor part of the assemblage, so are not included in this study. These bones are all postcranial, and of a relatively large size.

MAMMALIA
LEPIDAE
(Rabbits)
Lepus americanus Erxleben, 1777
(snowshoe rabbit)

Material: Several mandibles as well as isolated teeth. (Figure 4 to 6 provide the locations in which the cranial material of the rodent species was found)

The oldest known fossils of snowshoe rabbits date to the late Irvingtonian. Today they range into the southern Appalachian and Rocky Mountains. It is a small species with small ears and relatively large feet, adaptations for cold and snow. Typical habitats include swamps, forest and mountains. (Kurten and Anderson 1980).

SCIURIDAE
(Squirrels)
Marmota flaviventris (Audobon and Bachman), 1841
(yellow-bellied marmot)

Material: Several broken crania, several mandibles and post-cranial material. (Figure 4 to 6 for complete list)

Yellow-bellied marmots are found from central California to the foothills of Colorado, and south to the mountains of New Mexico. It is also common in the fossil record from Wisconsinan age. Marmots require a high moisture environment to provide the luxuriant plant growth they eat (Kurten and Anderson 1980). It presently inhabits high elevation in forests or along streams at lower elevations (Mead and Phillips 1981).

Spermophilus sp.
(ground squirrel)

Material: Several incomplete maxillae and mandibles. (Figure 4 to 6 for complete list)

Among different species of ground squirrels there is not a great deal of variation in tooth morphology. Identification is normally made from the dentition, cranial characteristics and the baculum (Kurten and Anderson 1980). This assemblage did not have a large enough sample to identify the species with any confidence.

Found in many habitats from Arctic circle to deserts, ground squirrels hibernate to escape climate extremes. The earliest records come from the Middle Miocene, and they are a very common Pleistocene fossils (Kurten and Anderson 1980).

MURIDAE
(Rats and Mice)
Peromyscus c.f. *maniculatus* (Wagner), 1843
(deer mouse)

Material: Teeth, mandibles, maxillae and crania (Figure 4 to 6 for complete list)

Deer mice have an enormous geographic range from Alaska to the southern United States. Because they are highly adaptable, they have come to occupy every type of environment except the extreme north and the southeast. Typically variation within this species can be greater than between other species (Kurten and Anderson 1980). Therefore I was not extremely confident in the species designation, but chose the most appropriate designation.

Neotoma c.f. *cinerea* (Ord), 1815
(bushytail woodrat)

Material: Isolated teeth, crania, mandibles, large volume of post cranial material. (Figure 4 to 6 for complete list)

Identification to the genus level was made using the occlusal pattern of the molars. The occlusal pattern in packrats is rather distinctive and consists of a simple pattern of 3 confluent or offset lophids. This pattern has three general subsets. One for the Blancan age taxa and two derived variants represented by *Neotoma alleni* and *Neotoma cinerea* (Zakarzewski 1993). In general the difference within subsets is not enough to differentiate species, only subsets. For this reason exact identification of the packrat species was not possible. However, *N. cinerea* is the most likely candidate because of tooth morphology, habitat, and midden building characteristics.

The folding pattern of the upper molars of *N. cinerea* tends to be distinctive. In M1 the anteriorbucal fold is in contact with the mesolingual fold. In *N. alleni*, the other modern type, the folds are offset (Appendix I A). This pattern is also repeated in the M2 and M3. In the lower molar set this is true for both species. However, N. alleni has S-shaped M3 that is rather distinct. This differs from the more symmetric M3 of N. cinerea. In some cases the upper M^3 has a closed anterior triangle and two confluent posterior loops (Appendix I B $M^{1\text{-}3}$) (Zakarzewski 1993).

It would be of great value to have specific quantifiable characteristics that could differentiate between species of packrats. There are several problems with developing this. First many species are closely related and are differentiated by unpreservable characteristics such as hair color. Secondly many species will occupy a given area and strongly overlap in range. There are 8 species of packrats north of Mexico in the western US. These species are known to overlap in range, but will have different habitats (Mead and Phillips 1981). Also the variability within a species can be greater than between species. Finally the greatest difficulty is in the most important characteristic of fossil: wear can change the occlusal pattern. Since it is so difficult to identify packrat species this creates significant biogeographic and paleoecological implications. *N. cinerea* is known from the Rancholabrean and Holocene in Wyoming, Idaho, Colorado, New Mexico and California. It inhabits mountain slopes and pinewoods in fissures and under logs. Of the common species of packrats *N. cinerea* is an almost obligate cliff or cave dweller. Their middens are an excellent source for quaternary vegetation and fauna.

In general mammal teeth tend to be the most identifiable element in the skeleton. This is especially true in animals with a similar body forms like rodents. One reason for this is that once an mammal has its adult teeth the teeth do not go grow. Therefore none of the variation can be from ontogeny. However some rodent species have molars that continue to grow and they also experience a kind of reverse ontogeny caused by wear. This is true in packrats. Their diet is often high in grasses which cause considerable wear because of microscopic silica particles in grasses. This causes a differences in the perceived degree of fold development and the expression of lophids. According to Zakarzewski (1993) all folds can be lost with enough wear. Folds are dependent on length of the fold on the side of the crown, the depth of the fold into the crown and the amount of wear.

Refer to Appendix II B and C and Appendix III A and B for variation in the occlusal patterns of packrats from Hidden Mine. Appendix II A shows general subset patterns (taken from Zakarzewski 1993)

These difficulties in identifying species have limited what can be said about an individual packrat species in situations where there are more than one species. Fortunately there is probably only one species responsible for the middens in all these sites. Any differences in the assemblages are likely to be intraspecific differences. This allows for a measure of how different middens can be in one species.

Given that the modern species of packrat found in the canyon is *N. cinerea* it is not unreasonable to assign the fossil packrats to this genus and species.

Microtus sp.
(vole)

Material: Isolated teeth, mandibles and maxillae (Figure 4 to 6 for complete list)

Microtus is the most common genus of vole. Molars are rootless and have cement in the reentrant angles (Kurten and Anderson 1980). This formed part of the basis for identification. Voles are found throughout North America.

URSIDAE
(Bears)
Ursus americanus Pallas, 1780
(black bear)

Material: 2 teeth; P4 and M2

The black bear is the most commonly found ursid in the Pleistocene of North America. During the Rancholabrean land mammal age their size increases leading to misidentification as grizzlies. However during the Holocene size has decreased, a phenomenon common in many large mammals (Kurten and Anderson 1980).

MUSTELIDAE
(Weasels, Martens, Skunks)
Martes americana (Turton), 1806
(pine marten)

Material: 2 teeth upper and lower M1

Martens prefer a dense spruce-fir forest habitat. The habitat near the cave is a mixed deciduous and conifer forest. In the early 1940 this species was listed as extremely rare or absent in the canyon (Hansen and Stokes 1941). Martens are somewhat omnivorous, and will eat rodents and other small mammals, plus birds, fruits, berries and nuts (Kurten and Anderson 1980).

Mustela vison Schreber, 1777
(mink)

Material: one mandible missing canine and incisors

Minks are known since the Irvingtonian. However they are generally uncommon fossils in the Pleistocene. Every Pleistocene site is found within the present range of the species. They are good indicators of permanent streams because they are typically amphibious. They prey on crayfish, fish, frogs, birds, muskrats, and other riparian mammals (Kurten and Anderson 1980).

