

National Park Service Paleontological Research



*To the
Volunteers and Interns
of the
National Park Service*

Copies of this report are available from the editors.

Geological Resources Division

12795 West Alameda Parkway

Academy Place, Room 480

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Cover Illustration

Life-reconstruction of Triassic bee nests in a conifer, *Araucarioxylon arizonicum*.

NATIONAL PARK SERVICE PALEONTOLOGICAL RESEARCH

EDITED BY

VINCENT L. SANTUCCI
FOSSIL BUTTE NATIONAL MONUMENT
P.O. Box 592
KEMMERER, WY 83101

AND

LINDSAY McCLELLAND
NATIONAL PARK SERVICE
Room 3229—MAIN INTERIOR
1849 C STREET, N.W.
WASHINGTON, D.C. 20240—0001

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FORMATTING AND TECHNICAL REVIEW

BY

*ARVID AASE
FOSSIL BUTTE NATIONAL MONUMENT
P.O. Box 592
KEMMERER, WY 83101*

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INTRODUCTION

Most of what is to be learned about the history of life remains buried within the sediments of the Earth's crust. Fossils preserved in approximately 120 units of the National Park Service contribute to our understanding of ancient plants, animals and ecosystems. Parks such as Agate Fossil Beds National Monument, Dinosaur National Monument, Fossil Butte National Monument, Petrified Forest National Park, were originally established based upon world-renowned paleontological resources. Many other national parks, such as Arches National Park, Death Valley National Park, Grand Canyon National Park, Yellowstone National Park, were not specifically established for the paleontological resources, but contain scientifically significant fossils.

This third National Park Service paleontological research volume compiles 38 articles representing paleontological research in 21 different national parks. The individual reports reflect a cross-section of the types of paleontological research activities recently undertaken throughout the National Park System. The contributions of each of the investigators, and their research teams are recognized and acknowledged in this volume.

I am proud to include reports documenting the multi-park-based Morrison Ecosystem Project, the fossil bee's nest at Petrified Forest National Park, and fossil mollusks from Alcatraz Island at Golden Gate National Recreation Area. This volume contains the first reports on paleontological inventories for Bryce Canyon National Park, Denali National Park, Great Smokey Mountains National Park, Mammoth Cave National Park, and Ozark National Scenic Riverway. Additionally, the unfortunate story regarding the abolished Fossil Cycad National Monument is included in this publication.

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This volume is dedicated to the many volunteers and paleontology interns who were funded by the NPS VIP Program, the NPS Geologic Resources Division Geologist-in-the-Park Program, the Geological Society of America, the Student Conservation Association Program, and other sources. It is difficult to imagine how the NPS Paleontological Resource Program would have the current level of success without the generous and enthusiastic contributions of these volunteers.

Finally, through the combined efforts of the men and women already mentioned, along with many others, the NPS Paleontological Resource Program continues to flourish. Many research questions remain to be explored within the national parks. Likewise, the increasing numbers of paleontological inventories being initiated in parks will certainly uncover clues buried in sediments and provide for a new and greater understanding of the ancient world. Parks are not merely beautiful and scenic places to visit, they also provide paleontologists with tremendous research opportunities.

Vincent L. Santucci
National Park Service

ADDITIONS AND COMMENTS ON THE FOSSIL BIRDS OF AGATE FOSSIL BEDS NATIONAL MONUMENT, SIOUX COUNTY, NEBRASKA

ROBERT M. CHANDLER

Department of Biological and Environmental Sciences
Georgia College & State University, Milledgeville, GA 31061-0490

ABSTRACT—Fossils from Agate Fossil Beds National Monument in western Nebraska have been a rich source of paleontological studies for many years. Fossil bird discoveries from the Monument have been far fewer than mammals and their reports have been sporadic and scattered throughout the literature. Although less common than mammals, the paleoavifauna of the Monument is very interesting in its level of diversity, ecological indicators, and from the perspective of historical biogeography with Old and New World representatives. The paleoavifauna has representatives from at least six families in four orders.

INTRODUCTION

IT HAS been more than ten years since Becker (1987a:25) briefly reviewed the fossil birds of the “Agate Fossil Quarries.” The specimens described herein were collected in 1908 by field crews from the University of Nebraska State Museum, but have never been identified or reported upon until now. This collection includes the first record of a crane, Gruiformes, and additional specimens of the fossil hawk, *Buteo ales* Wetmore. *Buteo typhoius* Wetmore should be removed from the list of species from Agate.

For historical accounts, the most comprehensive geologic data and the best paleoenvironmental interpretation for the Monument and surrounding fossil localities are discussed in the works of Robert M. Hunt, Jr. (1972, 1978, 1981, 1985, 1990, and 1995) and Hunt and Skolnick (1996).

SYSTEMATIC PALEONTOLOGY

[An asterisk (*) indicates genera or species described from the Agate Fossil Beds. The classification sequence followed below is that of the AOU Check-list, 6th edition. The following acronyms are used: American Museum of Natural History, Department of Vertebrate Paleontology (AMNH); Carnegie Museum of Natural History (CMNH); Harold J. Cook collection (HC); Museum of Comparative Zoology (MCZ); Princeton University Geological Museum (PUGM) now at Yale University, Peabody Museum; University of Nebraska State Museum (UNSM)].

Order FALCONIFORMES

(hawks, eagles, falcons, and allies)

Family ACCIPITRIDAE

(kites, hawks, eagles, and allies)

Subfamily ACCIPITRINAE

(kites, hawks, and eagles)

Genus PROMILIO Wetmore 1958

(extinct kite)

PROMILIO EFFERUS (Wetmore) 1923

Holotype.—AMNH 6299, left tarsometatarsus missing internal half of the shaft; Agate Fossil Beds National Monument, Upper Harrison (late Arikarean), Sioux Co., Nebraska.

Promilio efferus is the earliest record for a kite in North America (Brodkorb, 1964:274). Wetmore (1923:504) had tentatively placed *efferus* in the genus *Proictinia* Shufeldt (1915:301) from the late Miocene [latest Clarendonian or earliest Hemphillian, Long Island local fauna, Phillips County, Kansas; see Steadman (1981:171) for comments on age of Long Island local fauna]. Later, Wetmore (1958:2) decided that *Proictinia* was more closely related to the Everglade Kite, *Rostrhamus sociabilis*, and that *P. efferus* was more like the Old World carrion eating kites in the genus *Milvus*. *Promilio efferus* is equivalent in size and is similar osteologically to species of *Milvus*. Wetmore (1958:3) placed *efferus* in the subfamily Milvinae, but in a new genus, *Promilio*, based on perceived differences.

Genus BUTEO Lacepede, 1799 (hawks)

BUTEO TYPHOIUS Wetmore, 1923

Holotype.—AMNH 1754, distal two-thirds of the right tarsometatarsus missing the trochlea for Digit II; from the Lower Snake Creek, Olcott Formation (early Barstovian), 23 miles south of Agate, Sioux Co., Nebraska.

Referred material.—HC 477, distal one half of the right tibiotarsus, Agate Fossil Beds National Monument, Stenomylus Quarry 1.5 miles east of Carnegie Hill and University Hill quarries (referred by Wetmore, 1928:149).

Discussion.—*Buteo typhoius* is osteologically very similar to its living congeners. Wetmore compared *B. typhoius* exclusively to the eastern Red-tailed Hawk, *B. jamaicensis borealis*, from which it can be distinguished by subtle osteological differences and its much larger size (approximately 50 percent; see Wetmore, 1923:485-492; 1928:149-150).

None the less, because of the disparity in age of the type locality of *B. typhoius*, which is the Lower Snake Creek, early Barstovian, (see Becker, 1987b for the interesting history and insight into the age of the locality) and the age of the Monument, late Arikarean, I do not think *B. typhoius* occurs at Agate. The tibiotarsus (HC 477) that Wetmore (1928:149) referred to *B. typhoius* most likely belongs to the next species *B. ales* (Wetmore). Therefore, *B. typhoius* should be stricken from the Monument species list.

*BUTEO ALES (Wetmore) 1926

Holotype.—CMNH 1828, complete right tarsometatarsus; Agate Fossil Beds National Monument, Carnegie Hill (Quarry No. 2).

Referred material.—UNSM 3001, hallux; UNSM 3002, right humeral shaft; UNSM 3004, left ulna missing the olecranon; UNSM 3006, right femur, proximal end; UNSM 5782, left ulna, distal one/quarter; UNSM 5783, right tarsometatarsus, distal end missing trochlea of Digit 4; UNSM 5784, left tibiotarsus, proximal two-thirds; UNSM 5785, right tarsometatarsus, distal one/quarter missing anterior half of trochlea of Digit 3; UNSM 5786, left humerus, distal end missing the entepicondyle.

Discussion.—*Buteo ales* (Wetmore, 1926:403) was a large hawk. The length of the holotype tarsometatarsus, CMNH 1828, is 90.2mm with a distal width of 16.2mm. A hawk of this size is at the top of the size range for the eastern Red-tailed Hawk, *B. jamaicensis borealis*, given by Friedmann (1950:239). With the identification and referral of the UNSM fossils to *B. ales*, the assignment of this species to *Buteo* is affirmed. The ulna, UNSM 3003, may appear to be too long for this species (164.0mm), but is within reason when sexual size dimorphism is taken into consideration for North American raptors (Snyder and Wiley, 1976).

Measurements of selected fossils.—hallux (UNSM 3001) length of cord = 24.0mm; ulna (UNSM 3004) length missing the olecranon = [164.0mm], proximal width = 15.2mm, distal width = 11.0mm, depth of external condyle = 11.3mm, mid-shaft width/depth = 7.1/7.2mm; ulna (UNSM 5782) distal width/depth of external condyle = 10.8/11.2mm; tibiotarsus (UNSM 5784) width/depth across proximal articular surface = 13.5/17.5mm, length of fibular crest = 28.5mm, width/depth of shaft below fibular crest = 7.9/6.9mm; tarsometatarsus (UNSM 5785) distal width = 17.1, depth of trochlea Digit 4 = 8.3mm, width of trochlea Digit 2 = 7.2mm; humerus (UNSM 5786) distal width missing entepicondyle = [21.0mm].

ACCIPITRIDAE indeterminate

Wetmore identified three other fossils only to family rank with the following comments: HC 466, right ulna, proximal end about the size of a caracara, *Polyborus* (Wetmore, 1923:506); PUGM 12157, right tarsometatarsus, distal end which resembles a Marsh Hawk, *Circus hudsonius* (Wetmore, 1923:507); and CMNH 2207, large claw somewhat smaller than a Golden Eagle, *Aquila chrysaetos* (Wetmore, 1926:406). I have not seen any of these fossils, but the right ulna (HC 466) which is the size of a caracara should be re-examined with the UNSM ulnae referred to *B. ales*.

*Genus *Palaeastur**Species *Palaeastur atavus* Wetmore 1943

Holotype.—HC 693, right tarsometatarsus, distal one-third; Agate Fossil Beds National Monument, Stenomylus Quarry.

Discussion.—Wetmore (1943:230) likened this new genus and species of extinct hawk to the monotypic Black-and-

white Hawk-eagle (*Spizastur melanoleucus*). *Spizastur melanoleucus* is the smallest of the booted eagles, which are considered by Brown and Amadon (1968:22) to be “the most highly evolved members of the family and indeed of all birds of prey.” They live in dense, humid evergreen, and semideciduous forests in Central and South America (Blake, 1977; Howell and Webb, 1995).

Order GALLIFORMES

(grouse, quail, turkeys, and allies)

Family CRACIDAE

(curassows, guans, and chachalacas)

Genus BOREORTALIS

(extinct chachalacas)

*Species BOREORTALIS TANTALA (Wetmore) 1933

Holotype.—HC 498, right tibiotarsus, distal end; Agate Fossil Beds National Monument, Carnegie Hill. (This specimen is now in the AMNH collections).

Discussion.—In the Neogene there are five species of boreal chachalacas in the genus *Boreortalis* Brodkorb (1964:304-305). *Boreortalis* (Brodkorb, 1954:180) is closely related to *Ortalis*, the genus of living chachalacas found in southern Texas through Central America and into South America (Blake, 1977). It was Brodkorb's impression that chachalacas had a Nearctic origin and only during the Great American Biotic Interchange did they expand their range into South America. Although boreal today, the chachalacas from these North American fossil localities would have been much more tropical to subtropical in nature.

Family PHASIANIDAE

(grouse, quail, and turkeys)

Subfamily TETRAONINAE

(grouse)

Genus PALAEAELECTORIS

(extinct grouse)

*Species PALAEAELECTORIS INCERTUS Wetmore 1930

Holotype.—MCZ 2190, left humerus, proximal one-half and distal end with part of shaft missing; Agate Fossil Beds National Monument.

Discussion.—This fossil grouse is between a Northern Bobwhite, *Colinus virginianus*, and the Spruce Grouse, *Dendragapus canadensis*, in size. Wetmore (1930:152-153) thought it similar to the Spruce Grouse, but only distantly related. Today, the Spruce Grouse is a member of the boreal species community. *Palaeaelectoris* may represent an ancestral grouse living in a subtropical environment before the dichotomy we see today between boreal species like the Spruce Grouse and the prairie grouse like the Greater Prairie-Chicken, *Tympanuchus cupido*.

Order GRUIFORMES

(cranes, rails, limpkins, and their allies)

Family GRUIDAE

(cranes)

Genus and species indeterminate

Referred material.—UNSM 3003, right ulna mid-shaft;

UNSM 3005, right humerus, distal end; both are from Agate Fossil Beds National Monument, University Hill, University Quarry.

Discussion.—This right ulna (UNSM 3003) and humerus (3005) are the first crane fossils to be identified from the Monument. Although fragmentary, the fossils are from a species of crane approximately the size of the modern Sandhill Crane, *Grus canadensis* (Linnaeus). It should be kept in mind, however, that in the late Clarendonian there is an Old World crane (*Balearica*) in Nebraska (Feduccia and Voorhies, 1992:241), and the fossils from Agate may represent either of these cranes.

Order CHARADRIIFORMES

(thick-knees, plovers, sandpipers, and their allies)

Family GLAREOLIDAE

(coursers and pratincoles)

Genus PARACTIORNIS

(extinct pratincole)

* Species PARACTIORNIS PERPUSILLUS (Wetmore) 1930

Holotype.—MCZ 2191, left tarsometatarsus missing the intercylar prominence; Agate Fossil Beds National Monument, Carnegie Hill.

Discussion.—Wetmore (1930:153) originally named and described this new genus and species as the earliest representative of the modern oystercatchers, Haematopodidae. However, Olson and Steadman (1978:972-976) have shown this species to be the first New World record for the Old World pratincoles (Glareolinae). Pratincoles are short-legged insect feeders, which feed on the wing much like swallows. Once again, we have a member of the paleoavifauna from Agate which is representative of a greater, worldwide avifauna still in existence at the end of the Oligocene and into the early Miocene.

DISCUSSION

The fossil birds of the Agate Fossil Beds National Monument are very interesting at several levels. First, they are interesting at an alpha taxonomic level as new genera and species. Secondly, birds are frequently used as environmental indicators of certain habitats and to evaluate the health of the environment. The birds from the Monument support Hunt's interpretation of the paleoenvironment as an area with ephemeral stream channels, open plains, but with riparian areas along the streams. Thirdly, it is significant that the paleoavifauna represents a worldwide fauna, which only recently has been recognized at other important localities like Quercy, France; Messel, Germany; Green River, Wyoming; and the Naze in England. Olson (1989:2023-2029) has dubbed this the global avifauna, of which our world today has only relictual distribution patterns of that once cosmopolitan avifauna.

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A SYSTEMATIC REVIEW OF THE FOSSIL LIZARDS AND SNAKES (SQUAMATA) FROM THE WHITE RIVER GROUP OF BADLANDS NATIONAL PARK

DENNIS MADDOX¹ AND WILLIAM P. WALL²

¹Department of Physiology, Medical College of Georgia, Augusta, GA 30901

²Department of Biology, Georgia College & State University, Milledgeville, GA 31061

ABSTRACT—A general survey of the Squamata from the White River Group (37.0 to 26.9 MYA) from Badlands National Park is presented. New specimens are examined and described. Life habits of the fossil taxa are inferred from comparison with close living relatives where possible. Arboreal taxa are absent from the White River fauna. Since the Badlands region was open forest during much of that time, the absence of these taxa is probably the result of taphonomic bias. The reduction in herpetofauna diversity in this region during the Oligocene is believed to be the result of increasing aridity rather than the decline in temperature.

INTRODUCTION

PALEONTOLOGISTS HAVE collected vertebrate fossils from the sedimentary deposits of the Big Badlands in South Dakota since the late 1800's. Cenozoic squamates, however, because of their scarcity and fragmentary nature, have not enjoyed a great deal of attention over the years. Leidy (1851), Cope (1877), and Marsh (1890) were the first paleontologists to extensively study fossil reptiles from the Big Badlands. After more than one hundred years of study much confusion exists regarding these fossil squamates. Part of this problem is due to the misidentification of juvenile specimens as separate taxa from adults of the same species. Other taxa were named without giving sufficient consideration to intraspecific variation.

This paper, first, attempts to clarify some of the systematic confusion regarding the fossil lizards and snakes from the White River Group preserved in Badlands National Park. Second, based on interpretation of the life habits of these organisms, we hope to relate the herpetofauna to the habitats available in the Badlands region during the Oligocene.

STRATIGRAPHY AND PALEOECOLOGY

The rocks of Late Eocene through Oligocene age (37 - 27 million years ago) bear the majority of vertebrate fossil material (Clark, 1937; Clark, Beerbower, and Kietzke, 1967; Harris and Tuttle, 1977). The lowest unit of the White River group is the Chadron Formation. Deposition of this layer began during the Late Eocene time period, approximately 37mil-

lion years ago as determined by $^{40}\text{Ar}/^{39}\text{Ar}$ dating (see Prothero, 1994 for stratigraphic columns). It is divided into the Ahearn Member, the Crazy Johnson Member, and the Peanut Peak Member. Overlying the Peanut Peak Member of the Chadron is the Brule formation, and it is subdivided into the Scenic Member, and the Poleslide Member. Overlying the Poleslide Member of the Brule is the Sharps Formation. Prothero (1994) recently established that the Arikaree Member of the Sharps Formation was deposited during the late Oligocene. The Chadronian, Orellan, Whitneyan, and Arikareean land mammal "ages" were named from the White River Group.

The Eocene/Oligocene transition was a time of great change throughout the world, in both climate and species diversity (Clark, Beerbower, and Kietzke, 1967; Savage and Russell, 1983). The general trend was a transformation from an early Eocene rain forest type environment to a climate that was more like the modern arid semideserts (Prothero, 1994). Evidence from plant and marine fossils, and oxygen and carbon isotopes indicates that a significant cooling trend began about 50 million years ago and continued through the Oligocene. Hutchison (1992) compiled a listing of all the late Eocene through early Oligocene herpetofaunal taxa of North America. He determined that the percentage of aquatic taxa was decreasing during this time.

MATERIALS AND METHODS

The Georgia College & State University vertebrate paleontology (GCVP) collection houses the majority of specimens studied. Additional specimens from the South Dakota School of Mines and Technology (SDSM) and The Pratt Museum at Amherst College (ACM) were examined. Recent squamates from the Georgia College & State University herpetology collection (GCH) were used for comparative purposes. All material is identified, described, and placed in the correct stratigraphic position. Interpretations of life habits and climatology are based on analysis of fossil organisms, the depositional sedimentology of the area in which the fossil was found (when possible), and by comparing the fossil organism to modern relatives (when applicable). Relative abundance for each taxon over time is based on specimens in the GCVP collection.

All measurements were taken with Helios dial calipers to 0.05mm. Pictures of *Rhineura floridana* and *Rhineura hatcherii* were taken using a Polaroid model 618091 Microcam, an Olympus 20X binocular dissecting microscope, and a Dazor model 364 flexlight. These images were then scanned into a computer and modified using Adobe Photoshop and Illustrator software.

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA Merriam, 1820

Family ANGUIDAE Gray, 1825

Genus PELTOSAURUS Cope, 1873

PELTOSAURUS GRANULOSUS Cope, 1873

Peltosaurus abbotti Gilmore, 1928

Peltosaurus piger Gilmore, 1928

Peltosaurus floridanus Vanzolini, 1952

Holotype.—American Museum of Natural History (AMNH 1610).

Referred Material.—ACM 3900, left jaw fragment; GCVP 2130, partial skull and associated scutes; GCVP 2281, partial skull; GCVP 2429, partial skull; GCVP 2589, jaw fragment; GCVP 3015, partial skeleton and associated dermal osteoscutes; GCVP 3124, skull fragment and vertebrae; GCVP 3466, partial jaw with one tooth; GCVP 3483, fragmentary skull and jaw; GCVP 4266, jaw fragment; GCVP 4267, cranial scute; GCVP 4268, parietal scute; GCVP 4383, 2 dermal osteoscutes; SDSM 3189, complete skull with articulated dermal scutes and partial skeleton.

Diagnosis.—Gilmore (1928) lists the following as characteristics of *Peltosaurus*: Seven teeth on premaxillary; 10 teeth on the dentary; parietal bone broad and flat; frontals greatly narrowed and united; postorbital and postfrontal coalesced; parietal in contact with squamosal; head and body covered with unkeeled, finely granular scutes.

Remarks.—*Peltosaurus abbotti* is generally accepted as a valid taxon because its skull is greatly convex and its appearance is, as a result, drastically different from that of *Peltosaurus granulatus*. Recently, however, Sullivan (personal communication) has stated his opinion that the type specimen of *Peltosaurus abbotti* was probably an aberrant individual and, therefore, he considers the species invalid.

Age Distribution.—Known; Chadronian through Arikareean. Most abundant; Orellan.

Modern Relatives.—Modern members of the family Anguidae include the genera *Ophisaurus* (legless glass lizards) and *Gerrhonotus* ("alligator" lizard). Since *Ophisaurus* is a legless, burrowing lizard, it is *Gerrhonotus* that gives the better idea of the possible habits of peltosaurs. *Gerrhonotus* is a relatively slow-moving lizard with a prehensile tail. Its diet includes insects, spiders, newborn mice, small snakes, and lizards. It is restricted mainly to Texas.

Genus HELODERMOIDES Douglass, 1903

HELODERMOIDES TUBERCULATUS Douglass, 1903

Glyptosaurus tuberculatus Gilmore, 1928

Glyptosaurus montanus Gilmore, 1928

Glyptosaurus giganteus Gilmore, 1928

Holotype.—Carnegie Museum Catalogue No. 707

Referred Material.—GCVP 1256, dermal osteoscutes; GCVP 2121, dermal armor; GCVP 2132, 4 vertebrae; GCVP 2138, dermal armor; GCVP 3365, heavy cephalic armor; GCVP 3991, dermal armor; GCVP 3992, dermal armor; GCVP 3999, dermal armor.

Diagnosis.—Sullivan (1979) offers these characteristics as diagnostic of *Helodermoides*: frontals distinct; cephalic osteoderms bulbous; tubercles numerous, usually without definite arrangement (rarely a ring pattern is found on body osteoderms); six or seven rows of cephalic osteoderms between orbits; teeth subconical, posterior ones slightly recurved; jugal blade curved; maxilla straight; dentary moderately slender; supratemporal fenestra closed; skull highly vaulted.

Remarks.—The GCVP collection has a small sample of

Glyptosaurine material. The only specimens that are available are dermal osteoscutes (GCVF 6128, 6129, 6130, and 6131) and a small portion of the cranial region of one individual (GCVF 6132). This material is tentatively identified as *Helodermoides tuberculatus* because the cephalic osteoderms do not demonstrate concentrically arranged patterns of tubercles.

Age Distribution.—Known; Chadronian through Orellan. Most abundant; Chadronian through Orellan.

Modern Relatives.—Same as for *Peltosaurus*.

Family RHINEURIDAE Vanzolini, 1951

Genus RHINEURA Cope, 1861

RHINEURA HATCHERI Baur, 1893

Gilmoreia attenuatus Taylor, 1951

Lepidosternon sp. Gilmore, 1928

Pseudorhineura minuta Vanzolini, 1951

Rhineura amblyceps Taylor, 1951

Rhineura attenuatus Estes, 1983

Rhineura coloradoensis Gilmore, 1928

Rhineura hatcherii Baur, 1893

Rhineura hibbardi Taylor, 1951

Rhineura minutus Gilmore, 1938

Rhineura sternbergii Walker, 1932

Rhineura wilsoni Taylor, 1951

Holotype.—Princeton University, Yale Peabody Museum (YPM-PU 11389).

Referred Material.—GCVF 2223, skull and jaws; GCVF 2224, partial skull; GCVF 2707, partial skull; GCVF 3628, skull and jaws; GCVF 3686, skull and jaws; GCVF 3935, partial skull and jaws; GCVF 4068, skull and jaws.

Diagnosis.—A compact well-ossified skull, with pleurodont teeth lacking the postorbital and postfrontal squamosal arches and epipterygoid (Gilmore, 1928).

Remarks.—Sullivan and Holman (1996) question whether *Rhineura* is the proper generic name for the fossil amphisbaenids from the White River Group. We believe that the fossil specimens show a definite affinity with the Rhineurinae. We do, however, recognize two differences between *R. hatcherii* and *R. floridana*. First, the teeth of *R. floridana* are less robust and more recurved than are those of *R. hatcherii* (Figure 1). Second, the parietal regions of the skulls of *R. hatcherii* and *R. floridana* appear to vary greatly with *R. hatcherii* having a visibly more expanded parietal re-

gion. Parietal expansion was measured across the widest point of the squamosals, skull lengths were measured from the mid-point of the occipital condyle to the anterior tip of the premaxillary. All of our skulls of *R. hatcherii* are more brachycephalic than *R. floridana*. The smallest difference in ratios is between GCH 100 and GCVF 4068, 4.9%. If the expansion of the parietal area in *R. hatcherii* holds true for a larger sample size and a variety of age groups, this characteristic may be a useful diagnostic trait at the specific (or possibly the generic) level.

Age Distribution.—Known; Orellan through Whitneyan. Most abundant; Orellan.

Modern Relatives.—*Rhineura floridana* is the only extant member of the genus found in North America. Its body is segmented like that of an earthworm, but is covered in scales. This animal is adapted for burrowing and has no external eyes, limbs, or ear openings. Its range is restricted to the Florida peninsula where it lives in sand or soil and eats earthworms, spiders, and termites.

Family BOIDAE Gray, 1825

Subfamily ERYCINAE Bonaparte, 1831

Genus CALAMAGRAS Cope, 1873

CALAMAGRAS ANGULATUS Cope, 1873

Ogmophis angulatus Cope, 1874

Holotype.—American Museum of Natural History (AMNH 1654).

Referred Material.—GCVF 1864, five articulated vertebrae, Poleslide Member of the Brule; 3410, two articulated vertebrae, Scenic Member of the Brule.

Diagnosis.—The vertebrae of *Calamagras* are characterized as having short, thick neural spines. The vertebral centra of *Calamagras* are less than 9mm. The neural spine is less than one-half the total length of the centrum, but it is not tubular or dorsally swollen (Holman, 1979).

Remarks.—Holman (1979) believed this poorly defined small boa-like snake might have had vestiges of hind limbs. *Calamagras* is a member of the Infraorder Henophidia, and general characteristics for this group include: neural arches usually vaulted, condyles and cotyles usually round, foramina usually lacking on either side of the cotyles, and hemal keel poorly developed.

Age Distribution.—Known; Orellan through Arikarean. Most abundant; Orellan.

Modern relatives.—*Calamagras* is similar to the living North American genera *Lichanura* and *Charina* (Holman, 1979). *L. trivirgata*, the Rosy Boa, inhabits rocky brushlands and deserts (Stebbins, 1966). A burrowing snake, it is attracted to oases and permanent or intermittent streams and feeds on small mammals and birds. *Charina bottae*, the Rubber Boa, is a good swimmer, burrower, and climber, frequenting grasslands, woodlands, and forests. It is usually found under rocks, logs, or the bark of fallen trees, generally feeding on small mammals and lizards.

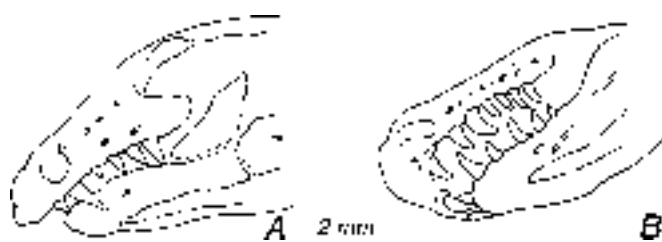


FIGURE 1—Oblique side views of skulls of A, *Rhineura hatcherii* and B, *Rhineura floridana* showing differences in dental curvature.

Genus *GERINGOPHIS* Holman 1976

GERINGOPHIS VETUS Holman, 1982

Holotype.—University of Kansas (KU 49126)

Referred Material.—GCVF 3460, 2 associated vertebrae.

Diagnosis.—This erycine boid is distinct from the other small boid genera found in the White River Group in that it has a flattened shape and a long, high neural spine. Holman (1979) describes *Geringophis* as having a "... unique combination of vertebral characters of a depressed neural arch, a long, well-developed, dorsally swollen neural spine, and a distinct hemal keel and sub-central ridges."

Remarks.—*Geringophis vetus* is the earliest occurrence of the genus *Geringophis* in the fossil record. It is quite interesting because of the variation of its vertebrae from the normal boid pattern. Sullivan and Holman (1996) state, "Whether this genus arose from *Cadurcoba* [from the late Eocene of France] and immigrated to North America from the Old World, or originated from an erycine boid with a flattened vertebral form such as *Calamagras angulatus*, is unknown". Two other members of this genus are known: Holman (1979) reports *G. depressus* from the Lower Miocene of Nebraska and *G. yatkolae* from the Upper Miocene of Nebraska.

Age Distribution.—Known; Orellan. Most abundant; Orellan.

Modern relatives.— See *Calamagras*.

DISCUSSION

Retallack (1992) stated that during the Orellan the Badlands region was open forest. It is necessary therefore, to explain the absence of any arboreal herpetofauna from the White River Group. The only herpetofauna observed from this time period are fossorial or ground dwelling, and if the area were, in fact, open forest, it seems that arboreal herpetofauna should be represented in the fossil record. This discrepancy, however, may be the result of taphonomic bias. The ground-dwelling forms had heavy dermal armor and their life habits may have increased the likelihood of preservation.

Prothero (1994) emphasized the decrease in temperature during the Eocene/Oligocene as the major climatic factor affecting species diversity. Hutchison (1992), however, stated that the increase in aridity (and accompanying decrease in aquatic habitats) had a greater impact on species diversity than the change in temperature. The squamate fauna tends to support Hutchison's interpretation. Aquatic lower vertebrates could find some measure of protection from cold weather by hibernating under water. The terrestrial vertebrates, however, would be more susceptible to cold weather. The aquatic lower vertebrates, particularly the boas, show a significant decline in abundance by the end of the Orellan. Since terrestrial lower vertebrates continue to flourish into the Whitneyan and Arikarean, it seems likely that the lack of aquatic habitats probably had the greater impact on squamate species diversity.

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REASSESSMENT OF CHARACTERISTICS DETERMINING GENERIC AFFINITY IN *GOPHERUS* AND *STYLEMYS* (TESTUDINIDAE) FROM THE WHITE RIVER GROUP, BADLANDS NATIONAL PARK

WILLIAM P. WALL¹ AND DENNIS MADDOX²

¹Department of Biology, Georgia College & State University, Milledgeville, GA 31061

²Department of Physiology, Medical College of Georgia, Augusta, GA 30901

ABSTRACT—A review of the White River Group's (37.0 to 26.9 MYA) land tortoises is presented. New specimens are examined and described. The generic characteristics of *Gopherus*, *Hesperotestudo*, and *Stylemys* are reexamined. The species *Stylemys amphithorax* is declared *nomen dubium*. Based on nuchal morphology, the common White River tortoises should be placed in *Gopherus*. *Stylemys* could be retained as a fossil morphotype similar to modern gopher tortoises.

INTRODUCTION

TORTOISE SHELLS, family Testudinidae, are among the most common fossils in the White River rocks of Late Eocene through Oligocene age (37–27 million years ago, see Prothero, 1994 for stratigraphic columns) exposed in Badlands National Park. The lowest unit of the White River group is the Chadron Formation. Deposition of this layer began during the Late Eocene, approximately 37 million years ago (Chadronian Land Mammal Age). Overlying the Chadron is the Brule formation, subdivided into the Scenic Member (Orellan Land Mammal Age) and the Poleslide Member (Whitneyan Land Mammal Age) which is overlain by the lower Sharps Formation (Arikareean Land Mammal Age).

The Eocene and Oligocene transition was a time of great change throughout the world, in both climate and species diversity (Clark, Beerbower, and Kietzke, 1967; Retallack, 1992). The general trend was a transformation from an early Eocene rain forest environment to a climate that was cooler and more like modern semiarid regions (Prothero, 1994).

Hutchison (1992) reviewed all herpetofaunal taxa in the late Eocene through early Oligocene of North America. After comparing the stratigraphic variance in the number of genera referable to terrestrial or aquatic habitats, he determined that the number of aquatic taxa was decreasing. Hutchison concluded that the declining diversity of herpetofaunal taxa was due in large part to the dwindling of aquatic environments.

Hay (1908) listed five genera of tortoises, *Geochelone*, *Gopherus*, *Hesperotestudo*, *Stylemys*, and *Testudo*, in the White River Group. He stated that the borders where the costals and peripherals meet are more rounded or more weakly sutured in *Gopherus* and in *Stylemys* than in *Geochelone* and *Testudo*. However, such qualitative characteristics are often difficult to interpret. The extent to which these sutures are more or less strongly interlocked is difficult to definitively measure, but traditionally when the costal/peripheral interface is rounded, *Stylemys* or *Gopherus* is indicated. However, suturing of the costal/peripheral interface is not indicative of generic affiliation. The most recent revision of these tortoises (Hutchison, 1996) recognized *Gopherus*, *Stylemys*, and

Hesperotestudo as valid taxa in the White River Group.

The question of what tortoise genera are actually present in the White River Group is the subject of this paper.

MATERIALS AND METHODS

The Georgia College & State University vertebrate paleontology (GCVP) collection provided the majority of specimens studied. Additional specimens from the South Dakota School of Mines and Technology (SDSM) were examined. Modern tortoises from the Georgia College & State University herpetology (GCH) collection were used for comparative purposes. The terminology of Zangerl (1969) is followed for turtle morphology (Figure 1). All material is identified, described, and placed in the correct stratigraphic position.

All measurements were taken with Helios dial calipers to .05mm. The method used to express neural formulae is modified from Hutchison (1996). Neural shape is indicated by a number. For example, the number "6" indicates that the neural is hexagonal. Numbering begins with the first neural and ends with the eighth. Numbers are followed by a parenthesis. An open parenthesis following the number indicates that the neural is widest anteriorly. A closed parenthesis following a number indicates that the neural is widest posteriorly. A neural formula of 4(8)4(8)6(6)6(6) indicates that the first neural is quadrangular and widest anteriorly. The second neural is octagonal and widest posteriorly, etc.

The following characteristics were used in this study: shell characters include nuchal dimensions, neural differentiation, costal alternation, positioning of the inguinal scale in relation to the femoral scale, and the presence or absence of peripheral bridge pits; cranial characteristics involve details of the premaxillary ridge. Hay (1908), Auffenberg (1962), Bramble (1982), Hutchison (1996), and others use nuchal dimensions as the primary means to differentiate among tortoise genera.

SYSTEMATIC PALEONTOLOGY

Hutchison (1996) states that *Gopherus* has a nuchal that is "as wide or wider than long," *Hesperotestudo* has a nuchal that is "longer than wide," and *Stylemys* has a nuchal that is "longer than wide." We examined modern specimens of *Gopherus agassizii* and found that all specimens, indeed,

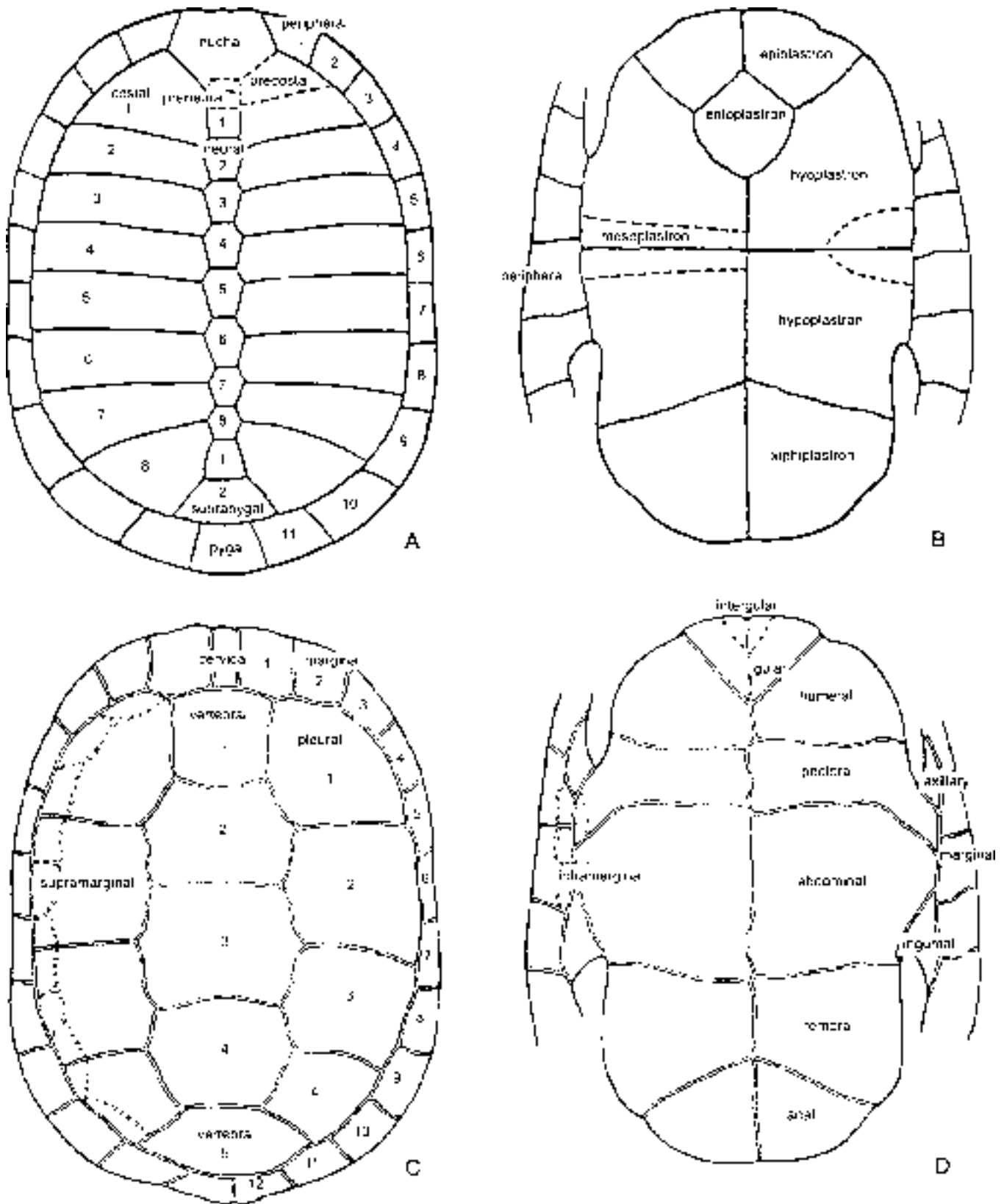


FIGURE 1—Generalized testudine carapace (A, C) and plastron (B, D) illustrating bone and scale terminology respectively (from Zangerl, 1969).

had a nuchal that was wider than long. We also examined all fossil tortoises in the GCVP collection and found no reason to discontinue the use of this characteristic as a diagnostic factor.

Characteristics of the premaxillary ridge are of questionable value. All three genera of the Family Testudinidae known from the White River Group may have a median premaxillary ridge. *Stylemys* has historically been accepted as differing from *Gopherus* in having a distinctive lack of the juncture between the longitudinal premaxillary ridge and the masticatory ridges. In skulls of modern *Gopherus*, the point where the masticatory ridges join with the longitudinal premaxillary ridge is exceedingly faint. We do not think it is practical to try to distinguish fossil remains by a characteristic that is barely observable when present in modern forms. Bramble (1982) and Hutchison (1996) state that *Gopherus* may occasionally have the median premaxillary ridge not joining the medial maxillary triturating ridge. Thus, the characteristic is sporadic and useless in diagnosing specimens.

Hutchison (1996) stated that the median premaxillary ridge of *Hesperotestudo* is reduced or absent. Qualitative characteristics are confusing and overlap causes much guesswork. We believe that *Gopherus* and *Stylemys* have the median premaxillary ridge, and that this characteristic is variable in *Hesperotestudo*.

Neural shape is often used in determining the taxonomic placement of a tortoise specimen. Hutchison (1996) has devised a useful method of describing these neurals (see materials and methods), and he gives some neural formulae as follows: *G. laticuneus* 6)6)4(6(6(6(6(6 or 4(8)4(6(6(6(6(6, *Gopherus* sp. 4(8)4(8)4(6(6(6 or 4(8)4(6(6(6(6(6, *Hesperotestudo brontops* 4(8)4(8)4(6(6(6, *Stylemys nebrascensis* 4(6(6(6(6(6(6(6 or 4(8)4(6(6(6(6(6.

All GCVP specimens available have a neural formula of 4(6(6(6(6(6(6(6(. If the neural pattern were the only defining trait then all testudines in the GCVP collection belong in the genus *Stylemys*. Nuchal measurements, however, do not support this taxonomic assignment. The nuchal scales in all of these specimens have a width greater than their length, a characteristic considered to be diagnostic of *Gopherus*.

We examined modern *Gopherus* specimens in an attempt to resolve this conflict. Modern *Gopherus* specimens have relatively indistinct neural shapes with the neural formula being closest to 4(6)6(6(6(6(6(6(. The first neurals did not compare well with the one shown by Hutchison (1996). Additionally, the first costal in modern *Gopherus* contacts the second neural. This condition is also true for all White River testudines in which this character can be observed in the GCVP collection.

Auffenberg (1964) stated that neural differentiation should not be used as a diagnostic characteristic. It is evident, as attested to by the fact that *Gopherus* and *Stylemys* have two different neural formulae each, that neural formulae are highly variable. We agree that neural differentiation has little diagnostic value.

According to Hutchison (1996), *Gopherus* has "costals distinctly alternately narrower and wider laterally",

Hesperotestudo has "costals moderately to distinctly alternately narrower and wider laterally", and *Stylemys* has "costals only slightly narrower and wider laterally". We believe that qualitative characteristics lead to the potential for overlap, and thereby increasing the probability of an erroneous identification.

Based on specimens in the GCVP collection that we recognize on independent criteria (primarily nuchal shape, see discussion above) as a single species, *Gopherus laticuneus*, we found a wide range of variation in the degree of costal alternation. The costals obviously alternate in some cases, while they alternate very little in other specimens.

Bramble (1982) used the contact or lack of contact between the inguinal scale and the femoral scale to determine generic assignment of tortoise specimens. Hutchison (1996) stated that *Gopherus* has an inguinal scale, which is "moderate to small but contacts FEM [femoral scale]." He also wrote that *Hesperotestudo* has an inguinal scale, which is "enlarged anteromedially and may broadly contact FEM," and that *Stylemys* has an inguinal scale, which is "moderate to small, never contact[ing] FEM".

We examined modern *Gopherus* specimens and found that the shape of the inguinal scale is highly variable, but the contact between it and the femoral scale was always present. This character is usually not apparent in fossil tortoises. The entire inguinal and femoral scales are evident in only two of seventeen specimens examined. These two specimens (GCVP 36 and GCVP 37) appeared to be *Gopherus laticuneus* except for the fact that there was no contact between the inguinal scale and the femoral scale.

Based on examination of the fossil tortoises in the GCVP collection, we believe that the contact, or lack thereof, between the inguinal scale and the femoral scale may be variable in all tortoises from the White River Group.

Leidy (1851) reported the presence of peripheral bridge pits in *Stylemys nebrascensis*. For many years the presence or lack of peripheral bridge pits was used to distinguish between *Stylemys* and *Gopherus*. Auffenberg (1962) re-described *Stylemys amphithorax*, citing the absence of peripheral bridge pits as one of the major distinguishing factors between *S. amphithorax* and *S. nebrascensis*.

Leidy (1851) originally described *Stylemys* from a specimen that was about seven inches long and four-fifths complete. He reported that this specimen had a gap of one-eighth of an inch (approximately 3 mm.) between the peripheral and costal bones. Later, Hay (1908) retained *Stylemys* as a valid genus and described it as having ribs at the distal ends of the costal plates which enter pits in the bridge peripherals. We believe the gap between the bones described by Leidy (1851) and Hay (1908) is an age variable trait and therefore not a useful diagnostic tool. Juveniles of some modern turtles (for example, *Geochelone radiata*), exhibit a gap between the costal and peripheral bones that is absent in adult specimens. Through this gap, the ribs can be seen to insert into grooves along the peripherals. Our observations do not support Hay's (1908) belief that the insertion of the rib heads was along the bridges. All tortoise specimens in the GCVP collection which

TABLE 1.—Comparison of characteristics distinguishing *S. amphithorax* and *S. nebrascensis*.

<i>S. amphithorax</i>	<i>S. nebrascensis</i>
*Lacks peripheral bridge pits for reception of rib heads.	*Peripheral pits present.
*Length of posterior lobe of plastron equal to or greater than length of bridge.	*Length of posterior lobe of plastron less than length of bridge.
#Thinner, more elongate shell.	#Thicker, more rounded shell.
#Narrow and elongate cervical.	#Broad and relatively short cervical.
#Distinct lateral notch on Xiphiplastron.	#Weak lateral notch on Xiphiplastron.

(*) indicates characteristics shown by Auffenberg (1964) to be juvenile or variable.
 (#) indicates characteristics that we believe are individually variable.

exhibit the gap between the peripherals and the costals show a range of insertion points for the rib heads all along the peripherals, they are not confined to the bridges.

Auffenberg (1964) discussed the ontogenetic changes that occur when observing bridge grooves/pits in *Gopherus*. He demonstrated that the presence of peripheral bridge pits is entirely based on the age of the organism. We do not think bridge pits are a valuable diagnostic character. The weakness of this character places the validity of *Stylemys amphithorax* (Auffenberg, 1962) in doubt since it was distinguished primarily from *S. nebrascensis* because it lacked peripheral bridge pits. Other characteristics attributed to *S. amphithorax* are individually variable (see Table 1). This leaves *S. amphithorax* with no unique characteristics. We, therefore, suggest that it be synonymized with *S. nebrascensis* (Leidy, 1851), which has priority.

Based on our analysis, all of the Badlands tortoises in the GCVP collection belong in the genus *Gopherus*. We believe the following classification best describes our tortoises from the White River Group.

Order TESTUDINES Linnaeus 1758
 Suborder CRYPODIRA Cope 1868
 Family TESTUDINIDAE GRAY, 1825
 Genus GOPHERUS Rafinesque, 1832

Gopherus laticuneus Cope, 1873
Testudo laticunea Cope, 1873
Testudo quadratus Cope, 1884
Testudo thompsoni Hay, 1908
Testudo praeextans Lambe, 1913
Gopherus laticunea (Cope, 1873), Williams, 1950
Geochelone thompsoni (Hay, 1908), Auffenberg, 1963
Scaptochelys laticunea (Cope, 1873), Bramble, 1982

Holotype.—American Museum of Natural History (AMNH 1160)

Selected Reference Specimens: GCVP 1, nearly perfect

shell; GCVP 36, complete shell; GCVP 37, complete shell and skeletal fragments; GCVP 43, complete shell; GCVP 3305, complete shell; GCVP 3501, complete shell; GCVP 3841, partial shell; GCVP 4118, complete shell; GCVP 4452, complete shell; GCVP 4454, complete shell; GCVP 4456, complete shell.

Diagnosis.—Ernst and Barbour (1989) indicate that *Gopherus* has a nuchal scute that is about as broad as it is long and an inguinal buttress which joins to the sixth costal. According to Hutchison (1996), *Gopherus* differs from *Stylemys* in that the inguinal buttress contacts the femoral sulcus and the costals of *Gopherus* are alternately wide and narrow. Hutchison (1996) says that the first two neurals of *Gopherus* are widest posteriorly, and that the neurals of *Gopherus* may be alternately octagonal or quadrangular or they may all be hexagonal.

Age Distribution.—Known: Chadronian through Whitneyan. GCVP Collection: Chadronian through Whitneyan.

Modern Relatives.—There are three modern members of the genus *Gopherus* (gopher tortoises) found in North America. These are *G. agassizii*, *G. berlandieri*, and *G. polyphemus* (Ernst and Barbour, 1989). All seem to prefer areas with sandy soil and open scrub brush. All extant species of *Gopherus* are herbivorous, and their food preferences include grasses, leaves, flowers (especially blossoms if available), and fruits. *G. agassizii* and *G. berlandieri*, which both dwell in desert or near-desert environments, eat cacti.

DISCUSSION

Table 2 lists those characteristics we believe may have diagnostic value for members of the Testudinidae from the White River Group. Comparative measurements are often used to distinguish *Gopherus* from *Stylemys*. We have previously stated our opinion that some of these measurements are of little diagnostic value. Our taxonomic assignment of the common Badlands tortoises into the genus *Gopherus* is based primarily on nuchal dimensions because that characteristic appears to us to be the most reliable.

Our interpretation of White River testudines raises the question of the validity of the genus *Stylemys* as a separate taxon from *Gopherus*. Both generic names are firmly entrenched in the scientific literature. Which genus is better known depends on the researcher's field. Herpetologists are certainly more familiar with the modern gopher tortoises in the genus *Gopherus*. On the other hand, paleontologists are probably more familiar with the Badlands fossil tortoises which are typically placed in the genus *Stylemys*. *Gopherus* (Rafinesque, 1832) has priority over *Stylemys* (Leidy, 1851), therefore if the two genera are the same, the badlands tortoises should be placed in the modern genus. We have tentatively adopted that philosophy in this paper. We do, however, propose a possible solution to this taxonomic dilemma. *Stylemys* could be recognized as a "chrono" genus in a manner similar to that for chronospecies in the paleontological literature.

TABLE 2—Potential diagnostic characteristics for the tortoise genera found in the White River Group.

Gopherus	Hesperotestudo	Stylemys
*Symphyseal groove	*No symphyseal groove	*Symphyseal groove
*Otolithic mass Nuchal scale wider than long	*No otolithic mass Nuchal scale longer than wide	*No otolithic mass Nuchal scale longer than wide
*Phalangeal formula 2-2-2-2-1 or less	*Phalangeal formula 2-2-2-2-2	Phalangeal formula 2-2-2-2-2
Premaxillary ridge present	Premaxillary ridge may be present or absent	Premaxillary ridge present
*Os transiliens present	Os transiliens absent	Os transiliens absent
*Caudal vertebrae with interpostzygopophyseal notches	*Caudal vertebrae with interpostzygopophyseal notches	*Some caudal vertebrae lacking interpostzygopophyseal notches

(*) Indicates characters not verified in this study and/or rarely observable in fossil tortoises (see Auffenberg, 1961).

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A COMPARISON OF FEEDING ADAPTATIONS IN TWO PRIMITIVE RUMINANTS, *HYPERTRAGULUS* AND *LEPTOMERYX*, FROM THE OLIGOCENE DEPOSITS OF BADLANDS NATIONAL PARK

WILLIAM P. WALL AND CHRISTOPHER M. COLLINS

Department of Biology, Georgia College & State University, Milledgeville, GA 31061

ABSTRACT—The craniodental morphology of two primitive Oligocene ruminants, *Hypertragulus calcaratus* and *Leptomeryx evansi*, was analyzed to determine the likely dietary habits of these sympatric species. Their craniodental morphologies were compared to each other and to a variety of extant ruminants whose dietary habits are known. A variety of quantitative measures, including hypsodonty index and relative premolar row length, were statistically analyzed. Ten qualitative characteristics were also used in comparison.

Hypertragulus showed overlap between browsers and mixed feeders for a variety of characters, but was most likely a mixed feeder. *Leptomeryx* grouped with browsers in almost all cases. It seems likely that these two closely related sympatric taxa reduced competition by consuming different food resources.

INTRODUCTION

HYPERTRAGULUS AND *Leptomeryx* are small, primitive, hornless ruminants belonging to the infraorder Tragulina that contains the families, Hypertragulidae, Tragulidae, and Leptomerycidae. The only extant members of this infraorder are the tragulids or chevrotains of southeastern Asia. Hypertragulids are the most primitive of the three families. Leptomerycids actually share more derived traits with horned ruminants than do the modern tragulids; therefore they are regarded as the most specialized of the tragulines (Webb and Taylor, 1980).

Hypertragulus calcaratus and *Leptomeryx evansi* are two of the most common taxa found in paleosols characteristic of savanna woodlands in the middle Oligocene beds exposed in Badlands National Park, South Dakota. *Hypertragulus* is not found in younger beds, but other species of *Leptomeryx* survive until the middle Miocene (Emry et al., 1987).

This study was conducted with two purposes in mind. First, to determine how much dietary overlap these two closely related sympatric taxa experienced. And second, to increase our knowledge of leptomerycids, a group that could have given rise to the horned ruminants, the most successful large terrestrial herbivores today.

PALEOECOLOGY AND GEOLOGY OF THE BRULE FORMATION

The middle Tertiary was a period of major climatic change. At the beginning of the Tertiary, during the Early Paleocene, the world was warm and equable with little latitudinal gradation. Broad-leaved deciduous forests adapted to regimes of seasonal darkness were found in the Polar Regions and subtropical woodland extended to within polar confines. Paleocene forests were denser and more closed-canopied than that of the Cretaceous (Prothero, 1994). The thermal high point and the maximum diversity of mammals are represented by the transition from the Early to Middle Eocene. Following this period, a cooling and drying trend occurred (Janis, 1993; Prothero, 1994). Annual precipitation in the region of Bad-

lands National Park was 1,000 mm in the early part of the late Eocene, 500-900 mm in the early Oligocene, and only 350-450 mm in the late Oligocene (Retallack, 1983).

The fauna of this period was transitional between the jungle-adapted fauna of the early Paleocene and the grassland fauna of today. Carnivores were more heavily proportioned and there is no evidence of pursuit predators. Ungulates were becoming more cursorial, but were still shorter-legged and less cursorial than modern forms (Janis, 1993).

Retallack (1983) studied the paleosols in Badlands National Park. From this he identified three major habitats found during deposition of the Scenic Member of the Brule (Orellan Land Mammal Age). These were stream-side swales with herbaceous vegetation that was probably mainly grasses, gallery woodlands lining the streams, and savanna woodland with scattered trees and intervening areas of bunch grasses, forbs, and small shrubs. Clark et al. (1967) and Retallack (1983) surveyed the fauna from each habitat. They found that in the gallery woodlands the predominant genera were *Mesohippus* and *Merycoidodon* while the fauna of the savanna woodlands was predominantly *Paleolagus*, *Leptomeryx*, and *Hypertragulus*. Little data were collected on the near-stream swales fauna, but according to Retallack, (1983), the aquatic rhinoceros *Metamynodon* was probably common (possibly restricted to this habitat).

The climate during deposition of the Scenic Member was changing from humid and subtropical to subhumid and warm temperate (Retallack, 1983). The dry season was becoming more severe and there were few flowing streams during the dry season. The greater abundance of *Celtis* seeds and increasing rarity of alligators also indicates that the climate was becoming cooler (Retallack, 1983).

The Poleslide Member of the Brule (Whitneyan Land Mammal Age) contains numerous calcareous nodules indicating a more arid environment than during deposition of the Scenic Member (Retallack, 1983). Few streams flowed permanently and the water table was generally below two meters.

The dry climate and sparse vegetation contributed to accelerated sediment accumulation and ash preservation.

SYSTEMATIC AND ANATOMICAL REVIEW

Members of the suborder Ruminantia are typically divided into two infraorders, the Tragulina and the Pecora. Webb and Taylor (1980) consider the hypertragulids to be the most primitive ruminants based on features found in *Hypertragulus*. Primitive cranial features cited by them include an incomplete postorbital bar, an extensively exposed mastoid, the marginal position of the tympanohyal, and the primitive structure of the petrosal. The premolars are also simple in that they have no lingual elaboration, but it is not clear whether this is a primitive condition or if they were secondarily simplified (Janis, 1987).

The family Tragulidae includes two extant genera with four species (Nowak, 1991). Living tragulids occur exclusively in the Old World and are most common in the subtropical latitudes. The fossil record of tragulids only extends back to the Miocene. Webb and Taylor (1980) place them below leptomerycids due to the concave articulation of the malleolar and calcaneum. The derived state of this articulation in leptomerycids, gelocids and all higher ruminants is concavo-convex. Tragulids also share with all other ruminants except hypertragulids fusion of the trapezoid and magnum, absence of the trapezium, loss of metacarpal I, an incomplete fibula and a distinct malleolar. These features indicate that tragulids diverged from the main lineage of ruminants after the Hypertragulidae.

The most advanced traguline family is the Leptomerycidae. Derived characteristics that separate them from all other tragulines and ally them with higher ruminants are: the posterior position and narrow exposure of the mastoid, fusion of the magnum and trapezoid, reduction of metacarpals II and V, loss of metacarpal I, a well developed malleolar, parallel ginglymi on each end of the astragulus, fused metatarsals III and IV, and the reduction of metatarsals II and V to fused proximal rudiments (Webb and Taylor, 1980).

The dentition of *Hypertragulus* is simpler than *Leptomeryx* (Figure 1) and is considerably different except for the molars, which are of the basic selenodont pattern in both animals. The dental formula of *Hypertragulus* is $0/3 \ 1/1 \ 4/4 \ 3/3$ and the dental formula of *Leptomeryx* is $0/3 \ 1/1 \ 3/4 \ 3/3$ (Scott, 1940).

The lower incisors of *Hypertragulus* are styliform with the crowns spatulate and outcurved. The canine is incisiform, and the first premolar takes the canines place both functionally and in shape. The first incisor in *Leptomeryx* is much larger than the others. It is procumbent and points almost directly forward. The second and third incisors are much smaller. The canine is incisiform and is closely appressed to the third incisor. P_1 is isolated from the other teeth by a diastema in front and behind. It is caniniform in shape but is very small and has only one root (Scott, 1940).

The large upper canines of *Hypertragulus* were possibly used as defensive fangs. However, the canines do show a significant separation into two size classes, which could indicate

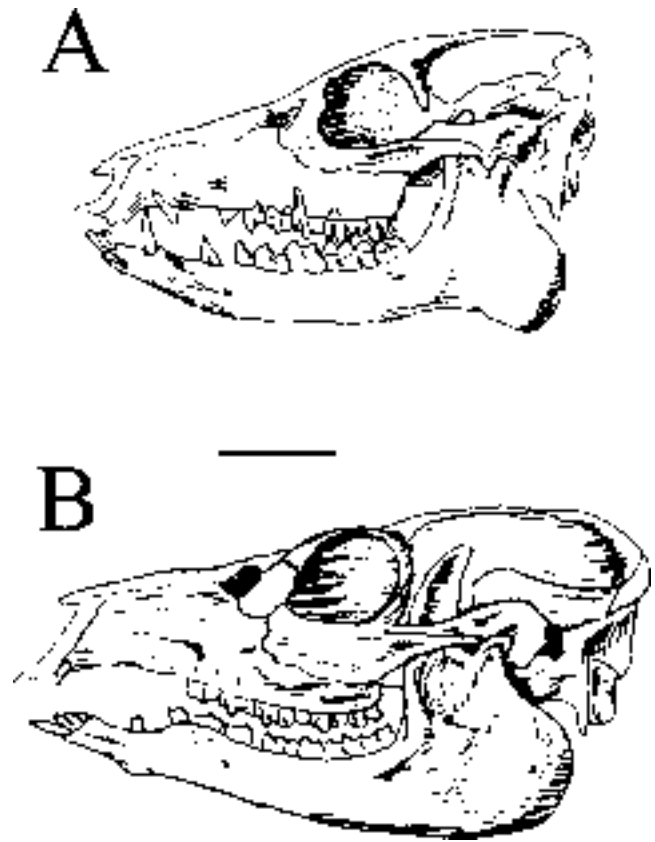


FIGURE 1—Lateral view of the skull and jaws of (A) *Hypertragulus* and (B), *Leptomeryx* (modified from Scott, 1940).

this character is sexually dimorphic. The upper canines of *Leptomeryx* were in contrast small and vestigial, but they probably protruded below the gum line (Scott, 1940; Webb and Taylor, 1980).

In *Hypertragulus*, P^1 is a small, sharp pointed tooth with a simple crown and has two widely divergent roots. It is separated by a diastema both anteriorly and posteriorly. P^1 in *Leptomeryx* is lost (Scott, 1940).

The premolars in the cheek teeth of *Hypertragulus* are simple compared to those of *Leptomeryx*. Both P^2 and P^3 are simple conical teeth. P^3 has a weak protocone and lingual cingulum, making it triangular, and P^3 has a weak metaconid and hypoconid, giving it a wedge-shaped appearance. P^4 and P^4 are more elaborate than the other premolars and a small paraconid is added to P^4 (Webb and Taylor, 1980).

The premolars in the cheek teeth of *Leptomeryx* are more complex. P^2 has three labial cusps, a large paracone with smaller basal cusps anteriorly and posteriorly. P^3 and P^4 have strong protocones in addition to the three labial cusps, with the protocone forming a crescent on P^4 . P^2 and P^3 have a paraconid, a tall protoconid, and a small hypoconid connected by three longitudinal crests. P^4 has a strong metaconid lingual to the protoconid in addition to the other three crests found on P^3 . *Leptomeryx* premolars are more submolariform than are those of *Hypertragulus*. The premolars of *Hypertragulus* show little wear, while those of *Leptomeryx*

often show considerable wear (Webb and Taylor, 1980).

The molars of both *Hypertragulus* and *Leptomeryx* are of the typical selenodont pattern, having four elongated cusps. The molars of *Hypertragulus* are somewhat higher crowned than those of *Leptomeryx*, but they are not hypsodont or even mesodont (Scott, 1940). The upper molars of *Leptomeryx* differ from those of *Hypertragulus* by the presence of a strong mesostyle, which is absent in *Hypertragulus* (Janis, 1987, Matthew, 1908). The lower molars of *Leptomeryx* differ from those of *Hypertragulus* by the presence of the *Palaeomeryx* fold. In *Leptomeryx*, a small fissure separates the entoconulid and hypoconulid on M₃ posteriorly, while in *Hypertragulus*, they are united (Heaton and Emry, 1996).

Hypertragulus first appears in the White River group in the Orellan and persists through to the end of the Whitneyan (Emry, 1978).

Retallack (1983) studied the paleosols found in Badlands National Park, and found that *Hypertragulus* fossils were most abundant in deposits that were formed in savanna woodlands that probably developed in broad floodplains adjacent to streams. Root traces and the nature of the paleosols indicated that they supported abundant herbaceous ground cover with well-spaced and only weakly clumped trees. *Celtis* seeds are also found in these paleosols, giving further evidence of trees.

The genus *Leptomeryx* includes seven species (Emry and Heaton, 1996). Some of the more primitive forms are placed in the genus *Hendryomeryx* by some workers (e.g., Black, 1978; Storer, 1981). The type species for this genus is *L. evansi*, which is common in Orellan deposits in the Great Plains, and is apparently the only species of *Leptomeryx* found during the Orellan. There was greater diversity in Chadronian forms, and they are found in deposits ranging from Saskatchewan to Texas (Emry and Heaton, 1996). Leptomerycids survived until the middle part of the Miocene.

According to Retallack (1983), *Leptomeryx* fossils are most common in the same type of deposits as those where *Hypertragulus* are the most common, but in greater abundance. In addition to these near stream savanna woodland deposits, *Leptomeryx* remains are also common in savanna woodland deposits that were not associated with streams.

MATERIALS AND METHODS

Craniodental measurements were taken on both fossil and recent specimens. With the exception of specimen number SDSM 3083 on loan from the South Dakota School of Mines, all fossil specimens used in this study are housed in the Georgia College & State University Vertebrate Paleontology collection (GCVP). Modern forms used for comparison are housed in the Georgia College & State University Mammal collection (GCM). Measurements were taken with Mitutoyo calipers accurate to within 0.05 mm.

The craniodental indices used were hypsodonty index, relative premolar row length, and relative muzzle width. Hypsodonty index was determined by dividing the height of M₃ by its width. Height was measured from the base of the crown to the tip of the protoconid on teeth that were fully erupted and showed only slight wear. Width was measured

between the outer surfaces of the protoconid and entoconid. Relative premolar row length was determined by dividing the premolar row length by the molar row length. Measurements were taken on the labial side of each series at the base of the crown. Relative muzzle width was determined by dividing the palatal width by the muzzle width. Palatal width was measured as the distance between the second molars at the level of the protocone, and muzzle width was measured at the junction of the premaxillary and maxillary bones.

Statistical analysis of the data was calculated by Instat 2.03. The test used to analyze the data was dependent on sample size and differences in standard deviations between the groups being compared. Because the unpaired t-test assumes equal standard deviations, this test was only used for sets of data with equal standard deviations. When comparing a trait from a single species with the same trait of a group of species within a certain feeding type, the standard deviations of each group would not be expected to be equal. When this occurred, the Mann Whitney test was used. This test checks for significant differences between the medians of the groups being analyzed and makes no assumptions about their standard deviations. This test was used to identify significant differences between *Hypertragulus* and *Leptomeryx* and the modern forms.

Measurements for relative muzzle width for all modern forms were taken from Janis and Ehrhardt, (1988). According to them, only grazers could be distinguished from other feeding types with a high degree of confidence, but mixed feeders in open habitats usually have the narrowest muzzles.

Several qualitative characteristics were also used to distinguish feeding types. These included 1) massiveness of the muzzle, 2) length of M³ versus M², 3) height of the molar basal pillars, 4) morphology of the central cavities of the molars, 5) size of the maxilla in lateral view, 6) presence or absence of a prominent protuberance above M¹, 7) the position of the orbit, 8) relative size of the ridge below the orbit, 9) relative size of the coronoid process, and 10) the shape of the ventral and posterior rims of the dentary.

Individual molar and premolar lengths were used to determine if a size difference existed between *Hypertragulus* and *Leptomeryx*. An unpaired t-test was used to determine if the size difference was significant for M₁ and M₂, and the Mann Whitney test was used to test for significant differences in M₃. Janis (1995) provides a thorough review of the reliability of comparing fossil and modern taxa.

RESULTS

Table 1 summarizes the data obtained for hypsodonty index for each group measured. *Hypertragulus* could not be distinguished from high level browsers ($p=.090$), unspecialized browsers ($p=.178$), and mixed feeders in closed habitats ($p=.467$). *Hypertragulus* is significantly more hypsodont than selective browsers are ($p=.026$), and significantly less hypsodont than mixed feeders in open habitats ($p=.005$), and grazers ($p=.036$). The Mann Whitney test was used to calculate p values for all groups except high level browsers and unspecialized browsers, whose p value was found using the

TABLE 1—Median, mean, and range of hypsodonty index for each group measured.

	n	Median	Mean	Range
<i>Hypertragulus</i>	2	2.15	2.15	2.12-2.17
<i>Leptomeryx</i>	7	1.67	1.67	1.62-1.72
High level browsers	5	1.32	1.45	1.18-2.23
Selective browsers	3	1.47	1.50	1.30-1.72
Unspecialized browsers	8	1.60	1.64	1.23-2.29
Mixed closed habitats	19	1.97	2.07	1.12-3.03
Mixed open habitats	37	3.90	3.90	2.12-5.30
Fresh grass grazers	7	3.59	3.39	2.35-4.05
Grazers	9	4.87	4.87	3.77-6.12

unpaired t test. There was not a large enough sample size to calculate a p value using the Mann Whitney test and the standard deviations were not equal so an unpaired t test could not be used to test for a significant difference between *Hypertragulus* and fresh grass grazers.

Leptomeryx could not be distinguished from high level browsers ($p=1.06$), selective browsers ($p=.383$), and unspecialized browsers ($p=.121$). *Leptomeryx* is significantly less hypsodont than mixed feeders in closed habitats ($p=.010$), mixed feeders in open habitats ($p<.0001$), fresh grass grazers ($p=.0006$), and grazers ($p=.0002$). The Mann Whitney test was used to calculate all p values.

Hypertragulus is significantly more hypsodont than *Leptomeryx* with an unpaired t test p value of $<.0001$. There was not a significant difference between the relative premolar row length of the browsers and mixed feeders that were measured ($p=0.1075$).

The mean relative premolar row length for *Leptomeryx* was .917 and the median was .915. This was not significantly different ($p=.257$) from browsers whose mean relative premolar row length was .859 and median was .822. *Leptomeryx* had a significantly longer relative premolar row length than mixed feeders ($p=.002$) whose mean was .734 and median was .762.

Table 2 lists the qualitative characteristics observed in *Hypertragulus* and *Leptomeryx* and whether they are more like browsers or grazers in these features.

The lengths of M^2 and M^3 were both browser-like in that they were approximately equal in both *Hypertragulus* and *Leptomeryx*. The molar basal pillars are also browser-like in that they are small and do not reach the occlusal surface. The molar central cavities are also browser-like, being simple crests with no complex folding.

In lateral view (Figure 1), the size of the maxilla in *Hypertragulus* and *Leptomeryx* is small like modern browsers. There is no maxillary protrusion like that often found in grazers in either *Hypertragulus* or *Leptomeryx*.

The position of the orbit in both *Hypertragulus* and *Leptomeryx* is browser-like in that it starts above M^2 in both. In *Hypertragulus*, the zygomandibularis leaves a pronounced ridge on the zygomatic arch like that found in grazers. In *Leptomeryx*, this ridge is small and browser-like.

Leptomeryx has a relatively more massive coronoid pro-

TABLE 2—Qualitative characteristics observed in *Hypertragulus* and *Leptomeryx*.

Characteristic	<i>Hypertragulus</i>	<i>Leptomeryx</i>
Muzzle massiveness	browser or mixed feeder	browser or mixed feeder
Length of M^2 versus M^3	browser	browser
Molar basal pillars	browser	browser
Molar central cavities	browser	browser
Size of maxilla	browser	browser
Prominence above M^1	—	browser
Position of orbit	browser	browser
Size of ridge below orbit	grazer	browser
Size of the Coronoid Process	mixed feeder	browser
Shape of the dentary	mixed feeder	browser?

cess than *Hypertragulus*. The large coronoid process in *Leptomeryx* would indicate that the temporalis muscle and therefore the orthal retraction phase of the chewing cycle were more important in this animal than in *Hypertragulus*. The ventral rim of the dentary of *Hypertragulus* is like that of mixed feeders in that it is concave and thin lateromedially. The ventral rim of the dentary of *Leptomeryx* is fuller and more like that of browsers. The posterior rims of the dentaries of both *Hypertragulus* and *Leptomeryx* are concave like those of browsers.

There was a significant size difference between *Hypertragulus* and *Leptomeryx*, with *Hypertragulus* being much smaller. The mean length of M_1 of *Hypertragulus* is 5.09 mm and the mean length of M_1 of *Leptomeryx* is 6.53mm. The unpaired t test p value is $<.0001$. The mean length of M_2 of *Hypertragulus* is 5.35 mm and the mean length of M_2 of *Leptomeryx* is 6.78mm. The unpaired t test p value is $<.0001$. The difference in standard deviations between M_3 was too large to calculate a p value using the unpaired t test. The Mann Whitney p value was significant at $<.0001$.

DISCUSSION

The molars in *Hypertragulus* are significantly higher crowned than those in *Leptomeryx* (Table 1), however, neither falls into the range required for hypsodonty (Janis, 1988). The crown height for both taxa falls into the mesodont range (*Leptomeryx* at the low end and *Hypertragulus* in the middle). The crown height in *Hypertragulus* groups it with high level browsers, unspecialized browsers, and mixed feeders in closed habitats. The crown height exhibited by *Leptomeryx* groups it clearly with the browsers (no overlap with either group of mixed feeders).

Hypertragulus groups with mixed feeders such as *Antilocapra*, the North American pronghorn, and *Boselaphus*, the Indian nilgais, with regard to relative premolar row length. *Leptomeryx* has a premolar row length typical of modern browsers.

A comparison of the qualitative characters examined (Table 2) reveals that *Leptomeryx* is browser-like in almost all traits, while *Hypertragulus* shares some traits with browsers and others with mixed feeders. Relative muzzle width is

not significantly different in *Hypertragulus* and *Leptomeryx*. The narrow muzzles of both taxa clearly indicate they are not like modern grazers in this feature. The relatively larger coronoid process on the lower jaw of *Leptomeryx* indicates orthal retraction, the food acquisition phase of mastication, took more effort in this animal than in *Hypertragulus*. This distinction could indicate *Hypertragulus* was more selective in its dietary habits than *Leptomeryx*. The angular shape of the lower jaw in *Hypertragulus* and *Leptomeryx* is clearly different (Figure 1). *Hypertragulus* is more like that of primitive artiodactyls, possibly indicating a more generalized jaw muscular pattern. *Leptomeryx* has a relatively full and thick mandibular angle indicating a more specialized jaw muscle arrangement. This trait would therefore imply a more specialized feeding pattern for *Leptomeryx*.

Based on their similar body size and anatomical traits, the closest modern analog for *Hypertragulus* appears to be *Moschus* the Asiatic musk deer. *Moschus* has a varied diet consisting of grass, moss, twigs, and other leafy material (Nowak, 1991). *Leptomeryx*, on the other hand compares most favorably to the modern *Pudu*, the South American pudu, and *Tragulus*, the Asiatic mouse deer. The pudu is a generalist browser and the mouse deer is a selective browser (Nowak, 1991).

CONCLUSIONS

Analysis of the craniodental morphology of these primitive ruminants indicates that *Hypertragulus* was probably a mixed feeder and *Leptomeryx* was a browser. These small herbivores were clearly sympatric spatially and temporally during much of the Orellan. Based on the results of this study, however, it would appear that these two taxa did not overlap significantly in food requirements. *Hypertragulus* does not appear in the fossil record after the Whitneyan. Whether *Leptomeryx* played an indirect role in the termination of the *Hypertragulus* lineage could not be determined from this study. Based on their success through the middle Miocene it would appear that leptomerycids were well adapted to a browsing mode of life. Questions regarding the adaptive radiation of the horned ruminants should consider the browsing mode of life as a likely starting point for the evolution of modern pecorans.

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PALEOECOLOGICAL IMPLICATIONS OF THE CRANIODENTAL AND PREMAXILLA MORPHOLOGIES OF TWO RHINOCEROTIDS (PERISSODACTYLA) FROM BADLANDS NATIONAL PARK, SOUTH DAKOTA

ALFRED J. MEAD¹ AND WILLIAM P. WALL²

¹University of Nebraska State Museum, Division of Vertebrate Paleontology, Lincoln, NE 68588-0514

²Department of Biology, Georgia College and State University, Milledgeville, GA 31061

ABSTRACT—Analysis of the craniodental and premaxilla morphologies suggests differing feeding strategies for two late Eocene/Oligocene rhinocerotoids, *Hyracodon* and *Subhyracodon*, from Badlands National Park, South Dakota. The relatively longer upper and lower premolar rows, wider central incisors, relatively wider and more stout premaxillae, complete anterior dentition, and strong cingula indicates that *Hyracodon* was morphologically similar to modern browsers and mixed feeders. The proportionately shorter premolar rows, enlarged lateral incisors, relatively narrower and more delicate premaxillae, and less well developed cingula in *Subhyracodon* illustrates similarities to modern grazers and mixed feeders. *Hyracodon* was likely a browser of nuts, twigs, and tougher vegetation growing on the distal reaches of a bushland floodplain. *Subhyracodon* appears to have been a selective-mixed feeder utilizing the more high-fiber vegetation of wooded habitats proximal to the Oligocene water courses.

INTRODUCTION

A THOROUGH understanding of the paleoautecology of extinct mammalian species enables researchers to generate more accurate interpretations of paleoenvironments. Among the ecological attributes, dietary preference is possibly the most informative. Various cranial morphological traits (e.g. premaxilla shape) have been used to determine dietary preferences of extinct ungulate species (Gordon and Illius, 1988; Solounias and Saunders, 1988; Solounias et al., 1988; Solounias and Moelleken, 1993a; Dompierre and Churcher, 1996). Tooth microwear analysis (Solounias and Moelleken, 1992a, b, 1993b, 1994), tooth wear facet analysis (Janis, 1990a), and enamel isotope composition (Wang et al., 1994) have also been used to discern dietary preference. Additionally, craniodental indices have been employed to compare and contrast ungulate feeding strategies (Janis, 1988, 1990b, c, 1995; Janis and Ehrhardt, 1988). These craniodental indices include the hypsodonty index (HI), relative muzzle width (RMW), relative incisor width (RIW), and relative lengths of the upper and lower premolar series (RLPM).