Procyonidae
(Raccoons)
Procyon lotor (Linnaeus), 1758
(raccoon)

Material: One ulna

Found throughout North America from Panama to Canada in forested areas with water source or wetlands. Late Pleistocene variants tent to be larger, as do ones that inhabit colder, northern regions. Nocturnal and omnivorous in habit, they are a very common species that has adapted to many different environments (Kurten and Anderson 1980).

BOVIDAE
(Sheep)
Ovis canadensis Shaw, 1804
(mountain or bighorn sheep)

Material: By far the most common large mammal in Timpanogos Cave National Monument. It is represented by mostly postcranial bones. There are several maxillas and mandibles as well as isolated teeth and the anterior portion of a cranium (Figure 1 for complete list)

Ovis canadensis had a very wide distribution in Pleistocene, but in modern times they have become extremely reduced. Suitable habitat has become reduced and discontinuous distribution in the mountains from BC to southern Mexico and Baja. Competition with livestock, overhunting, and diseases introduced by domestic sheep have also reduced populations. (Kurten and Anderson 1980).

Ovis canadensis

Bighorn sheep are significantly represented in the collection. This is the only large mammal to be represented to a significant degree. The distribution of differs markedly from the rodent species. Figure 16 shows the distribution of bighorn sheep elements.

Even though many species are represented by only one or two elements they still form a significant part of this assemblage. There is a fair number of the rodent and carnivore species represented in this collection. Looking at this from an ecological perspective the most conspicuously missing species are large herbivores. Only bighorn sheep are represented even though three cervid species are known from the canyon. This is not unexpected given the rugged terrain surrounding the caves and the high elevation. Deer may have trouble negotiating the steep slopes found around the caves.

DISCUSSION

The significance of this assemblage is not in its age nor in the species that populate it, but in its state of preservation. The condition is a result of the taphonomic factors that have affected it. This assemblage was created by the midden build-

TABLE 2—The Minimum Number of Individuals (MNI) for each group was used to calculate the percentage of expected representatives for each element.

	Entrance Room				Hidden Mine				Boneyard	
	large rodent		small rodent		large rodent		small rodent		large rodent	
Element	n	Percent of expected	n	Percent of expected	n	Percent of expected	n	Percent of expected	n	Percent of expected
Mandible	15	68.2	11	91.7	42	87.5	30	100	0	0
Maxilla	17	77.3	1	8.33	29	60.4	5	16.7	1	25
Vertebrae	33	11.5	15	9.62	66	10.6	13	3.33	14	26.9
Pelvis	5	22.7	7	58.3	15	31.3	23	76.7	1	25
Sacrum	0	0	1	16.7	5	20.8	1	6.67	0	0
Scapula	11	50	3	25	14	29.2	5	16.7	1	25
Humerus	22	100	10	83.3	30	62.5	19	63.3	3	75
Ulna	10	45.5	5	41.7	26	54.2	7	23.3	0	0
Radius	10	45.5	6	50	22	45.8	9	30	0	0
Femur	10	45.5	8	66.7	19	39.6	19	63.3	1	25
Tibia	11	50	6	50	38	79.2	25	83.3	4	100
Calcaneum	12	54.5	5	41.7	18	37.5	5	16.7	2	50
Metapodia	10	4.55	3	2.5	3	0.63	26	8.67	5	12.5
Phalanges	12	4.96	12	9.09	14	2.65	9	2.73	2	4.55

ing activities of the packrats. This has lead to several taphonomic process that affect the bones. There are two primary taphonomic processes that work on this assemblage, the collecting behavior of the packrats and the collecting biases that occurred during excavation.

The first taphonomic process at work is the formation of this assemblage by packrats. In numbers of specimens small mammals form the largest percentage of the fauna. The only other significantly represented species is *Ovis canadensis*. The other animals are only represented by teeth and mandibles. This fits with the description provided by Guilday et al (1969) of cave fauna in the eastern United States. Natural trap sites that had not experienced any secondary collecting biases should be dominated by small mammals.

There are two distinct parts to the rodent assemblage: cranial and postcranial elements. An analysis of the postcranial elements is important because it shows both what the packrats collected and the nature of the packrats' own state of preservation.

Figure 2 shows the unidentified elements of large rodents and Figure 3 shows the unidentified elements of small rodents. For most elements there are more large than small. Also of interest is that there are almost always more elements represented from Hidden Mine than the Entrance Room, in most cases there are about twice as many. This provides strong evidence for better preservation at Hidden Mine. This is also supported in other groups.

From this data the MNI was calculated by element. The MNI for each group was then used to calculate the percentage of the expected representation for each element (Table 2). This is an indicator of the completeness of an assemblage. Vertebrae are the most common element of large rodents, and metapodials are the most common element of small rodents. However, they only represent about 10% of the amount they should. It is logical that a large percentage of these have been lost because they are two of the smaller elements.

CRANIAL ELEMENTS

Figures 4, 5 and 6 show the distribution of rodent cranial elements from the Boneyard, the Entrance Room and Hidden Mine. The sample from the Boneyard is small enough to be considered insignificant. Isolated teeth, mandibles and maxillae were used in the identification of six rodent species. As these figures show there is a preponderance of *N. cinerea* elements represented. This is to be expected given that they formed these middens. The distinctive occlusal pattern of *N. cinerea* allowed for the specific identification of molars. The other taxa are only represented by generic molars.

Comparing the cranial elements from the Entrance Room to Hidden Mine (Figures 5 and 6) shows that there are more mandibles and maxillae preserved in Hidden Mine than the Entrance Room. Though the Entrance Room has a higher species diversity by one this is too small to be used as a preservation indicator. There is a higher MNI of *Peromyscus* in Hidden Mine. The deer mouse is the smallest rodent represented and the least likely to be preserved. Its presence in abundance in Hidden Mine is yet another support for good preservation of the fauna.

Though these inferences about preservation are good it is important to consider the actual site. The Entrance Room consists of middens on the floor. Much of this area was once covered with over 200 tons of rock from the tunnel blasting. Some of the sites are along the cave trail where people pass daily. It is logical then that the fossils found in a relatively undisturbed fissure would be better preserved.

There are several factors that have influenced the formation and alteration of this fossil assemblage. The first set of factors include the age, ecology and climatic conditions that the fauna lived in. The second set are essentially taphonomic factors that have led to the present condition of the fossils.

The age, ecology and climatic conditions are all related phenomena. As shown in the results all of the fauna in this assemblage are all extant species that can still be found in the American Fork Canyon. Although some of the species in this assemblage have wide, unconstrained geographic ranges, several species have specific habitat requirements. Minks and marmots both need to live near water. Snowshoe hares, bushy-tailed woodrats, and bighorn sheep are all mountain species. These are constraints that the fauna put on the type of environment that they can occupy. These constraints closely match the canyon today.

There is a good correlation between the species identified by Hansen and Stokes in the American Fork Cave, and the species identified here. They identified some bat bones, an unknown species of bear, marten, weasel, skunk, lynx, porcupine, woodchuck, prairie dog, packrat, mule deer, elk, and mountain sheep. Differences between these two assemblages can be attributed to agency and elevation. Since this material was the result of human activity, it is more likely that it would contain large mammals like deer and elk. They are also more common at lower elevations. The prairie dog is an anomalous specimen since it no longer inhabits the Utah valley and is not known from that high an elevation. The authors propose that it was brought to the site by the humans. An interesting correlation in fauna is that American Fork Cave is also rich in mountain sheep. Hansen and Stokes identified over 100 individuals. This may have been the primary prey of the hunters (Hansen and Stokes 1941).