Hyracodon (Hyracodontidae) and *Subhyracodon* (Rhinocerotidae) were two temporally sympatric rhinocerotoids that inhabited the area of Badlands National Park (BADL), South Dakota, during the latest Eocene through the late-middle Oligocene (Emry et al., 1987). Their fossilized remains are commonly found in the same White River Group horizons within BADL, but usually in differing lithofacies. This apparent dichotomous facies distribution has led researchers to suggest that *Hyracodon* was an open plains dweller and *Subhyracodon* was a denizen of the riparian strip (Matthew, 1901; Clarke et al., 1967). The purpose of this study is: 1) to utilize craniodental indices and premaxilla shapes as indicators of dietary preferences in *Hyracodon* and *Subhyracodon*;

and 2) to speculate on modern analogues for these two Oligocene rhinocerotoids.

MATERIALS AND METHODS

The *Hyracodon* and *Subhyracodon* material examined in this study was collected from BADL and is housed in the Georgia College & State University Vertebrate Paleontology (GCVP) and South Dakota School of Mines (SDSM) collections. Only molars that were fully erupted and exhibited light wear were used for the calculation of HI values ($HI = H/W$). The heights and widths of m3's were taken at the protoconid on the labial side of the lower molars. The heights and widths of M3's were measured on the labial side at the paracone. Height was measured as the distance from the occlusal surface to the dentine/enamel junction, and the width measured as the maximum tooth width normal to the trend of the cheek tooth row. For the calculation of the relative muzzle width ($RMW = MW/PW$), palatal width (PW) and muzzle width (MW) were measured between the M2 protocones and at the maxilla/premaxilla suture respectively. The lower incisors were measured at their widest point above the alveolar rim for the calculation of the relative incisor width ($RIW = i1/i2$ or $i1/i3$). To determine the relative length of the premolar series ($RLPM = PM/M$), upper and lower premolar (PM) and molar series (M) were measured parallel to the labial side of the cheek tooth row at bone height. Additional RLPM measurements were obtained from the extant rhinoceroses *Ceratotherium simum*, *Diceros bicornis*, *Rhinoceros unicornis*, and the Miocene rhinoceroses *Aphelops* and *Teleoceras* in the University of Nebraska State Museum (UNSM) collections. The Student's t-test was used to analyze the comparative data. Photographs of the extant *Dicerorhinus sumatrensis* (Groves and Kurt, 1972) were examined to determine its RLPM values. Published HI and RMW values (Janis, 1988; Janis and

Ehrhardt, 1988) for extant perissodactyls with known dietary preferences and habitat usage were used for comparative purposes. Habitat usage and dietary preferences of extant ungulates comes from Nowak (1991) unless otherwise stated.

The premaxillae morphologies of *Hyracodon* and *Subhyracodon* were qualitatively compared to a variety of modern browsers (*Tapirus terrestris*, *T. bairdii*, *D. bicornis*, *Odocoileus virginianus*, *O. hemionus*, *Giraffa camelopardalis*), grazers (*Equus caballus*, *E. burchelli*, *E. grevyi*, *C. simum*), and mixed feeders (grasses represent between 10% and 90% of the diet; *R. unicornis*, *Tayassu tajacu*, *Antilocapra americana*, *Cervus elaphus*, *Boselaphus tragocamelus*) in the Georgia College & State University Mammal (GCM) and UNSM collections.

RESULTS

Both *Hyracodon* and *Subhyracodon* are brachydont, lophodont rhinocerotoids exhibiting some degree of upper premolar molarization. *Hyracodon* retains complete anterior dentition and strong cingula on the cheek teeth. *Subhyracodon* exhibits a reduced number of incisors, absence of canines, and less well developed cingula on the cheek teeth. HI values (Table 1) for both m3's and M3's are nearly identical between *Hyracodon* and *Subhyracodon*, and when compared to HI values for extant perissodactyls, fall between those of the browsing *T. terrestris* and the mixed feeding *R. unicornis*.

A discernible difference exists between the lower RLPM values for *Hyracodon* and *Subhyracodon* denoting a proportionately longer lower premolar row in *Hyracodon*. The rela-

tive length of the upper premolar series is significantly ($\alpha = .10$) longer in *Hyracodon*. *Hyracodon* and the Miocene rhinocerotid *Aphelops* exhibit nearly identical RLPM values while the *Subhyracodon* RLPM values are intermediate between those of *Aphelops* and *Teleoceras*.

The extant *D. bicornis* exhibits an upper RLPM ratio intermediate between those of *Hyracodon* and *Subhyracodon*, and a lower RLPM value nearly equal to that of *Subhyracodon*. The *R. unicornis* lower RLPM values are nearer those of *Hyracodon* while the upper RLPM values are more similar to those of *Subhyracodon*. Both RLPM ratios of *C. simum* are nearly equal to those of *Subhyracodon*. Photographs of the upper cheek tooth rows of *Dicerorhinus sumatrensis* demonstrates that the upper premolar series is longer than the molar series, similar to the upper RLPM condition of *Hyracodon*.

The central incisors of *Hyracodon* are nearly the same size as the lateral incisors while the central incisors in *Subhyracodon* are much smaller than the lateral incisors. The RMW of study specimens exhibiting non-distorted MW and PW is not significantly different for *Hyracodon* and *Subhyracodon*. Several extant perissodactyls exhibit RMW values similar to those of *Hyracodon* and *Subhyracodon*. The RMW value of 0.840 for *Hyracodon* is within 0.2 of *Equus grevyi* (0.822), *E. hemionus* (0.838), *Ceratotherium simum* (0.842), and *Diceros sumatrensis* (0.847). The average RMW of 0.910 for *Subhyracodon* is very similar to that of *E. kiang* (0.900) and within 0.025 of *E. przewalskii* (0.885). The relatively widest muzzles in extant perissodactyls belong to the mixed feeding *R. unicornis* and the browsing *R. sondaicus*. The browsing perissodactyls *Diceros bicornis*, *T. indicus*, and *T. terrestris* exhibit the relatively narrowest muzzles. However, *D. bicornis* lacks upper incisors and exhibits greatly reduced premaxillae.

The premaxillae of *Hyracodon* (Figure 1A) are rounded and stout, whereas those of *Subhyracodon* (Figure 1B) are more pointed and delicate. Qualitative comparisons to the artiodactyl premaxillae morphologies figured by Gordon and Illius (1988) and Solounias et al. (1988) indicate that the shape of the *Hyracodon* premaxillae more closely resembles the mixed feeding artiodactyls (e.g. *Cervus elaphus*, Fig. 1N) while the premaxillae of *Subhyracodon* (Figure 1B) more closely resembles those of the browsing artiodactyls (e.g. *G. camelopardalis*, Figure 1D). The same results are obtained when the quantitative method of premaxillae analysis (Dompierre and Churcher, 1996) is applied. In terms of robustness, the *Hyracodon* premaxillae is similar to that exhibited by *Tayassu tajacu* (Figure 1M).

A comparison of the premaxillae of *Hyracodon* (Figure 1A) with modern perissodactyls demonstrates a striking similarity to *Tapirus terrestris* (Figure 1C). None of the extant perissodactyls examined provides a reasonable modern analogue for the premaxilla shape of *Subhyracodon*. Unlike *Hyracodon* or *Subhyracodon*, the premaxillae of extant grazers (Figures 1G, H, I, and J) are more bulbous with broader incisor arcades. The only mixed feeding perissodactyl figured (*Rhinoceros unicornis*, Figure 1K) exhibits much wider premaxillae than either *Hyracodon* or *Subhyracodon*. The

TABLE 1—Calculated craniodental indices. () = number of individuals sampled.

Oligocene rhinocerotids			
	<i>Hyracodon</i>	<i>Subhyracodon</i>	
dental formula	3/3,1/1,4/3,3/3	2/2,0/0,4/4-3,3/3	
Hypsodonty index (HI = H/W)			
m3 light wear	0.983 (10)	0.938 (5)	
M3 light wear	0.826 (13)	0.730 (5)	
Relative length of premolars (RLPM = PM/M)			
lower premolar series	0.869 (25)	0.783 (14)	
upper premolar series	1.050 (21)	0.859 (11)	
Relative incisor width (RIW = i1/i3 or i1/i2)	1.030 (8)	0.471 (10)	
Relative muzzle width (RMW = MW/PW)	0.840 (14)	0.910 (4)	
Miocene rhinocerotids			
	<i>Aphelops</i>	<i>Teleoceras</i>	
RLPM = PM/M			
lower premolar series	0.820 (3)	0.488 (9)	
upper premolar series	1.050 (3)	0.671 (10)	
Extant rhinocerotids			
	<i>D. bicornis</i>	<i>R. unicornis</i>	<i>C. simum</i>
RLPM = PM/M			
lower premolar series	0.788 (1)	0.957 (1)	0.762 (2)
upper premolar series	0.901 (1)	0.737 (1)	0.819 (2)

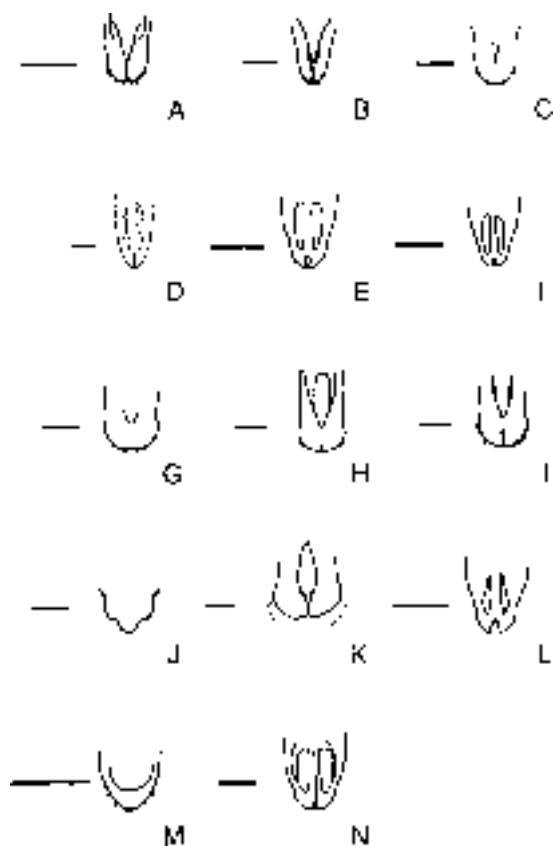


FIGURE 1—Premaxillae of (A) *Hyracodon*, (B) *Subhyracodon*, extant browsers [(C) *Tapirus terrestris*, (D) *Giraffa camelopardalis*, (E) *Odocoileus virginianus*, (F) *O. hemionus*], grazers [(G) *Equus burchelli*, (H) *E. caballus*, (I) *E. grevyi*, (J) *Ceratotherium simum*], and mixed feeders [(K) *Rhinoceros unicornis*, (L) *Antilocapra americana*, (M) *Tayassu tajacu*, (N) *Cervus elaphus*]. Scale bars = 4 cm.

premaxillae of *C. simum* (Figure 1J) and *D. bicornis* (not figured) are greatly reduced. *C. simum*, a grazer, possesses a broad, squarish lip that functions as a cropping mechanism. *D. bicornis*, a browser, has a narrow prehensile lip (hook lip) used to pull browse items into the mouth. Both *Hyracodon* and *Subhyracodon* lack the elevated and retracted nasals, expanded nasal incisions, and rostral muscle scars indicative of a prehensile lip or proboscis (Wall, 1980).

DISCUSSION

Paleosol analyses suggest that the paleo-vegetation of the BADL region was transitional from middle Eocene tropical forests, to early Oligocene open woodlands, to late Oligocene open bushland (Retallack, 1983). Some of the paleosols in the Pinnacles area of BADL preserve root traces suggestive of low desert scrub (Retallack, 1983). Although direct botanical evidence is sparse, wooded areas with succulent vegetation most likely existed in the riparian strips, while dry scrub and tougher vegetation was more abundant distal to the Oligocene stream courses.

Janis (1995) used the combination of HI, RLPM, and RMW to determine the general characteristics of the three

major feeding groups for extant ungulates. When compared to grazers, browsers exhibit a low HI, long premolar row, and medium width muzzle. Grazers have a higher HI, shorter premolar row, and a relatively broader muzzle. Mixed feeders exhibit a moderate HI, short premolar row, and narrow muzzle (narrowest of the three groups). Tests of these dietary divisions on extant ungulates show that grazers and browsers are nearly always correctly identified.

The HI values for *Hyracodon* and *Subhyracodon* suggest that the cheek teeth were optimally suited for browsing. *Hyracodon* possessed minimally enlarged central lower incisors and *Subhyracodon* exhibited enlarged lateral lower incisors. Modern grazers tend to possess subequal lower incisors that are relatively broad, browsers possess enlarged central incisors, and intermediate feeders possess significantly wider lateral incisors than browsers (Janis and Ehrhardt, 1988). Direct analogy would suggest browsing habits for *Hyracodon* and mixed feeding habits for *Subhyracodon*. However, enlarged lateral lower incisors are a defining characteristic of the Rhinocerotidae and may not reflect a feeding adaptation in *Subhyracodon*.

The RMW values of *Hyracodon* are most similar to the extant *E. grevyi*, *E. hemionus*, *C. simum*, and *Dicerorhinus sumatrensis*. *Equus grevyi* is a grazer that consumes fibrous grasses that are inedible to cattle and other ungulates in sub-desert grasslands. *Equus hemionus* inhabits the flat deserts of Asia subsisting on grass and low succulent plants. *Ceratotherium simum* inhabits the open forests and plains of Africa consuming a variety of grasses (Groves, 1972) and *D. sumatrensis* inhabits hilly, humid forests, eating fruits, leaves, twigs, and bark (Groves and Kurt, 1972). The RMW of *Subhyracodon* is most similar to the extant *E. kiang* and extinct *E. przewalskii*. *Equus kiang* inhabits the Tibetan Plateau and grazes on grasses and low succulent plants. *Equus przewalskii* inhabited the plains and hills of eastern Europe and grazed on a variety of grasses.

The proportionately longer upper premolar row in *Hyracodon* is similar to the conditions found in the browsing Miocene rhinocerotid *Aphelops* (Prothero et al., 1989) and the extant browsing *Dicerorhinus sumatrensis*. The proportionately shorter premolar row in *Subhyracodon* is similar to the mixed-feeding *R. unicornis* and grazing *C. simum*. Both the upper and lower RLPM values of the browsing *Diceros bicornis* are intermediate between the values for *Hyracodon* and *Subhyracodon*. When compared to the standard craniodental morphologies determined by Janis (1995), *Hyracodon* most closely resembles a modern browsing ungulate while *Subhyracodon* favors the mixed feeding group. Well developed cingula on the cheek teeth, as exhibited by *Hyracodon*, are generally recognized as an indication of an herbivore utilizing thorny or rough vegetation. Less well developed cingula on the cheek teeth, as in *Subhyracodon*, suggests an organism not optimally suited to utilize such vegetation.

The premaxillae morphology of *Hyracodon* is similar to that exhibited by *Cervus elaphus*, *Tayassu tajacu*, and *Tapirus terrestris*. *Cervus elaphus* is both a grazer and a browser,

utilizing fresh grasses in the spring and early summer, and browsing forbs, woody plants, shrubs and conifers in the late summer, fall, and winter. *Tayassu tajacu* is a browsing artiodactyl of the southwestern United States that grubs for fruits, berries, tubers, bulbs, and rhizomes. *Tapirus terrestris* is a browser of leaves, buds, twigs, and fruits of low-growing terrestrial plants. The premaxillae morphology of *Subhyracodon* is most similar to *G. camelopardalis*, a select browser that consumes mainly leafy vegetation from acacia, mimosa, and wild apricot trees.

Speculation concerning modern analogs for *Hyracodon* and *Subhyracodon* requires comparisons to both perissodactyls and artiodactyls. Taking into consideration the craniodental indices, incisor arcade structure, apparent habitat usage, and appendicular morphology, *Tayassu tajacu* of Arizona and Texas may be the most appropriate modern analog for *Hyracodon*. Although *T. tajacu* is an artiodactyl, it lacks the rumen digestive system found in the more diverse ruminants. *Tayassu tajacu* inhabits desert scrub and arid woodlands, escaping danger with quick bursts of speed. Bio-mechanical analysis of locomotor morphology suggests that *Hyracodon* was functionally similar to modern wild pigs (Wall and Hickerson, 1995). The robust snout of *T. tajacu* is used to grub for food. Cactus fruit, berries, and bulbs are the primary dietary components. A grubbing nature for *Hyracodon* could help to explain the presence of the robust premaxillae and nasals. *Subhyracodon* is enigmatic in comparison to extant ungulates. The craniodental indices suggest an organism more suited as a mixed feeder/grazer, yet the premaxilla morphology, which is very similar to *G. camelopardalis*, indicates a select browser. Although the premaxillae morphologies differ, the South American *Tapirus terrestris* may provide a legitimate ecological analogue for *Subhyracodon*.

CONCLUSIONS

The analysis of craniodental and premaxilla morphologies suggests differing feeding habits for the Oligocene rhinocerotoids *Hyracodon* and *Subhyracodon*. The relatively longer upper and lower premolar rows, wider central incisors, relatively wider and more stout premaxillae, complete anterior dentition, and well developed cingula suggests that *Hyracodon* was morphologically similar to modern browsers and mixed feeders. The proportionately shorter premolar rows, enlarged lateral incisors, narrower and more delicate premaxillae, and less well developed cingula in *Subhyracodon* suggests an herbivore more morphologically suited as a grazer and mixed feeder. The distinctive premaxillae shape exhibited by *Subhyracodon* is suggestive of a selective mixed feeding perissodactyl. This evidence suggests that *Hyracodon* was a browser of the nuts, fruits, twigs, and tougher vegetation growing on the distal reaches of bushland floodplains present in the region of BADL during the Oligocene. *Subhyracodon* was likely a mixed feeder utilizing the more high-fiber vegetation and succulent browse in the wooded habitats proximal to Oligocene water courses.

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DIETARY IMPLICATIONS OF JAW BIOMECHANICS IN THE RHINOCEROTOIDS *HYRACODON* AND *SUBHYRACODON* FROM BADLANDS NATIONAL PARK, SOUTH DAKOTA

ALFRED J. MEAD¹ AND WILLIAM P. WALL²

¹University of Nebraska State Museum, Division of Vertebrate Paleontology, Lincoln, NE 68588-0514

²Department of Biology, Georgia College and State University, Milledgeville, GA 31061

ABSTRACT—Analysis of the cranial morphologies of the two rhinocerotoids, *Hyracodon* and *Subhyracodon*, from Badlands National Park, South Dakota, suggests differing feeding modes for these sympatric herbivores. Morphological differences are distinguished by means of distortion grids and mandibular angle quadrant analyses. The biomechanical ability of each rhinoceros is estimated using adductor muscle mass reconstruction and median muscle fiber lengths and moment arm ratios. *Hyracodon* was a brachydont hyracodontid with a brachy- to mesocephalic skull, posteriorly expanded mandibular angle, more anteriorly inclined deep masseter, enlarged coronoid process, and a relatively larger temporalis. *Subhyracodon* was a brachydont rhinocerotid with a dolichocephalic skull, vertically enlarged masseteric fossa, more vertically inclined deep masseter, and a proportionately smaller temporalis. Given an Oligocene mosaic landscape of lush succulent and woody riparian vegetation bordered by bunch grass bushland floodplain, *Hyracodon* was morphologically and functionally better adapted to browse the rougher low vegetation (twigs, buds, bark, and tough leafy material) of the bushland distal to the water courses, whereas *Subhyracodon* was more suited to utilize the succulent vegetation and high browse of the wooded riparian strip.

INTRODUCTION

DETERMINING THE diets of extinct species is vital for an understanding of the paleoecology of a fossil fauna. Direct evidence of paleodiet (e.g. Voorhies and Thomasson, 1979) is seldom available to the vertebrate paleontologist, and thus alternative avenues of analysis must be pursued. It is readily apparent that the structure of the jaws and teeth and the muscles that move them are indicative of particular modes of feeding (Smith and Savage, 1959; Janis, 1995). Since the shapes and masses of the jaw adductor muscles can never be known (only approximated), biomechanical studies of fossils require that the feeding mechanisms be reduced to a system of forces and levers (DeMar and Barghusen, 1972). Studies of jaw biomechanics utilizing vector analysis have proven useful in the analysis of fossil species (Gingerich, 1971; Naples, 1987; Joeckel, 1990).

The late Eocene/Oligocene sediments of the White River Group in Badlands National Park (BADL), South Dakota, have yielded a wide array of Chadronian, Orellan, and Whitneyan (North American Land Mammal Ages) mammalian taxa. If their fossil record is a valid indicator of past abundance, *Hyracodon* (Hyracodontidae) and *Subhyracodon* (Rhinocerotidae) were the most common large (> 100 kg) herbivores (horses and oreodonts being medium-sized) of the Orellan in the central Great Plains region. *Subhyracodon* was approximately 120 cm at the shoulder and, although larger, exhibited similar skeletal proportions to modern tapirs such as *Tapirus terrestris* (Scott, 1941). The dental formula is 2/2, 0/0, 4/4-3, 3/3. *Hyracodon* was smaller than *Subhyracodon* and more agile, as suggested by the elongate metapodials. It was approximately 80 cm at the shoulders with a proportionately longer neck than that of any known rhinocerotoid (Scott, 1941). The dental formula is 3/3, 1/1, 4/3, 3/3. Recent bio-

mechanical analysis of the locomotor abilities of *Hyracodon* suggest subcursorial habits, similar to extant wild pigs and peccaries (Wall and Hickerson, 1995).

Hyracodon and *Subhyracodon* have been cited as indicator species of separate sedimentary facies in BADL. Matthew (1901) determined *Hyracodon* to be indicative of his Clay fauna (plains dwellers) and *Subhyracodon* indicative of the Sandstone fauna (forest dwellers). Clark et al. (1967) concluded that *Subhyracodon* was indicative of a Near Stream fauna of the Lower Nodular Zone (Orellan) while *Hyracodon* was representative of the Open Plains fauna. Wilson (1975) reported the occurrence of *Subhyracodon* exclusively in the *Protoceras* Channels and *Hyracodon* only in the overbank mudstones of the *Leptauchenia* Beds (Whitneyan) in the Palmer Creek area.

The purpose of the present study is to: 1) illustrate cranial morphological differences; 2) attempt to reconstruct the jaw adductor musculature; 3) estimate jaw biomechanical abilities; and 4) suggest possible feeding modes for *Hyracodon* and *Subhyracodon* that may explain the observed dichotomous facies distribution.

MATERIALS AND METHODS

Adult *Hyracodon* (4 skull/jaws) and *Subhyracodon* (3 skull/jaws, 4 jaws) material examined in the present study was collected from BADL and is housed in the Georgia College & State University Vertebrate Paleontology (GCVP) collection. Comparisons with recent mammals are based on study of specimens housed in the Georgia College & State University Mammalogy (GCM) collection. To illustrate relative morphological differences, Cartesian transformations were constructed (as described by Thompson, 1961) in both the lateral (Figure 1) and dorsal (Figure 2) aspects for *Hyrachyus* (a primitive rhinocerotoid), *Hyracodon* and *Subhyracodon*. Quadrant analyses (Figure 3) of the mandibular angles of

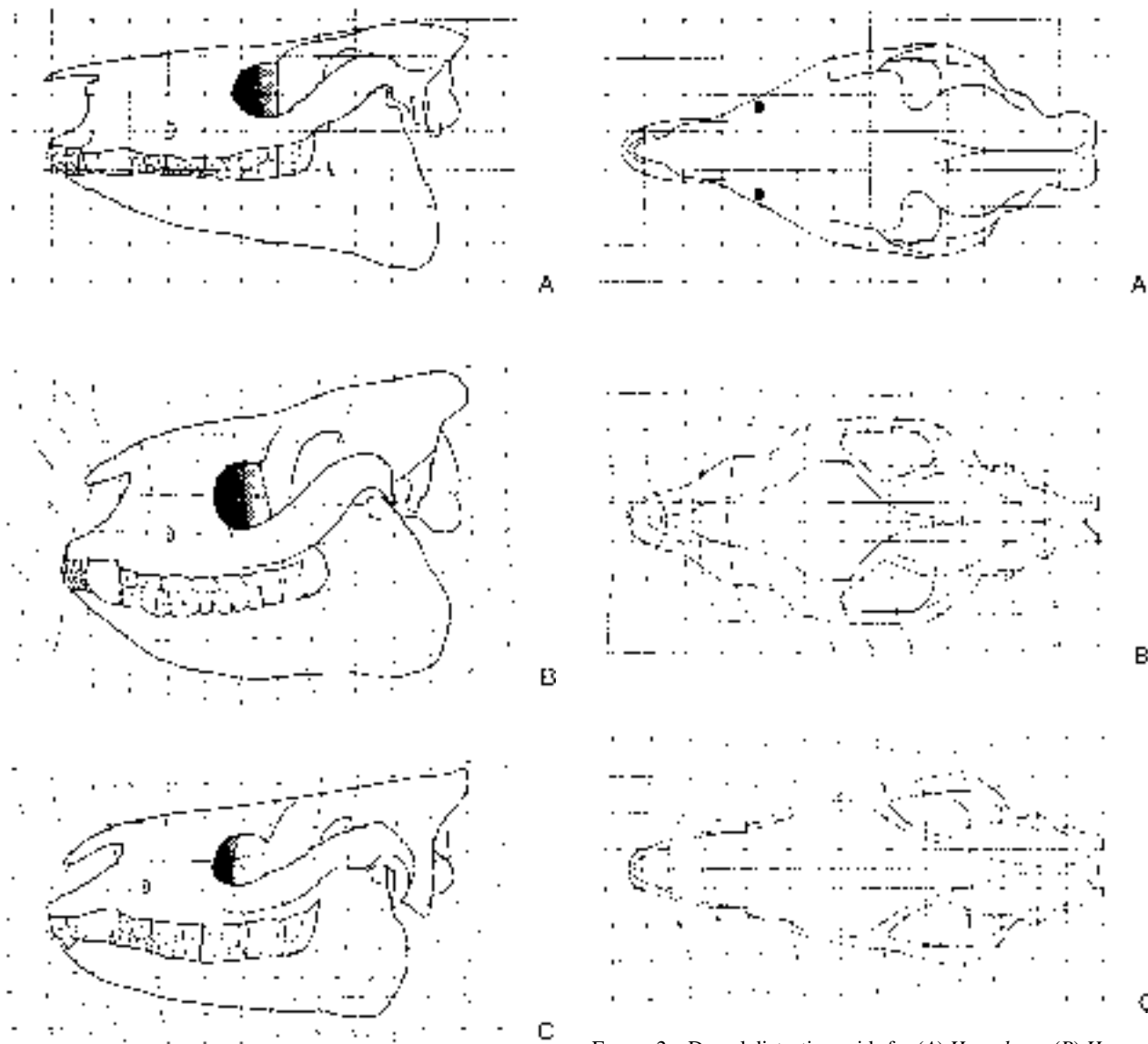


FIGURE 1—Lateral distortion grids constructed for (A) *Hyrachyus*, (B) *Hyracodon*, and (C) *Subhyracodon*. *Hyrachyus* modified from Osborn and Wortman (1894: Plate 2).

Hyracodon and *Subhyracodon* were performed to quantify the attachment areas for the deep and superficial masseters in relation to the cranio-mandibular joint (CMJ). The mandibular angle was systematically divided into four quadrants and a dot grid was used to determine the percentage of the total occurring within each quadrant.

Jaw adductor muscle reconstructions were attempted for *Hyracodon* and *Subhyracodon* with the aid of muscle scars on the fossil material mentioned above. Although unknown, all muscles are assumed to exhibit parallel fibers. Fresh heads of the extant *Odocoileus virginianus*, *Alces alces*, *Antilocapra americana*, and *Cervus elaphus* were dissected and served as general templates for the reconstructions. The following estimates were used for the origins of the adductor musculature: superficial masseter, anterior to the zygomatic arch, above the

FIGURE 2—Dorsal distortion grids for (A) *Hyrachyus*, (B) *Hyracodon*, and (C) *Subhyracodon*. *Hyrachyus* modified from Osborn and Wortman (1894: Plate 2). *Hyracodon* and *Subhyracodon* modified from Scott (1941).

middle of M1 in both genera; deep masseter, on the zygomatic arch with muscle fibers perpendicular to the central axis of the arch; temporalis, the distal end of the temporal fossa, anterior edge of the occipital ridge.

Muscle mass proportions were estimated using modeling clay as described by Turnbull (1976). The masseter group includes the superficial masseter, deep masseter, and zygomaticomandibularis. The pterygoid estimate includes the lateral and medial pterygoid. The temporalis estimate includes the deep and superficial temporalis. The proportions of the superficial and deep masseter and zygomaticomandibularis in the total masseter group mass were estimated using known percentages for modern ungulates exhibiting similarly oriented zygomatic arches and similarly shaped mandibular angles (Turnbull, 1970). *Ovis aries* (30% superficial; 70% deep) was used for *Subhyracodon* and *Odocoileus virginianus* (38%

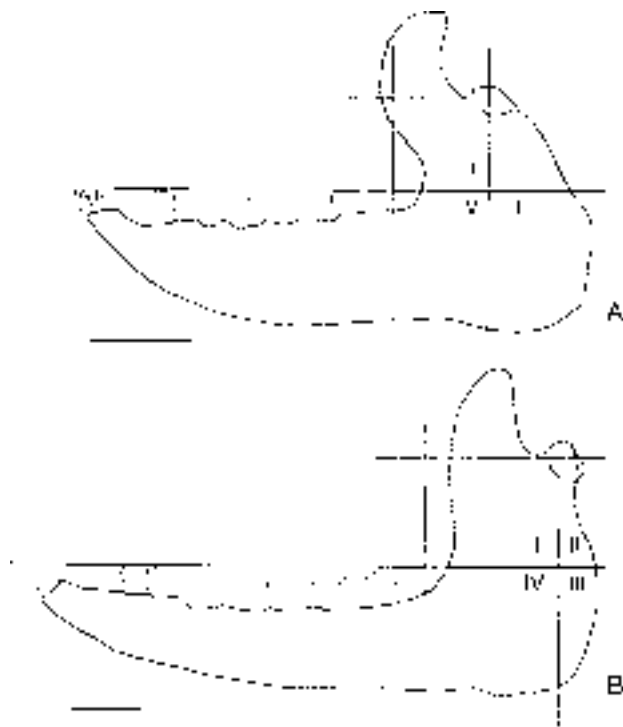


FIGURE 3—Labial views of left lower jaws of (A) *Hyracodon* and (B) *Subhyracodon* with mandibular angles divided into quadrants as discussed in text. Scale = 4 cm.

superficial; 62% deep) was used for *Hyracodon*.

Lengths of the median muscle fibers for the superficial masseter, deep masseter, and temporalis were estimated using nylon string cut to lengths connecting the middle of the muscle scars for each origin and its corresponding insertion (Naples, 1987; Joeckel, 1990). The median muscle fibers were superimposed upon line drawings of the skulls (Figure 4) at the mid-point of observed muscle scars. Perpendicular moment arms were inserted between the median fibers and the mandibular condyle (CMJ). Force vectors (Figure 5) were estimated based on the lengths and orientation of the median fibers and the approximate proportions of the total adductor muscle mass of each muscle. A total vector length of 15 cm was arbitrarily chosen for each analysis. The angle of each vector was measured against a reference line in the occlusal plane of the cheek teeth. Estimation of the role of the medial and lateral pterygoid in fossil mammals is difficult due in part to the variability exhibited in modern mammals (Janis, 1983). For this reason the pterygoid group is treated as a single force with a line of action the same as the deep masseter.

RESULTS

Distinct differences are evident when the skulls of *Hyracodon* and *Subhyracodon* are compared to the primitive rhinocerotoid cranial morphology exhibited by *Hyrachyus* (Figures 1A and 2A). *Hyracodon* (Figure 1B) exhibits a vertically expanded temporal fossa and sagittal crest, and a shorter, deeper rostrum. The coronoid process is expanded both vertically and horizontally, as is the posterior half of the zygo-

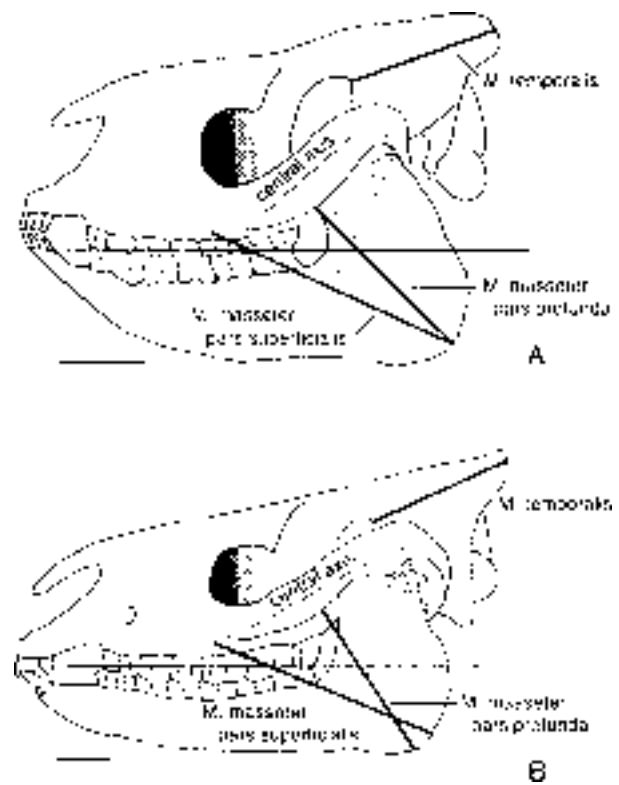


FIGURE 4—Left lateral view of the skulls of (A) *Hyracodon* and (B) *Subhyracodon* illustrating the length and orientation of each median muscle fiber (heavy solid line), the moment arm of each fiber (light dashed line), and the trend of the central axis of each zygomatic arch (heavy dashed line). Scale = 4 cm.

matic arch. The premaxilla is shortened and the maxilla expanded anteroposteriorly. The mandibular angle is enlarged primarily ventrally, but also slightly posteriorly. The frontals are anteroposteriorly expanded above and anterior to the orbits, and also in the posterior-most region of the parietals (Figure 2B). The posterior parietals are laterally constricted. The anterior and posterior zygomatic arch and premolar region of the rostrum are laterally expanded. The nasals above the premolars are anteroposteriorly and laterally reduced.

The temporal region of *Subhyracodon* (Figure 1C) is enlarged but not to the extent seen in *Hyracodon*. The rostrum is longer immediately anterior to the orbit and above the premaxillae, but shortened in the region of the narial notch. The coronoid process is not noticeably changed. The zygomatic arch is enlarged above the CMJ and M_3 . The premaxillae and maxillae are expanded both anteroposteriorly and vertically. The ascending ramus of the dentary is vertically expanded, the masseteric fossa is enlarged, and the posterior portion of the mandibular angle is reduced. The anterior dentary is vertically thickened below the diastema, and anteroposteriorly expanded below the premolars. The nasals, frontals, and anterior parietals (above the orbits) are anteroposteriorly expanded (Figure 2C). The nasals are laterally expanded above the premolars, yet slightly constricted in the molar region. The posterior region of the zygomatic arch is marginally ex-

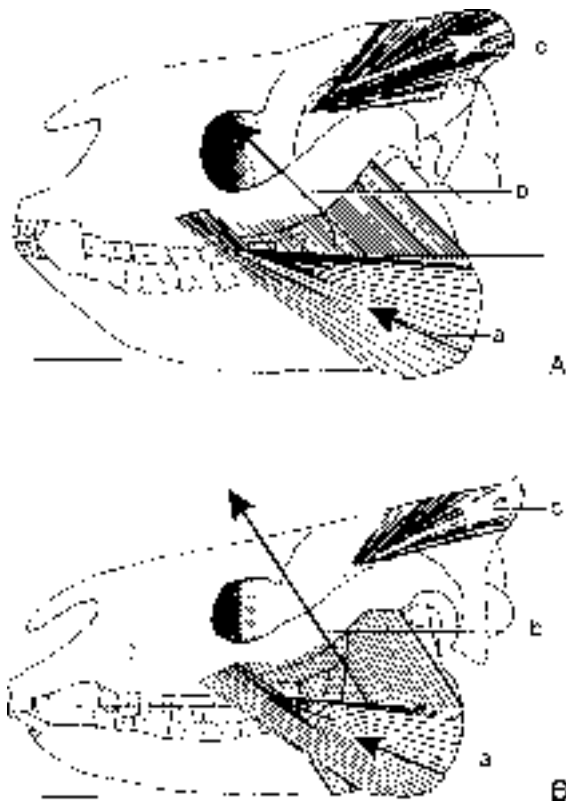


FIGURE 5—Vector analysis and adductor muscle reconstruction of (A) *Hyracodon* and (B) *Subhyracodon*. a = M. masseter pars superficialis; b = M. masseter pars profunda, M. pterygoideus medialis, and M. pterygoideus lateralis; c = M. temporalis. Scale = 4 cm.

panded and the anterior region is medially constricted. The maxillae are laterally expanded in the premolar region.

Nearly half (Table 1) of the mandibular angle of *Subhyracodon* (Figure 3B) lies within quadrant IV and 83% lies anterior to the CMJ (quads I and IV). Sixty percent lies beneath the occlusal plane (quads III and IV). The distribution of bone is more uniform across the quadrants in *Hyracodon* (Figure 3A). Fifty percent of the mandibular angle lies anterior to the CMJ and 66% lies beneath the occlusal plane. *Hyracodon* exhibits a dominantly larger quadrant III posterior to the CMJ.

Modeling clay muscle mass estimates suggest a proportionately larger temporalis in *Hyracodon* and larger masseter group in *Subhyracodon* (Table 1). When compared to known values for modern mammals (Turnbull, 1970), the temporalis, pterygoid, and masseter group percentages of *Hyracodon* are most similar to those of *Odocoileus virginianus* and *Sus scrofa*, while the percentages of *Subhyracodon* most closely resembles those of *Ovis aries* and a zebra (GCM 575, *Equus* sp.). The superficial/deep masseter median fiber ratios are the same for both species. The temporalis/deep masseter median fiber ratios of 0.88 in *Subhyracodon* and 0.79 in *Hyracodon* indicate that the latter has a relatively longer temporalis or shorter deep masseter (Figure 4A, B). The superficial/deep masseter moment arm ratios are also identical. *Hyracodon* exhibits a

TABLE 1—Cranial morphological parameters.

	<i>Hyracodon</i>	<i>Subhyracodon</i>
Mandibular angle analysis		
quad I	20%	34%
quad II	13 %	6 %
quad III	33 %	11 %
quad IV	33 %	49 %
Adductor muscle mass est.		
% temporalis	24	20
% pterygoid	32	32
% masseter group	44	48
Median muscle fiber ratios		
superficial/deep masseter	1.38	1.39
temporalis/deep masseter	0.79	0.88
Moment arm ratios		
superficial/deep masseter	1.57	1.53
temporalis/deep masseter	0.89	0.66
temporalis/superficial masseter	0.57	0.43
Angle of zygomatic arch	41°	30°
Vector angles		
superficial masseter	25°	23°
deep masseter	45°	57°
temporalis	20°	25°

proportionately longer temporalis moment arm. A more inclined (41° as opposed to 30°) central axis of the zygomatic arch is evident in *Hyracodon*. Vector orientations illustrate a more anteriorly inclined deep masseter in *Hyracodon* and a more vertically elevated temporalis in *Subhyracodon* (Figure 5A, B).

DISCUSSION

Analysis of the cranial morphology of *Hyracodon* and *Subhyracodon* reveals many differences which suggest differing functional abilities that ultimately determine the feeding category of each rhinocerotoid. For fossil mammalian herbivores, the assigned feeding modes must coincide with available vegetation. The diversity of White River mammalian fauna indicates that a number of habitats existed during the late-Eocene through early-Oligocene in the area of BADL including well drained open gallery forests, bushland prairies, and vegetated swamps (Clark et al., 1967). Paleosols and fossil gastropods in sediments of the White River Group suggest that the general paleo-environment of central North America progressed from moist forests to dry woodlands to wooded bushlands (Retallack, 1992; Evanoff et al., 1992). Evidence of true grasses is absent, but the flora likely included shrubs and bunch grasses (Retallack, 1983).

The limitations of muscle mass reconstructions and vector analyses must be recognized. The absolute size of a given muscle in a fossil species can never be known. The absolute force generated by an estimated muscle mass is indeterminate and not always directly proportional to the mass. However, in light of these limitations, it is possible to discuss meaningful relative differences.

The muscle mass estimations and superficial/deep masseter moment arm ratios (Table 1) suggest typical ungulate-

style masseter-driven mechanical systems in both genera. The low profile of the *Subhyracodon* skull gives the impression that the deep masseter vector (Figure 5B.b) is considerably longer than that in *Hyracodon* (Figure 5A.b) when in fact they are nearly identical in length. The primary difference lies in the direction of the vectors.

Hyracodon exhibits a more anteriorly inclined deep masseter due largely to the postero-ventral expansion of the mandibular angle (Figure 3A) and a 41° inclination of the central axis of the zygomatic arch (Figure 4A). A more anteriorly inclined masseter translates into a greater anterior movement of the lower jaw during the initial phase of the chew cycle, allowing for increased shear as the teeth move into centric occlusion and is beneficial for the comminution of tough browse. Greaves (1991) concluded that the area of attachment for the masseter and pterygoids reflects the gross size of the muscles. The expanded posterior half of the zygomatic arch (Figures 1B, 2B) increases the area of origin for the deep masseter and zygomaticomandibularis. Lateral expansion of the zygomatic arch allows for an increase in the mass of the superficial and deep masseters and the zygomaticomandibularis (44% of the adductor muscle mass).

The postero-ventral expansion of the mandibular angle in *Hyracodon* (Figures 1B, 2B, 3A) also allows for an increased distance between the origin and insertion of the superficial and deep masseters and pterygoids. The distance over which a muscle can effect a movement is proportional to its length (Hildebrand, 1995). Assuming that the occlusion of the cheek teeth does not vary with a change in muscle size, absolute greater muscle mass likely reflects greater overall force generation.

The expanded temporal fossa (Figure 2B) and sagittal crest (Figure 1B), enlarged coronoid (Figure 1B), and proportionately longer moment arm (Figure 4A) suggests that the temporalis is of greater importance in *Hyracodon* than *Subhyracodon*. The expanded temporal fossa and sagittal crest provide a larger area of origin for the temporalis and the enlargement of the coronoid increases the area of insertion. The proportionately longer moment arm increases the mechanical advantage of the muscle. Increased temporalis leverage could correspond to an increase in orthal retraction movements necessary to snip tough browse.

The less well developed coronoid process, proportionately smaller temporal fossa (Figures 1C, 2C) and estimated temporalis muscle mass, along with a relatively shorter temporalis moment arm (Figure 4B), reflects a reduced importance of the temporalis in *Subhyracodon*. This condition suggests a lesser importance of orthal retraction movements during food acquisition in *Subhyracodon*. Vertical expansion of the mandibular angle in *Subhyracodon* (Figure 1C) increases the area of insertion for the deep masseter (masseteric fossa) and medial pterygoid (pterygoid fossa) anterior to the CMJ (Figure 3B). A muscle mass producing a more vertically oriented (57° to the occlusal plane) force (Figure 5B) would likely increase the occlusal pressure during centric occlusion and thus increase the grinding ability in *Subhyracodon*.

The mandibular condyle is more elevated above the tooth

row in *Subhyracodon* (Figure 1C). A more elevated condyle allows the maintenance of vertically oriented occlusal forces (Greaves, 1974), and would benefit the grinding phase of the chew cycle. The expansion of quadrant IV (49%) in *Subhyracodon* allows for a more anteriorly positioned deep masseter point of insertion (Figure 3B). Coupled with a decreased angle (30°) of the central axis of the zygomatic arch (Figure 4B), enlarged posterior and reduced anterior zygomatic arch (Figure 1C), the total effect is a posterior shift of the origin and anterior shift of the insertion maintaining an effective moment arm for the deep masseter. The medial constriction of the anterior zygomatic arch decreases the area of origin and suggests a decreased importance of the superficial masseter.

The laterally expanded premaxillae, frontals, zygomatic arches, and parietals along with anteroposteriorly reduced anterior maxillae and anterior parietals illustrate the brachy- to mesocephalic nature of the *Hyracodon* skull (Figure 2B). The laterally constricted maxillae, anterior parietals, and zygomatic arches in combination with anteroposteriorly expanded premaxillae, maxillae, frontals, and parietals illustrate the more dolichocephalic, wedge shaped nature of the *Subhyracodon* skull (Figure 2C). The relative orientation of the occipital condyles (Figure 1B, C) suggests that head carriage may have varied as indicated by Scott (1941). The skull of *Hyracodon* was likely held in a snout-down orientation while the *Subhyracodon* skull was held in a snout-forward manner. The Zeuner (1945) method of estimating rhinoceros feeding habits based on the average head carriage suggests differing feeding modes for *Hyracodon* and *Subhyracodon*.

A herbivore utilizing tough browse as a food source would benefit more from cranial musculature arranged to produce a larger amount of shear at the occlusal surface. One utilizing more succulent browse (material that will not break under shearing forces) would derive the greatest benefit from an increase in grinding abilities. In an open bushland environment, the short wide muzzle of a brachycephalic skull and well developed orthal retraction in the chew cycle would be more advantageous to a non-selective browser of tough vegetation. The modern browsing perissodactyls (e.g. tapirs and browsing rhinos) generally exhibit brachycephalic or mesocephalic skulls. The long narrow muzzle of a dolichocephalic skull would allow a selective browser to be very precise in its acquisition of food materials. Dolichocephalic skulls are more indicative of the grazing modern perissodactyls (e.g. horses, zebras, and wild asses) and selective browsing artiodactyls (e.g. giraffe).

CONCLUSIONS

Past sedimentological studies have concluded that *Hyracodon* is more prevalent in the floodplain facies and *Subhyracodon* generally restricted to the stream channel facies of BADL suggesting different habitat usage and feeding modes in these temporally sympatric rhinocerotoids. Differing cranial morphologies in *Hyracodon* and *Subhyracodon* suggest differences in jaw biomechanical abilities and support the earlier conclusions concerning differing habitat us-

age. A brachy- to mesocephalic skull, complete anterior dentition, well developed temporalis, and more anteriorly directed masseter/pterygoid muscle group, along with a snout-down carriage, relatively long neck, and subcursorial locomotor abilities, indicates that *Hyracodon* was likely a non-selective browser of tough, low vegetation distal to the Oligocene streams. The dolichocephalic skull, reduced anterior dentition, lesser developed temporalis, vertically enlarged masseteric fossa, more vertically oriented deep masseter and medial pterygoids, and snout-forward carriage suggests that *Subhyracodon* was a mixed feeder more suited to utilize the succulent vegetation and high browse of the riparian strips.

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PRELIMINARY REPORT ON A NEW SAUROPOD LOCALITY IN THE JAVELINA FORMATION (LATE CRETACEOUS), BIG BEND NATIONAL PARK, TEXAS

ANTHONY R. FIORILLO

Dallas Museum of Natural History, P.O. Box 150349, Dallas, TX 75315

ABSTRACT—A newly discovered sauropod bonebed, that has yielded several dozen bones, has been discovered in the Upper Cretaceous Javelina Formation of Big Bend National Park. The sauropod is tentatively identified as *Alamosaurus sanjuanensis*. This bonebed consists of the disarticulated remains of possibly three individuals, one adult and two juveniles that are approximately half the adult size. Excavation of this site has thus far shown this accumulation of material to be monospecific.

The locality is within the floodplain facies of the Javelina Formation. Further, based on the occurrence of some steeply plunging bones, this site may have been a focal point for trampling activity, such as an area around a waterhole.

INTRODUCTION

IN THE spring of 1995, members of a dinosaur class from the University of Texas at Dallas were engaged in a tour of the Late Cretaceous section in Big Bend National Park. During this tour, the class discovered a new sauropod bonebed in the Javelina Formation of the Park. During the winter of 1996, excavation of this bonebed became a joint Dallas Museum of Natural History-University of Texas at Dallas endeavor. Since the spring of 1997 the bonebed has been excavated by joint field parties from these two institutions. The purpose of this report is to discuss the ongoing work in light of the general depositional setting, the taxonomic makeup of the quarry, and the general taphonomic setting.

Langston et al. (1989) provided a detailed overview of the history of vertebrate fossil collecting in the Big Bend area. Saurian remains from this region have been known since 1907 and subsequently the area has received a good deal of attention from paleontologists (Langston et al., 1989). However, despite this lengthy history, few large concentrations of bones have been found in the Cretaceous section of the Big Bend area. Perhaps the most notable exception to this pattern is the W.P.A. Quarry I which yielded the remains of several ceratopsian dinosaurs from the Aguja Formation (Lehman, 1982; 1989). Therefore, with respect to non-microvertebrate material, this new bonebed represents an unusual concentration of vertebrate fossil material in this region.

GEOLOGIC SETTING

The Maastrichtian sedimentation pattern for the latest Cretaceous in Big Bend National Park was a general southeastwardly-directed paleoflow direction on an alluvial plain (Lehman, 1986). The terminology for the latest Cretaceous units in Big Bend National Park has been the subject of some controversy. Schiebout et al. (1987, 1988) referred to the Javelina Member of the Tornillo Formation while Lehman (1988) maintained that the Javelina Member should be given the rank of formation. For the purposes of this report, I am following the discussion presented by Lehman (1988) and recognizing the Javelina Formation. Within this context, the *Alamosaurus*

quarry discussed here is located in the Javelina Formation of Big Bend National Park. Precise stratigraphic position is difficult to discern because the outcrop exposure is sporadic in the vicinity of the quarry.

The quarry is comprised of two basic lithologies. The lower unit is a light to medium gray to greenish-gray siltstone, generally massive in appearance. Brownish-gray clay clasts, up to 1 cm in diameter (though most are only 1-2 mm in diameter), are locally abundant. Clay slickensides are common. Carbonate nodules are present throughout and many contain bone. This unit is at least 2m thick with bones occurring through the approximately upper 1.5 m. The greenish siltstone has weak, "swirled" bedding occurring irregularly through the unit. The upper contact is sharp and irregular (Figure 1).

The overlying unit is also a siltstone but maroon in color. This unit also contains carbonate nodules, none of which contain bone. There appear to be remnants of horizontal bedding in this siltstone. Based on the fine-grained nature of both of these units, the general depositional setting for this bonebed is taken as part of the floodplain facies.

TAPHONOMIC SETTING

All vertebrate fossil material recovered from this site thus far is attributed to *Alamosaurus sanjuanensis* is based on the morphology of the ilium, pubis, and cervical neural spines

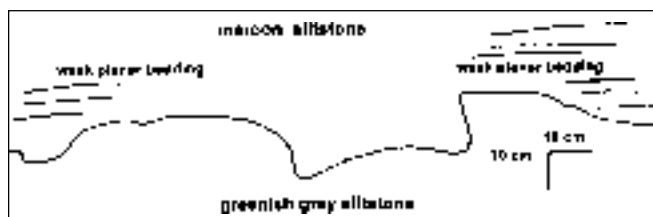


FIGURE 1—Contact between the maroon siltstone and the bone-bearing gray to greenish siltstone at the *Alamosaurus* quarry, Big Bend National Park, Texas. The feature shown in the center of this figure is suggestive of a sauropod footprint in cross section. No planar bedding is present directly overlying the downward extension of the maroon siltstone.

(Gilmore, 1946; Mateer, 1981; Lucas and Hunt, 1989; Geomani, pers. comm.). These bones appear to belong to 3 individuals, namely 1 adult and 2 juveniles. Based on element length, the juvenile individuals are approximately 50% adult size.

All bones from this site are disarticulated. Most elements are isolated, though there are some exceptions. The most notable exception recovered so far has been an unprepared mass of six ribs and a scapulocoracoid (?). All bones are preserved within carbonate nodules. The thickness of the encasing nodule varies from bone to bone. This carbonate crust is typically 0.5 cm to 2.5 cm thick.

Though most bones are found oriented close to the same plane as the dip plane, a small sample of steeply plunging bones have been found. The most spectacular example was the discovery of an isolated femur of a juvenile in a nearly vertical orientation, an anomalous orientation given the low-energy sedimentological setting of the site. The occurrence of high-angle bones in the fossil record is somewhat problematic, and in the absence of corroborative sedimentological data, such orientations were typically attributed to trampling (Hill and Walker, 1972). In an experiment involving modern bones subjected to trampling by ungulates, it has been demonstrated that trampling is a viable means for introducing high-angle bones into a muddy substrate (Fiorillo, 1989). Another characteristic for identifying trampling is the occurrence of shallow scratch marks on the bone surface (Fiorillo, 1984, 1988, 1989), but not the occurrence of this feature is correlated with the sand content of the surrounding matrix (Fiorillo, 1991). Given the fine-grained nature of the matrix at the *Alamosaurus* quarry, it is expected that similar scratch marks will not be found there. Therefore, the orientation of these high-angle bones at the quarry, and the lack of corroborative sedimentological evidence of high-energy stream flow with rapid deposition, suggests that the subset of bones is evidence for trampling at this site during the formation of this locality.

DISCUSSION

With respect to the fossil record, it is generally accepted that bonebeds are "snapshots", that is, they represent very short intervals of time. Given the similarities of preservation and the proximity of the various bones at this site, it is realistic to suggest that these three individuals shared some interaction during their life history. Continued excavation of this quarry and its group of sauropods may provide insight into the population dynamics of these animals as well as more detailed information regarding habitat preferences.

As mentioned above, the contact is irregular but has the appearance in some cases of large footprints in cross-section (sensu Loope, 1986). Given the size and shape of the better defined of these features, it seemed reasonable to suggest that these features were made by sauropod dinosaurs. However, careful excavation of this contact revealed no evidence of skin or claw impressions. Thulborn et al. (1996) described sauropod tracks from the Lower Cretaceous Broome Sandstone in Western Australia. In their description they described "transmitted plates", hardened prints resulting from the pressure of

a multi-ton creature walking thereby causing differential compaction of the substrate (Foulkes, pers. comm.). This type of sedimentological structure provides a criterion for identifying features. Therefore, the presence of trampling at the *Alamosaurus* quarry currently cannot be refuted or corroborated by the sedimentology of the site.

Sauropod remains are infrequently recovered from the Upper Cretaceous of North America. The known distribution of these remains has made some workers recognize an "*ALAMOSAUROS* community" during the latest Cretaceous, a community extending from west Texas up through New Mexico and into Utah, with possible extension into Wyoming (Sloan, 1970; Lehman, 1987). In contrast, no sauropods are known from the latest Cretaceous of more northern regions such as the North Slope of Alaska (Rich, 1996; Rich et al., 1997), tempting one to conclude that environmental factors related to northern regions explain the distribution of sauropods in North America during this time. However, Rich (1996) and Rich et al. (1997) summarized the distribution of polar dinosaurs and show that sauropods have in fact existed in paleo-Arctic climates in the past. Therefore, the explanation for the global distribution of sauropods is ecologically complex. Continued excavation of the *Alamosaurus* quarry is likely to contribute to a better understanding of the biogeographic distribution of sauropod dinosaurs.

CONCLUSIONS

A bonebed containing several dozen bones has been discovered in the Upper Cretaceous Javelina Formation of Big Bend National Park. This bonebed, thus far, has proven to be monospecific and yielded only the remains of the sauropod dinosaur *Alamosaurus sanjuanensis*. This quarry consists of the disarticulated remains of possibly three individuals, one adult and two juveniles that are approximately half the adult size.

The locality is within the floodplain facies of the Javelina Formation. Further, based on the occurrence of some steeply plunging bones, this site may have been a focal point for trampling activity, such as an area around a waterhole.

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LOUISIANA STATE UNIVERSITY MUSEUM OF NATURAL SCIENCE COLLECTIONS FROM LATE CRETACEOUS THROUGH EARLY EOCENE MICROVERTEBRATE SITES, BIG BEND NATIONAL PARK, TEXAS

JUDITH A. SCHIEBOUT¹, JULIA T. SANKEY¹, BARBARA R. STANDHARDT², AND JASON RAMCHARAN¹

¹Louisiana State University Museum of Natural Science and Department of Geology and Geophysics,
Louisiana State University, Baton Rouge, LA 70803

²2313 W. Alabama, Hobbs, New Mexico 88242

ABSTRACT—Over twenty years of research by Louisiana State University scientists on the Late Cretaceous through early Eocene rocks of Big Bend National Park has focused on the recovery of microvertebrates by bulk screening. This research has produced vertebrate paleontological collections from 95 sites, and a total of 1,822 specimens or lots have been entered into the LSU Museum of Natural Science computerized database summarized in Table 1. Every stratigraphic unit studied has yielded vertebrate microsites, even though the Big Bend section is relatively thin for the time spanned, and although classic bonebeds are scarce. Computerization of sites and of currently identified fossils has been completed, allowing an examination of patterns of productivity. Floodplain sites are the most productive, particularly one, Joe's Bonebed Conglomerate, a conglomerate including carbonate nodules concentrated from soils. Conglomerates rich in pedogenic nodules, formed in channels in a marsh, have also been productive.

INTRODUCTION

IN BIG Bend National Park, deposition of the Javelina Member of the Tornillo Formation spans the Cretaceous-Tertiary boundary, and the Paleocene/Eocene boundary lies between the overlying Black Peaks Member and the Hannold Hill Member of the Tornillo Formation. Lehman (1991) discussed the sedimentological and tectonic significance of these deposits in the Laramide Tornillo Basin. The Cretaceous Aguja Formation and the Tornillo Formation have been the focus of vertebrate paleontological research at Louisiana State University since 1976 (Hartnell, 1980, Rigsby, 1982, Rapp, 1983, Rapp et al., 1983, Sankey, 1995, 1996, 1997, Sankey and Schiebout, 1997, Schiebout, 1979A, 1979B, 1981, 1995, Schiebout et al., 1987, 1988, Standhardt 1986, 1995, Sankey 1998, Schiebout et al., in press). The stratigraphically lowest major sites considered here are from the Late Cretaceous (Campanian), from the base of the upper shale member of the Aguja Formation, deposited during the last regression of the Interior Seaway from the region. Within the overlying Tornillo Formation, the Black Peaks/Hannold Hill Member contact marks the transition from deposition low on a floodplain to a higher elevation floodplain. The contact of the Tornillo Formation and the overlying Chisos Formation marks the initiation of local volcanism (Schiebout et al., 1987).

Where paleomagnetic work has been done and rates of net sedimentation can be calculated, rates in Big Bend are considerably lower than those in classic northern sites of comparable age. From Tiffanian zone Ti3 (late Paleocene) to Wasatchian zone Wa1 (early Eocene), the rate was 21 meters per million years (Schiebout, 1995, p. 43). Sedimentation rates of 90 to 200 meters per million years occurred in the Bighorn Basin in Wyoming at approximately the same time (Sloan, 1987). In general, Big Bend sites were in a coastal plain setting further from uplands and had lower rates of sedimentation than comparable northern sites. Faunal differences

between Big Bend and the northern sites have been an ongoing research focus, with the goal of producing a more geographically complete picture of life for the time. The abundance of carbonate pedogenic nodules in parts of the Big Bend section, such as the late Paleocene, is a major difference from northern sites, attributed to climate differences (Schiebout, 1979B). Nodules have hampered paleontological study by encrusting and breaking bone and covering weathered outcrop surfaces, thereby obscuring fossils.

Much of the LSU work has focused on microvertebrate sites, in part because Big Bend quarry sites had been extensively worked earlier. Late Cretaceous dinosaur and large crocodile quarries in the Aguja Formation in the vicinity of Talley Mountain had been collected by WPA (Works Progress Administration), American Museum of Natural History, and University of Texas at Austin crews since the 1940's. The early Eocene Hannold Hill Member site on Exhibit Ridge, the first in-place exhibit of Tertiary mammal remains in the United States, had been located and the large vertebrates from it studied previously (Wilson, 1967). Most fossils in the LSU collection, including those listed in Table 2, have been recovered by screening. Only Ray's (Wilson, 1967, Schiebout, 1974) and Joe's Bonebeds (Schiebout, 1974) have yielded appreciable larger specimens to the collections, and neither "bonebed" would qualify for the term in comparison to sites where several partial skeletons or hundreds of bones have been recovered. Identifiable fossils from screening in Big Bend are usually individual teeth, the hardest part of the vertebrate skeleton, but can include bones, small jaws or jaw pieces, seeds, invertebrates, and even ostracodes (Standhardt, 1986).

TECHNIQUES

Prior to 1970, major bulk screening had not been done on the Late Cretaceous to early Eocene rocks of Big Bend National Park. The first bulk screening done in the area was on Joe's Bonebed Conglomerate, a small lens of pedogenic

TABLE 1—Late Cretaceous through early Eocene stratigraphy, Big Bend National Park, Texas, and related vertebrate collections in the Louisiana State University Museum of Natural Science. NALMA is an abbreviation for North American Land Mammal Age.

Age	NALMA or Epoch	Formation/ Member	Vertebrate Localities	Locs. over 10 specimens	Total # specimens
Eocene	Wasatchian	Tornillo/ Hannold Hill	2	1	91
Paleocene	Tiffanian	Tornillo/ Black Peaks	2	2	255
Paleocene	Torrejonian	Tornillo/Black Peaks	5	2	56
Paleocene	Puercan	Tornillo/Javelina	15	7	563
Late K or Pal.	?	Tornillo/Javelina	4	0	10
Late K	Maastrichtian	Tornillo/Javelina	49	11	504
Late K	Late Campanian	Aguja	18	8	343

nodules and sand, winnowed out of floodplain mudstones in the late Paleocene (Schiebout, 1974). A bulk sample was transported to the University of Texas Vertebrate Paleontology Laboratory, dried and warmed, and soaked in varsol, a dry-cleaning solvent. The varsol was decanted and water added, displacing the lighter varsol and breaking down the clays, allowing the rock to be screened.

Vertebrate paleontological research at LSU began with work at late Paleocene Joe's and Ray's Bonebeds and early Eocene TT-Jack's site, all three of which had previously been worked by University of Texas at Austin researchers (Wilson, 1967, Schiebout, 1974). In the 1970s, rock was treated with varsol or broken down by ultrasonic vibration in a Bransonic-brand ultrasonic. Next, LSU work focused on the Cretaceous-Tertiary boundary rocks, and bulk wet screening of mudstone, without chemical treatment, began from many sites (Standhardt, 1986). Recently, LSU work has focused on Late Campanian microvertebrate sites in the upper Aguja Formation near Talley Mountain. Five horizons of extremely hard fossiliferous conglomerate containing pedogenic nodules have been bulk sampled, disaggregated with dilute acetic acid, and wet screened at LSU (Sankey, 1995, 1996, 1997; Sankey and Schiebout, 1997, Sankey, 1998).

DISCUSSION

Several questions can be asked of the results shown in Table 1 and 2. What lithologies are highest in productivity? How are sites distributed with respect to the ages and stratigraphic units? In the summaries in Tables 1 and 2, the decision to include sites yielding 10 and 50 catalogue numbers, respectively, was arbitrary.

The pattern of productivity reflects both the discovery of fossil concentrations like Joe's Bonebed Conglomerate, which resulted in a concentration of work at its level, and research emphasis on segments of the section for scientific reasons, even if rich concentrations were not available. The Big Bend sites Joe's Bonebed and Ray's Bonebed remain the southernmost North American major sites for the late Paleocene Tiffanian Land Mammal Age, so screening at both continued even when the rich carbonate nodule concentration at Joe's Bonebed was expended. This explains the relatively small numbers recovered at LSU from Joe's Bonebed (Table 2) versus the productivity from Joe's collected prior to 1974. Joe's

Bonebed's original lens of conglomerate yielded 450 catalogued specimens from approximately a ton of rock disaggregated (Schiebout, 1974). Joe's Bonebed conglomerate was a small lens in floodplain mudstone, mainly composed of nodules from local soils with a high component of vertebrate remains from the same source. It is more productive per ton washed than the Talley Mountain conglomerate sites, which have yielded a total of 267 catalogued specimens from 1.9 tons. Rock collected from these sites for processing was pedogenic-nodule-bearing conglomerate, deposited in channels, some showing marine influence (Sankey, 1998), on a marshy coastal plain. Considerable coarse material, such as limestone pebbles, was also being carried by the flow in addition to pedogenic nodules and vertebrate remains.

No early Eocene screening sites were known before 1976, which resulted in an emphasis on screening at TT Jack's Site, which had yielded medium and large sized mammals of early Eocene age (Wilson, 1967; Hartnell, 1980). The fine-grained floodplain sites of Table 2, like TT-Jacks, differ in depositional microenvironment from one to another and are not totally comparable. For example, Ray's Bonebed has been interpreted as a near-river backswamp and contains a comparatively high level of freshwater lower vertebrates, compared to TT-Jack's. TT-Jack's is not as closely associated with any major fluvial sandstone and is much poorer in freshwater lower vertebrates.

No sites were recognized as definitely early Paleocene (earlier than late Torrejonian) for Big Bend before Standhardt's (1986) research, which resulted in emphasis on the appropriate stratigraphic level, and culminated in bulk sampling and intense study of Dogie Site (Table 2) and discovery and processing at other early Paleocene, as well as Cretaceous sites. Of the microsites in floodplain fine-grained deposits, the one most heavily worked by researchers from LSU was the Dogie Site, from which 3.3 metric tons were processed (Standhardt, 1986). The high amount of material screened is reflected in the high number of Dogie Site specimens (Table 2).

The most productive (per weight processed) of the screening microsites in this part of the Big Bend section remains the first one worked, classic Joe's Bonebed Conglomerate, studied before the work at LSU began. Further search has yielded sites in all relevant formations and members, but not faunas belonging to all NALMA'S. No definitely Clarkforkian ani-

TABLE 2—Big Bend National Park Late Cretaceous through early Eocene microvertebrate sites which have produced over 50 catalogued specimens based on material from Louisiana State University Museum of Natural Science (Geoscience section, LSUMG). * Values for “total number of vertebrates” and for the following categories include fossils from surface search, screening, and quarrying. Detailed locality information is on file in the Vertebrate Paleontology collections at LSUMNS.

Age	NALMA or Zone	Formation/Member	LSUMNS Vertebrate Locality Name, (#)	Lithology and Depositional Environment	Total verts.*	Total fish, sharks, rays	Total non dino. reptiles & amphibians	Total dinosaurs	Total mammals
Eocene	Wasatchian	Tornillo-Hannold Hill	TT Jack's (1)	floodplain mudstone	76	2	7	0	66
Paleocene	Tiffanian	Tornillo/Black Peaks	Joe's Bonebed(3)	conglomerate lens and floodplain mudstone	76	3	6	0	67
	Tiffanian	Tornillo/Black Peaks	Ray's Bonebed(9)	floodplain mudstone	77	12	32	0	33
	Puercan	Tornillo/Javelina	Dogie (108)	floodplain mudstone w. limonitic concretions	279	75	51	0	153
			Tom's Top(111)	floodplain silts and fine ss w/ limonitic concretions	96	11	31	0	54
Late Cretaceous	Early-Maastrichtian	Tornillo/Javelina	Running Lizard(113)	mudstone, fine ss, marls, prob. lacustrine	93	34	38	7	14
	Late Campanian	Aguja	Judy's Conglomerate (140, 489)	carbonate-cemented conglomerate; lag of distributary channel	120	64	29	7	20

mals are known from outcrops stratigraphically between Joe's Bonebed (clearly Tiffanian) and the first Wasatchian fossil sites (Schiebout, 1995). This contrasts with the more complete record for this interval in Wyoming.

Continued LSU field work has not located a single new major quarrying site for medium to large animals. TT-Jack's and Ray's were previously known quarry sites of moderate productivity of medium- and large-sized animals which also became useful microsites, but nothing new equally productive for quarrying has been found, suggesting that initial surveys were very successful in locating concentrations of larger vertebrate remains, and that these sites are rarer than they are in more rapidly deposited rocks, such as the northern sites of Wyoming and Montana. Slower deposition in Big Bend resulted in more weathering and reworking of vertebrate remains and less frequent development and preservation of the type of situations yielding quarryable bonebeds, which explains the preeminence of microsites in the Big Bend Late Cretaceous through early Eocene interval.

CONCLUSIONS

The Big Bend area, less thoroughly studied twenty years ago than northern areas exposing Late Cretaceous to early Eocene rocks, in part because of lower richness and nodule-rich ancient soils in Big Bend, was further from sediment sources and more stratigraphically condensed. Although relatively low in real “bonebed” style quarry sites, the Big Bend section has yielded many useful microsites. Although not all North American Land Mammal Ages (NALMA's) are represented, every Big Bend stratigraphic unit for the time span under consideration has microsites of consequence. Vertebrates have been recovered whenever concentrations of soil-

formed nodules, like Joe's Bonebed Conglomerate and the Talley Mountain conglomerates, have been collected. Locating more such concentrations will continue to be a goal of work in the Big Bend section.

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A NEW VERTEBRATE FOSSIL LOCALITY WITHIN THE WAHWEAP FORMATION (UPPER CRETACEOUS) OF BRYCE CANYON NATIONAL PARK AND ITS BEARING ON THE PRESENCE OF THE KAIPAROWITS FORMATION ON THE PAUNSAUGUNT PLATEAU

JEFFREY G. EATON, HEIDI MUNK, AND MEGAN A. HARDMAN

Department of Geosciences, Weber State University, Ogden, UT 84408-2507

ABSTRACT—Vertebrate fossils have been recovered previously from the stratigraphically highest Upper Cretaceous rocks on the Paunsaugunt Plateau, just west of Bryce Canyon National Park. The fauna that was recovered includes dinosaurs, crocodilians, turtles, herptiles, and a mammalian fauna of moderate diversity; however, no chondrichthians (sharks or rays) were recovered. The rock sequence that produced the vertebrate fauna has been variously referred to either the Wahweap or Kaiparowits formations. The Kaiparowits Formation overlies the Wahweap Formation in their type areas on the Kaiparowits Plateau to the east. Previous comparison of the mammalian fauna to those of the Wahweap and Kaiparowits formations supports correlation with the latter. The relatively common occurrence of ceratopsian teeth, the turtle *Compsemys*, along with the absence of sharks also suggests correlation with Kaiparowits Formation faunas. However, the fauna did not match well with that known from the Kaiparowits Formation and there was some concern at the time of the original faunal description that the fauna could represent a facies of the Wahweap Formation not previously sampled.

In the 1997 field season a locality containing abundant vertebrate fossils was located within the Wahweap Formation within Bryce Canyon National Park. The locality has yielded fossils of mammals, dinosaurs, turtles, crocodilians, fish, and herptiles as well as invertebrates such as gastropods and ostracods. The mammals are more primitive than those recovered from the Kaiparowits Formation, and sharks and rays are abundant as they are in the type area of the Wahweap Formation. We have also significantly increased sampling of the uppermost Cretaceous rocks on the Paunsaugunt Plateau and the additional material confirms the distinct differences between this fauna and that of the Wahweap Formation. This data strongly suggests that the uppermost Cretaceous rocks along the southern margin of the Paunsaugunt Plateau and Bryce Canyon National Park are equivalent to the Kaiparowits Formation.

INTRODUCTION

BRYCE CANYON National Park is situated along the eastern margin of the Paunsaugunt Plateau, southwestern Utah. The plateau is bounded to the east by the Paunsaugunt fault system and to the west by the Sand Pass and Sevier fault systems (Figure 1) (Eaton et al., 1993). The southern margin of the plateau is an erosional scarp formed above the Skutumpah Terrace. The top of the plateau is formed by the pink and white resistant caprocks of the Claron Formation of Early Tertiary age.

Below the colorful cliff-forming rocks of the Claron Formation is a problematic series of Upper Cretaceous rocks. The Paunsaugunt Plateau contains less than half the thickness (approximately 900 m, Figure 2) of Cretaceous rocks that are present immediately to the east on the Kaiparowits Plateau (approximately 2000 m) (Eaton et al., 1993). Critical to interpretation of regional history and tectonics is why the Cretaceous sequence on the Paunsaugunt Plateau is so much thinner than that of the Kaiparowits Plateau.

STRATIGRAPHY

The presence of the Dakota Formation, Tropic Shale, and the Tippet Canyon, Smoky Hollow, and John Henry Members of the Straight Cliffs Formation has been documented on the Paunsaugunt Plateau (Gregory, 1951; Eaton, 1993a; 1993b; Eaton et al., 1993). Difficulties arise in interpreting the equivalency of the uppermost Cretaceous rocks on the Paunsaugunt

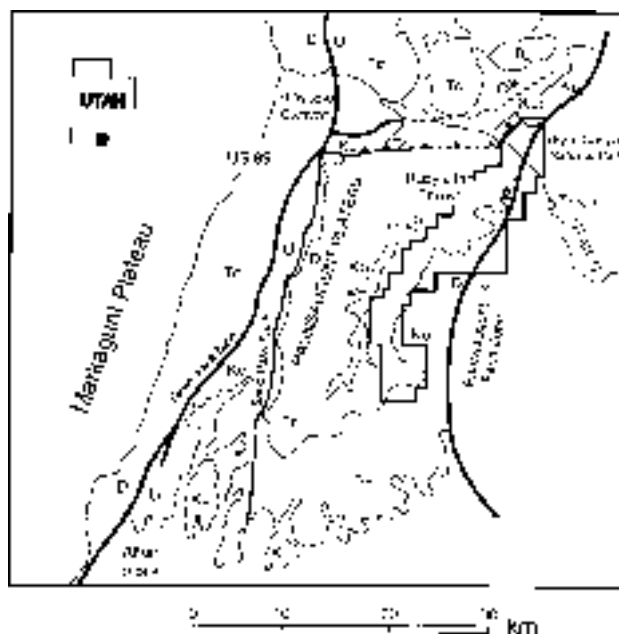


FIGURE 1—Map of the Paunsaugunt Plateau area showing the major faults, distribution of undifferentiated Cretaceous formations (Ku), the Claron Formation (Cl), Tertiary basalts and other volcanics (Tb), Quaternary alluvium (Qa), and the area from which most of the Cretaceous vertebrates have been recovered from the uppermost Cretaceous rocks (indicated by the "1") and from the Wahweap Formation (indicated by the "2") (modified from Eaton, 1993a). Outline of Bryce Canyon National Park is approximate.

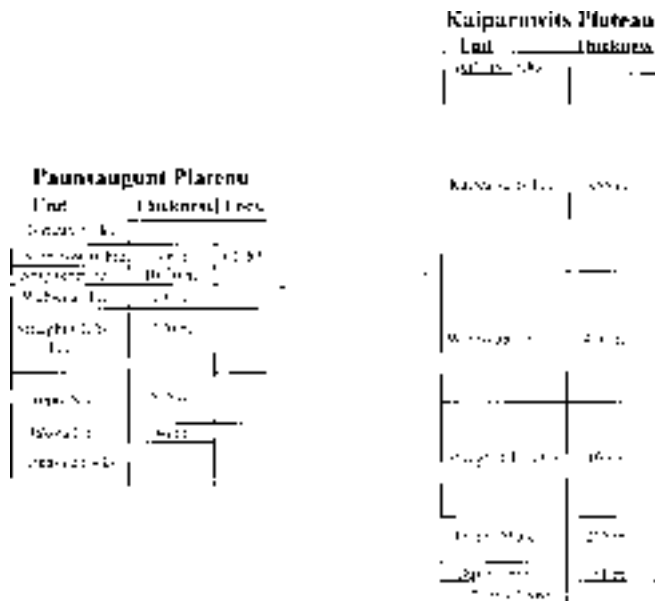


FIGURE 2—A preliminary interpretation of a generalized stratigraphic section on the Paunsaugunt Plateau (see Eaton et al., 1993, and Eaton, 1993a, for other interpretations) compared to the section on the adjacent Kaiparowits Plateau (based on Eaton, 1991). Only the stratigraphic position of localities within the Kaiparowits(?) and Wahweap formations of the Paunsaugunt Plateau are indicated.

Plateau. Gregory (1951) was unable to distinguish the Straight Cliffs Formation from the Wahweap Formation and mapped them as a single unit (Ksw). Gregory (1951) placed a conglomerate high in the Cretaceous section at the base of the Kaiparowits Formation and considered it to lie unconformably on top of the combined Straight Cliffs-Wahweap formations (Ksw). Overlying the conglomerate are gray and variegated mudstones and sandstones that Gregory included, along with the basal conglomerate, in the Kaiparowits Formation. Doelling and Davis (1989) also maintained that the Kaiparowits Formation is present on the Paunsaugunt Plateau (and to the west) and suggested that the Straight Cliffs Formation is very thin (30-80 m) on the plateau but provided no justification for this hypothesis.