No radiometric dates were determined for this assemblage. Since the fauna is similar to modern species it is most likely a few hundred to a few thousand years old, certainly representing the Holocene. Naturally the climate and ecosystem of an area will determine what animals will make up the source of an assemblage. Since the assemblage is similar to today the climate and ecosystem are also likely to have been similar. Radiometric dates would show at least how long these conditions have existed.

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I thank Vincent Santucci of Fossil Butte for introducing me to this project and providing support towards the publication of this paper. Rod Horrocks, former Cave Specialist at Timpanogos Cave National Monument, provided me a great deal of help in the excavation and information about the cave. Roger Thomas, Professor of Geology and Paleontology at Franklin & Marshall College, served as my advisor this past year and provided a great deal of help in my research and writing of this paper. Ron Kerbo, Cave Management Specialist with the National Park Service Geologic Resources Division, provided financial support for radiometric analysis. I thank Franklin & Marshall College's Committee on Grants and the John Marshall Scholarship program for the funding that made this project possible.

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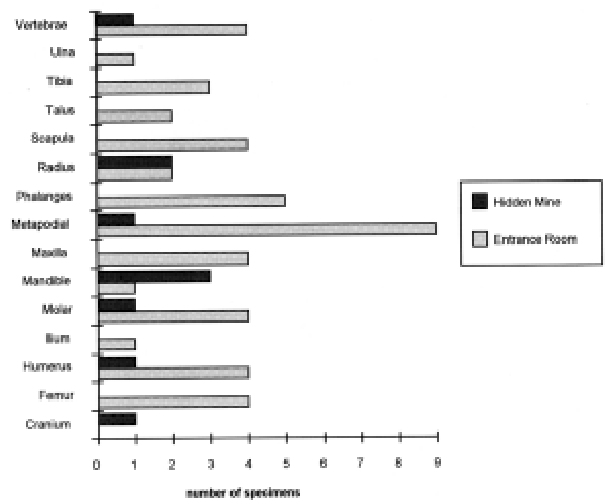

FIGURE 1—Elements of Ovis canadensis by excavation area. No elements were found in the Boneyard.

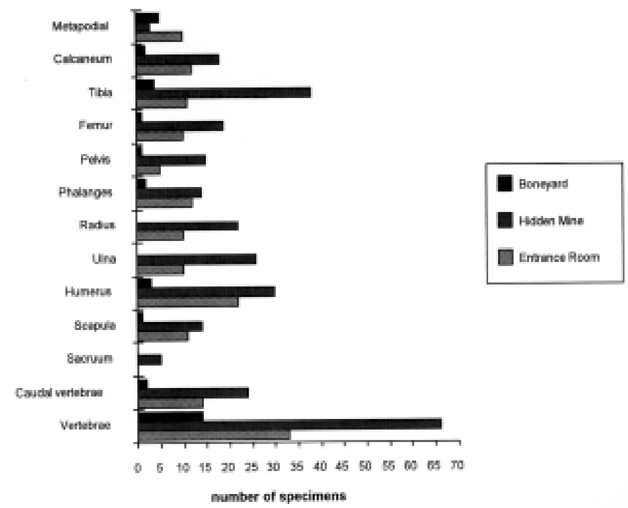

FIGURE 2—Postcranial elements of large rodents.

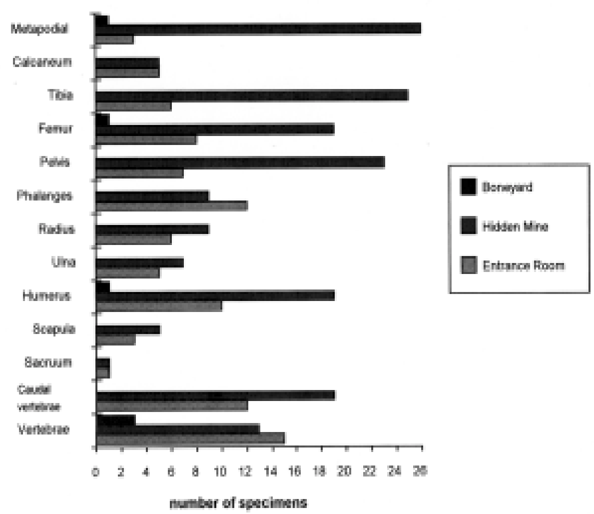

FIGURE 3—Postcranial elements of small rodents.

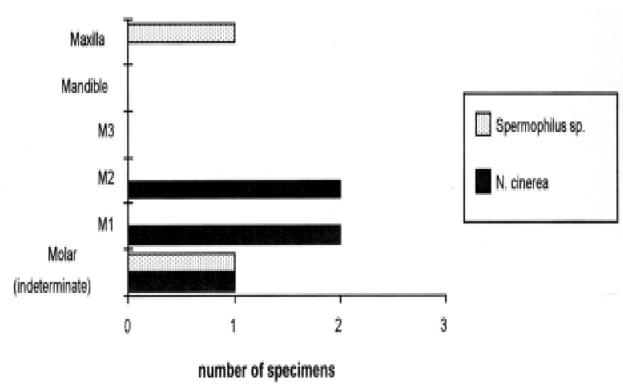

FIGURE 4—Cranial elements of rodent species found in the Boneyard.

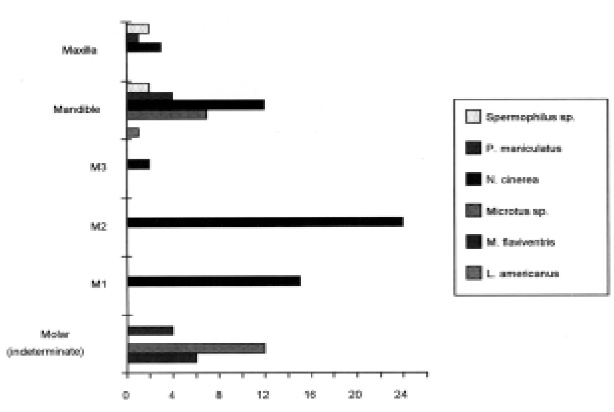

FIGURE 5—Cranial elements of rodent species found in the Entrance Room.

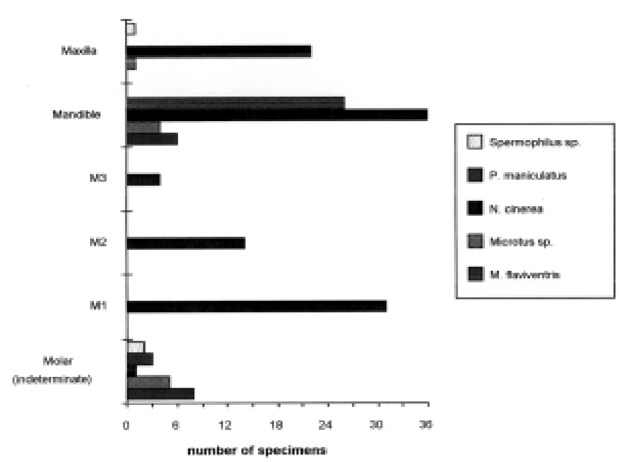

FIGURE 6—Cranial elements of rodent species found in Hidden Mine.