Bowers (1990) and Tilton (1991) suggested that the conglomerate did not represent an unconformity at the base of the Kaiparowits Formation, but rather the uppermost member of the Straight Cliffs Formation, the Drip Tank Member, which can be conglomeratic on the Kaiparowits Plateau (Eaton, 1991). Both Bowers (1990) and Tilton (1991) suggested that the beds immediately overlying the conglomerate belong to the lower part of the Wahweap Formation rather than to the Kaiparowits Formation. This is certainly the most parsimonious explanation as it requires only a single erosional unconformity prior to deposition of Tertiary rocks.

Goldstrand (1994), Goldstrand et al. (1993), and Eaton et al. (1993) suggested that the Kaiparowits Formation may be present on the plateau based on comparisons of sandstone petrology between the uppermost rocks of the Paunsaugunt

and Kaiparowits plateaus. Eaton et al. (1993) suggested several possible scenarios that might preserve a remnant of the Kaiparowits Formation on the Paunsaugunt Plateau. All of these scenarios require a major unconformity within the Cretaceous sequence on that plateau that is either absent or undetected on the adjacent Kaiparowits Plateau.

An attempt to compare the mammalian fauna recovered from the uppermost Cretaceous rocks of the Paunsaugunt Plateau to faunas from the Wahweap and Kaiparowits formations on the Kaiparowits Plateau yielded equivocal results. Eaton (1993a) tentatively suggested that the fauna recovered from the uppermost Cretaceous rocks of the Paunsaugunt Plateau correlated more closely to the fauna of the Kaiparowits Formation rather than that of the Wahweap Formation. There was some concern at the time as to whether the fauna might represent a more upland facies of the Wahweap Formation than had been sampled on the Kaiparowits Plateau.

VERTEBRATE FAUNAS

Vertebrate localities are common throughout the Cretaceous sequence on the Paunsaugunt Plateau; however, access is extremely limited due to localities occurring on cliff faces far from roads. As a result, few localities have been screen-washed for vertebrates.

Vertebrates have been recovered from the Dakota Formation along the western margin of the plateau near the town of Alton and the mammals recovered from that locality (Museum of Northern Arizona Locality 939) have been described in Eaton (1993b, 1995).

No vertebrates have been recovered from the Smoky Hollow Member of the Straight Cliffs Formation around the margins of the plateau, but vertebrates have been recovered on the nearby Kaiparowits Plateau (Cifelli, 1990a; Eaton, 1995). Fossils are relatively common from stratigraphically higher rocks variously interpreted to represent the Straight Cliffs or Wahweap formations, particularly in the area of Bryce Canyon National Park (Eaton, 1994). There is no road access to any of these localities as most are high on roadless cliff faces. As such, surface collection of crocodilian, dinosaur, and turtle scrap are common, but small, biostratigraphically useful materials have not been recovered until recently. A single test screen-washing of a small sample from a locality within Bryce Canyon National Park yielded microvertebrate fossils including a partial upper molar of a marsupial (Eaton, 1994). During the 1997 field season, a locality was discovered in the Wahweap Formation within Bryce Canyon National Park (Utah Museum of Natural History Vertebrate Paleontology (=UMNH VP) Locality 77). This locality is considered to represent the Wahweap Formation rather than the Straight Cliffs Formation because there is no evidence of the brackish water or coal deposits that characterize the Straight Cliffs Formation, the mudstone sequences (floodplain deposits) are proportionally thicker relative to sandstones as in the Wahweap Formation in its type area on the Kaiparowits Plateau, a thick conglomerate that appears to be equivalent to the Drip Tank Member of the Straight Cliffs Formation is present at the base of the section, and the area of the locality (Campbell Canyon) was

mapped as the Wahweap Formation by Bowers (1990).

Eighteen sacks of matrix were hauled by backpack from this locality and processed. At the time of this writing most of the concentrate has been picked, but there has been relatively little taxonomic study. The material recovered to date includes the teeth of mammals (a pediomyid marsupial and a multituberculate with teeth smaller than, but morphologically similar to, those of *Cimolodon similis*), dinosaurs, sharks, rays, fragmentary jaws and postcrania of herptiles, and shell material of turtles (Table 1). These fossils will be accessioned into the collections at the Utah Museum of Natural History.

The vertebrate fauna described by Eaton (1993a) is from the top of the plateau in an erosional window cut through the Claron Formation into the uppermost Cretaceous rocks (Figure 1). Approximately 2,000 kg of matrix were processed for microvertebrates during the 1988-1989 field seasons. The fauna includes material of dinosaurs, herptiles, and mammals, which are housed at the Museum of Northern Arizona, Flagstaff (mostly from MNA localities 1073 and 1074). An additional 4,000 kg was processed during the 1996-1997 field seasons and will be accessioned into the collections at the Utah Museum of Natural History in Salt Lake City (mostly from UMNH VP Locality 83, the same locality as MNA 1073, but also from two new localities UMNH VP Locs. 61 and 84). Much of this new material remains to be picked and studied.

TABLE 1—Vertebrates from the Wahweap Formation (UMNH VP Loc. 77), Bryce Canyon National Park.

Class Chondrichthyes	Class Reptilia
Order Orectolobiformes	Order Chelonia
Family	Family Pleurosternidae?
Ginglymostomatidae	<i>Compsemys</i> sp.
<i>Squatirhina</i> sp.	Order Squamata
<i>Squatirhina</i>	Infraorder Scincomorpha
<i>americana</i>	Family Teiidae
Order Rajiformes	<i>Chamops segnis</i>
Family Rhinobatidae	Family Scincidae
cf. <i>Myledaphus</i> sp.	<i>Contogenys</i> sp.
Family	Order Crocodylia
Sclerorhynchidae	Subclass Dinosauria
cf. <i>Ischyryza</i> sp.	Order Saurischia
Family indet.	Suborder Theropoda indet.
<i>Ptychotrigon</i> sp.	Order Ornithischia
Class Osteichthys	Family Hadrosauridae indet.
Order Lepisosteiformes	Family ?Ankylosauridae
Family Lepisosteus	indet.
<i>Lepisosteus</i> or	Class Mammalia
<i>Astracosteus</i> sp.	Order Multituberculata
Order Amiiformes	Family Neoplagiaulacidae
Family Amiidae	cf. <i>Mesodma</i> sp.
<i>Amia</i> sp.	Family Cimolodontidae
Class Amphibia	<i>Cimolodon</i> sp.
Order Urodela	Order Marsupialia
Family	Family Pediomyidae indet.
Scapherpetontidae	Family Alphadontidae
<i>Scapherpeton</i> sp.	cf. <i>Alphadon</i> sp.

The material discovered to date from this uppermost Cretaceous unit does not include a single shark or ray tooth. The turtle *Compsemys* is relatively abundant as are ceratopsian teeth. Only the mammals have been studied in detail and the list presented in Table 2 is essentially the same as that presented in Eaton (1993a). Differing from the original faunal list is the question mark preceding *Cimexomys gregoryi*. Eaton (1995) noted the similarity of this taxon to *Bryceomys* described from the Smoky Hollow Member of the Straight Cliffs Formation. More material of the Paunsaugunt Plateau taxon would be required to confirm this synonymy. An M² recently recovered strongly suggests the presence of *Bryceomys* in the fauna and compares closely to MNA (Museum of Northern Arizona) 7042 from the Kaiparowits Formation.

FAUNAL AGE AND CORRELATION

The material from the new Wahweap locality is consistent with previous known localities from the Wahweap Formation of the Kaiparowits Plateau (see Eaton, Cifelli et al., in press). Sharks and rays are abundant. The rays are similar to

TABLE 2—Vertebrates from the uppermost Cretaceous rocks of the Paunsaugunt Plateau.

Class Osteichthys	Neoplagiaulacidae
Order Lepisosteiformes	<i>Mesodma</i> sp., cf. <i>M. formosa</i>
Family Lepisosteus	<i>Mesodma</i> sp., cf. <i>M. hensleighi</i>
<i>Lepisosteus</i> or	<i>Mesodma</i> sp.
<i>Astracosteus</i> sp.	Family Cimolodontidae
Order Amiiformes	<i>Cimolodon</i> sp., cf. <i>C. nitidus</i>
Family Amiidae	? <i>Cimolodon</i> sp.
<i>Amia</i> or <i>Melvius</i> sp.	Family Cimolomyidae
Class Amphibia	<i>Cimolomys</i>
Order Urodela	<i>milliensis</i>
Family Scapherpetontidae	Family ?Cimolomyidae
<i>Lisserpeton</i> sp.	indet.
Family Sirenidae	Suborder and Family
<i>Habrosaurus</i> sp.	incertae sedis
Class Reptilia	? <i>Cimexomys</i>
Order Chelonia	<i>gregoryi</i>
Family	<i>Paracimexomys</i> sp.
Pleurosternidae?	Order Symmetrodonta
<i>Compsemys</i> sp.	Family Spalacotheriidae
Order Crocodylia	<i>Symmetrodontoides</i>
Subclass Dinosauria	<i>foxi</i>
Order Saurischia	Order Marsupialia
Suborder Theropoda	Family Alphadontidae
indet.	<i>Alphadon</i> sp., cf. <i>A. wilsoni</i>
Order Ornithischia	<i>Alphadon</i> sp., cf. <i>A. russelli</i>
Family Hadrosauridae	<i>Alphadon</i> sp., cf. <i>A. attaragos</i>
indet.	<i>Turgidodon</i> sp. indet.
Family Ceratopsidae	cf. <i>Turgidodon</i> sp.
indet.	
Class Mammalia	
Order Multituberculata	
Suborder Ptilodontoidea	
Family	

the species of *Myledaphus* from the Kaiparowits Formation but appear to be more primitive. There is another taxon of ray informally referred to as “smile button” which is known from the Wahweap Formation, but not the Kaiparowits. The turtle *Compsemys* is present, but rare relative to other turtles, whereas *Compsemys* is a common element of Kaiparowits faunas. The mammals are similar to those known from the Wahweap, particularly the specimen of *Cimolodon*. The single pEDIOMYID tooth is a deciduous fourth premolar and compares almost identically to a tooth recovered from the uppermost Cretaceous beds on the Markagunt Plateau interpreted to be either latest Santonian or earliest Campanian in age (Eaton, Diem et al., in press). Nothing like this odd pEDIOMYID tooth is known from the Kaiparowits Formation.

Eaton (1993a) considered the fauna from the uppermost Cretaceous rocks of the Paunsaugunt Plateau to be more closely equivalent to Kaiparowits (most closely correlative to the Judithian Land-Mammal “Age”) than to Wahweap (most closely correlative to the Aquilan Land-Mammal “Age”) faunas. The species of *Alphadon* and *Mesodma* appear to be even younger than those known from the Kaiparowits Formation. Unfortunately, many of these species are based primarily on size and it is now clear (see Eaton, Diem et al., in press) that species of *Alphadon* and *Mesodma* appear to have had a wide range of sizes throughout the Late Cretaceous and that size alone is not a reliable taxonomic guide. Two new specimens (M1s) of *Mesodma* (UMNH VP 6789, 6794) compare closely to specimens from the Kaiparowits Plateau specimens (MNA V5291 and V7525 respectively) and are similar to *M. hensleighi*, also supporting correlation to the Kaiparowits Formation. *Turgidodon* was described from the Kaiparowits Formation by Cifelli (1990b) and is unknown from the Wahweap Formation. Its presence strongly supports correlation of the fauna to that of the Kaiparowits Formation. A recently recovered upper molar that is *Turgidodon*-like (but lacks stylar cusp C; B and D are subequal) compares closely to an undescribed Kaiparowits Formation molar (Oklahoma Museum of Natural History (=OMNH) 23320). This indicates a diversity of *Turgidodon*-like taxa in the uppermost Cretaceous of the Paunsaugunt Plateau which would not be expected if this unit represented the Wahweap Formation.

The presence of *Symmetrodontoides foxi* originally argued strongly against correlation to Kaiparowits faunas as symmetrodonts were completely unknown from the Kaiparowits Formation and the type of this species was recovered from the Wahweap Formation. However, a single symmetrodont tooth (probably *Symmetrodontoides*) has now been reported from the Kaiparowits Formation (Eaton, Cifelli et al., in press).

The complete absence of sharks and rays suggests the seaway was well to the east. The sea was at its greatest distance from the area (during the time represented by Cretaceous strata on the Kaiparowits Plateau) during deposition of the Kaiparowits Formation and sharks are unknown from that formation except from near the base. Teeth of ceratopsian dinosaurs are relatively common in the uppermost Cretaceous beds of the Paunsaugunt Plateau. Although ceratopsians may

have an older record (Wolfe et al., 1997), they are not found commonly in this region until after deposition of the Wahweap Formation. Also the occurrence of the salamander *Habrosaurus* from the uppermost beds on the Paunsaugunt Plateau suggests a Late Campanian age (Kaiparowits equivalence) as this salamander is not known from older rocks.

So in the years that have followed the original description of the fauna from the uppermost Cretaceous beds of the Paunsaugunt Plateau (Eaton, 1993a), the age of this fauna still remains somewhat equivocal but the specimens recently recovered more strongly indicate an equivalence of this fauna to that of the Kaiparowits Formation.

In the 1997 field season we resampled the uppermost Cretaceous localities on the Paunsaugunt Plateau and plan to increase our sampling of the Wahweap Formation in Bryce Canyon National Park over the next several field seasons. It is hoped that this continued work will provide final resolution to the question of the presence or absence of the Kaiparowits Formation on the Paunsaugunt Plateau.

The thinning of the Cretaceous section across the Paunsaugunt Plateau remains somewhat of a mystery. The thinning occurs 130–150 km from the thrust belt and may reflect a short wavelength forebulge associated with a zone of crustal weakness (Eaton et al., 1997); however, this is only one of many possible hypotheses and further work is needed.

CONCLUSIONS

A new locality from the Wahweap Formation of Bryce Canyon National Park has produced a fauna typical of the Wahweap to the east on the Kaiparowits Plateau. The fauna contains abundant sharks and rays, mammals, and other taxa consistent with an interpretation of an Early Campanian age (approximately correlative to the Aquilan Land Mammal “Age”). Most of the vertebrates previously recovered from the Paunsaugunt Plateau were from the stratigraphically highest Cretaceous rocks on the plateau. This fauna appears to be correlative to those of the Kaiparowits Formation (approximately correlative to Judithian Land Mammal “Age”) based on comparison of the mammalian and herptile taxa to those from the Kaiparowits Formation, the occurrence of abundant ceratopsian teeth along with the common occurrence of the turtle *Compsemys*, and the absence of sharks or rays. Continued work on these sequences should produce final resolution of this problem over the next few years.

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A PRELIMINARY REPORT ON LATE CRETACEOUS HERPTILES WITHIN OR NEAR BRYCE CANYON NATIONAL PARK, UTAH

HEIDI MUNK

Department of Geosciences, Weber State University, Ogden, Utah 84408-2507

ABSTRACT—A research project was started in 1997 to determine if the Kaiparowits Formation (Upper Campanian) is present in Bryce Canyon National Park. Previously known localities from beds thought to represent the Kaiparowits Formation were resampled and a new locality has been found in the Wahweap Formation (Lower Campanian) of Campbell Canyon in Bryce Canyon National Park. The herptiles that have been recovered from the Wahweap locality are compared to herptiles recovered from the stratigraphically highest Cretaceous beds of the Paunsaugunt Plateau. The presence of a Late Campanian salamander, *Habrosaurus*, suggests correlation of the uppermost beds to the Kaiparowits Formation.

INTRODUCTION

IN AN effort to determine if the Kaiparowits Formation (Upper Campanian) is present in Bryce Canyon National Park, I, with the help of a few colleagues, have undertaken an undergraduate research project in Bryce Canyon National Park (beginning in 1997) and on the top of the Paunsaugunt Plateau, in the area of Podunk and Mill creeks, to compare fossils from the Wahweap Formation and from units that have been considered to represent the Kaiparowits Formation by

Eaton (1993) and Eaton et al. (1993) (Figure 1).

Gregory (1951) identified the Kaiparowits Formation as present on the Paunsaugunt Plateau. Bryce Canyon National Park occupies the eastern margin. Subsequent work has challenged Gregory's assessment. Doelling and Davis omit the formation in their 1989 map, as does Bowers in his 1990 map (following the work of Tilton, 1991). Eaton et al. (1993) and Eaton (1993) have, based on both sedimentological and paleontologic data, suggested that at least some of the Kaiparowits Formation may be present on the plateau (and within Bryce Canyon National Park) (Figure 2).

A new locality was recently discovered in the Wahweap Formation of Campbell Canyon within Bryce Canyon National Park (Figure 1). The herptile fossils (lizards, frogs

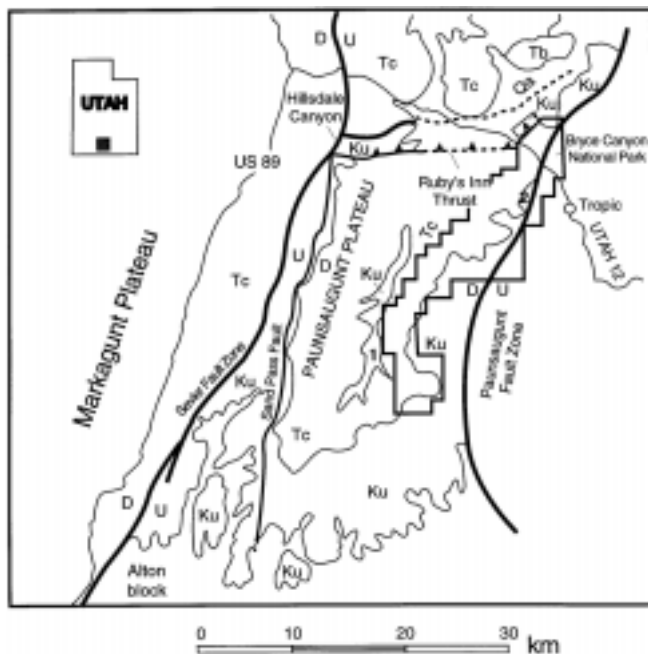


FIGURE 1—Map of the Paunsaugunt Plateau area showing the major faults, distribution of undifferentiated Cretaceous formations (KU), the Claron Formation (Cl), Tertiary basalts and other volcanics (Tb), Quaternary alluvium (Qa), and the area from which most of the Cretaceous vertebrates have been recovered from the uppermost Cretaceous rocks (indicated by the "1") and from the Wahweap Formation (indicated by the "2") (modified from Eaton, 1993). Bryce Canyon National park boundaries are approximate.

Paunsaugunt Plateau

Unit	Thickness	Locs.
Tertiary rocks		
?Kaiparowits Fm.	0-90 m	61, 83
conglomerate	10-70 m	
Wahweap Fm.	100 m	73
Straight Cliffs Fm.	270 m	
Tropic Shale	213 m	
Dakota Fm.	84 m	
Jurassic rocks		

FIGURE 2—A preliminary interpretation of a generalized section of the Paunsaugunt Plateau (based on Eaton et al., 1993, and Eaton, 1993). Only the stratigraphic position of localities discussed in this report are indicated.

and salamanders) that have been recovered to date from both the uppermost Cretaceous rocks on the Paunsaugunt Plateau and the new locality from the Wahweap Formation will be compared to taxa known from the Kaiparowits Formation. The resulting identifications will be used to help determine the absence or presence of the Kaiparowits Formation on the Paunsaugunt Plateau.

METHODS

The field localities were Campbell Canyon in Bryce Canyon National Park and areas near Podunk and Mill creeks on the Paunsaugunt Plateau (Figure 1). We identified possible localities for sampling and collection by examining the ground surface for pieces of jaw, tooth (mammal or fish), bone, scale and/or turtle shell. When fossils were found, we located the producing layer by looking for the highest occurrence of the fossils. We then carefully removed the surface matrix of the layer in question and examine the exposed matrix for any fossils. Samples were shoveled into bags, labeled, and then carried back to base camp for washing. The matrix was then poured into nested double screens for drying in the sun before the first wash. When dry, the double screens were placed in troughs of water for breakdown of the clays and silts by the water. The top screen is a coarse window screen mesh that allows the small fossils to wash through to the bottom screen which is a finer mesh. Large fossils were retained in the upper screen as are any remaining large chunks of matrix. Smaller fossils and pieces of matrix were collected in the finer screen. With gentle agitation of the screens, the clays and silts were washed from both of the screens and into the troughs to prevent redeposition of the finer particles. After each layer of screen had been individually agitated, the screens were placed in the sun to dry. After drying for the second time, the screens were nested and washed again as above. After the second wash and dry, the fine screens were emptied into a common bucket and the coarse screens were emptied into another common but separate bucket. The matrix was then taken to Weber State University (Ogden, Utah) for removal of fossils. The matrix was then spread a little at a time on a picking tray, and then examined under a microscope for fossils. The fossils are removed with tweezers and sorted taxonomically into vials.

RESULTS

At present, the results are few. The concentrated matrix has not been completely picked. There have been few specific identifications of the recovered fossils and this process is currently in progress. The specimens have been grouped into general taxonomic categories (e.g. crocodiles, mammals, fish, etc.). Although herptile jaws are being found, intact specimens are rare. The identifications made here are from jaws that have complete teeth in place and relatively complete vertebrae.

At the newly discovered Campbell Canyon locality (Wahweap Formation) in Bryce Canyon National Park (UMNH VP Loc. 77), teeth have been found representing sharks, rays, crocodiles, fish, mammals as well as jaw fragments of lizards, salamanders and frogs.

Specimen UMNH VP 6992 (NPS accession number 417,

catalogue number 3944) (Figure 3D) has been identified as Order Squamata, Infraorder Scincomorpha, Family Teiidae, *Chamops segnis* (Keebol and Fox, 1996). The specimen is an incomplete left maxillary. The specimen had six well-preserved tricuspid teeth which show some wear. The teeth are slightly recurved posteriorly with tooth replacement pits at the bases of the teeth.

Specimen UMNH VP 6994 (NPS accession number 417, catalogue number 3946) (Figure 4A,B) is identified as Order Squamata, Infraorder Scincomorpha, Family Scincidae, Subfamily Scincinae, *Contogenys* sp. There are three complete teeth on the jaw with the bases of three teeth showing through the attached matrix. The cusps of the teeth are flattened on the top.

Specimen UMNH VP 6995 (NPS accession number 417, catalogue number 3947) (Figure 4D) is a jaw fragment identified as Order Caudata, Suborder Ambystomatidae, Family Scapherpetonidae, *Scapherpeton* sp. The jaw is broken on the labial side so any other distinguishing features of species are missing. There are locations for nine teeth on this specimen.

At UMNH VP locality 61, from the stratigraphically uppermost Cretaceous rocks on the Paunsaugunt Plateau near Mill Creek, bones and teeth representing fish, crocodiles, dinosaurs, turtles and mammals have been found. Herptile fossils include vertebrae and jaw fragments of lizards, frogs, and salamanders. At this locality, specimen UMNH VP 7365 (Figure 4C) was found. The specimen is identified as Class Amphibia, Order Urodela, Family Sirenidae, *Habrosaurus* sp., a fragmentary tooth plate. The specimen has seven to eight rows of teeth in the fragment.

At UMNH VP locality 83, also representing the stratigraphically uppermost Cretaceous rocks on the Paunsaugunt Plateau near Mill Creek, tooth and bone fragments of hadrosaur and fish have been found. Jaw fragments representing lizards and salamanders were found here along with mammal and crocodile teeth as well as fragments of turtle shell. Gastropods and ostracods are also present at this locality. Present in the material are vertebrae from Class Amphibia, Order Urodela, Family Scapherpetonidae, *Lisserpeton* sp. (UMNH VP 6986) (Figure 3A-C). Several other similar specimens have also been found. The distinct triangular outline of the atlantes and the half round shape of the centrum are diagnostic of the genus (Estes, 1981). The rib-bearing part of the vertebrae is bicipital. The neural arch is missing from all specimens.

DISCUSSION

The herptile jaws that have been recovered are most often edentulous, but occasionally there are teeth in them. The jaws have been identified to order on the basis of the shape of the jaw and whether it has a tooth bearing ridge (lizards), is continuously rounded with the teeth resting on the rounded lingual surface of the jaw as opposed to the shelf (salamanders). If the jaw is relatively flat with a textured labial side having the small ridges of the teeth then it is from a frog.

In the picked fragments of bone material from all of the

FIGURE 3—A-C, *Lisserpeton* sp. atlas vertebra. D, *Chamops* sp. UMNH VP 6992. Scale bar = 1 mm..

localities discussed above, there are bone fragments that would seem to indicate similar taxa are present in the different localities. The Campbell Canyon locality (Loc. 77), in the Wahweap Formation, is distinctly different from the stratigraphically uppermost Cretaceous beds on the plateau because sharks and rays are present at this locality. Fragments of frogs and salamanders are common to all three localities.

The *Habrosaurus* specimen (UMNH VP 7365) from UMNH VP locality 61, is important because the salamander is only known from Late Campanian and Maastrichtian rocks (Estes, 1964). The fossil suggests that the uppermost rocks on the plateau are equivalent to the Late Campanian Kaiparowits Formation rather than the Early Campanian Wahweap Formation. The occurrence of *Habrosaurus* may be a potential marker fossil in the region making biostratigraphic correlation of other localities easier. The other genera discussed above are known to occur from the Santonian to Maastrichtian. Their occurrence over a broad range of time

makes them poor for biostratigraphic correlation.

CONCLUSION

The presence of the Kaiparowits Formation is suggested by the occurrence of the Late Campanian salamander *Habrosaurus* (Figure 3C). Identification of the Kaiparowits Formation within Bryce Canyon National Park will influence the way maps of the park are drawn in the future. Our understanding of the environmental history of the park will increase as the fossils from the area help to develop a picture of the area in the Cretaceous. Our understanding of the influence of the Western Interior Seaway on nonmarine rock sequences and animal life of the past will increase with future study.

ACKNOWLEDGMENTS

Many thanks to the National Park Service, Richard Bryant and the Bryce Canyon Natural History Association (under the guidance of Gayle Pollack), who have assisted me

FIGURE 4—A-C, *Lisserpeton sp. atlas vertebra*. D, *Chamops sp. UMNH VP 6992*. Scale bar = 1 mm.

in my research in Bryce Canyon National Park. The cooperation of the U.S. Forest Service is also appreciated for our work on the top of the plateau. Many thanks also to my mentors, Jeff Eaton and Janet Gillette, without whose guidance I would not have discovered my love of paleontology and the many wonders of Bryce Canyon National Park. Megan Hardman, Judy Wilkinson, Roger Jackman and Angie Nebeker have assisted me in the collection of the fossil bearing matrix. My greatest thanks to George, Davin and Ryan Munk without whose unending support I could have never thought about beginning a project this big, not to mention finishing the project in the future. The Petroleum Research Fund of the American Chemical Society (30989-GB8) and the Bryce Canyon Natural History Association are funding my current work on the plateau.

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AN OCCURRENCE OF REPTILE SUBAQUEOUS TRACES IN THE MOENKOPI FORMATION (TRIASSIC) OF CAPITOL REEF NATIONAL PARK, SOUTH CENTRAL UTAH, USA.

JAMES MCALLISTER¹ AND JOHN KIRBY²

¹Biology Department, Indiana University of Pennsylvania, Indiana, PA 15701

²Biology Department, Mansfield University, Mansfield, PA 16933

ABSTRACT—Capitol Reef National Park has been long known for the occurrence of fossil reptile tracks and traces. Recent exploration in the park has revealed new sites of subaqueous traces within the Triassic Moenkopi Formation. Previous workers noted subaqueous traces but could not identify consecutive traceways or provide as complete an account of recognition criteria as the new material allows. A brief description of the new sites are provided here. The sites are important because they are either extensive and assessable (providing excellent sampling opportunities), or have consecutive subaqueous traces of a single buoyant tracemaker. The new material increases the recognition criteria with information about kick-off scours, z-traces, and variably preserved traces.

INTRODUCTION

HISTORICALLY FOSSIL tracks have been treated as novelties of passing interest, or as a footnote in the context of a site report. When reported, tracks were typically the best examples found and rarely included mention of average or poor quality tracks. Ambiguous tracks and traces (such as subaqueous forms) were rarely acknowledged. Papers by Peabody (1948, 1956) and Lammers (1964), along with an abstract by Webb (1980) are exceptional. They describe and provide understanding to some poorly preserved traces considered to have been produced by swimming tetrapods. These reports are some of the earliest references of fossil subaqueous traces. These authors found their samples in the Moenkopi Formation within and adjacent to Capitol Reef National Park, south-central Utah.

Previous contributions are important and progressive, but reevaluation is necessary and expected with advances in methods, context, and when new specimens are found. Peabody serves as an excellent example of research which emphasized rigor in understanding locomotory processes applied to descriptive morphology. With that basis, behavioral interpretations now have become the focus of trackway workers, especially since the publication of Ostrom (1972). The emphasis of our paper is to add to the Capitol Reef National Park (CARE) vertebrate trace fossil story in two ways. First we can increase further the criteria to corroborate subaqueous interpretations; second, we can document sites which we do not believe previous authors studied.

MATERIALS AND METHODS

Localities.—Three study sites are within the boundaries of CARE. The sites are in the Torrey Member of the Moenkopi Fm. and are estimated to be late Scythian (Spathian) (Hintze, 1988). All contain examples of subaqueous traces formed by tetrapods. Traces occur as sandstone casts which filled in the impressions (molds) found in the underlying mudstone. The mudstone is friable and crumbles upon exposure. The traces are not underprints (secondary structures created by compres-

sion of layers deeper than the original substrate surface) as evidenced by primary structures on the trace (features created by direct contact of the sediment by the tracemaker; example: striations) and occurrence at a discontinuous sediment interface.

Site 1 is a low ridge, at approximately the 5560 ft. contour. The site curves from the southeast to the southwest approximately 87 meters and broadens into a wide slope. The ridge is west of the Headquarters/Visitor Center, bounded on the east and south by Sulphur Creek. The trace layer studied at this site covers approximately 297 sq. m. of surface area and has a strike and dip of 30° NW and 12° NE, respectively. At this location four smaller study sites were chosen and these sections of the trace layer were flipped for study. The surface areas of flipped rock at each of these sites are: Site 1a = 3.38 sq. m., Site 1b = 5.0 sq. m., Site 1c = 2.0 sq. m., Site 1d = 1.42 sq. m. Numerous large traces occur at each site, and are abundant over the entire ridge exposure. No individual traces can be assigned to specific traceways due to the trace density. The flipped blocks were arranged downslope in the mirror image of their original orientation and aligned to their original compass bearing. The blocks were cleaned, photographed, and samples of the surface duplicated by latex molds. The blocks were subsequently restored to their original position.

Site 2 is a broad slope about 1/4 mile due west of Site 1 along Route 24. This location includes both large and small traces. They are plentiful but less numerous than Site 1; individual traceways are scarce. Site 2 was not as well documented as the others. Study was limited to exposure of the undersurface to find local areas of future interest. Pictures and latex molds were made of selected displaced slabs which could not be oriented *in situ*.

Site 3 is located approximately 2.5 miles west of Site 2 and then south of Route 24 near a dry streambed. The fossil site is at the base of a small cliff where a number of large blocks have fallen. The traces at this site are on two large blocks whose original orientation and placement within the

nearby outcrop are unknown. There are over 40 traces on the two blocks which include two distinct traceways. These traceways and remaining traces were made by a relatively large tracemaker similar in size to those at Site 1. The two displaced large blocks of Site 3 were gridded for analysis using chalk lines at intervals of 25 by 25 cm. A Plumb BarbaraTM (computer-enhanced plumb bob) was used to create an artificial base line for this grid. No directional orientation is implied by the base line. The individual traces of each traceway were then photographed and described. The traceways on both blocks were duplicated using latex peels.

RESULTS

Site 1—A hodgepodge of traces oriented to the southwest: no discernible traceways are apparent. All traces are subaqueous and large. Marks of individual traces range from 8 - 20 mm at greatest width and 21 - 90 mm in axis length. Most trace prints range from one to three digit impressions.

Site 2—Orientation is not apparent for all traces. Many small traces exhibit subaqueous characteristics. Larger traces are indistinct and lack features that indicate subaqueous formation. Variation in sandstone thickness and block size makes this site less amenable to flipping and reconstruction of lower surface. A few large traces are present but the majority are small. The small traces consist of marks from one, two or three digits. Single digit traces can have a width of 3-4 mm and a length of 18 mm. The three-digit traces can have greatest width and axis length of 11 mm and 21 mm, respectively.

Site 3—Two traceways are recognized. The original orientation of the trace block is unknown but each traceway is oriented at 40 degrees to the apparent direction of the current. Both traceways have evidence of locomotion by all four appendages. One traceway, composed of 13 traces, has three z-shaped traces. The individual z-traces, appear to be formed from the action of one digit and have a greatest width and total axis length of 41 mm and 87 mm, respectively. Most associated marks have two digits associated with the trace and have total trace greatest widths and axis lengths of 57 mm and 114 mm, respectively. The second oriented traceway is composed of 20 traces.

DISCUSSION

Vertebrate subaqueous traces described in the literature occur as sandstone casts that had filled imprints preserved in underlying mudstone. Exposed traces occur on the underside of resistant sandstone ledges where the mudstone eroded away. This typically makes the traces difficult to examine as it requires removal and flipping of the sandstone layer to expose the traces. At CARE the concordance of stratigraphic dip and hillside slope (forming a small hogback) combined with the lateral extensiveness of the trace-bearing sandstones allows sampling along a large uninterrupted surface. Furthermore, the sandstone is jointed and the underside can be exposed by flipping blocks which are neither so small that there is destruction of many traces, nor too large to require excessive physical effort. These factors combine to make these localities extraordinary. A large exposure can be sampled by two people equipped with handtools.

Prior work by Peabody (1956) and Lammers (1964) at

CARE were especially important in documenting subaqueous traces. Although there was no specific listing of recognition criteria, the important characteristics they used to justify their interpretations can be interpreted from their writings. Peabody was impressed by the lack of distinctiveness of the "swim" traces. The lack of definitive series (trail continuity), poorly defined imprints that appeared as if digit tips formed the traces, and the corroboration of the physical environment were important to his interpretation. Salt crystal pseudomorphs, shrinkage cracks, and ripple marks occur elsewhere in the park sediments but not near the "swim" traces.

The sedimentary criteria that form the environmental interpretation should agree with the expected environment of the trace fossils. For example, the lack of salt pseudomorphs, shrinkage cracks, and ripple marks were considered important to Peabody (1956). He used these characters to refine his initial subaqueous track paleoenvironmental interpretation as one which did not undergo subaerial desiccation. Peabody (1956, pg. 738) also considered the traces to have been made in a particular environment, "...shallow but extensive pools of a floodplain." However, observations of current produced sedimentary features (especially at Site 3), the offset nature of some traceways (Sites 2 and 3), and the presence of ripplemarks (Site 2) indicate a need to reevaluate the specific environmental interpretation as one which was highly influenced by currents. Although the sedimentary evidence indicates a sub-aquatic environment in general, and is consistent with the evidence of the traces, each individual character can be used in the interpretation of a variety of environments which underwent similar processes. Sometimes the characters may not simply be a checklist but rather may build several lines of independent evidence which together corroborate an interpretation.

In addition to evidence from the tracks and evidence relating to the depositional environment, Peabody also mentioned an association of a limuloid trackway with subaqueous traces. The presence of this traceway enhances the interpretation of the proximity of an aqueous environment for the CARE Moenkopi Formation.

Lammers (1964) provides additional recognition criteria for Capitol Reef subaqueous traces. He noted that individual traces had striations caused by scales and nails which obscured expected track details. Overhangs along the posterior of the traces would be unusual for non-buoyant tetrapods. Further, the general confusion of the traces, lack of full foot impressions, the abnormal elongation and smearing of the traces, lack of consecutive series, randomness, disorder, and overlapping indicated to Lammers random swimming movements.

McAllister (1989) listed subaqueous features which can be separated into three categories: criteria inherent to individual traces, criteria inherent to sequential traces, and corroborative evidence from sediments/paleoenvironment. The characters used to distinguish subaqueous traces are considered to be easily made by a buoyant paddler, but unlikely to be consistently made during normal terrestrial locomotion. The descriptions of the subaqueous traces by Peabody and Lammers were examined and interpreted to correspond to our list of

TABLE 1—Criteria helpful for subaqueous interpretation.

Individual Traces	
	reflecture of digits
	depth/arc
	elongation
	posterior overhang*
	striations parallel to propulsion*
	impression of distal digits*
	kick-off scours**
	z-traces**
Sequential or Multiple Traces	
	variability in pace angulation
	trace lengths variable compared to widths*
	manus and pes trace count unequal*
	unexpected configurations*
	buoyancy/size-mitigated variably-preserved traces**
Sedimentary and Paleoenvironmental	
	expected fauna/flora*
	expected sedimentary features*
	paleoenvironmental interpretation*
* noted by Peabody (1948, 1956) or Lammers (1964) from CARE Moenkopi Fm. traces.	
** new criterion described from CARE Moenkopi Fm. traces.	

criteria (Table 1). Comparison of these published CARE descriptions to the later compilation of subaqueous traceway criteria is very favorable. The criteria used by Peabody and Lammers are indicated by an asterisk in Table 1.

Criteria inherent to individual traces are: reflecture of digits (retraction mark of digit tips made from posterior of trace anteriorly), depth of the mark corresponding to arc of limb, elongation of traces, posterior overhangs (continuations of the digit tips posteriorly into the sediment, creating a hanging edge in the cast), striations parallel to direction of propulsion, and preferential impression of distal ends of digits. Criteria inherent in multiple trace comparison or traceways are: great variability in pace angulation, trace lengths excessively variable compared to widths, ratio of manus and pes traces unequal (manus typically underrepresented), and unexpected configurations (lack of traces or extra traces in an expected sequence). Sedimentary and environmental criteria are: association with other appropriate fauna/flora, association with expected sedimentary features, and environmental interpretation.

Our examination of the CARE specimens allows us to include additional recognition criteria. They are the presence of kick-off scours, z-traces, and buoyancy/size-mitigated variably-preserved traces.