AN INVENTORY OF PALEONTOLOGICAL RESOURCES FROM WALNUT CANYON NATIONAL MONUMENT, ARIZONA

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Abstract—Walnut Canyon is carved into Permian sedimentary rocks on the southern margin of the Colorado Plateau in Arizona. The Coconino Sandstone and the Kaibab Limestone are well exposed fossiliferous units within Walnut Canyon. The canyon developed during the gradual uplift of the region, increasing stream downcutting. The ruins of approximately 300 rooms are preserved in the sedimentary cliffs within Walnut Canyon.

COCONINO SANDSTONE

The Coconino Sandstone is well exposed in Walnut Canyon National Monument. This Permian unit consists of a light colored, cross-bedded, aeolian sandstone. This unit occurs throughout northern Arizona on the southern limits of the Colorado Plateau.

Low diversity vertebrate and invertebrate ichnofauna are reported from within the Coconino Sandstone, however, not specifically from Walnut Canyon National Monument. Lull (1918) provides the first scientific description of Coconino tetrapods from Arizona. During the 1920s, Charles Gilmore produced a series of monographs on fossil vertebrate tracks from late Paleozoic strata in Grand Canyon National Park (Gilmore, 1926, 1927, 1928).

A revised ichnotaxonomy of Coconino vertebrate tracks was developed by McKeever and Haubold (1996). All Coconino tetrapod traces were identified within three ichnospecies of *Chelichnus*. *Chelichnus* is characterized by rounded manual and pedal impressions that are nearly equal in size and exhibit five short, rounded toe impressions. Trackways have a pace angulation of about 90 degrees and the manual and pedal impressions are close together (McKeever and Haubold, 1996). The three valid ichnospecies of *Chelichnus* are distinguished on the basis of size alone and are presumed to be the tracks of caseid-like reptiles.

KAIBAB LIMESTONE

The Kaibab Limestone overlies the Coconino Sandstone in Walnut Canyon. The Kaibab is a grey, sandy, marine limestone unit that forms the capping rock throughout the Colorado Plateau in north-central Arizona. The overhanging ledges formed at the base of the Kaibab Limestone were areas frequently utilized by the cliff dwellers of Walnut Canyon.

The Kaibab is very fossiliferous. The most comprehensive review of the Kaibab fauna was produced by McKee (1938), who divided the formation into three members: Alpha (top), Beta (middle) and Gamma (lower). Hopkins (1990) more recently divided the Kaibab into two members. The Fossil Mountain Member equates to McKee's beta and gamma members. The Harrisburg Dome Member equates to McKee's alpha member. Many dozens of marine invertebrate species have been reported from the Kaibab Limestone in Arizona. The assemblage of fossils from the Alpha member include pelecypods, gastropods and scaphopods. This assemblage indicates a shallow, near-shore, brackish, marine depositional environment.

Fossil sponges are often contained within silica concre-

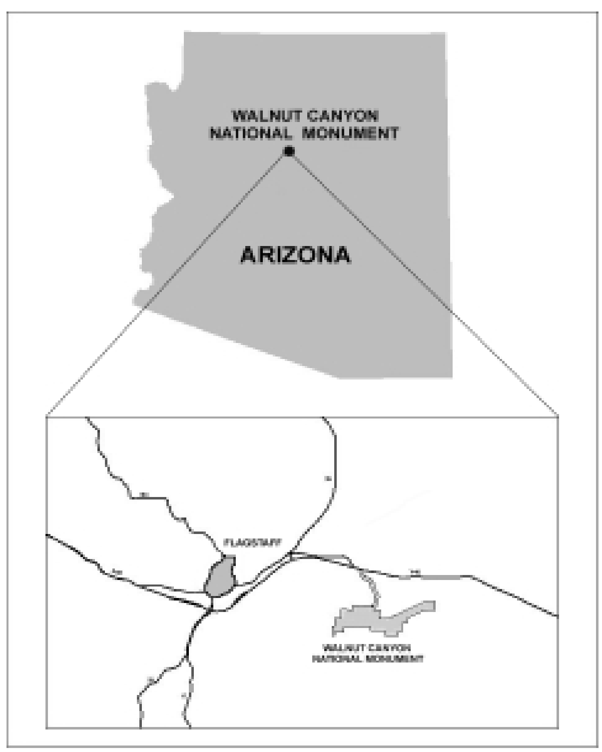

Figure 1. Map showing the geographic location of Walnut Canyon National Monument, Arizona.

tions in the Kaibab. The brachiopods include productid and spiriferid species. Below is a composite list of paleontological resources from Walnut Canyon and the surrounding area.

PHYLUM BRYOZOA

Unidentified bryozoans are known only as fragmentary remains from the lower portion of the Alpha Member of the Kaibab Limestone.

PHYLUM MOLLUSCA

Class Gastropoda
- *Baylea* sp.
- *Bellerophon deflectus*
- *Euomphalus* sp.
- *Euphemites* sp.
- *Goniasma* sp.
- *Murchisonia* sp.
- *Naticopsis* sp.
- *Pennotrochus arizonensis*
- *Soleniscus* sp.
- Busyconid gastropods

Class Pelecypoda
- *Allorisma* sp.
- *Astarella* sp.
- *Aviculopecten kaibabensis*
- *Dozierella* sp.
- *Edmondia* sp.
- *Gramatodon politus*
- *Janeia* sp.
- *Kaibabella curvilinata*
- *Myalina* sp.
- *Myalinella adunca*
- *Nuculana* sp.
- *Nuculopsis* sp.
- *Palaeonucula levatiformis*
- *Parallelodon* sp.
- *Permophorous albequus*
- *Pleurophorus albequus*
- *Schizodus texanus*
- *Solemya* sp.
- *Solenomorpha* sp.

Class Scaphopoda
- *Plagioglypta canna*

Class Cephalopoda
- *Aulometacoceras* sp.
- *Metacoceras unklesbayi*
- *Stearoceras* sp.
- *Tainoceras* sp.

PHYLUM BRACHIOPODA

- *Chonetes* sp.
- *Composita arizonica*
- *Dictyoclostus* sp.
- *Marginifera* sp.
- *Peniculauris bassi*
- *Quadrochonetes kaibabensis*
- *Rugatia paraindica*

PHYLUM ARTHROPODA

Class Trilobita
- *Anisopyge* sp.
- *Ditomopyge* sp.

PHYLUM ANNELIDA

Worm tubes have been identified on a specimen of the brachiopod *Marginifera.*

PHYLUM CHORDATA

A variety of shark's teeth are known from the Kaibab Limestone including: *Sandalodus, Deltodus, Symmorium, Petalodus, Orrodus* and phyllodont tooth plates.

PALEOECOLOGY

According to McKee (1938) the Alpha member of the Kaibab formation represents a regressive shallow marine facies. This member consists of dolomites, dolomitic sandstones and intraformational conglomerates. Nicol (1944) suggests that the pelecypod *Schizodus* indicates a shallow hypersaline environment within the Alpha member of the Kaibab Formation. The assemblage represents a near shore brackish environment which is supported by the absence of corals. Bryozoans are known only as fragmentary remains from the lower portion of the Alpha Member. The fossil assemblages also reflect a thanatocoenoses (a collection of dead organisms or parts of organisms that have accumulated after death - death assemblage). The Beta member (Nicol, 1944) includes sponges and echinoderms.

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CONTINENTAL ICHNOFOSSILS FROM THE UPPER JURASSIC MORRISON FORMATION, WESTERN INTERIOR, USA: WHAT ORGANISM BEHAVIOR TELLS US ABOUT JURASSIC ENVIRONMENTS AND CLIMATES

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Abstract—A large number of previously undescribed continental trace fossils are now known from the Late Jurassic as a result of the three year interdisciplinary project "The Morrison Formation Extinct Ecosystem Project" funded by the National Park Service. This study examined rocks of the Upper Jurassic Morrison Formation associated with national parks, monuments, and historical sites and adjacent areas in the Western Interior of the United States. Continental ichnofossils are extremely important pieces of evidence for understanding ancient environmental, ecological, and climatic settings. First, ichnofossils, which preserve evidence of organism-substrate interactions, record invertebrate, vertebrate, and plant biodiversity under-represented by body fossils in the Morrison. This new ichnofossil evidence demonstrates that there was an abundance of invertebrates predominantly representing terrestrial and freshwater insects. Ecological tiering of these traces provides vertical and lateral evidence of ancient soil development and water table and soil moisture levels dictated by the local paleohydrologic regime. The local and regional climatic setting controls these components of the environment, in turn. Invertebrates and plants are particularly sensitive to changes in the physical, chemical, and biological components of their environment, and thus, are useful paleoclimatic barometers.

Ichnofossil diversity and community composition from the base to the top of the Morrison suggest that the climate in the lower part of the Morrison (Tidwell, Salt Wash Members) was semi-arid to seasonal with pronounced wet and dry periods. Through time, the climate became wetter with a less pronounced drier interval and more annually distributed rainfall in the upper part of the Morrison (Recapture, Westwater, and Brushy Basin Members). Some areas in the western part of the Morrison depositional basin experienced a possible rainshadow effect due to mountains/highlands to the west. This likely produced locally drier climates as a result of annually reduced rainfall that is reflected in depauperate ichnofossil assemblages. However, further to the east (Utah/Colorado/Wyoming borders) ichnofossil diversity is much higher, reflecting annually wetter climates.

INTRODUCTION

The National Park Service funded a three year interdisciplinary project entitled "The Morrison Formation Extinct Ecosystem Project" that gathered geologic, paleontologic, and geochemical data used to more accurately reconstruct the Late Jurassic ecosystem inhabited by gigantic herbivores, small armored herbivores and omnivores, and ferocious meat eaters. This study examined the Upper Jurassic Morrison Formation associated with national parks, monuments, paleontological areas, historical sites, and adjacent areas in the Western Interior of the United States (Turner and Peterson, 1998).

One of the results of this project was the discovery of a large number of previously undescribed continental trace fossils (Fig.1), some of which have evolutionary and ecological implications for understanding organisms and ecosystems in the Mesozoic. The traces of Jurassic plants and animals reveal important information about ancient environmental, ecologic, and climatic settings in the Rocky Mountain region between 155-145 million years ago. Organisms like bees, ants, termites, wasps, dung beetles, carrion beetles, crayfish, caddisflys, mayflys, and many others have burrows, nests, and other traces of their existence in lakes, rivers, floodplains, and dunes (e.g., Hasiotis and Demko, 1996, 1998; Hasiotis, 1998b; Hasiotis *et al.*, 1998a, b). This study is the first systematic search for evidence of terrestrial and freshwater organisms not preserved or under-represented by body fossils in Jurassic continental rocks in North America. Root patterns, burrows, nests, tracks, and trails preserve details about organism behavior-substrate interactions that reflect physical, chemical, and biological conditions of the: (1) depositional setting, (2) ecosystem, (3) hydrologic regime, (4) soil formation, (5) seasonality of precipitation and temperature, and (6) climatic trends throughout the Late Jurassic (Hasiotis, 1998a).

RESEARCH SUMMARY

At least 38 Jurassic outcrop localities were studied between the 1994 and 1996 field seasons in the Rocky Mountain region from northwestern New Mexico to northwestern Montana. Numerous outcrops were visited in and around national parks and monuments and paleontological areas.

These include Arches National Park [ARCH] (UT), Bighorn Canyon National Recreation Area [BICA] (WY), Canyonlands National Park [CANY] (UT), Capital Reef National Monument [CARE] (UT), Cleveland-Lloyd Quarry [CLQ] (UT), Colorado National Monument [COLM] (CO), Comanche National Grasslands [CNG] (CO), Curecanti National Recreation Area [CURE] (CO), Garden Park Paleontological Area [GPP] (CO), Dinosaur National Monument [DINO] (UT/CO), Dinosaur Ridge National Historic Site [DRN] (CO), Fruita Paleontological Area [FPA] (CO), Picket Wire Natural Area [PWN] (CO), Red Rocks State Park [RRS] (NM), and Roxborough State Park [RSP] (CO). Other Morrison localities were investigated in portions of Colorado (Boulder [BO], Dillon [DI], Glenwood Springs [GS], Park Creek Reservoir [PCR], Rabbit Valley [RV]), Montana (Bridger [BR], Belt [BE], Gibson Reservoir [GR], Great Falls [GF]), New Mexico (Aneth [AN], Gallup [GP]), Utah (I-70 Corridor [I-70U], Beclabito Dome [BD], Hanna [HA], Moore Cutoff [MC], Montezuma Creek [MZ], Ruby Ranch [RR], Salt Valley Anticline [SVA]), and Wyoming (Arminto [AR], Alcova [AV], Como Bluff [CB], Grey Bull [GB], Thermopolis [TH]).

Ichnofossils from these areas have been documented and photographed. In some cases, specimens were collected for further study, after which they will be deposited in the Geology Section of the University of Colorado Museum, Boulder.

RESULTS

The Morrison ichnofossils and their implications are presented as a suite of observations used to interpret environmental, ecological and climatic settings for terrestrial and freshwater deposits within one or more closely related intervals. Nine intervals were defined from formal and informal members of the Morrison (Peterson and Turner, 1989; Turner and Fishman, 1991; Peterson, 1995) as "time-related sequences" and were based on relative stratigraphic equivalency and chronostratigraphic data such as age dates from volcanic ash beds and biostratigraphic ages of microfossils, like pollen and ostracodes. The intervals are as follows:

1). Basal contact surface/interval of the Morrison Formation and correlative rocks (J-5 and correlative surface).

2). Windy Hill and Tidwell Members beneath the lower alluvial complex (or lower rim Salt Wash Member) in the Colorado Plateau region, lowermost beds of the Bluff Sandstone and Junction Creek Sandstone Member, and Swift Member in Wyoming and Montana.

3). Lower alluvial complex and "Lower Rim" of the Salt Wash Member in western Colorado Plateau, as well as correlative beds of the Tidwell, Bluff, and Junction Creek Members, and correlative beds in the Recapture Member.

4). Middle alluvial sandstone and mudstone complex of the Salt Wash Member in the Colorado Plateau and middle mudstone unit in the eastern part of the Plateau; also includes correlative beds in the Tidwell Member where the lower beds of the Salt Wash pinch-out, Bluff and Junction Creek Members, and correlative beds of the Recapture Member.

5). Upper alluvial sandstones and mudstones of the Salt Wash member in the western part of the Colorado Plateau and "Upper Rim" of the Salt Wash in the eastern Colorado Plateau; also includes correlative beds in the Tidwell Member, Bluff and Junction Creek Members, and correlative beds of the Recapture Member.

6). Lower part of the Brushy Basin Member from the top of the Salt Wash to the clay change within the Brushy Basin; near the top includes the lower part of the Westwater Canyon Member in eastern Colorado Plateau, the lower and middle mudstones and alluvial sandstones of the Fiftymile Member in the Kaiparowits Plateau, and the uppermost Recapture Member in the southern Colorado Plateau.