Kick-off scours (Fig. 1) occur immediately posterior to the traces. The sandstone cast infilled the scour and is seen as the irregular positive relief behind the digit scrapes. They represent the action of the water eddies created behind the digits as they pass close over the sediment. At the end of the propulsive phase (kick-off phase of Thulborn and Wade, 1989),

FIGURE 1—Selected traces from Site 3. Note kick-off scours behind the traces. Scale equals 10 cm.

the eddies created by the tips of the digits scour out the area immediately behind the trace. Most of the excavated material disperses into the water column. In a terrestrial case, much of the propulsive phase has the force of the weight-bearing subphase directed downward compressing the sediment. For a fully buoyant tracemaker, the touchdown and weight bearing phases are less well defined, and include pushing sediment (typically fine-grained mud) out of the trace to scatter posteriorly. In the terrestrial trace Thulborn and Wade indicate the manner in which a tracemaker can create striations (retro-scratches) along the imprinted track with a continuation of a backsliding kick-off phase. In this terrestrial situation sediment which is scooped or squeezed out of the track will be deposited on the substrate. If a cast were made of the terrestrial track, the squeezed out or scooped out material would create negative relief. This is an important difference in the modes of formation between buoyant and non-buoyant traces and leads to a fundamental difference in the disposition of the displaced sediment. The difference in mode of formation also helps understand why underprints are not likely to be created by a buoyant tracemaker. Under expected buoyant conditions there will be an extremely small component of substrate compression (downward), compared to a non-buoyant locomotion.

Z-traces (Fig. 2) are interpreted as little double kicks of the tracemaker as the tips of the toes graze the substrate. These traces are made by feet on the side of the tracemaker opposite of the striking current. The trace begins with the typical im-

FIGURE 2—Selected traces from Site 3. Note Z-traces. Scale equals 10 cm.

print of one digit entering the sediment in an arc during protraction. The entrance is slightly wider than the rest of the trace (as seen in the entry of other traces), and the depth of the arc does not progress all the way through the sediment as do the two digits on the current side. The digit then retracts anterolaterally a short distance leaving a continuous striated path and trace. The digit continues protracting posteriorly, entering deeper into the substrate, leaving an overhang in the trace cast.

Initial interpretation of the Z-trace establishes the basic mode of formation. The shallow entry and progressive arc-depth indicate that this part of the trace was made first. The continuity of the trace (especially continuity of depth and striations) through the middle of the Z connecting the sides, indicates the creation by one digit. The overhang indicates that this is the end of propulsion; the part of the trace made last. The overhang indicates the direction of the tracemaker movement (toward top of page in Fig. 2) as opposite of the direction the overhang points.

Continued interpretation becomes more speculative, but also more interesting. The initial protraction, quick retraction, and continued final protraction, is interpreted as the tracemaker being at the limits of limb extension (barely touching the substrate) while in an offsetting current. Seemingly these Z-traces indicate an extra little attempt to gain additional grip on the substrate with an immediate second try or extra little flip of the distal limb. For the tracemaker, the sense of one digit barely touching substrate on this side (possibly because the animal is leaning into the current, away from this side) may have caused the tracemaker to try and dig in a bit deeper. Additionally, the side leading into the current may emphasize propulsion, while the side opposite the current may emphasize prevention of current offset. Most importantly, the movement of the limb as described would require a degree of freedom which would only be consistently provided in a buoyant state.

Buoyancy/size-mitigated variably-preserved traces are present at Site 2. Details of some traces are better defined than in other traces (variably preserved). For example, at Site 2 small traces with subaqueous characteristics are well preserved, while large traces are most often poorly preserved with no recognizable subaqueous characteristics. The large ones appear to be full prints of tracks which are deformed and amorphous. Sediment may have been compressed, squeezed, and stuck to the foot as it was removed from the track. The significance of the variably preserved traces is interpreted as relating to the size of the tracemaker versus the water depth and opportunity to become buoyant (buoyancy/size-mitigated). Essentially small tetrapods floated in shallow water while large ones waded. Other variables need to be taken into consideration for a complete interpretation, (ability of small tetrapods to walk along the substrate bottom (Brand 1979), variation in water level over time, and non-contemporaneous trackways). However, the presence of these disparately preserved traces will contribute to a more complete understanding of the subaqueous environment at CARE.

SUMMARY

The importance of the Capitol Reef National Park Moenkopi Formation vertebrate traces is clearly evidenced by early references in the literature. Some of the first recognized subaqueous traceways came from the park. Today the extensive deposits and accessibility of the sediments allows continued advancement in traceway interpretations. Previous recognition of subaqueous vertebrate traces include criteria inherent to individual traces, inherent to sequential traces, and correlative criteria from sediments/paleoenvironment. Many of these criteria were originally recognized from CARE specimens. We have further documented criteria not described for this material. Most notable of these are kick-off scours (individual traces), z-traces (individual traces), and buoyancy/size-mitigated variably-preserved traces (sediments/paleoenvironment). These three criteria all rely on buoyancy of the tracemaker to make their characteristic mark of subaqueous formation.

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COMPARATIVE GRAPTOLITE BIOSTRATIGRAPHY OF THE JUTLAND KLIPPE TO THE MARTINSBURG FORMATION AT DELAWARE WATER GAP NATIONAL RECREATION AREA

DAVID C. PARRIS¹, LOUISE F. MILLER¹, AND STANLEY C. FINNEY²

¹Bureau of Natural History, New Jersey State Museum
205 W. State St., PO Box 530, Trenton, NJ 08625-0530

²Department of Geological Sciences, California State University-Long Beach,
1250 Bellflower Boulevard, Long Beach, CA 90840

ABSTRACT—Investigations in and near Delaware Water Gap National Recreation Area have established the age span of the graptolite-bearing Martinsburg Formation. Ranging in age from the *Climacograptus bicornis* Zone to the *Climacograptus spiniferus* Zone, its lowermost portions conformably overlie the Jacksonburg Formation (which has a shelly fauna). Correlations remain doubtful for various outlier outcrops and allochthons which are found to the southeast of the main body, although our recent work has correlated the Port Murray outlier to the *Corynoides americanus* Zone and to the Bushkill Member of the Martinsburg Formation.

Current work in the Jutland Klippe of Union Township, Hunterdon County, New Jersey has confirmed various past studies of ages ranging from the *Adelograptus-Clonograptus* Zone to the *Climacograptus bicornis* Zone. However, the sites currently being studied are in original sequence, not overturned as suggested in some previous publications. To date, no certain overlap has been found in graptolite ages of the Jutland Klippe with those of the main body of the Martinsburg Formation of Delaware Water Gap National Recreation Area.

INTRODUCTIONS

THROUGHOUT THIS century the Ordovician rocks near Jutland, Hunterdon County, New Jersey have presented challenges to structural and paleontological work (Figure 1). Weller (1903) noted the presence of well-preserved graptolites there in fair abundance, in contrast with other rocks of the Ordovician System in New Jersey. Noting the unusually complicated structure, Weller's report foreshadowed other efforts to interpret the area, which mostly lies within Union Township. Various workers sought precise dates, structural interpretations, and a better understanding of the Taconic Orogeny, (Dodge, 1952; Perissoratis, 1974; Perissoratis et al., 1979; Markewicz, 1984; Parris and Cruikshank, 1986). Al-

though the outcrop area is small, the Jutland Sequence (also called the Jutland Klippe) has great potential for interpretation of Taconic-area movements and for comparison to other Ordovician sequences. Among these, the Martinsburg Formation, which overlies the Jacksonburg Formation at Delaware Water Gap National Recreation Area, is the most significant. New faunal information from previously inaccessible exposures near Jutland can now be presented. Some of our results were published in preliminary form (Parris *et al.*, 1995). The information presented herein has confirmed and expanded our preliminary conclusions, but work continues, and the results cannot yet be considered a final report. The ultimate objective of our studies is a comprehensive biostratigraphy that relates the allochthons and outliers to the Martinsburg Forma-

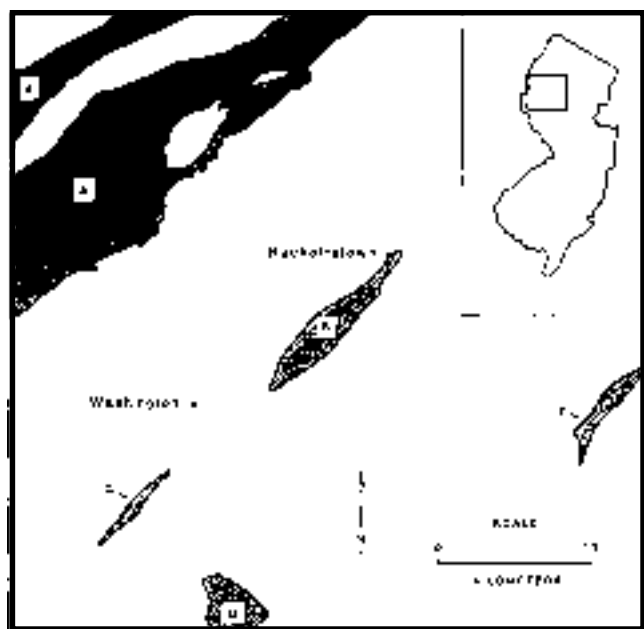


FIGURE 1—Martinsburg Formation and other Ordovician fine-grained clastic rock exposures in western New Jersey. A—Main body of Martinsburg Formation. B—Port Murray Outlier, C—Asbury Outlier, D—Jutland Klippe and E—Peapack Klippe.(after Parris *et al.*, 1993).

tion at Delaware Water Gap National Recreation Area, where previous studies have established a range from the *Climacograptus bicornis* Zone to the *Climacograptus spiniferus* Zone (Parris and Cruikshank, 1992). One outlier has thus far been confidently correlated (Parris *et al.*, 1993). The Port Murray Outlier correlates to the Bushkill Member of the Martinsburg Formation and the *Corynoides americanus* Zone.

CURRENT INVESTIGATION

Only a few specimens from previous studies have been located thus far in repositories. We have restudied all such materials available to us and have accepted the competent identifications of our predecessors for the most part (Parris *et al.*, 1995).

We also have prospected the Jutland sequence in search of more faunal material, including inspection of sites previously reported. The one major new site, herein described, was inspected in detail for the sake of a more detailed lithologic description of its fossiliferous sequence. It includes the first exposure of a section in which an estimate of thickness is possible, as well as an approximation of the positions of the fossiliferous zones.

FIGURE 2—Major excavation at Clinton Block and Supply Site showing generally consistent dip in sequence. Human figure for scale.

RESULTS

The Clinton Block and Supply Site in Union Township (Figure 2) is the major source of new information on the Jutland Sequence. Four graptolite-bearing levels have thus far been collected. Although significant deformation is present at the site, these collections are in an apparent sequence, numbered herein as Collections 19-22. The units generally strike N55°E and dip 24°SE, in apparent consistency, with collection 19 lowest, and collection 22 highest. Collection 21 is from a metabentonite high in the quarry face. The other collections are from marine clastic units.

Table 1 lists the faunal collections numbered 19-22 as currently identified. Zonation numbers are those of Berry (1960, 1968). Previous collections range from Zone 2 (*Adelograptus-Clonograptus*) to Zone 12 (*Climacograptus bicornis*). Those of the Clinton Block and Supply Site are in the later ranges of that span.

Numbers currently assigned to specimens from the Clinton Block and Supply Site are as follows: NJSM 16481-16490 from Locality 19; NJSM 16564 for Locality 20; NJSM 16565 for Locality 21. Specimens from Locality 22 are New Jersey Geological Survey specimens, currently unnumbered, but under study at the New Jersey State Museum.

Exposures of the Jutland section of the Clinton Block and Supply Site enable an approximation of section thickness and notation of key beds (Figures 2 and 3). The sequence ranging from the level of Zone 8 to Zone 9 is approximately 50 meters thick and from Zone 9 to Zone 10 another 20 meters.

TABLE 1—Faunal collections numbered 19-22 as currently identified. Zonation numbers are those of Berry (1960, 1968). Previous collections range from Zone 2 (*Adelograptus-Clonograptus*) to Zone 12 (*Climacograptus bicornis*). Those of the Clinton Block and Supply Site are in the later ranges of that span.

Locality Number	Taxon	Graptolite Zone
19	<i>Isograptus forcipiformis</i> (Ruedemann)	8
	<i>Didymograptus</i> sp. (<i>extensus</i> ?)	
	<i>Pseudotrigonograptus ensiformis</i> (Hall)	
	<i>Tetragraptus</i> sp. (<i>bigbyi</i> or <i>serra</i>)	
	<i>Xiphograptus svalbardensis</i> (Archer and Fortey)	
	<i>Isograptus victoriae maximus</i> (Harris)	
20	<i>Pseudisograptus</i> sp.	9
	<i>Isograptus</i> sp.	
	<i>Cryptograptus tricornis</i> (Carruthers)	
	<i>Glossograptus</i> sp. (<i>holmi</i> ?)	
21	<i>Climacograptus</i> sp.	10
	<i>Glyptograptus teretiusculus</i> (Hissinger)	
	Dichograptidae, genus indet.	
	<i>Pseudoclimacograptus angulatus</i>	
	<i>Cryptograptus tricornis</i> (Carruthers)	
	? <i>Reteograptus geinitzianus</i> Hall	
22	<i>Climacograptus</i> sp.	11
	<i>Hallograptus</i> ?	
	<i>Dicellograptus</i> ?	
	<i>Nemagraptus</i> ?	
	<i>Glyptograptus</i> ?	
	<i>Climacograptus</i> sp.	
	<i>Didymograptus</i> sp.	
	<i>Glossograptus</i> sp.	
	<i>Cryptograptus</i> sp.	
	<i>Pseudoclimacograptus</i> sp.	

FIGURE 3—View toward quarry face at Clinton Block and Supply Site, facing southeast. Fauna 21 is from light banded level (metabentonite) high in quarry (note arrows). Human figure for scale.

DISCUSSION

The graptolite biostratigraphy is but one aspect of a structural interpretation. However, the work of Perissoratis et al. (1979) antedates the majority of discoveries at the Clinton Block and Supply site, and the faunal evidence from that site does not support their interpretation, that is, that the sequence is overturned. No previous faunal collections from the Jutland sequence could be compared directly in continuous exposures with measureable sections. The Clinton Block and Supply Site has produced four faunal levels in sequence represented by collections 19-22, which are demonstrably older basal faunas to younger upper faunas. There is no reason to conclude that this differs from the Jutland Sequence as a whole, which thus appears to be an original sequence, not overturned. A new structural interpretation will be expected once other investigations are completed.

The youngest rocks of the Jutland sequence closely approach the ages of the oldest rocks of the Martinsburg Formation, both being correlated to the *Climacograptus bicornis* Zone. However, no overlap in the ages of the two sequences can yet be demonstrated.

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INITIATING A PALEONTOLOGY INVENTORY AND DATABASE AT DENALI NATIONAL PARK AND PRESERVE, ALASKA

PHIL F. BREASE

Denali National Park & Preserve, P.O. Box 9, Denali Park, AK 99755

ABSTRACT—Denali, at 6 million acres, is one of several large-acreage National Park Service units in Alaska where paleontological resources are poorly known, and the large volume of existing geologic and paleontologic data is inadequately organized. With the help of a Geologic Society of America volunteer, Denali began an evaluation of the existing literature, and catalogued 1068 cited fossils from 276 localities as reported in 46 journal articles, government documents, and other sources. Additionally, site localities were checked on maps and entered into the park Geographic Information System (GIS) to make preliminary determinations on reported locality accuracy and precision. Fossil materials at Denali include Paleozoic and Mesozoic marine invertebrates and microfossils, Mesozoic and Cenozoic plant material, and Cenozoic insect and pollen detritus.

INTRODUCTION

DENALI NATIONAL Park and Preserve is located in South-central Alaska, where there is a long history of marine deposition (Precambrian to late Mesozoic) which has been continually affected by tectonic shortening and/or accretion since at least the late Paleozoic (Csejtey, et al, 1982). Although most of the park geology is only reconnaissance mapped at a scale of 1:250,000, and the structural history of tectonic accretion is less than favorable to fossil preservation, some 40 rock units (see table 2.) have been identified that exhibit fossil remains. These fossil occurrences are reported in various publications, reports, theses, maps, manuscripts, inventory forms, and journal articles. Some of these records exist in obscure forms or in limited print (grey literature), many duplicate or overlap information, and no single systematic database exists that can be used for park paleontological resource management, or for research evaluations. Additionally, the park has fewer than 5% of reference samples from major fossil localities.

To rectify these conditions, a proposal was developed to do a literature search, design a useful database format, input known paleontology literature and citations, delineate descriptive (mapped) localities, and perform locality checks for accuracy and for providing park examples of some sites and fossils. This proposal was provided to the NPS Geologic Resources Division in the Winter of 1997 for assistance in personnel and/or operational funding. In early December, the project description was forwarded to the Geological Society of America (GSA) for consideration in the intern program within their Institute for Environmental Education. GSA approved of the project and offered to advertise, screen applicants, and provide a stipend to the selected intern.

After advertisement in the magazine "GSA Today," GSA received some 35 applications for the intern position in Denali. Through this process, an intern with previous relational database experience was selected, and arrived at the park in mid-May, 1997. The intern worked as a team member of the Physical Sciences Branch, Research and Resource Preservation Division, at Denali National Park. The primary duties involved the design, set-up and record entry of a new Paleontol-

ogy database for the park, coupled with a few site visits for data confirmation.

RELATIONAL DATABASE MANAGEMENT SYSTEM

Database requirements for paleontological information are similar to many other database themes. The database must provide for data organization, offer a search or find function, and have variable presentation formats to satisfy a wide range of investigation or report requirements. We choose Microsoft Access (2.0) because it provided these capabilities, is commonly available within government computer purchase packages, and is the current, NPS sanctioned database program.

The paleontology database design at Denali originally involved about 15 fields, but numerous design revisions were made through the course of data input to accommodate differing citation data and evolving search and cross-correlation database manipulations. Some of the more difficult field categories requiring custom designs included multiple authors, multiple citations, varying and sometimes conflicting taxonomic details, varieties of coordinate and common locality descriptions, varying geologic descriptors, and multiple collector/repository combinations. To track data input and to record location confidence, additional yes/no fields were included for citations, maps, and actual field locations.

The database fields are given below in three major form-entry categories:

- *Citation Fields* include: Citation ID, Source ID, Locality ID, Fossil Type, General Fossil Type, Invertebrate Type, Era, Phylum, Class, Order, Genus, Species, Age in Years, Repository, Collection Number, Collector, Year, and Notes;
- *Locality Fields* include: Map Number, Locality ID, Cited Locality Number, Precise Locality, Terrane, Quad, Quad Number, Section, Range, Township, Latdeg., Latmin, Latsec, Longdeg, Longmin, Longsec, Rock Unit, Lithology, and Notes;
- *Publications Fields* include: Source ID, Title, Author 1, Author 2, Other authors, Year, Journal, Publisher, Vol/Page, and Notes.

In addition to three input forms, the database is structured with 8 tables, 16 queries, and 5 reports which provide

TABLE 1—Paleo-taxonomy in Denali National Park and Preserve.

	<u>PHYLUM (or type)</u>	<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u>	<u>GENUS</u>	<u>SPECIES</u>
*ALL RECORDS	10	17	26	47	306	161
	<i>Mollusca</i> (271)	<i>Bivalves</i> (143)	<i>Dysodonta</i> (54)		<i>Inoceramus</i> (12)	
					<i>Gryphea</i> (3)	
					<i>Buchia</i> (21)	
					<i>Minotis</i> (7)	
					<i>Ostrea</i> (2)	
					<i>Halobia</i> (2)	
					<i>Lima</i> (3)	
			<i>Desmodonta</i> (13)		<i>Pleuromya</i> (11)	
			<i>Isodonta</i> (1)			
		<i>Cephalapoda</i> (100)	<i>Amminoids</i> (78)		(24+ varieties)	
			<i>Blemnoids</i> (19)		(2+ varieties)	
		<i>Gastropoda</i> (19)			(+3 varieties)	
	<i>Brachiopoda</i> (107)	<i>Articulata</i> (40)	(7+ varieties)			
					(19+ varieties)	
	<i>Cnidaria</i> (170)	<i>Anthozoa</i> (136)	<i>Tabulata</i> (21)		(8+ varieties)	
			<i>Rugosa</i> (20)		(2+ varieties)	
			<i>Scleractinia</i> (15)			
		<i>Hydrozoa</i> (34)	(3+ varieties)			
	<i>Arthropoda</i> (95)	<i>Trilobita</i> (6)			(2+ varieties)	
		<i>Arachnida</i> (9)	(2 varieties)			
		<i>Insecta</i> (78)	<i>Coleoptera</i> (69)	(14+ varieties)		
			<i>Hymenoptera</i> (6)			
			<i>Hemiptera</i> (1)			
			<i>Trichoptera</i> (2)			
		<i>Crustacea</i> (2)	<i>Cladocera</i> (2)		<i>Daphnia</i> (2)	
	<i>Echinodermata</i> (48)	<i>Crinoidea</i> (15)				
		(33 unspecified)				
	<i>Gymnolamatea</i> (7)					
	<i>Bryophyta</i> (5)			<i>Sphagnaceae</i> (3)		
	<i>Porifera</i> (2)					
	<i>Conodonts</i> (93)				(19+ varieties)	
	<i>Radiolarians</i> (86)				(17+ varieties)	
	<i>Pollen</i> (83)				(35+ varieties)	
	<i>Plants</i> (58)	<i>Angiospermae</i> (15)		(9+ varieties)		
		<i>Gymnospermae</i> (4)				
	<i>Dinoflagillates</i> (2)					
	<i>Foraminifera</i> (2)					
	<i>Alga</i> (2)					
	<i>Vertebrate</i> (1)				(Fish skeletal remains)	
	<i>Trace Fossils</i> (1)				(Worm burrows)	

* specified taxa/numbers represent abundance at lowest identifiable levels.

* this table represents park record as of January 1998.

for rapid data filters, correlations and cross-tabulations. However, customized data manipulations are quite simple in Microsoft Access.

For the spatial database, record locations were originally placed on USGS 1:63,360 scale topographic quadrangle maps for initial assessment of descriptive precision. If significant problems or conflicts were not identified by this process (i.e. questionable physiography, wrong rock units, or conflicting location reports) then the localities were transferred to the

park GIS database through our ArcView software. Citations/localities were thus bounded by reported sites within a 49-quadrangle window. Although this boundary limit includes some lands outside Denali National Park, it also encompasses most rock units and terranes of central Alaska, in their entirety.

DATABASE RESULTS AND STATUS

The Denali paleontology database consists of 1068 cited fossil records from 276 localities as reported in 46 documents.

TABLE 2—Rock units, age, and fossil types in Denali National Park and Preserve. Numbers in parantheses indicate number of records currently recorded from the park.

*UNIT	LITHOLOGY	AGE	FOSSIL TYPES - TAXA - NUMBER OF RECORDS
Oc	limey shales, sanstone, siltstone	Early-Mid Ordovician	<i>mega-invert.</i> (2)
Sl	marblized limestone	Early-Mid Silurian	<i>Cnidaria & algae</i> (5)
Dos	limestones & shales	Ordovician - Devonian	<i>Brachiopoda, Cnidaria, Mollusca, conodonts & radiolarians</i> (15)
Dms	marble	Ordovician - Permian	<i>Cnidaria & Echinodermata</i> (16)
Kms	argillite & chert	Ordovician - Penn.	<i>conodonts & radiolarians</i> (11)
msl	dolomite-limestone (melange)	Silurian - Devonian?	<i>Brachiopoda, Cnidaria, Echinodermata, Porifera, Gymnolaemata, Arthropoda & conodonts</i> (39)
mnl	limestone (melange)	Devonian - Cretaceous	<i>Brachiopoda, Cnidaria, Echinodermata, Mollusca & conodonts</i> (35)
TRPs	cherts, carbonates & congl.	Devonian - Permian	<i>Brachiopoda, Cnidaria, Mollusca, Echinodermata, & conodonts</i> (41)
Pzus	clastics & carbonates	Mid-Devonian - Penn.	<i>Brachiopoda, Cnidaria, Mollusca, Echinodermata, Gymnolaemata, Arthropoda & Forams</i> (35)
ls	limestone	Midille Devonian	<i>Cnidaria</i> (3)
DI	clastics & carbonates	mid-late Devonian	<i>Brachiopoda, Cnidaria, Mollusca & Echinodermata</i> (61)
Dsb	chert	Late Devonian	<i>Mollusca, radiolarians & conodonts</i> (11)
TRdv	limestone, chert, volcanic breccia	Late Devonian - Triassic	<i>Brachiopoda, Cnidaria, Mollusca, Echinodermata, Gymnolaemata, conodonts & radiolarians</i> (67)
Kmn	argillites, chert & conglomerate	Missip. - Cretaceous	<i>Cnidaria, Mollusca & radiolarians</i> (4)
Pd	continental clastics	Middle Pennsylvanian	<i>plant</i> (1)
TRcg	conglomerate w/ chert clasts	Permian - Late Triassic	<i>Cnidaria, conodonts & radiolarians</i> (4)
TRrb	red sandstones & conglomerates	Permian - Late Triassic	<i>Cnidaria</i> (2)
TRcs	silty limestone	Triassic	<i>conodonts</i> (5)
JTRlb	limestone	Triassic	<i>Brachiopoda & Cnidaria</i> (4)
TRbd	siltstone, greenstone & argillite	Late Triassic	<i>Cnidaria, Mollusca, Porifera & radiolarians</i> (13)
TRlb	limestone	Late Triassic	<i>Brachiopoda, Cnidaria, Mollusca & radiolarians</i> (16)
Pzsl	carbonaceous/calcareous shale	Late Triassic	<i>conodonts</i> (1)
JTRrs	calcareous sandstone	Late Triassic	<i>Cnidaria & Mollusca</i> (5)
JTRs	limestone & calcareous sandstone	Upper Triassic	<i>Cnidaria, Mollusca & Echinodermata</i> (57)
TRvs	argillites & marble	Late Triassic	<i>Cnidaria & Mollusca</i> (11)
Js	limestone & calcareous sandstone	Early Jurassic	<i>Mollusca</i> (41)
JTRta	chert, limestones & tuff	Jurassic	<i>Mollusca & radiolarians</i> (33)
KJa	chert & argillite	Jurassic - Cretaceous	<i>Mollusca, & radiolarians</i> (29)
KJs	flysch sequence	Jurassic - Cretaceous	<i>Brachiopoda & Mollusca</i> (28)
KJfk	limestone & flysch	Early Cretaceous	<i>Mollusca</i> (4)
KJf	argillite & chert	Mid Cretaceous	<i>Mollusca, & radiolarians</i> (5)
KJfl	limestones, clastics & argillites	Cretaceous	<i>Brachiopoda, Mollusca, & conodonts</i> (31)
Tcs	siltstone, sandstone & shale	Cretaceous - Paleocene	<i>plants, pollen, conodonts, dinoflagellates & vertebrate [fish skeletal elements]</i> (128)
Ts	conglomerates & sandstone	Tertiary (Paleocene)	<i>plant</i> (6)
Tfv	clastics & carbonates	Eocene?	<i>conodonts & plants</i> (17)
Tcb	argillaceous sandstone & siltstone	Oligocene - Miocene	<i>plant</i> (17)
Q,Qs,Qa	sands, gravels & unconsolidated	Quaternary	<i>plants, insects, pollen</i>

* Rock unit nomenclature from Reed and Nelson, 1980, and Csejtey, et al, 1992.

The records show the dominate fossil type to be mega-invertebrates (729 records), but a small variety of other flora and fauna are also present in the park. Table 1., "Paleo-Taxonomy in Denali National Park and Preserve," provides a view of those taxonomic numbers and diversity with ten mostly marine invertebrate phyla, two major marine categories, as well as insects, spiders, plants, mosses, pollen, algae, trace fossil records, and 1 vertebrate record. The Phylum Mollusca, particularly Class Pelecypoda, represent the greatest numbers and greatest diversity, while the lone vertebrate record (fish skeletal elements) stands as the most limited in diversity and numbers.

Age representation is currently split between 414 Paleozoic records, 465 Mesozoic records, 165 Cenozoic records, and 24 records of undetermined age. Although the greatest number of fossil records was found in the Mesozoic, the greatest faunal diversity is within the Paleozoic Era. Table 2, "Rock Units, Age, and Fossil Types in Denali National Park and Pre-

serve," demonstrates this greater Paleozoic diversity, with the majority of fossil records falling in the early Paleozoic, and most of those fall within the Devonian Period, or in a range encompassing the Devonian Period. Much of this record can be attributed to the abundance of fossiliferous carbonate shelf and upper slope deposits in the early Paleozoic rocks of Denali, and conversely, the lack of such fossiliferous carbonate rocks in the flysch sequences that dominate the Mesozoic rock units.

Of the 276 localities, approximately 80% have been precisely located on hard copy maps (1:63,360 USGS Topographic Quadrangles) and the remaining 20% lacked adequate information to plot exact positions.

Although it is assumed that the bulk of the paleontology data within and around the park has been entered in the database, several external and less formal citations, collections, and other reports are not yet included. Continued database development and field inventories are planned for future field seasons. We wish to thank the Geological Society of America

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A WALK THROUGH TIME AT FOSSIL BUTTE: HISTORICAL GEOLOGY OF THE GREEN RIVER FORMATION AT FOSSIL BUTTE NATIONAL MONUMENT

H. P. BUCHHEIM

Geology Section, Department of Natural Sciences, Loma Linda University
 Loma Linda, CA 92350

ABSTRACT—The type section of the Fossil Butte Member of the Green River Formation at the east of Fossil Butte provides a nearly complete history of Fossil Lake throughout its history. The base of formation rests on the red fluvial Wasatch Formation. The limestones of the Green River Formation grade laterally into the Wasatch Formation as well. The Green River Formation is easily divided into three basic units here, each representing a significantly different phase of Fossil Lake.

The lower unit is composed primarily of bioturbated limestones, but grades southward into a well developed lake deposit with laminated micrites containing abundant fossil fish.

The middle unit is composed of kerogen-rich laminated-micrite that has been extensively quarried for its abundant fossil fish. Fossil Lake expanded to its maximum size during middle unit time, however it suffered periods of near total evaporation, as evidenced by beds of dolomicrite. The fossil resources of this deposit are spectacular and unique, but may be threatened by multiplied commercial quarrying activities over the past few years.

The upper unit is composed largely of dolomicrite containing salt casts of sodium carbonates. Fossil fish are absent from the upper unit at Fossil Butte. Fossil Lake freshened only briefly for a short period of time before being totally filled in by the encroaching fluvial systems surrounding the lake.

Much remains to be discovered about this unique lake deposit, and no doubt our view of Fossil Lake will change with those new discoveries.

INTRODUCTION

ALTHOUGH WE do not have time machines to visit the past, we can come pretty close with the modern tools of geology and paleontology and with the skills to apply them. It is the unknown and mystery of the past that motivates many of us to pursue our professions as geologists and paleontologists. It is like putting the pieces of a puzzle together... the more pieces that we can fit together, the clearer the picture becomes. The Eocene lake deposits (Fossil Lake) of Fossil Butte National Monument and surrounding areas (known in total as Fossil Basin) provide an opportunity to recreate the puzzle and interpret the past in nearly complete way. Most of the puzzle pieces are there because of continuous deposition without periods of erosion, because of incredible preservation of life rarely seen elsewhere, and because of the way nature has

dissected these ancient lake beds into a suite of canyons and buttes that provide a nearly complete three dimensional view of Eocene Fossil Lake. We will now take a walk through time as we walk up through the type section at Fossil Butte National Monument; we shall imagine standing on the ancient shore of this unique lake, and we shall observe the physical lake environment, as well as the life and death of the myriad of creatures that inhabited the lake and it's surroundings. This paper will serve as an introduction to more detailed papers in this volume about Fossil Butte National Monument that provide in depth views of Fossil Lake in regards to specific topics and time periods.

THE TYPE SECTION OVERVIEW

Stratigraphic Nomenclature.—Figure 1 provides a stratigraphic overview of the Green River Formation at Fossil Butte.

FIGURE 1—The Green River Formation in Fossil Basin at Fossil Butte is divided into three units as indicated. Note the marker beds to the right of the section that are referred to in the text. XRD mineralogy provides a view of the relative amounts of calcite, dolomite, and total silicate minerals (quartz, feldspar, zeolites, clays). Fossil fish occur in units indicated with solid bars.

The basic lacustrine stratigraphy was first described and divided into the Fossil Butte and Angelo Members by Oriel and Tracey (1970) and later studied in more detail by Buchheim (1994a and 1994b) and Buchheim and Eugster (1998). Buchheim (1994a) informally divided the Fossil Butte and Angelo Members of the Green River Formation up into the lower, middle, and upper units. This was necessary in order to accurately incorporate new knowledge obtained about the stratigraphy including the discovery of a thick sequence of fluvial-lacustrine rocks best developed in the Little Muddy Creek and more southern canyons and described in detail by Biaggi (1989). In addition, Buchheim (1994a) found that Fossil Lake underwent three phases: a shallow freshwater phase (lower unit); a relatively deeper freshwater to saline phase (middle unit) and a mostly hyper saline-alkaline phase (upper unit). The boundaries of these units can be accurately located at most locations and are identified by mapable marker beds.

Previous stratigraphic and paleontologic investigations.—Cope (1877 and 1884). Peale (1879, p. 535) first described the geology and fossil fishes of the Green River Formation. The geologic history with emphasis on paleontology was summarized by McGrew and Casilliano (1975). A detailed description of the paleontology of the entire Green River Formation was provided by Grande (1984). Grande and Buchheim (1994) provided a detailed analysis of lateral variations in paleontology and sedimentology in Fossil Lake. A detailed summary of the Green River Formation of Fossil Basin was completed recently by Buchheim and Eugster (1998).

Recent Investigators who have made detailed descriptions of the sedimentology, stratigraphy, and paleontology of Fossil Lake include: Biaggi (1989), who studied an early phase of Fossil Lake during which the lower unit was deposited; Loewen and Buchheim (1997) who reported on the saline to freshwater transitions in Fossil Lake as revealed in the upper unit; Cushman (1983) who conducted the only study on fossil pollen in the lake beds of Fossil Basin; Leggitt and Buchheim (1997) who reported on a significant mass mortality beds of fossil birds in the southern part of Fossil Basin (see also Leggitt, 1996); Trivino (1996) who completed a detailed spatial analysis of unit 5b, an oil shale bed (kerogen-rich laminated-micrite) and recreated the paleogeography of Fossil Lake during one period of Fossil Lake's history.

A WALK THROUGH TIME

Lower Unit time.—At Fossil Butte one is impressed with the bold white cliffs of the Green River Formation that contrast markedly with the underlying slope-forming and variegated red and purple Wasatch Formation. The Wasatch Formation represents a vegetated, fluvial food plain that was crossed by numerous rivers and streams. If you stand at the base of the contact between these two formations and look south and imagine yourself back in early Eocene time, you would actually be standing on the north shore of a lake that was well developed in the southern part of Fossil Basin. However, the lake was usually shallow and was frequently filled in by fluvial sedimentation. It was surrounded by broad mudflats that were mud-cracked. These mudflats were frequently

swallowed up by a lake that experienced numerous expansions and contractions. Subsidence in Fossil Basin eventually exceeded sedimentation and the lake deepened and flooded the fluvial plain until it stretched north of Fossil Butte another 30 kilometers.

Fossil Lake never attained depths greater than four or five meters at Fossil Butte during lower unit time. It formed a hyper saline lake at least twice and probably totally desiccated. The two meter-plus thick beds of dolomite are evidence of this. The massive white limestones of this unit are heavily bioturbated as indicated by abundant trace fossils with meniscus fillings indicating sediment-feeding organisms, such as insect larvae, worms, or shrimp.

As you near the top of the lower unit you observe a 3-4 meter thick sequence of alternating siliciclastic mudstones and laminated micrites. Close study of the micrites reveal that they are composed of alternating laminae of micrite and clay. This unit grades southward into the sandstone tongue of the Wasatch Formation, that provides a prominent marker bed throughout the southern half of Fossil Basin. This sandstone has been interpreted as a prograding delta (Peterson, 1987). At Fossil Butte, the mudstones of this unit represent a pro-delta deposit. Only a few kilometers north of Fossil Butte, Fossil Lake was replaced by a fluvial flood plain during this time.

Lower unit time ended with a hypersaline lake where dolomite precipitated from a shallow body of water and was clear and free of siliciclastic input. The lake again freshened for a short period of time before drying up again in one last gasp before the onset of a dramatic change marking the beginning of middle unit time.

Cushman (this volume) concludes that the climate during lower unit time was warm temperate as indicated by the palynofloral assemblage.

Middle unit time.—Middle unit time was a time of fascinating events in Fossil Basin. It began with a loud roar as the climate must have changed abruptly, transcending to a wet-humid period of high rainfall. The lower oil shale at the base of the middle unit was deposited as a result of the most expansive phase of Fossil Lake's history. A mudstone unit (coaly mudstone) rich in coalified plant material with a 2-3 cm thick coal at the top can be traced throughout the basin. There are no roots associated. A thin oil shale known as the lower oil shale (kerogen-rich laminated-micrite) about 30 cm thick overlies the coal bed. It contains small *Knightia* in abundant numbers along with fossil insects and plant fragments. This sequence is interpreted as being deposited in a lake undergoing a rapid transgression. The transgression appears to have been initiated abruptly during a single episodic event that transported huge amounts of plant material into the lake, resulting in the thin coal deposit. The high organic-carbon content and dense fossil fish concentrations are consistent with a lake in its early stages of expansion. Nutrient levels are high and are inherited from the rich soils recently flooded. The lower oil shale can be traced throughout Fossil Basin wherever the middle unit outcrops and provides an excellent marker bed to the experienced stratigrapher.

Fossil Lake remained very productive throughout middle unit time resulting in the deposition of the fish beds that the Green River Formation is so famous for. One of these beds, known as the lower sandwich bed, has been studied intensively throughout Fossil Basin at over 70 locations (Trivino, 1996). The two tuff beds delineating the top and bottom of this unit allow precise stratigraphic correlations and spatial analysis studies. Studies conducted of bed thickness, laminae number, stable isotopes, mineralogy, and paleontology have provided a detailed recreation of the paleogeography of Fossil Lake during this time. Most of the inflow areas were concentrated in the southern half of the lake; however a significant inflow point was present in the northeastern part of the lake as is indicated by a dramatic thickening of laminae in the vicinity. The laminae thickening is thought to be a result of a high rate of calcite precipitation in this area. In addition, a fluvial channel filled with conglomerate replaces most of the middle unit a few kilometers east of the thick laminae anomaly. Buchheim and Biaggi (1988) and Buchheim (1994b) concluded that the laminae of this unit are not true varves because laminae number between the two tuff beds increases from about 1100 to 1600 from lake center to margin. Deposition of a greater number of laminae near the lake-margins occurred where calcium-rich inflow water first mixed with the bicarbonate-rich (alkaline) lake water (Buchheim, 1994a).