7). Upper part of the Brushy Basin Member from the clay change to the base of the uppermost Morrison alluvial sandstone beds including the middle and upper Westwater Canyon Member and upper alluvial sandstones in the Fiftymile Member.

8). Uppermost part of the Brushy Basin Member, including the Jackpile Sandstone Member in the southern Colorado Plateau and correlative, unnamed alluvial Morrison sandstones elsewhere.

9). Upper contact/interval of the Morrison Formation with the Lower Cretaceous rocks above the K-1 or K-2 where present.

The following section contains the environmental, ecological, and climatic interpretations of the intervals described above. The groups of intervals are based on their ichnofossil diversity, distributions, and relationship to paleosols. Each section begins with a summary of ichnofossil occurrences, a brief description of the paleoenvironments present, and a paleoecologic and paleoclimatic interpretation of the setting.

INTERVALS 1-2

In the area of the Colorado Plateau (Shitamoring Canyon [SC], Trachyte Ranch [TR], Hanna [HA], Alcova [AV], Colorado National Monument [COLM], Dinosaur National Monument [DINO], Como Bluff [CB], etc.), ichnofossils include marine and brackish-water stromatolites (with and without bivalve borings), oyster encrusting grounds, horseshoe crab trails, unidentified crustacean burrows and surface feeding traces, clam resting traces, amphipod suspension feeding burrows, polychaete deposit-feeding burrows, snail grazing trails, nematode crawling trails, pterosaur tracks and feeding traces, and theropod and sauropod dinosaur tracks. Most of these traces are found in low diversity, high abundance assemblages found in shallow, single to compound tiers of no more than 2-3 cm thick. These traces suggest marine and marginal-marine to tidal environments (Windy Hill Member) with low to high depositional energy and salinity-stressed deposystems in warm to hot humid settings. The brackish-water and tidal ichnofossils imply that coastlines had several embayments to form sequences of tidal sediments.The traces in lacustrine settings (Tidwell Member) include mayfly deposit-feeding burrows, midge fly and crane fly deposit-feeding burrows (Diptera), aquatic earthworm trails, nematode trail, pterosaur tracks and feeding traces (scratched surfaces), clam resting traces, crayfish burrows and crawling trails and small horizontal burrows, and theropod and sauropod dinosaur footprints. Ichnofossils are found in single 2-4 cm deep tiers that are subdivided into shallow and deep tiering compartments; small traces are typically in the shallow part (mayfly, caddisfly burrows), while larger, deeper traces are in the deep compartment (crayfish burrows). These continental traces suggest that the marginal-lacustrine and lacustrine environments had episodic depositional rates and seasonally high water tables, which would have also resulted in imperfectly drained and poorly developed paleosols.

Trace fossils in fluvial and overbank deposits (Salt Wash Member), modified by pedogenesis, contain solitary and social bee nests, crayfish burrows, beetle burrows, bug burrows, root traces and mottling patterns, pith casts (not true trace fossils) of large 10 cm diameter horsetails (*Neocalamites*), and theropod and sauropod dinosaur footprints. Up to four tiers are present in these environments, the deepest of which approximate the water table depth; however, in most places the deepest tier reflects the intermediate vadose zone. Alluvial environments had weakly developed soils, many with simple to mature, cumulative and compound profiles resulting in successions of weakly modified distal overbank deposits. Many of these ancient soils contain weakly-developed B horizons, or zones of clay accumulation due to water infiltration and animal activity, with mottling of gray, green, yellow, and purple. These colors suggest seasonally imperfectly drained settings (gray, green, and yellow) with drier intermediate periods (purple and red).

Small eolian dune fields persisted in the Four Corners area and were scattered up through western Colorado and Wyoming. Ichnofossils are sparse and simple, composed of mainly indistinct horizontal and vertical burrows. These dunes were associated with the marginal-marine and marginal-lacustrine environments.

In the Front Range of Colorado (Horsetooth Reservoir [HR], Park Creek Reservoir [PCR]), ichnofossils are similar to that of the Colorado Plateau, but are dominated by stromatolites (also with borings) and polychaete feeding burrows. These traces indicate that predominately marine and marginal-marine (estuarine and tidal) environments existed in the Fort Collins area. Lacking is the more common high-abundance, low-diversity brackish-water to stressed-marine assemblages of the Colorado Plateau region. Here, ichnofossil tiering is similar to marine and marginal-marine environments on the Plateau. These Front Range ichnofossil occurrences suggest a more restricted environment with either higher salinity or higher energy settings. The climatic setting in the Front Range was probably similar to that of the Plateau; however, there may have been less precipitation and higher evaporation in the Front Range due to the orographic effects to the west in western Utah.

INTERVAL 3-5

In the Colorado Plateau and surrounding areas (Shitamoring Canyon [SC], Trachyte Ranch [TR], Hanna [HA], Alcova [AV], Dinosaur National Monument [DINO], Como Bluff [CB], etc.), abundant and diverse ichnofossils include at least four types of large and small termite nests, four types of ant nests, three types of bee nests, wasp cocoons, at least five types of beetle burrows (vertical and horizontal), dung beetle nests, soil bug burrows, bivalve resting traces, snail trails, crayfish burrows, various types of plant roots (small plants up to large trees), and several types of sauropod and theropod footprints. These traces suggest the environments were dominated by proximal and distal alluvial floodplains that formed on and between channel and sheet sandstones with less intercalated overbank fine-grained sediments (greater amounts of fines in western Colorado Plateau). In several localities termite and ant nests co-occur with several types of beetle burrows and solitary bees' nests in moderately to well-developed simple paleosols. Up to four tiers are present in these environments, the deepest of which approximate the water table depth. In places where the water table is very deep, the deepest tier reflects the intermediate vadose zone. Many of the paleosols that contain discernible trace fossils (e.g., Shitamoring Canyon, Bullfrog, Curecanti) indicate that bioturbation out-paced pedoturbation (soil-forming processes) and sedimentation. For other types of mature paleosols (e.g., Hanna, Salt Valley Anticline), pedoturbation out-paced bioturbation and sedimentation. In general, many localities contained paleosols that had parent material and pedogenic characters that were strongly dominated by sedimentation rates that out-paced pedoturbation.

In the Four Corners area (Bluff Member and Eolian Facies of the Recapture Members) isolated eolian erg fields persisted from Interval 1-5. During these intervals, the sedimentary facies and ichnofossils suggest increasingly wetter settings that eventually stabilized the erg systems with vegetation and paleosols. These vegetated surfaces included intensive nesting by solitary and social insects. In the area of Gallup, New Mexico, the upper parts of the ergs (Recapture) contain rhizoliths and giant termite nests. The uppermost part contains termite nests 30+ m long that followed rhizoliths of trees and small shrubs below the surface. The bulk of the nests are within the top 15 m. However, galleries and stacked chambers can be traced to the base of the Bluff, for a total length of nearly 40 m. In this area, termite galleries that are interpreted to reach the paleo-water table at a depth of nearly 32 m represent the deepest ichnofossil tier.

INTERVAL 6-7

In the Colorado Plateau and surrounding areas (Beclabito Dome [BD], Bighorn Res. [BR], Hanksville [HK], Canon City-Marsh Felch [MF at GPP], Montezuma Creek [MZ], Moore

FIGURE 1—A few examples of Morrison trace fossils. A-B, Ant nest from Hanksville (UT) area and a rock cross-section through part of the nest; C-D, Termite nests from the Gallup (NM) area with clos-up of internal morphology; E-F, Bees nest from the southern Henry Mountains (UT) area with close-up of some of the cell morphology.