Similar results were obtained from a paleogeographic study (Buchheim, 1993) of the "18-inch layer". This unit has been extensively excavated for its well-preserved fossil fish fauna since the late 1800's. Grande and Buchheim (1994) provide a detailed analysis of the lateral variation of paleontological and sedimentological characteristics of this unit. The 18 inch layer (as a kerogen-rich laminated micrite containing abundant fossil fishes) is spatially limited to only about a hundred kilometer area from about the Fossil Butte National Monument Visitor's center on the north to about 10 kilometers south; and from about the middle of R119W to the middle of R118W. About 60% of this area has been eroded out, leaving only about 40 square kilometers of area where this incredible paleontological resource is still preserved. The 18 inch layer only crops out over a linear distance of about 30 kilometers. Of this only about 10 kilometers is accessible to major paleontologic excavation activities, because of steep slopes over most of it that require excessive overburden removal before collection can begin. These are rough estimates, but it is clear that the preservation of this unique paleontological heritage is at risk. Of the 10 accessible kilometers, up to half may be under private or state lease to commercial quarry operators! The so called "split fish" layers at more marginal geographical localities is not within the 18 inch layer, but within the lower sandwich beds. The sandwich beds extend over a 40 by 20 kilometer square area centered around location 1306, about 6 kilometers south of Fossil Butte National Monument.

The glory period of Fossil Lake finally faded with the temporary onset of arid conditions leading to nearly total dessication of the lake during middle dolomicrite bed time. Fossil Lake during this period was clear with little siliciclastic input. Although this bed is dolomicrite at the center of the

basin, it grades laterally into calcimicrite. This observation suggests that fresher conditions existed at the margins of the lake, a trend that dominates the lake system throughout its history. This relationship suggests that the dolomite was precipitated either directly from the water column or formed syndepositionally (Buchheim, 1994a), rather than generated on marginal mudflats. The ostracodal dolomicrite is a prominent marker bed in the southern half of the basin, where it forms a hard, dense and blocky unit that leaves "bricks" of gray limestone scattered over an otherwise soft weathered slope.

Fossil Lake did not experience a major expansion again until k-spar tuff time (from the top of the ostracodal dolostone to one meter above the k-spar tuff: a major marker bed that is composed of authigenic potassium feldspar), but remained brackish to saline. Abundant fish fossils are presently being quarried from this unit at some the basin center quarries. Along with fossil fish occur abundant *Goniobasis* gastropods. The significance of this relationship is not well understood because gastropods generally signal very shallow water and well oxygenated conditions (Surdam and Stanley, 1979). Shallow water conditions are indicated by the nearly basin-wide distribution of kerogen-poor laminated-micrite, a facies deposited in shallower near-shore water (Buchheim, 1994b) along with the occurrence of gastropods and abundant burrow traces. The potassium feldspar mineralogy of the k-spar tuff suggests hyper saline conditions during this period. Authigenic feldspar is produced by the reaction of hypersaline-alkaline water (rich in potassium) with volcanic ash (Sheppard and Gude, 1968, 1969; Surdam and Stanley, 1979). However, the relationship of feldspar and zeolite mineralogy to salinity is not as clean as expected. Although authigenic potassium feldspar tuff beds (rather than zeolite or clay beds) nearly always occur in dolomite sequences, they occasionally occur in calcitic sequences as well (Buchheim, 1998). The calcite mineralogy of the laminated micrite, occurrence of gastropods, and abundant fossil fishes suggests the lake was fresh to saline, but not hyper saline.

Cushman (this volume) suggests that the abundance of hardwood, riparian and conifer taxa provide a picture of moist lowlands and flood plains around Fossil Lake with upland forests on the surrounding ridges and mountains. Pine and other upland taxa grew in the highlands surrounded the lake. The palynofloral assemblages of the lower and middle units and the lower part of the upper unit indicate that a mixed mesophytic forest grew near Fossil Lake. The climate during middle unit time was probably more subtropical than during lower unit time.

Upper Unit Time.—Fossil Lake developed into a large, but shallow, hyper saline lake during upper unit time, generally devoid of fossils in central basin areas (Buchheim, 1994a). Salt casts of sodium carbonate minerals are abundant beginning about four meters above the k-spar tuff, indicating hypersalinity. A series of 3-4 oil shales (kerogen-rich laminated-micrite) within the lower half of the upper unit provide marker beds that can be traced throughout the basin. The lenticular nature of the laminae suggest these were deposited in shallow water.

Did fish entirely disappear from Fossil Lake during upper unit time? Loewen and Buchheim (1997) recently reported the first occurrence of fossil fish including very abundant numbers of *Priscacara hypsacantha* (perch) and *Lepisosteus* (gar) in the upper unit at a near-shore locality south of Elk Mountain in the southwest part of Fossil Butte (see Loewen and Buchheim, this volume, for further details). Their preliminary study indicated that a relatively fresher-water apron existed on the margins of Fossil Lake. In addition a lateral trend (lake-center to margin) in mineralogy (dolomite to calcite), oxygen stable isotopes (heavy to light), petrology (kerogen-rich laminated-micrite, highly disrupted by salt casts to laminated calcimicrite to bioturbated calcimicrite) all provide corroborating evidence of a salinity gradient in Fossil Lake during upper unit time.

About 16 meters above the k-spar tuff in the upper unit a four meter thick sequence of chert nodules and bedded chert occurs in a dolomicrite (chert horizon). The chert horizon can be correlated throughout Fossil Basin and provides an excellent marker unit. Lake water pH probably exceeded 10 during this time driving most silicates into solution. The dissolved silica precipitated out as silica gel and eventually converted to chert nodules or bedded chert (Buchheim, 1994b).

Abundant fossil birds of the genus *Presbyornis* frequented the shorelines of Fossil Lake during upper unit time (Leggitt and Buchheim, 1997), as indicated by a mass mortality bird bed that occurs in the vicinity of Warfield Creek about 40 meters above the k-spar tuff. Egg shell fragments, gastropods and ostracods are commonly associated. The reader is referred to Leggitt and Buchheim (this volume) for further details.

Volcanism increased significantly during upper unit time as indicated by a higher percentage of silicate minerals in the carbonate rocks (see XRD mineralogy in Figure 1). Tuff beds tend to be thicker as well. The k-spar tuff, that marks the lower boundary of the upper unit, averages 13 cm and increases to a maximum of 25 cm in the northwest corner of the basin at the head of Watercress Canyon. Most of the tuff beds in the underlying units are thinner (1-3 cm) and the carbonates contain generally less than 10% silicate minerals. The local thickening of the k-spar tuff suggests that a local volcanic source existed nearby. If the source was hundreds of kilometers away, the ash would be more evenly distributed across the basin.

Pollen collected and studied by Cushman (this volume) suggest that the climate gradually cooled during upper unit time, but may have returned to a warmer, subtropical climate during its final phase. This conclusion is supported by the occurrence of *Reevesia* (a tropical to subtropical element) at the top of the upper unit (Cushman, this volume) and is corroborated by the presence of about a meter of laminated micrite containing fossil fish. This essentially marked the end of Fossil Lake's history. Subsidence within the basin apparently slowed and the fluvial Wasatch Formation the lake. A few limestones in the Wasatch Formation above the upper unit indicate that a few short-lived ponds or less extensive shallow lakes attempted a come back.

We have now completed our walk through time. Our view is still somewhat hazy, but as research continues in Fossil Basin it will sharpen and maybe even change. New discoveries await the motivated researcher; new fossils, new views of processes occurring in Fossil Lake. This walk will be made again... and with each walk we will see Fossil Lake with a clearer perspective!

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THE STRATIGRAPHIC SETTING OF THREE *PRESBYORNIS* NESTING SITES: EOCENE FOSSIL LAKE, LINCOLN COUNTY, WYOMING

V. LEROY LEGGITT, H. PAUL BUCHHEIM, AND ROBERTO E. BIAGGI

Geology Section, Department of Natural Sciences, Loma Linda University, Loma Linda, California 92350

ABSTRACT—Autochthonous *Presbyornis* sp. (Aves: Anseriformes) eggshell from three Eocene Fossil Lake sites is strong evidence for multiple avian nesting sites within Fossil Basin. Two of these nesting sites (the Bear Divide and Warfield Creek sites) occur near the base of the lower unit of the Fossil Butte Member of the Green River Formation. The third nesting site (the Powerline site) occurs near the top of the upper unit of the Fossil Butte Member. The *Presbyornis* nesting sites span Green River Formation time in Fossil Basin.

The Green River Formation in Fossil Basin is completely encased in the late early Eocene Wasatch Formation. The “K-spar tuff” at the junction between the upper and middle units of the Fossil Butte Member has been dated at 50.2 \pm 1.9 mya. Palynomorph data from the lower, middle, and upper units of the Fossil Butte Member are consistent with a late early Eocene or an early middle Eocene age.

It is likely that the Bear Divide and Warfield Creek nesting sites are late early Eocene in age, and that the Powerline nesting site may be early middle Eocene in age.

INTRODUCTION

THE SHOREBIRD-DUCK mosaic bird *Presbyornis*, with its duck-like head, and long-legged shorebird-like body, was first described from the Green River Formation of Utah by Wetmore (1926). Since then, *Presbyornis* has been reported in great concentrations of associated skeletons from all of the Eocene Green River Formation lakes: Lake Gosiute (Simmacher, 1970; McGrew and Feduccia, 1973; Feduccia and McGrew, 1974, 1984; Feduccia, 1978, 1980; McGrew, 1980; Olson and Feduccia, 1980a); Fossil Lake, (Leggitt and Buchheim, 1993); Lake Uinta (Zawiskie et al., 1991); and ?late Paleocene Lake Flagstaff (Zawiskie et al., 1991).

Non-Green River Formation *Presbyornis* occurrences include: Eocene rocks in Mongolia (Zawiskie et al., 1991), the Lower Eocene Casamayor Formation of Patagonia (Howard, 1955; Cracraft, 1970; Feduccia and McGrew, 1974), and most recently, the marine late Paleocene Aquia Formation of Mary-

land and Virginia (Olson, 1994). Apparently *Presbyornis* had a worldwide distribution in the Paleocene and Eocene.

In addition to its widespread distribution, *Presbyornis* is important because its duck like cranial elements and shorebird-like postcranial elements link two modern orders of birds that were never thought to be related before the discovery of its fossils (Olson and Feduccia, 1980b; Olson, 1981; Feduccia, 1996).

Descriptions of avian nesting sites are rare in the paleontologic literature. Mohabey et al. (1993), reported a clutch of small oblong-shaped eggs of avian-like affinity associated with sauropod nesting sites from the Lameta Formation (upper Cretaceous) of India. In the Cretaceous of Mongolia, Gobipterygiform bird eggs are found in clutches and as individual eggs at several stratigraphic levels (Mikhailov et al., 1994). Both occurrences of Indian and Mongolian avian eggs have been interpreted as nesting sites.

There are numerous descriptions of Tertiary avian egg-

FIGURE 1—*Presbyornis* bones and eggshell from the Powerline nesting site. 1, a humerus (H), femur (F), coracoid (C), and tibiotarsus (T), from a lake margin strandline of *Presbyornis* bones. 2, a scanning electron micrograph of *Presbyornis* eggshell showing a distinct prismatic morphotype (radial cross section).

shell in the paleontologic literature (Mikhailov, 1997), but few of the reports emphasize a nesting site hypothesis. A good example of an Eocene avian nesting site was reported by McGrew and Feduccia (1973). This site was located in shoreline facies of the Wilkins Peak Member of the Green River Formation of Lake Gosiute, and contained hundreds of bones of *Presbyornis*, abundant eggshell fragments, tufa-encrusted logs, and skeletal elements of turtles, crocodiles, and fish. The sedimentology and paleoecology of the site were consistent with a nesting site hypothesis, but the eggshell fragments were not well described and might have been derived from the birds, turtles or crocodiles.

Avian eggshell fragments of prismatic morphotype have been identified by scanning electron microscopy from three Green River Formation localities along the southern shoreline of Eocene Fossil Lake (Leggitt and Buchheim, 1997). The three eggshell sites occur in close association with monospecific, single horizon, bonebeds of adult *Presbyornis* which are suggestive of mass mortality events (Figure 1).

Because of this close association of the avian eggshell fragments with the monospecific *Presbyornis* bonebeds, the eggshell has been referred to *Presbyornis* (Leggitt and Buchheim, 1997). The autochthonous nature of one site (the Powerline site) has been clearly established (Leggitt, 1996), and the remaining sites are believed to be autochthonous because of their proximity to the southern shoreline of Fossil Lake. Autochthonous *Presbyornis* eggshell is strong evidence in support of the nesting site hypothesis.

It is the purpose of this paper to document the precise stratigraphic position of the three nesting sites so that temporal, spatial and morphologic comparisons can be made between these Fossil Lake avian nesting sites.

STRUCTURE AND STRATIGRAPHY OF FOSSIL BASIN

Fossil Basin is a small north-south trending structural basin in southwestern Wyoming (Figure 2). Both the western and eastern margins of Fossil Basin were topographically elevated at the beginning of Wasatch and Green River deposition by reactivated thrust uplift and footwall uplift (Coogan, 1992). Basin margin uplift continued throughout Wasatch deposition as evidenced by a belt of the Tump Conglomerate Member of the Wasatch Formation, which interfingers with other Fossil Basin sediments on the west, north and east basin margins (Oriol and Tracey, 1970; Hurst and Steidtmann, 1986; Coogan, 1992). This basin margin uplift resulted in symmetrical (west to east) Wasatch and Green River facies deposition (Coogan, 1992).

The Tertiary stratigraphy of Fossil Basin has been described by several authors (Oriol and Tracey, 1970; Rubey et al., 1975; Hurst and Steidtmann, 1986). Oriol and Tracey (1970) described more than 7,000 feet of uppermost Cretaceous and Tertiary continental strata in northern Fossil Basin. These sediments include the Adaville, Evanston, Wasatch, Green River, and Fowkes Formations.

The Green River Formation in Fossil Basin can be characterized as a large lens of heterogeneous lacustrine sediments which includes well laminated limestone, siltstone, marlstone, and claystone with layers of oil shale (Rubey et al., 1975). This lens of lacustrine sediments is encased in the red, detrital, coarse grained strata of the Wasatch Formation (Rubey et al., 1975).

The red Wasatch sediments are roughly 3,000 feet thick and have been divided into seven mapped members by Oriol and Tracey (1970): 1) the basal conglomerate member, 2) the lower unnamed member, 3) the main body, which underlies the Green River Formation, 4) the sandstone tongue, which

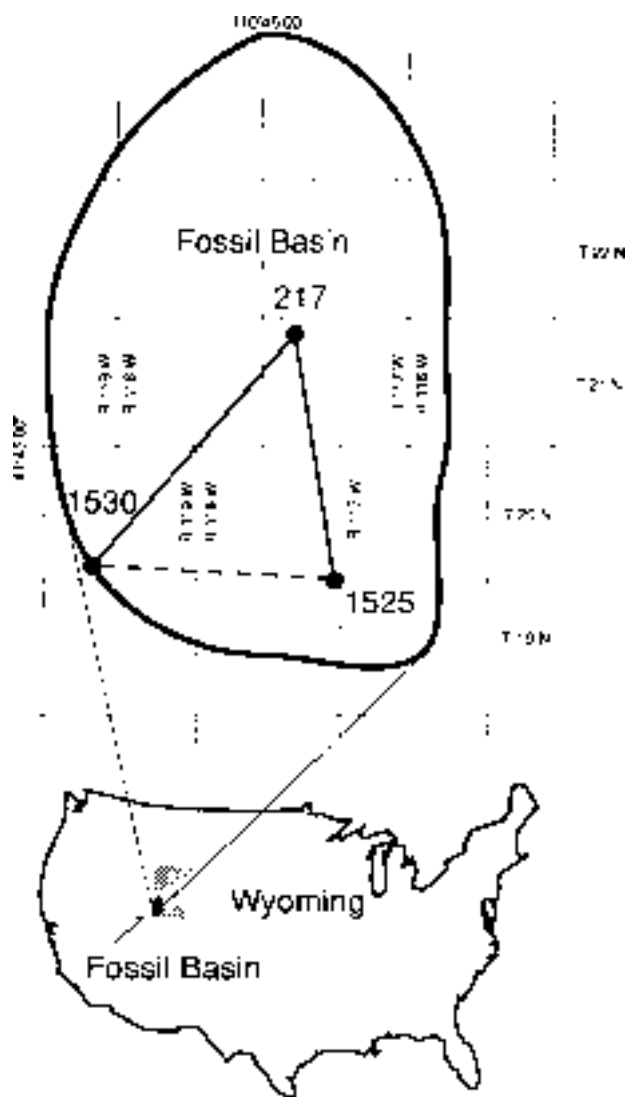


FIGURE 2—Map showing the location of measured sections in Fossil Basin. Location 217 is the type section of the Fossil Butte Member of the Green River Formation and is located within the boundaries of Fossil Butte National Monument. The solid correlation line represents middle unit correlations with the type section. The dashed correlation line represents lower unit correlations between locations 1525 and 1530.

divides the Fossil Butte Member of the Green River Formation, 5) the mudstone tongue, which divides the Fossil Butte and Angelo Members of the Green River Formation, and is characterized by abundant tufa-encrusted logs, 6) the Bullpen Member, which overlies the Green River Formation, and 7) the Tump Member, which is a peripheral member which interfingers with units 2-6 (Figure 3).

The Green River Formation in Fossil Basin has been divided into the Fossil Butte Member and the overlying Angelo Member by Oriol and Tracey (1970). The two members of the Green River Formation are separated by the time-transgressive mudstone tongue of the Wasatch Formation.

Buchheim (1994), and Buchheim and Eugster (1998), noticed that the Fossil Butte Member could be divided into

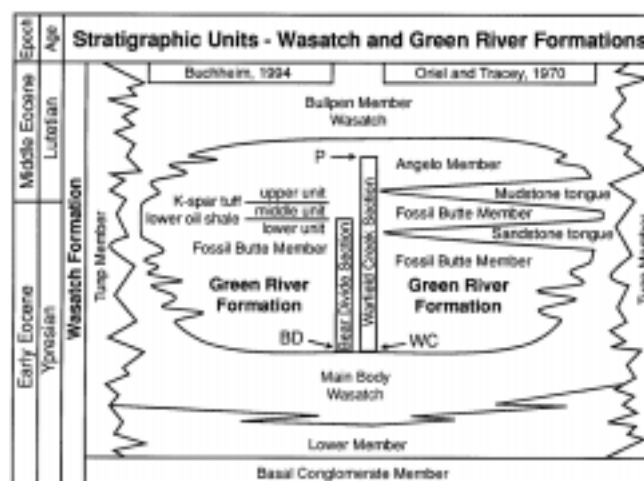


FIGURE 3—Schematic diagram of Wasatch and Green River Formation sediments in Fossil Basin. The right side of the diagram shows the divisions of the Green River Formation as proposed by Oriol and Tracey (1970). The left side of the diagram shows the divisions of the Green River Formation as proposed by Buchheim (1994). The study sections are included to show the location of the nesting sites: P is the Powerline nesting site, WC is the Warfield Creek nesting site, BD is the Bear Divide nesting site.

three units on the basis of major facies changes in Fossil Lake history: 1) a lower unit, recently studied by Biaggi (1989), which contains a record of the early development of Fossil Lake; 2) a middle unit, which is characterized by high-stand freshwater calcimicrite and which contains the famous fossil fish deposits; and 3) an upper unit, which is characterized by low-stand saline minerals and dolomicrite. This upper unit includes most of Oriol and Tracey's Angelo Member.

Buchheim and Eugster (1998) used time synchronous horizons to divide the Fossil Butte Member into units. The division between the lower and middle units was set at the lower oil shale and the overlying lower sandwich horizon (a pair of thin tuff beds about 50 cm apart). The middle and upper units were divided by the "K-spar tuff". Both marker horizons can be widely mapped in Fossil Basin and are used in this paper to correlate sections.

The stratigraphy of the lower unit was described in detail by Biaggi (1989). The lower unit was subdivided into the following ascending stratigraphic subunits: 1) the lower shale horizon (LSH) subunit, characterized by its brown-greenish-gray color; 2) the lower white marker (LWM) subunit, characterized by its distinctive white color and bench forming units; 3) the upper limestone (ULS) subunit, characterized by its golden or buff color; and 4) the sandstone (SS) subunit, characterized by its brown color. This sandstone subunit is equivalent to the sandstone tongue of the Wasatch as described by Oriol and Tracey (1970).

These subunit bands of color indicate facies changes within the lower unit and are present across most lower unit outcrops (Biaggi, 1989). The color bands are useful for stratigraphic correlation even though they represent time-transgressive facies.

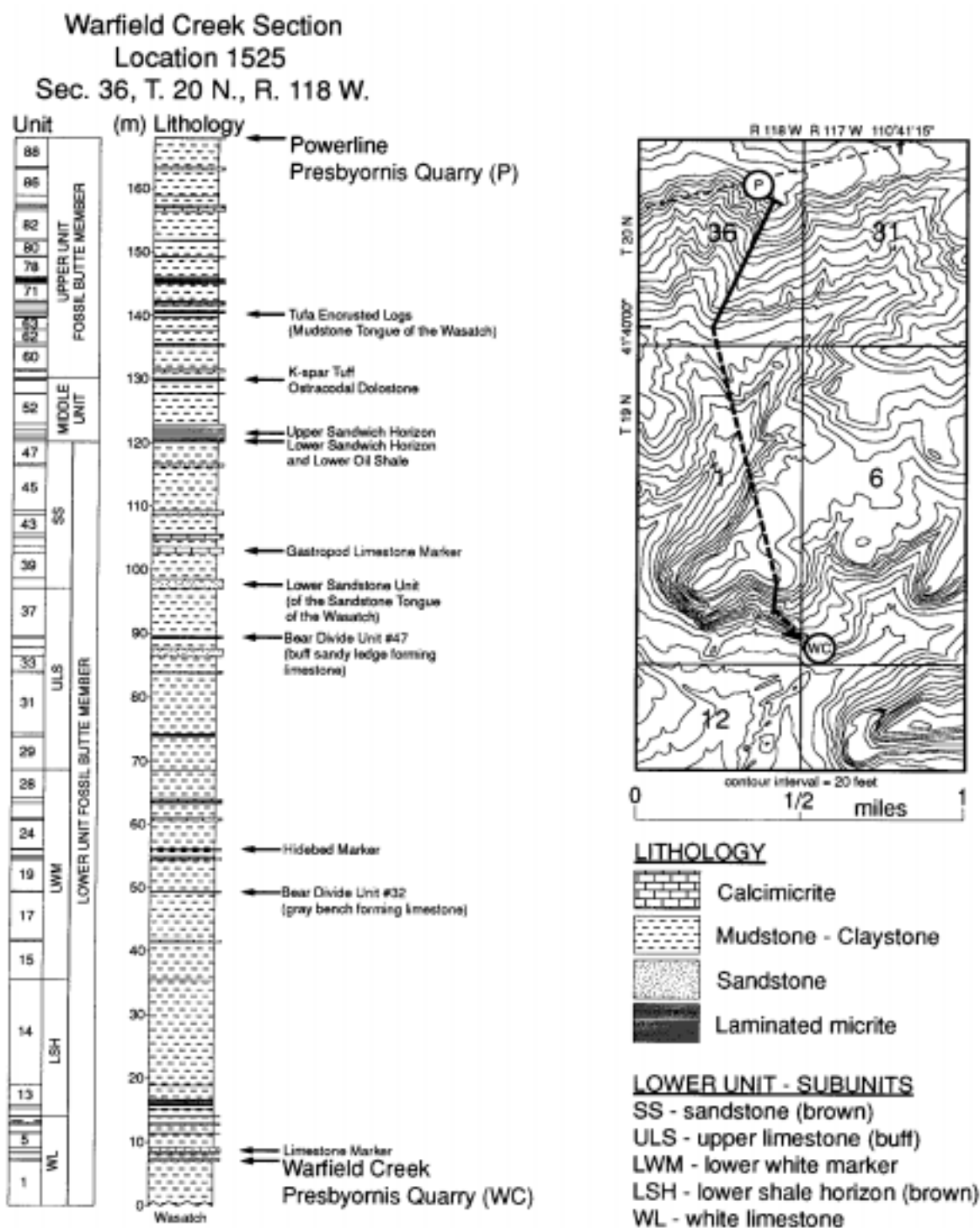


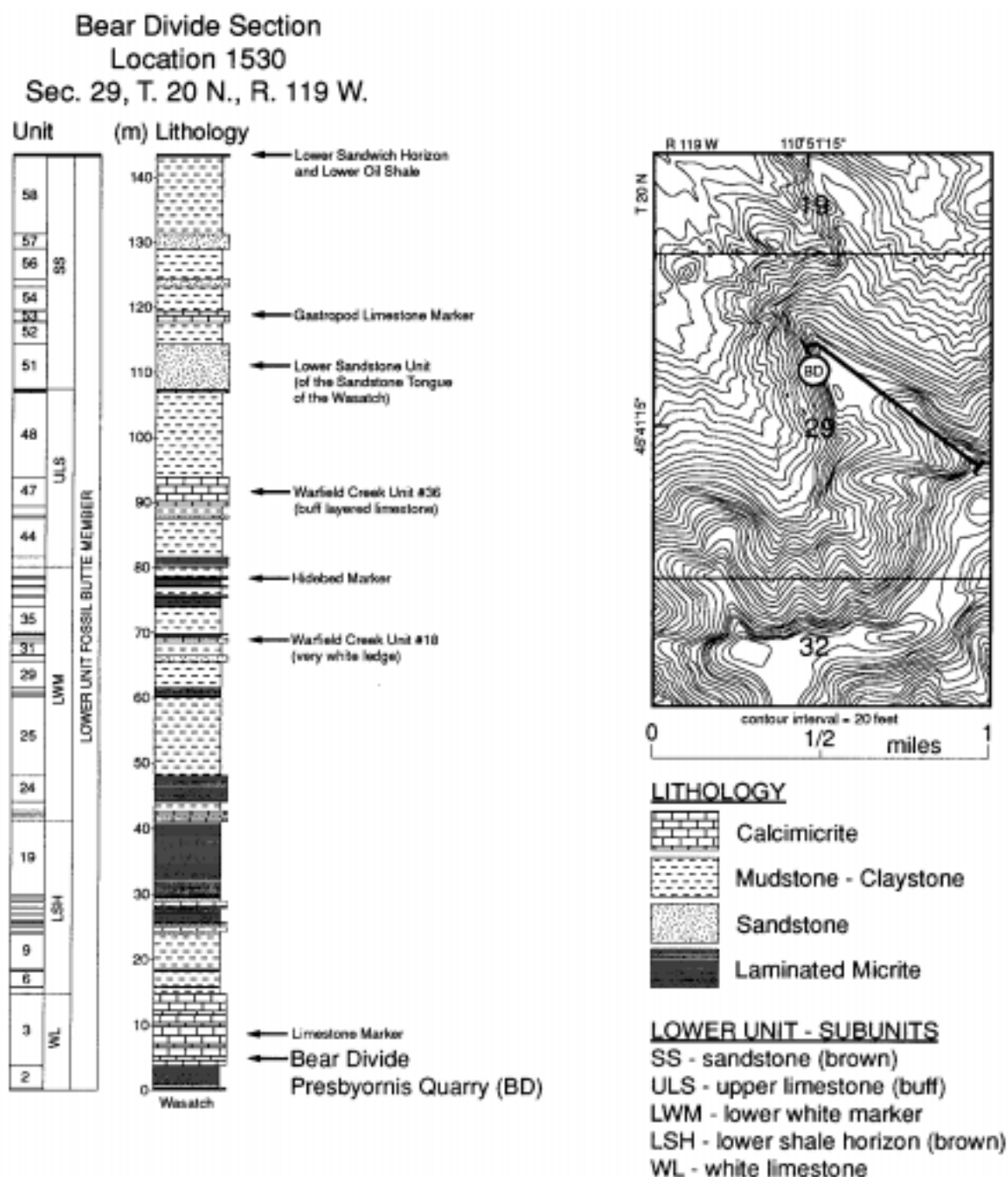
FIGURE 4—Warfield Creek section and the stratigraphic position of the Powerline nesting site and the Warfield Creek nesting site within the Green River Formation.

THE AGE OF FOSSIL BASIN SEDIMENTS

Most of the Wasatch Formation is of early Eocene age on the basis of pollen, invertebrate and vertebrate fossils (Gazin, 1952, 1956; Oriel and Tracey, 1970), but the basal conglomerate member may be partly Paleocene (Hurst and Steidtmann, 1986), and the Bullpen member may be partly early middle

Eocene (Oriel and Tracey, 1970). The age of the Wasatch formation is important because it completely encases the Green River Formation and therefore constrains Fossil Basin Green River time. The Green River Formation in turn encases the *Presbyornis* Nesting Sites.

The late early Eocene Green River Formation age, as determined using Wasatch fossils, is independently corroborated



by palynomorph analysis of the lower, middle, and upper units of the Fossil Butte Member of the Green River Formation (Cushman, 1983). The “K-spar tuff” which divides the middle and upper units of the Fossil Butte Member has been dated at 50.2 ± 1.9 mya (Buchheim and Eugster, 1998). This date suggests that the upper unit may be early middle Eocene in age.

THE NESTING SITE STRATIGRAPHY

Stratigraphic sections, which include the lower sandwich horizon tuff beds and the lower oil shale, were measured at

the fossil quarries and compared with the type section of the Fossil Butte Member of the Green River Formation (Figure 2). The locations of the three *Presbyornis* nesting sites are as follows: 1) the Powerline site (Figure 4), section number 1525, quarry location NE 1/4 Sec. 36, T. 20 N., R. 118 W., Warfield Creek Quadrangle, Lincoln County, Wyoming; 2) the Warfield Creek site (Figure 4), section number 1525, quarry location SW 1/4 Sec. 6, T. 19 N., R. 117 W., Warfield Creek Quadrangle, Lincoln County, Wyoming; and 3) the Bear Divide site (Figure 5), section number 1530, quarry location NW 1/4

Sec. 29, T. 20 N., R. 119 W., Windy Point Quadrangle, Lincoln County Wyoming.

The correlations between the two measured sections at the fossil sites and the type section of the Fossil Butte Member are shown in Figure 6. The lower sandwich horizon tuff beds and the lower oil shale, separate the lower and middle unit of the Fossil Butte Member and were used as a datum for correlation. Correlations were made by the marker units described by Buchheim and Eugster (1998), and Biaggi (1989).

DISCUSSION AND CONCLUSIONS

Although fossil avian nesting sites are rarely described, *Presbyornis* nesting sites appear to be common in the shoreline facies of the Green River Formation (Leggitt and Buchheim, 1997; McGrew, 1980). Within Fossil Basin, the stratigraphic position of three of these nesting sites was described using standard stratigraphic technique. We found that more than 160 meters of sediment separated the lowest and highest *Presbyornis* occurrence.

This stratigraphic interval includes the complete Fossil Butte Member of the Green River Formation and most of the overlying Angelo Member. The lowest *Presbyornis* nesting sites (Bear Divide and Warfield Creek) are found at the base of the Green River Formation at a time when Fossil Lake was developing. The highest *Presbyornis* nesting site (Powerline) is found at the top of the Green River Formation at a time when Fossil Lake was shrinking in size.

Most lines of evidence suggest that these *Presbyornis* nesting sites are late early Eocene in age. It is possible that the Powerline nesting site is early middle Eocene in Age.

ACKNOWLEDGMENTS

We are grateful to Storrs L. Olson of the National Museum, who identified the *Presbyornis* bones at the Powerline quarry. The staff at Fossil Butte National Monument provided useful support, and Laurie Bryant and the Wyoming Bureau of Land Management are acknowledged for arranging the permits for this use of public lands.

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PALYNOSTRATIGRAPHY AND AGE OF THE GREEN RIVER FORMATION IN FOSSIL BASIN, WYOMING

ROBERT A. CUSHMAN, JR.

Geology Section, Department of Natural Sciences, Loma Linda University
Loma Linda, California 92350, <bcushman@ccmail.llu.edu>

ABSTRACT—The palynoflora of the Green River Formation in Fossil Basin, Wyoming, provides a method for estimating the age of the formation. Outcrop samples were collected and processed for plant microfossils from three measured sections representing the center and marginal areas of Fossil Lake.

A reported occurrence of *Lambdotherium* in the middle unit suggests a Lostcabinian (Ypresian) age for most of the Green River Formation in Fossil Basin. A potassium-argon age determination of 50.2 ± 1.9 Ma on a potassium-feldspar tuff near the top of the middle unit of the Fossil Butte Member suggests a late early to early middle Eocene age. A late early Eocene (Ypresian) to early middle Eocene (Lutetian) age range for the Fossil Butte palynoflora is suggested by the co-occurrence of *Bombacacidites*, *Eucommia*, *Pistillipollenites mcgregorii*, *Platycarya platycaryoides*, and *Momipites triradiatus*. Consequently, the palynoflora does not rule out the possibility that the upper part of the Green River Formation in Fossil Basin may be early middle Eocene (early Lutetian or Bridgerian) in age.

The late early to early middle Eocene age of the Green River Formation in Fossil Basin correlates with deposition of the Wilkins Peak Member of the Green River Formation in the Green River Basin, Wyoming.

INTRODUCTION

THE PURPOSE of this study was to use plant microfossils to estimate the age 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 Tump Range form the western boundary; Oyster Ridge forms the eastern boundary; and the Uinta Mountains form 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. 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 (see Biaggi and Buchheim, this volume). 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 (Oriel and

FIGURE 1—Geographic and geologic features in the vicinity of Fossil Basin, Wyoming. Study localities are FBM, CCS, and LMC in the left-hand figure. (After Biaggi and Buchheim, this volume).

Tracey, 1970). 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 (see Loewen and Buchheim, this volume). 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 (see Figure 2 and Buchheim, 1994).

PREVIOUS STUDIES

The Green River Formation in Fossil Basin contains a rich assemblage of fossils. Fossils reported from the Fossil Butte Member include fish (Cope, 1877, 1884; Thorpe, 1938; Hesse, 1939; Grande, 1984), sting rays (Schaeffer and Mangus, 1965), birds (Wetmore, 1933; Leggitt, 1996; Leggitt and Buchheim, 1997), a bat (Jepsen, 1966), a snake (Schaeffer and Mangus, 1965), insects (Scudder, 1890; Cockerell, 1920), plants (Lesquereux, 1883; Brown, 1929, 1934), and freshwater mollusks, ostracods, and algal limestones (Bradley, 1926). Until recently, the age of the Green River Formation in Fossil

Basin was based on mammal fossils from the intertonguing Wasatch Formation (Gazin, 1959). The Green River Formation was interpreted as Lostcabinian (North American Land Mammal Age), although no mammals of that age were known from Fossil Basin (Gazin, 1959; Schaeffer and Mangus, 1965). Two recent vertebrate fossil discoveries have shed more light on the age of the Fossil Butte Member. Breithaupt (1990) reported the occurrence of *Orohippus* in the middle unit. Because of this find, he questioned the Lostcabinian age assignment for the Fossil Butte Member. However, the more recent discovery of *Lambdotherium* (Froehlich and Breithaupt, 1997) in the F2 or “split fish” zone of the Fossil Butte Member (within the middle unit of Buchheim, 1994), supports the Lostcabinian Land Mammal Age for at least some of the Green River Formation in Fossil Basin. Plant microfossil studies by Wodehouse (1933) from the Parachute Creek Member (specifically the Mahogany Ledge) of the Green River Formation in Colorado and Utah led him to conclude that the Green River Formation was Middle Eocene in age. In later studies of the Piceance Creek and Uinta basins, Newman (1974, 1980) developed palynomorph range zones for the Green River Formation (Douglas Creek, Garden Gulch, Anvil Points, Parachute Creek, and Evacuation Creek members). Newman assigned Early and Middle Eocene age estimates and land mammal ages to each of the plant microfossil biozones.

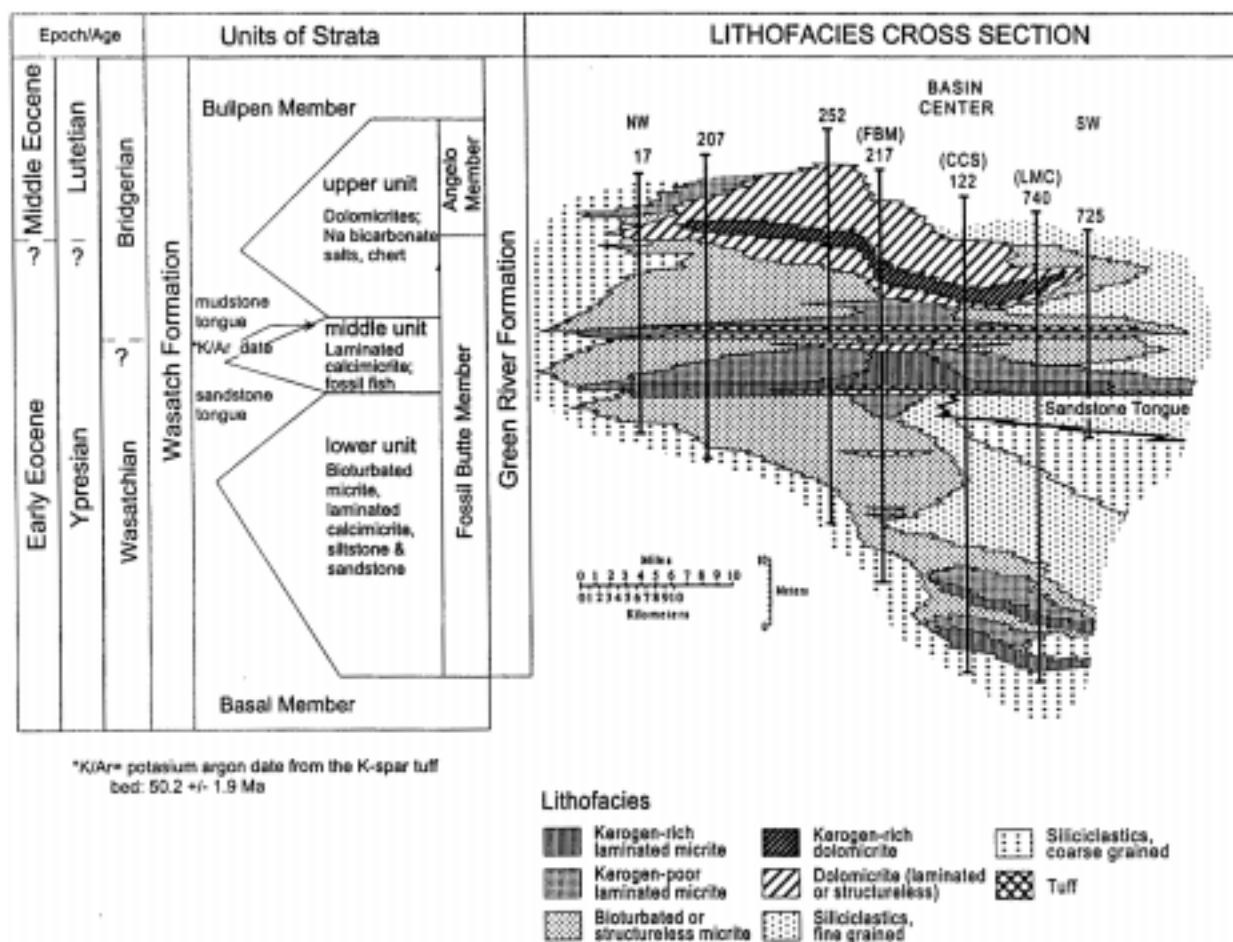


FIGURE 2—Stratigraphic chart illustrating stratigraphic units, facies relationships and relationships of measured sections. Locality 217 = FBM, 122 = CCS, and 740 = LMC. (Modified from Buchheim and Eugster, 1998).