Cutoff [MC]), the trace fossils included crayfish burrows, termite nests, ant nests, cicada burrows, beetle burrows (horizontal and vertical), rare beetle larvae burrows (*Scoyenia*), beetle-borings (pupal chambers) in dinosaur bones, earthworm pellets and burrows, various sizes of plant roots (small to large diameter, tree-size), and several types of sauropod and theropod footprints.

The ichnofossils in these rocks suggest that larger amounts of precipitation fell during the rainy season in these intervals and intervals 8-9. Crayfish burrows are more abundant than ant nests and termite nests in proximal overbank deposits in the Brushy Basin and Recapture Members (GPP, RV, AN, MC). In more distal facies (also better drained paleosols) ant nests are more dominant than termite nests in most areas (HA, MC, SC), but both are shallower in overall depth compared to similar structures in the lower part of the Morrison. There are more occurrences of solitary to primitively-social bees' nests in these intervals as well (MZ, GPP). Ichnofossil tiering is similar, but the overall depth of all four tiers is shallower due to higher water tables.

INTERVAL 8-9

Ichnofossils in these intervals include indistinct horizontal and vertical burrows, large (but rare) termite nests, beetle burrows, soil bug burrows, crayfish burrows, and various sized root traces. These traces predominantly occur in paleosols developed on fine-grained overbank deposits and in buried channel/levee deposits on floodplains. In interval 8, numerous paleosols occur as immature to mature, simple and cumulative sequences. Many of the paleosols developed on paludal to marginal-lacustrine settings in Wyoming, or were developed on poorly drained overbank floodplains with episodic deposition. Near the end of this interval and including interval 9 (the boundary), paleosols became increasingly better developed and more mature.

Paleosols that formed at interval 9 are quite variable and were the result of different lengths of subaerial exposure under particular types of groundwater regimes and depositional settings. For example, the thick sequence of paleosols (10 m+) developed at Ruby Ranch are composed of cumulative and compound profiles dominated by crayfish burrows and rhizoliths. These paleosols formed during seasonally high and fluctuating groundwater table conditions in an imperfectly drained area. Four ichnofossil tiers are present, a little deeper than in the previous intervals, possibly due to environmental or climatic changes. These ichnofossils and paleosols were later calcretized by an early Cretaceous event. The boundary paleosols (2 m+) at Salt Valley Anticline are drab-colored olive-green, mottled red, yellow, and brown produced by interactions between the primary and secondary taproot rhizoliths (with finer-scale rootlets) and the substrate. The boundary paleosol at Dinosaur Ridge National Historic Site is a thick, clay accumulation (2 m) that is well developed and represents a long-term surface of exposure. The paleosol is dominated by red and purple mottles with minor amounts of yellow and white mottles and is intensely bioturbated with fine rootlets, soil bugs and beetle burrows.

CONCLUSIONS

Based on the ichnofossil assemblages and their association with paleosols in the rocks of the Upper Jurassic Morrison Formation, the Morrison environments became increasingly wetter from the Tidwell and Salt Wash to the end of Brushy Basin and equivalent deposits. Paleosols are local and regional discontinuity features (e.g., Kraus and Bown, 1986; Bown and Kraus, 1987; Hasiotis 1997; Demko *et al.*, 1998) that, in the Morrison, also reflect increasingly wetter climates through time. They also record extensive bioturbation by rooted vegetation from the Salt Wash up through the Brushy Basin. Paleosols also preserve short to long periods of infrequent deposition and regional subaerial exposure. On these surfaces, trace-making organisms, from plant roots and beetles to huge sauropods, left attributes that reflect the hydrologic and climatic setting of that time. The various paleosols resulted in surfaces that could be used as sequence stratigraphic boundaries signaling changes in regional base level, sedimentation, climate, and tectonics through time.

Morrison ichnofossils are important because they represent the activity of different types of invertebrates, vertebrates, and plants that otherwise are not preserved as body fossils. Ichnofossils also record the interactions of paleocommunity elements with one another. Since traces are found *in place*, understanding their presence and distribution produces more accurate paleoecological interpretations (e.g., Hasiotis and Bown, 1992). Invertebrate ichnofossils are the most useful paleoenvironmental and paleoecological indicators because they are physiologically constrained to specific moisture and substrate conditions, and salinity ranges, by their environment. Thus, ichnofossils provide information that is complementary to interpretations inferred from body fossils. Together they can resolve: 1) salinity gradients, 2) frequency and magnitude of depositional events, 3) sedimentation rates, 4) soil moisture and water table regimes, 5) other physico-chemical gradients, 6) habitat energy flow, 7) environmental stability, 8) changes in paleoecosystems, and 9) changes and trends in paleoclimate.

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AFTERWORD

A review of currently published scientific articles associated with National Park Service (NPS) areas reveals an inconsistent use of park abbreviations and acronyms. Authors frequently utilize a self-generated abbreviation to reference a national park within a publication (e.g., GCNP = Grand Canyon NP; PFNP = Petrified Forest NP). These abbreviations can be highly variable and can present some difficulties in communication.

The National Park Service has established acronyms for each of the management units including national parks, monuments, historic sites, recreation areas, etc. The use of these established acronyms in publications is recommended. This system will standardize the referencing of the NPS units and facilitate communication between researchers and park management. These acronyms are also utilized by park staff in the curation of park museum collections. The consistent use of established acronyms should also accommodate bibliographic searches.

The standard National Park Service acronyms have been incorporated during the preparation of this document and the previous NPS Paleontological Research Volumes. Listed below is an updated list of the acronyms established for most of the national park units that have recognized paleontological resources.

AGFO	AGATE FOSSIL BEDS NATIONAL MONUMENT
AMIS	AMISTAD NATIONAL RECREATION AREA
ANIA	ANIAKCHAK NATIONAL MONUMENT
APPA	APPALACHIAN NATIONAL SCENIC TRAIL
ARCH	ARCHES NATIONAL PARK
ASIS	ASSATEAGUE ISLAND NATIONAL SEASHORE
BADL	BADLANDS NATIONAL PARK
BEOL	BENT'S OLD FORT NATIONAL HISTORIC SITE
BELA	BERING LAND BRIDGE NATIONAL PRESERVE
BIBE	BIG BEND NATIONAL PARK
BICA	BIGHORN CANYON NATIONAL RECREATION AREA
BISO	BIG SOUTH FORK NATIONAL RIVER
BISC	BISCAYNE NATIONAL PARK
BLCA	BLACK CANYON OF THE GUNNISON NATIONAL PARK
BLRI	BLUE RIDGE PARKWAY
BRCA	BRYCE CANYON NATIONAL PARK
BUFF	BUFFALO NATIONAL RIVER
CABR	CABRILLO NATIONAL MONUMENT
CACH	CANYON DE CHELLY NATIONAL MONUMENT
CANY	CANYONLANDS NATIONAL PARK
CARE	CAPITOL REEF NATIONAL PARK
CACA	CARLSBAD CAVERNS NATIONAL PARK
CEBR	CEDAR BREAKS NATIONAL MONUMENT
CHCU	CHACO CULTURE NATIONAL HISTORIC PARK
CHIS	CHANNEL ISLANDS NATIONAL PARK
CHCH	CHICKAMAUGA & CHATTANOOGA NATIONAL MILITARY PARK
CHIC	CHICKASAW NATIONAL RECREATION AREA
CHOH	C & O CANAL NATIONAL HISTORIC PARK
COLO	COLONIAL NATIONAL HISTORIC PARK
COLM	COLORADO NATIONAL MONUMENT
CRMO	CRATERS OF THE MOON NATIONAL MONUMENT
CUGA	CUMBERLAND GAP NATIONAL HISTORICAL PARK
CURE	CURECANTI NATIONAL RECREATION AREA
DESO	DESOTO NATIONAL MEMORIAL
DEVA	DEATH VALLEY NATIONAL MONUMENT
DEWA	DELAWARE WATER GAP NATIONAL RECREATION AREA
DENA	DENALI NATIONAL PARK
DETO	DEVIL'S TOWER NATIONAL MONUMENT
DINO	DINOSAUR NATIONAL MONUMENT
DRTO	DRY TORTUGAS NATIONAL PARK
EFMO	EFFIGY MOUNDS NATIONAL MONUMENT
EVER	EVERGLADES NATIONAL PARK
FIIS	FIRE ISLAND NATIONAL SEASHORE
FLFO	FLORISSANT FOSSIL BEDS NATIONAL MONUMENT
FONE	FORT NECESSITY NATIONAL BATTLEFIELD
FOBU	FOSSIL BUTTE NATIONAL MONUMENT
GAAR	GATES OF THE ARCTIC NATIONAL PARK
GEWA	GEORGE WASHINGTON BIRTHPLACE NATIONAL MONUMENT
GWMP	GEORGE WASHINGTON MEMORIAL PARKWAY
GETT	GETTYSBURG NATIONAL MILITARY PARK
GLAC	GLACIER NATIONAL PARK
GLBA	GLACIER BAY NATIONAL MONUMENT
GLCA	GLEN CANYON NATIONAL RECREATION AREA
GOGA	GOLDEN GATE NATIONAL RECREATION AREA
GOSP	GOLDEN SPIKE NATIONAL HISTORIC SITE
GRCA	GRAND CANYON NATIONAL PARK
GRTE	GRAND TETON NATIONAL PARK
GRBA	GREAT BASIN NATIONAL PARK
GRSA	GREAT SAND DUNES NATIONAL MONUMENT
GUMO	GUADALUPE MOUNTAINS NATIONAL PARK
HAFE	HARPERS FERRY NATIONAL HISTORICAL PARK
HAFO	HAGERMAN FOSSIL BEDS NATIONAL MONUMENT
HALE	HALEAKALA NATIONAL PARK
HAVO	HAWAII VOLCANOES NATIONAL PARK
HOSP	HOT SPRINGS NATIONAL PARK
HOVE	HOVENWEEP NATIONAL MONUMENT
HUTR	HUBBELL TRADING POST NATIONAL HISTORIC SITE
ICAG	ICE AGE NATIONAL SCIENTIFIC PRESERVE
INDE	INDEPENDENCE NATIONAL HISTORICAL PARK
INDU	INDIANA DUNES NATIONAL LAKESHORE
JECA	JEWEL CAVE NATIONAL MONUMENT
JODA	JOHN DAY FOSSIL BEDS NATIONAL MONUMENT
JOMU	JOHN MUIR NATIONAL HISTORIC SITE
JOTR	JOSHUA TREE NATIONAL MONUMENT
KATM	KATMAI NATIONAL PARK
KEFJ	KENAI FJORDS NATIONAL PARK
KOVA	KOBUK VALLEY NATIONAL PARK
LACL	LAKE CLARK NATIONAL PARK
LAME	LAKE MEAD NATIONAL RECREATION AREA
LAMR	LAKE MEREDITH NATIONAL RECREATION AREA
LABE	LAVA BEDS NATIONAL MONUMENT
MACA	MAMMOTH CAVE NATIONAL PARK
MANA	MANASSAS NATIONAL BATTLEFIELD PARK
MEVE	MESA VERDE NATIONAL PARK
MNRR	MISSOURI NATIONAL RECREATIONAL RIVER
MOJA	MOJAVE NATIONAL PRESERVE
MOCA	MONTEZUMA'S CASTLE NATIONAL MONUMENT
MOCI	MOUND CITY GROUP NATIONAL MONUMENT
MORA	MOUNT RAINIER NATIONAL PARK
NATR	NATCHEZ TRACE PARKWAY
NABR	NATURAL BRIDGES NATIONAL MONUMENT
NAVA	NAVAJO NATIONAL MONUMENT
NERI	NEW RIVER GORGE NATIONAL SCENIC RIVER
NIOB	NIOBRARA NATIONAL SCENIC RIVERWAY
NOAT	NOATAK NATIONAL PRESERVE
NOCA	NORTH CASCADES NATIONAL PARK
OLYM	OLYMPIC NATIONAL PARK
ORCA	OREGON CAVES NATIONAL MONUMENT
OZAR	OZARK NATIONAL SCENIC RIVERWAYS
PAIS	PADRE ISLAND NATIONAL SEASHORE
PETE	PETERSBURG NATIONAL BATTLEFIELD
PEFO	PETRIFIED FOREST NATIONAL PARK
PINN	PINNACLES NATIONAL MONUMENT
PIRO	PICTURED ROCKS NATIONAL LAKESHORE
PISP	PIPE SPRING NATIONAL MONUMENT
PORE	POINT REYES NATIONAL SEASHORE
PRWI	PRINCE WILLIAM FOREST PARK
RABR	RAINBOW BRIDGE NATIONAL MONUMENT
REDW	REDWOOD NATIONAL PARK
RICH	RICHMOND NATIONAL BATTLEFIELD PARK
RIGR	RIO GRANDE WILD & SCENIC RIVER
ROMO	ROCKY MOUNTAIN NATIONAL PARK
RUCA	RUSSELL CAVE NATIONAL MONUMENT
SAJU	SAN JUAN NATIONAL HISTORIC SITE
SAMO	SANTA MONICA MOUNTAINS NATIONAL RECREATION AREA
SCBL	SCOTT'S BLUFF NATIONAL MONUMENT
SACN	ST CROIX NATIONAL SCENIC RIVERWAY
SEKI	SEQUOIA/KINGS CANYON NATIONAL PARKS
SHEN	SHENANDOAH NATIONAL PARK
SPAR	SPRINGFIELD ARMORY NATIONAL HISTORIC PARK
THRO	THEODORE ROOSEVELT NATIONAL PARK
TICA	TIMPANOGOS CAVE NATIONAL MONUMENT
VAFO	VALLEY FORGE NATIONAL HISTORICAL PARK
VICK	VICKSBURG NATIONAL MILITARY PARK
VIIS	VIRGIN ISLAND NATIONAL PARK
WACA	WALNUT CANYON NATIONAL MONUMENT
WAPA	WAR IN THE PACIFIC NATIONAL HISTORICAL PARK
WHSA	WHITE SANDS NATIONAL MONUMENT
WICA	WIND CAVE NATIONAL PARK
WRST	WRANGELL-ST ELIAS NATIONAL PARK
WUPA	WUPATKI NATIONAL MONUMENT
YELL	YELLOWSTONE NATIONAL PARK
YUHO	YUCCA HOUSE NATIONAL MONUMENT
YUCH	YUKON-CHARLEY RIVERS NATIONAL PARK
ZION	ZION NATIONAL PARK

As the nation's principle conservation agency, the Department of Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the bests interests of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship can citizen responsibility for the public lands and promoting citizen partcipation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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