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 (Figure 2). These three sections are equivalent to localities FBM, CCS, and LMC, respectively (Figure 1). The Fossil Butte section (FBM, 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 (LMC, 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.

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 are 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.

PALYOSTRATIGRAPHY AND AGE

Biostratigraphically significant plant microfossil taxa from the Green River Formation in Fossil Basin include *Bombacacidites*, *Eucommia*, *Pistillipollenites mcgregorii*, *Platycarya platycaryoides*, and *Momipites triradiatus*. Figure 3 shows the vertical distribution of significant taxa present in the lower, middle, and upper units of the Green River Formation in Fossil Basin, Wyoming. The Fossil Butte palynofloral assemblage is compared with other palynological studies of the Wasatch and Green River formations (Leopold

Section and Sample#								Units
FBM	CCS	LMC						Upper Unit
13	16	12						
	12							
10								Middle Unit
7	8							
6								
4	6							
	3							Lower Unit
		1						
			<i>Platycarya platycaryoides</i>	<i>Eucommia</i>	<i>Momipites triradiatus</i>	<i>Bombacacidites</i>	<i>Pistillipollenites mcgregorii</i>	GREEN RIVER FORMATION

FIGURE 3—Stratigraphic distribution of biostratigraphically significant plant microfossils of the Green River Formation in Fossil Basin, Wyoming.

and MacGinitie, 1972; Newman, 1974, 1980; and Nichols, 1987) to determine the stratigraphic ranges of the significant taxa. The results of this comparison confirm that most of the Fossil Butte palynoflora is late early Eocene (late Ypresian or Lostcabinian) in age as suggested by the occurrence of *Lambdotherium* in the middle unit (Froehlich and Breithaupt, 1997). However, the stratigraphic ranges of *Bombacacidites*, *Eucommia*, *Pistillipollenites mcgregorii*, *Platycarya platycaryoides*, and *Momipites triradiatus* extend into the lower middle Eocene (lower Lutetian or Bridgerian). Consequently, the palynoflora does not rule out the possibility that the upper part of the Green River Formation in Fossil Basin may be early middle Eocene (early Lutetian or Bridgerian) in age.

The early middle Eocene age is suggested by a series of K-Ar age dates on a tuff (known as the "K-spar tuff" by Buchheim, 1994) in the uppermost part of the middle unit. In the early 1980's, four samples of this tuff from four different localities were age dated for Buchheim by Geochron Laboratories. The results were as follows: locality 242 (in the northern part of Fossil Basin) yielded a K-Ar age of 43.6 ± 1.6 Ma; locality 217 (FBM in Figure 1) yielded a K-Ar age of 49.1 ± 1.8 Ma; locality 252 (252 in Figure 1) yielded a K-Ar age of 50.2 ± 1.9 Ma; and locality 122 (CCS in Figure 1) yielded a K-Ar age of 52.2 ± 2.0 Ma. The date from locality 242 is clearly anomalous with the other three dates. Buchheim and Eugster (1998) reported the 50.2 ± 1.9 Ma date because it represents the median of the three more consistent age dates. Although the variability among the three age dates needs to be resolved, the ages suggest that the upper part of the Green River Formation may be early middle Eocene (early Lutetian or Bridgerian) in age.

However, that scenario is complicated by the uncertainty

surrounding the absolute ages for the Wasatchian-Bridgerian Land Mammal Age boundary and the Ypresian-Lutetian boundary. The accepted age of the Ypresian-Lutetian (Early-Middle Eocene) boundary is 49 Ma (Berggren et al., 1995) and is placed at the top of Chron C22n on the paleomagnetic polarity scale. In the same volume, Prothero (1995) placed the age of the Wasatchian-Bridgerian Land Mammal Age boundary at 50.4 Ma and within Chron C22r. In the past, the Wasatchian-Bridgerian boundary was considered correlative with the Early-Middle Eocene (and hence the Ypresian-Lutetian) boundary. The results of Prothero's (1995) work suggest that the Wasatchian-Bridgerian boundary is slightly older than the Early-Middle Eocene boundary. Further taxonomic and stratigraphic resolution of the Fossil Butte palynoflora, new tuff samples for age dating utilizing new analytical techniques, and additional study of the mammal fossils in Fossil Basin is needed to resolve this confusing situation.

CONCLUSIONS

The reported occurrence of *Lambdotherium* (Froehlich and Breithaupt, 1997) in the middle unit suggests a Lostcabinian (Ypresian) age for most of the Green River Formation in Fossil Basin. Potassium-argon age determinations of 49.1 ± 1.8 , 50.2 ± 1.9 , and 52.2 ± 2.0 Ma on a potassium-feldspar tuff near the top of the middle unit suggest that the upper part of the Green River Formation in Fossil Basin may be early middle Eocene in age. The co-occurrence of *Bombacacidites*, *Eucommia*, *Pistillipollenites mcgregorii*, *Platycarya platycaryoides*, and *Momipites triradiatus* support a late early Eocene (Ypresian) to early middle Eocene (Lutetian) age range for the Fossil Butte palynoflora. Consequently, the palynoflora does not rule out the possibility that the upper part of the Green River Formation in Fossil Basin may be early middle Eocene (early Lutetian or Bridgerian) in age. A late early (to possibly early middle) Eocene age for deposition of the Green River Formation in Fossil Basin correlates with deposition of the Wilkins Peak Member of the Green River Formation in the Green River Basin, Wyoming.

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PALEONTOLOGY AND PALEOECOLOGY OF THE CULMINATING PHASE OF EOCENE FOSSIL LAKE, FOSSIL BUTTE NATIONAL MONUMENT, WYOMING

MARK A. LOEWEN AND H. PAUL BUCHHEIM

Geology Section, Department of Natural Sciences, Loma Linda University
Loma Linda, CA 92350

ABSTRACT—While many studies have described the paleontology and paleoecology of the Green River Formation in Fossil Basin, few have focused on the latter stages of Fossil Lake's history. The upper portion of the Fossil Butte Member and the Angelo Member of the Green River Formation represent the latter stages of Fossil Lake.

Dolomite and evaporites characterize the upper unit. Desiccation cracks, flat pebble conglomerates and sediments disrupted by evaporites are common, suggesting an arid depositional environment. Sharp bottom contacts of lithologic beds suggest rapid changes in lake levels.

The flora includes prokaryotic algae, stromatolites, algal tufa and vascular plants. Angiosperms are relatively scarce, and the palynoflora is dominated by gymnosperms. The fauna and other organisms include bacteria, protists, invertebrates, fish, birds and reptiles. Fish communities of the upper unit are restricted to facies deposited under relatively fresh conditions, and include *Priscacara liops*, *P. hypsacantha*, *Lepisosteus*, *Knightsia*, *Diplomystus* and *Asineops squamifrons*. The shorebird *Presbyornis* is present in marginal facies.

The latter stages of Fossil Lake exhibit different communities than those present during most of Fossil Lake's history. Stromatolites and tufa become common. The tiny fish *Priscacara hypsacantha* dominates fish populations, while the major predator was *Lepisosteus*. These fish adjusted to increasing alkalinity and salinity by retreating to nearshore freshwater environments. Cooler gymnosperm-dominated floras replaced subtropical angiosperm floras.

The flora and faunas of the upper unit represent a unique paleocommunity that represents a response to the changing conditions of upper unit time. These organisms dealt with increasing alkalinity, salinity and fluctuating lake levels.

INTRODUCTION

THE PURPOSE of this paper is to present paleontologic data recently collected in Fossil Basin. It will also review the information currently available about the paleontology and paleoecology of the upper part of the Green River Formation in Fossil Basin.

Fossil Butte National Monument lies in the structural basin formed at the end of the Mesozoic by the ancestral Wyoming Thrust Belt, Wasatch and Uinta Mountains. This intermountain basin exhibited distinct depositional and paleontological

histories from those of contemporaneous deposits in nearby basins. For a complete review of the structural history and stratigraphic relationships of Fossil Basin, see Lamerson (1982), McGrew and Casilliano (1975) or Oriel and Tracey (1970).

The Wasatch and Green River formations represent the alluvial, fluvial and lacustrine sediments deposited in Fossil Basin during the Eocene. The Wasatch Formation underlies, interfingers with, grades into and overlies the Green River Formation (Figure 1). Oriel and Tracey (1970) divided the Green River Formation in Fossil Basin into the Fossil Butte

FIGURE 1—Lakes of the Green River Formation and stratigraphic relationships of the Green River and Wasatch Formations in Fossil Basin (modified after Oriel and Tracey, 1970; McGrew and Casilliano, 1975 and Buchheim, 1994a).

and Angelo Members. The mudstone tongue of the Wasatch Formation divides the two members.

Buchheim (1994a) informally divided the Green River Formation of Fossil Basin into lower, middle and upper units based on lithologic characteristics. The upper unit is equivalent to the uppermost part of Oriel and Tracey's Fossil Butte Member and the Angelo Member (Figure 1). Its bottom contact is the top of the 8 cm K-spar tuff above the fish bearing layers of the middle unit. The middle and upper units are best represented at the type locality of the Fossil Butte Member on the southeast face of Fossil Butte National Monument.

Siliciclastics, bioturbated micrites and kerogen-poor calcimicrites dominate the lower unit, and kerogen-rich laminated micrites characterize the middle unit (Buchheim and Eugster, 1998). The famous fish deposits such as the "18 inch" and "split fish" layers are located in the middle unit.

The upper unit is characterized by dolomicrites and evaporite minerals (Buchheim 1994b). Several kerogen-rich laminated dolomicrites form the prominent "oil shales" found throughout the basin. Desiccation cracks, flat pebble conglomerates and sediments disrupted by evaporites are common.

Fossil Basin has been the focus of many excellent paleontologic studies. Bradley (1929), Grande (1984), McGrew and Casilliano (1975) and Oriel and Tracey (1970) have studied the flora and fauna of Fossil Basin in detail among others. MacGinitie (1969), Cushman (1983) and Cushman et al. (1984) studied the flora of Fossil Basin. The fish of Fossil Basin have been studied in detail by Cope (1874, 1877, 1879, 1884, others); Grande (1979, 1982a, 1982b, 1984, 1985, 1994); Grande and Bemis (1991); Grande and Buchheim (1994); Quo-Qing, Grande and Wilson (1997); Quo-Qing, Wilson and Grande (1997) and Wiley (1976). Ferber and Wells (1995) and McGrew (1975) studied fish taphonomy. Most of these studies have focused on the famous fossil fish bearing layers of the middle unit.

Upper unit studies include Cushman (1983), who studied the palynoflora, the study of *Presbyornis* by Leggitt (1996) and Leggitt and Buchheim (1996, 1997) and the paleoenvironmental study of the maroon oil shale by Loewen and Buchheim (1997).

AGE

Ambrose et al. (1997) placed the Wasatch Formation underlying the Fossil Butte Member in the Lostcabinian subage of the Wasatchian (NALMA, Wa₇). Froehlich and Breithaupt (1997) reported a specimen of *Lambdaotherium* that dates the split fish layers of the Fossil Butte Member as Lostcabinian. The upper unit is Lostcabinian in age or younger.

DEPOSITIONAL ENVIRONMENT

Sedimentological and stratigraphic data suggest that Fossil Lake existed in a closed basin with a low topographic gradient during most of upper unit time (Buchheim, 1994a, 1994b; Loewen and Buchheim, 1997). Saline deposits dominate the upper unit. They represent a closure of the hydrographic basin, in contrast to the open basin of middle unit time. The

closed nature of the basin produced lake sediments that were dynamically influenced by inflow. When precipitation significantly exceeded evaporation, freshwater sediments were deposited. During times of drought, evaporites were deposited. Rapid transgressions are represented by flat pebble conglomerates of ripped up mud-cracks grading into kerogen-rich purple oil shales with sharp bottom contacts and finally evaporite sequences. Mud-cracks, strandlines of algal encrusted tufa logs, evaporite minerals and Magadi-type chert were deposited during periods of desiccation. Evaporites and hypersaline layers directly overlie relatively fresher deposits.

Although the lake experienced periods of hypersalinity, lateral gradients from relatively fresh at the margin to hypersaline in the center existed in Fossil Lake (Buchheim, 1994a; Loewen and Buchheim, 1997). Facies in these salinity gradient horizons change from partly bioturbated calcimicrite to kerogen rich dolomicrite with evaporites in the center on the lake. The low topographic nature of the basin may have allowed this gradient to exist, similar to the salinity gradient in Bear River Bay where it joins the Great Salt Lake (Buchheim, 1994a).

Marker beds in the upper unit are correlatable basin wide (Figure 2). The maroon oil shale exhibits a lateral change from laminated calcimicrite with fish in marginal facies to dolomicrite with salt casts at the center of the basin. Kerogen-rich oil shales with sharp bottom contacts directly overlie mudstone beds. Mud-cracks, strandlines of algal encrusted tufa logs, evaporite minerals and Magadi-type chert occur at several horizons in the upper unit.

The two major paleoenvironments recognized in Fossil Lake are littoral and limnetic. Siliciclastics, bioturbated facies, algal growth, invertebrate and vertebrate fossils characterize littoral paleoenvironments of the upper unit. Most of the limnetic paleoenvironments of the upper unit lack fossils and are dominated by dolomite and evaporites.

PALEONTOLOGY

The flora and fauna of the upper stages of Fossil Lake represent communities different than those present throughout the earlier history of Fossil Lake. In general, the communities of the Fossil Basin upper unit reflect a more arid, cooler, less hospitable climate. See Table 1 for a review of known taxa from the upper unit.

Monera, stromatolites, and tufa.—Single celled prokaryotes, consisting of bacteria and cyanobacteria, are represented by stromatolites, tufa (Figure 3), and the amorphous kerogen of its numerous oil shales.

Cushman (1983) reports that the kerogen present in the lower and upper purple oil shales is made up of over 90% amorphous kerogen derived from non-structured algal debris. The remaining fraction consists of vitrinite derived from woody plant tissue.

Although there is no direct evidence of bacteria from the upper unit, Leggitt and Buchheim (1996) suggest *Clostridium botulinum* as a cause of death for the shorebird *Presbyornis*. Indirect evidence of cyanobacteria is prevalent in the numerous stromatolites and tufa of the upper unit.

FIGURE 2—Detailed section of the upper unit at Fossil Butte National Monument and lithofacies cross section across the basin. Fossils occur in layers specified or equivalent marginal facies. (one cm K-spar tuff in the maroon oil shale is used as stratigraphic datum.

TABLE 1—Fossil Basin taxa from the latter stages of Fossil Lake.

	MONERANS:	Angiosperms:		Ostracods:	
Bacteria:	<i>Clostridium botulinum</i>	<i>Ailanthus</i>	<i>Myrica</i>	<i>Hemicyprinus</i>	<i>Pseudocypris</i>
Cyanobacteria:		<i>Bombacaceae</i>	<i>Platycarya</i>	<i>Procypris</i>	
	Stromatolites and tufa	<i>Carya</i>	<i>Podocarpus</i>		
		<i>Castanea</i>	<i>Populus</i>		
		<i>Chenopodiaceae</i>	<i>Pterocarya</i>		VERTEBRATES:
	PROTISTS:	<i>Ephedra</i>	<i>Quercus</i>	Fishes:	
Pyrophytes:	<i>Micrhystridium</i>	<i>Eucommia</i>	<i>Reevesia</i>	<i>Asineops squamifrons</i>	
Acritarchs:	<i>Baltispheridium</i>	<i>Ilex</i>	<i>Salix</i>	<i>Diplomystus</i>	
		<i>Juglans</i>	<i>Tilia</i>	<i>Knightia</i>	
	PLANTS:	<i>Momipites</i>	<i>Ulmus</i>	<i>Lepisosteus</i>	
Uncertain:	<i>Pistillipollenites</i>			<i>Priscacara hypsacantha</i> *	
Pteridophytes:				<i>Priscacara liops</i>	
	<i>Cyathidites</i>	<i>Laevigatosporites</i>	INVERTEBRATES:	Reptiles:	
	<i>Deltoidospora</i>		Gastropods:	<i>Trionyx</i> sp. turtles	
			<i>Bellamyia paludinaeformis</i>	Crocodyles	
Gymnosperms:			<i>Biomphalaria pseudoammonius</i>	Birds:	
	<i>Abies</i>	<i>Sabalites</i>	<i>Elimia nodulifera</i>	<i>Presbyornis pervetus</i>	
	<i>Picea</i>	<i>Taxodiaceae</i>	<i>Goniopasis</i>	Mammals:	
	<i>Pinus</i>	<i>Tsuga</i>	<i>Gyraulus</i>	unidentified bone fragments	
			<i>Oreoconus</i>		

* probably a new Percoid genus (see Grande, 1984)

Several species of cyanobacteria and algae trap and bind calcite directly from the water column. As these photosynthetic organisms grow and trap successive layers of calcite, they form biogenic sedimentary structures. The resultant morphologies range from loosely consolidated, porous tufa, to

finely laminated stromatolites in columnar and domal forms.

The upper unit contains several horizons of tufa encrusted logs. Tufa encrusted logs are porous calcite structures that preserve faint remnant laminations and molds of the wood on which they initially grew (Figure 3). They coated everything

FIGURE 3—A, Tufa encrusted branch. B, Surface texture of stromatolite growing on a tufa encrusted log. C, Stromatolite with rippled surface morphology growing on a tufa log. D, Bark impression on the reverse side of tufa encrusted log.

from entire logs over a meter long to tiny twigs. Interpreted as algal in origin, these layers of tufa represent biogenic calcite deposited on sticks and logs that littered the paleoshorelines of Fossil Lake. Several horizons of tufa logs are several kilometers wide, suggesting low gradient surfaces in Fossil Basin over which the shoreline transgressed and regressed.

Stromatolites occur in three horizons within the upper unit. These are restricted to marginal environments around the periphery of the basin. These stromatolites exhibit fine lamination and represent growth in relatively shallow lacustrine environments. Both stromatolites and stromatolitic tufa

deposits, absent in the lower and middle units of the Fossil Butte Member, are relatively common in the upper unit.

Protists.—The dinoflagellates and acritarchs of the upper unit include *Micrhystridium* and *Baltispheridium* (Cushman, 1983). These occur in the lower purple oil shale.

Plants.—The flora of the upper unit is poorly known because no detailed paleobotanical studies have focused specifically on the penultimate history of Fossil Lake. Most of our knowledge of the upper unit flora is based on the palynological study of Cushman (1983). He found that the palynoflora of three upper unit oil shales is different from the palynoflora

of the middle and lower units. The palynoflora of the middle unit is dominated by subtropical vegetation, suggesting a relatively warm and moist climate. The upper unit has the least diverse palynoflora preserved in the Fossil Butte Member, reflecting a warm temperate ecosystem dominated by spruce, fir, pine, and other gymnosperms. Angiosperms occur in the upper unit, but they are a relatively small part of the flora (Cushman, 1983).

Fern spores from the upper unit make up a tiny fraction of the total palynoflora. They include *Laevigatosporites*, *Cyathidites* and *Deltoidospora* (Cushman, 1983). These occur in the lower and upper purple oil shales and the oil shale directly above the K-spar tuff.

Indicators of a cooler climate such as *Abies*, *Castanea*, *Picea*, *Pterocarya* and *Tsuga* are more prevalent in the upper unit. The presence of *Ephedra* in the basin suggests periodic droughts, because of its leaves with a thick, waxy cuticle that prevent desiccation in times of drought (McGrew and Casilliano, 1975).

Plant macrofossils from the upper unit include deciduous leaf fragments and wood. The blue oil shale contains *Sabalites* sp. palm fronds and *Ailanthus* sp. (Tree of Heaven) seedpods (Figure 4c).

Cushman (1983) found a variety of microfossils and palynomorphs in the upper unit. Gymnosperm pollen (over 70% relative abundance) dominate the palynoflora of the upper unit and angiosperm pollen occur less frequently than in the lower and middle units (near 15% relative abundance). This gymnosperm to angiosperm ratio of 7:3 is distinctly different than the ratios of the lower and middle units (3:7 for the lower unit and 1:9 in the middle unit).

Invertebrates.—The invertebrates of the upper unit include mollusks, arthropods and crustaceans. Oriel and Tracey (1970) reported the gastropods *Biomphalaria pseudoammonius*, *Plesielliptro* sp., *Physa pleromatis*, *Elimia nodulifera*, and *Bellamyia paludinaeformis* from the upper unit. The gastropod *Oreoconus* occurs just below the maroon oil shale in the southern part of the basin (Figure 4b). Leggitt (1996) found the freshwater gastropods *Goniobasis*, *Physa*, and *Gyraulus* in marginal facies of the upper unit in the southern part of the basin. Gastropods are restricted to marginal facies in the upper unit.

Ostracods are tiny crustaceans enclosed in a bivalve shell. They are interpreted as indicators of marginal or shallow facies (Bradley, 1926). The ostracod genera *Hemicyprius*, *Procypris* and *Pseudocypris* occur in the upper unit (Oriel and Tracey, 1970). Ostracods occur in several horizons near the margins of the lake, and some horizons extend far out into the basin. Both larval and adult insects also occur in upper unit sediments.

Fishes.—Unlike the famous fish bearing deposits of the middle unit, fish are relatively scarce in the upper unit. Buchheim (1994a) reported *Knightia* from some of the freshwater shales near the top of the upper unit. Recent studies of the maroon oil shale demonstrated that, at times, large populations of fish lived along the fringes of Fossil Lake (Loewen and Buchheim, 1997). The blue oil shale of the upper unit

contains fossil fish at many locations throughout the basin. Other layers have also produced a few fish fossils.

Immediately above the K-spar tuff is a laminated calcimicrite horizon that contains *Knightia*, *Diplomystus* and *Priscacara*. It was deposited in shallow, freshwater lake conditions similar to those of the middle unit. The K-spar tuff does not represent a depositional hiatus. Therefore, the fish bearing bed above it represents a continuation of the sedimentation patterns of the fossiliferous middle unit.

The blue oil shale (about 2 meters above the K-spar tuff) contains fish, plant material, insects and feathers. This kero-gen-rich, finely laminated calcimicrite, exhibits fossil preservation different from any other in the basin. The partial outlines of the body and bones are preserved as dark films on the surface of the limestone (Figure 4f).

The maroon oil shale exhibits a distinct fish fauna near the southwestern shores of Fossil Lake. *Priscacara hypsacantha* (Figure 4e) make up the majority of the fish fauna, while *Lepisosteus* sp. and *Asineops squamifrons* (Figure 4d) are minor components. *Priscacara hypsacantha* were first recognized by Cope (1886). Grande (1984) refers to these fish as Percoid genus A (since a revision of the family Priscacaridae has not been made to date, we will refer to this fish as *P. hypsacantha*). A single *Priscacara liops* and *Lepisosteus* (gar) have been found in marginal facies of the maroon oil shale. Fry and juvenile *P. hypsacantha* are relatively common near the margin (Figure 4a).

Near the top of the upper unit, just above the chert horizon, two small limestone units contain *Knightia* (Buchheim, 1994a). They represent brief freshwater lacustrine intervals within dominantly alluvial-fluvial conditions.

Birds.—Bird tracks occur in marginal facies of the upper unit at the southern end of the basin. Leggitt (1996) reported a mass mortality of the shorebird-duck mosaic *Presbyornis* in the upper part of the upper unit. These are the same birds described by Olson (1994) as *Presbyornis pervetus*. Disarticulated bird bones, eggshell and gastropods form strand line deposits along the southern end of the basin (Leggitt and Buchheim, 1997). *Presbyornis* bones and eggshell occur in at least three horizons in the upper unit.

Tetrapods.—Crocodile remains and large coprolites occur in marginal facies of the "maroon oil shale." The soft-shell turtle *Trionyx* sp. occurs in marginal facies just above the K-spar tuff. Fragments of turtle shell, crocodile teeth and mammal bones occur in sandstones that interfinger with the upper unit at the southern end of the basin.

PALEOECOLOGY

The deposits at the bottom of the upper unit (from the K-spar tuff through the blue oil shale) exhibit similar paleocommunities to those of the middle unit. These communities are consistent with deposition in a freshwater lake, and probably represent a continuation of the conditions present during middle unit time.

The prevalence of stromatolites and tufa, often associated with saline-alkaline lakes in physiographically low-gradient basins, reflects a change in the lake conditions from those of

FIGURE 4—A, twelve mm long juvenile *Priscacara hypsacantha* from maroon oil shale. B, *Oreoconus* sp. from below the maroon oil shale. C, *Ailanthus* sp. (Tree of Heaven) seed pod from the lower blue oil shale. D, Tail of *Asineops squamifrons* from maroon oil shale. E, *Priscacara hypsacantha* from maroon oil shale. F, “Ghost” outline of *Knightia* from the lower blue oil shale.

lower and middle unit time.

The palynology suggests that the climate during upper unit time became warm temperate, in contrast to the more subtropical climate of lower and middle unit time. Indicators

of a cooler climate are more prevalent in the upper unit than in the middle and lower units. Unlike the lush tropical angiosperm flora of the middle unit, the upper unit reflects a warm temperate paleocommunity of conifers. These gymno-

sperms probably lived on the uplands and mountains surrounding Fossil Lake. Angiosperms and ferns may have lived at the base of these mountains, but they are drastically reduced in relative abundance. McGrew and Casilliano (1975) suggested that the upland flora of gymnosperms existed at elevations of 6000 – 8000 feet above sea level.

As hydrologic conditions changed from open to closed, the salinity and alkalinity of the lake increased. Small communities of fish living on the fringes of the lake replaced the diverse freshwater fish faunas of the lower and middle units. Fish faunas are less diverse than those of the lower and middle units. Previously rare fish are the major constituent of the fauna. *Priscacara hypsacantha* may have been able to survive salinity fluctuations better than other species. While the affinities of *Priscacara* are poorly known, gar are known to occur in fresh to brackish water. They are considered secondary freshwater fish and cannot survive in saline environments. All fish occurring in the upper unit are restricted to freshwater facies.

Grande (1984) states that all of the aquatic mollusks of the Green River Formation indicate freshwater conditions. Gastropods are uncommon in the upper unit and occur only in marginal facies consistent with freshwater deposition.

The paleontologic data allow reconstructions of trophic relationships of the maroon salt cast layer. Ostracods are detritivores, which feed on decaying organic matter from plants and animals. Algal blooms resulted in high fractions of organic material in the sediment. The presence of *P. hypsacantha* associated with abundant ostracods suggests that *P. hypsacantha* may have preyed on these tiny arthropods. *Asineops squamifrons* and gar may have preyed on the large *P. hypsacantha* population. Crocodiles were the top carnivores in the ecosystem.

Communities of the wading shorebird lived and died along the southern end of the lake. *Presbyornis* eggshell material suggests possible nesting sites. The presence of *Presbyornis* from the basal Member of the Wasatch Formation, and evidence in several layers of the upper unit, suggest that *Presbyornis* inhabited the region for a long time. *Presbyornis* may imply saline conditions in the lake. The frontal and nasal bones of *Presbyornis* have depressions for very large salt glands (Feduccia, 1980). This suggests that the birds had an affinity to more saline waters.

Sedimentary structures, mineralogy, evaporites and the paleontology of the upper unit all suggest that the flora and fauna of the basin endured periods of drought. The picture emerges of a community dramatically influenced by climatic changes. These fluctuations between periods of drought and more moist climates may have led to the final infilling of Fossil Lake. The relatively cool arid interval of the upper unit ends with a return to freshwater deposits at the top of the upper unit. These lake deposits were ultimately drowned by sedimentation from the ancestral Wasatch and Uinta Mountains.

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A COMPARISON OF FISH COMMUNITY STRUCTURE AMONG SEVERAL PALEOENVIRONMENTS OF EOCENE FOSSIL LAKE, WYOMING: A PRELIMINARY REPORT

TERRY R. FINGER
9882 Rt. N, Columbia, Missouri 65203

ABSTRACT—Genus, standard length, and stratigraphic position were recorded for 3341 fossil fishes at three sites within the basin of Eocene Fossil Lake near Fossil Butte National Monument, southwestern Wyoming. Two sites were at different stratigraphic positions near the lake center (Lewis Ranch sites) and one site, nearly contemporaneous with the stratigraphically lower mid-lake site, was near the lake shore (Thompson Ranch site). Preliminary analysis has documented distinct differences in fish community structure between the near-shore and stratigraphically lower mid-lake sites. The near-shore site is dominated by *Knightia* and small *Diplomystus*, while the lower mid-lake site is characterized by proportionately fewer *Knightia*, larger *Diplomystus*, and *Priscacara*. Overall fish fossil density at the near-shore site was approximately five times that of the lower mid-lake site. The fish community structure of the stratigraphically upper mid-lake site was similar to the near-shore site, suggesting that the mid-lake habitat may have become shallow during later lake stages. Further data analysis is continuing, including detailed documentation of the size distribution of the fishes at each site and an examination of stratigraphic changes in fish community structure within each site. Sampling is also underway at a second near-shore site.

INTRODUCTION

ECOLOGISTS HAVE long been interested in determining factors that affect biological community structure, i.e., the species present in a given area and their relative abundances. The effects of species interactions and environmental perturbations on fish community structure is a topic of considerable interest and debate (Grossman et al. 1982, 1985, 1990, Rahel et al. 1984, Yant et al. 1984, Herbold 1984, Moyle and Vondracek 1985, Ross et al. 1985, Matthews 1982, 1986, Finger and Stewart 1987). Ecological studies of extant communities are, however, limited in their time perspective. At best, such investigations can track changes in communities over several decades, while significant alterations in community structure may only occur over much longer time periods.

Ecological analysis of the fossil record provides an opportunity to assess long-term trends in community structure (Boucot 1978). Sites where the fossil record is sufficiently complete to consider such analyses are, however, rare, especially for vertebrates. The fossil fish localities of Eocene Fossil Lake (Fossil Butte Member, Green River Formation), in and near Fossil Butte National Monument, southwestern Wyoming, provide a unique opportunity for the study of long-term trends in fish community structure. Fishes from Fossil Lake are among the most numerous and best preserved vertebrate fossils in the world, and commercial quarries in the area provide access to large quantities of fossil material in several stratigraphic sections. The purpose of this study is to document fish community structure at localities within the basin of Eocene Fossil Lake and to relate those findings to paleoenvironmental conditions. In this paper I present preliminary findings from three distinct paleoenvironments.

STUDY AREA

Fossil Lake persisted for several million years during the late early Eocene, and at its largest size covered several hun-

dred km². It was the smallest and most short-lived of a system of three lakes that existed for approximately 15 million years from the late Paleocene to the middle or late Eocene. The environment was subtropical and the lake supported a freshwater fauna, although there may have been periods when at least part of the water column was saline (McGrew and Casilliano 1975, Grande 1994, Grande and Buchheim 1994). The taxonomy of the fish fauna of Fossil Lake has been thoroughly summarized by Grande (1984, 1994) and Grande and Buchheim (1994). Sedimentological studies assessing paleoenvironmental conditions have been conducted by Buchheim (1993, 1994) and others.

This paper includes preliminary findings from three fossil fish sites within the deposits of the middle and upper units of the Fossil Butte Member.

Sample Site A-1: Lewis Ranch quarry site of James E. Tynsky; SE1/4, SE1/4, Sec. 19, T.21N., R.117W., and NE1/4, NE1/4, Sec. 30, T.21N., R.117W., Kemmerer 15-minute quadrangle (U.S.G.S.). This quarry is locality A of Grande and Buchheim (1994). Stratigraphically, this sample site encompassed the "18-inch layer" deposits; i.e., the F-1 deposits of Grande (1984) and Grande and Buchheim (1994). Paleontological and sedimentological evidence indicates that these are mid-lake deposits.

Sample Site A-2: The same quarry location as sample site A-1. Stratigraphically, however, this sample site encompassed deposits approximately 10 m above the strata sampled at site A-1, and approximately 3 m above the "K-spar" tuff layer (see Grande and Buchheim 1994, Figure 2). The paleontological characteristics of this later lake stage are not well known, but sedimentological data suggest that there may have been periods of fluctuating salinity and depth.

Sample Site H-1: Thompson Ranch quarry site of Richard Hebdon, NW1/4, SW1/4, Sec. 22, T.22N., R.117W., Kemmerer 15-minute quadrangle (U.S.G.S.). This is locality

TABLE 1—Sample characteristics for sites A-1, A-2, and H-1. Sampling occurred during 1993 and 1995 field seasons.

Sample Characteristic	Sample Sites		
	A-1	A-2	H-1
volume sampled (dm ³)	14197.3	1577.3	2126.0
stratigraphic column sampled (cm)	36.5	94.3	291.1

H of Grande and Buchheim (1994), located approximately 11 km northeast of sample sites A-1 and A-2. Stratigraphically, this sample site encompassed the F-2 deposits of Grande (1984) and Grande and Buchheim (1994). Paleontological and sedimentological evidence indicates that these are near-shore deposits.

The deposits sampled at site H-1 are the sandwich bed deposits that can be traced throughout the lake basin because of their distinct pattern of tuff layers (see Grande and Buchheim 1994, Figure 2). At site A-1, the top of these deposits is less than 2 m below the sampled 18-inch layer deposits, and the two deposits were considered nearly contemporaneous by Grande and Buchheim (1994). Thus, comparison of sites A-1 and H-1 provides a view of mid-lake and near-shore fish communities at approximately the same stage in the lake's history, while comparison of sites A-1 and A-2 provides a perspective on temporal changes in the fish community within the same geographical location in the lake.

METHODS

Fish were collected in 1993 and 1995 (Table 1). Each locality was sampled by digging through the entire targeted stratigraphic column with techniques appropriate for the site. Similar techniques were described and illustrated by Grande (1984). At site A-1, where large, thin sheets of the deposits can be excavated, sampling was conducted in conjunction with the work of a quarry crew. Areas of 15 to 30 m² were excavated by defining layers averaging approximately 2 cm in thickness. Within each layer, sheets were removed and split as finely as possible, typically in sublayers 1.0 to 1.5 cm thick. At sites A-2 and H-1, areas of approximately 1 m² were excavated by defining layers approximately 4 cm in thickness. Within each layer, blocks were removed and split as finely as possible, typically in sublayers approximately 0.5 cm thick. At all sites, fish were identified to genus, measured for standard length (SL; the distance parallel to the vertebral column from the tip of the snout to the posterior end of the hypurals), and recorded separately for each defined stratigraphic layer. Stratigraphic positions were determined by measuring distances from tuff layer markers.

RESULTS AND DISCUSSION

At total of 3341 fish were collected from the three localities, including 312 very young juvenile *Diplomystus* less than 25 mm SL from site A-1 (Table 2).

The A-1 site, geographically located near the center of

TABLE 2—Number of fish of each genus collected at each sample site. See text for descriptions of sites. Data from site A-1 are compiled separately with and without 312 very young juvenile *Diplomystus* (<25 mm SL). For each site, no. = number of fish collected; % = percentage of the total number of specimens collected at that site.

Genus	Sample Sites							
	A-1 w/ juv.		A-1 w/o juv.		A-2		H-1	
	no.	%	no.	%	no.	%	no.	%
<i>Knightia</i>	484	32.1	484	40.5	498	59.9	566	56.4
<i>Diplomystus</i>	620	41.2	308	25.8	268	32.2	329	32.8
<i>Priscacara</i>	298	19.8	298	25.0	11	1.3	3	0.3
<i>Mioplosus</i>	39	2.6	39	3.3	25	3.0	21	2.1
<i>Phareodus</i>	16	1.1	16	1.3	0	0	6	0.6
<i>Notogoneus</i>	12	0.8	12	1.0	0	0	0	0
<i>Amphiplaga</i>	0	0	0	0	0	0	3	0.3
<i>Eohiodon</i>	0	0	0	0	0	0	1	0.1
<i>Heliobatis</i>	0	0	0	0	0	0	1	0.1
Unknown	37	2.5	37	3.1	29	3.5	74	7.4
Total No.	1506		1194		831		1004	
No./m ³	106.3		84.1		526.8		472.2	

the basin, is dominated by *Knightia*, *Diplomystus*, and *Priscacara*. *Mioplosus*, *Phareodus*, and *Notogoneus* are also relatively common. Many of the *Diplomystus* are large, exceeding 300 mm SL, and the only juveniles in abundance are very young *Diplomystus*. These findings parallel those of Grande (1984) and Grande and Buchheim (1994) for mid-lake deposits. Sedimentological analyses of these deposits also indicate a mid-lake site (Buchheim 1993, 1994). The composition of the fish community at site A-1 therefore appears to be characteristic of a relatively deep-water, pelagic habitat. The presence of very young *Diplomystus* may be an indication of open-water spawning by this genus.

The H-1 site, geographically located near the northeast shore of the basin, is dominated by a greater proportion of *Knightia* than site A-1. *Diplomystus* is also abundant, but unlike site A-1, few individuals exceed 150 mm SL and very young juveniles are rare. *Mioplosus* and *Phareodus* are quite common, as at site A-1, but *Priscacara* is considerably less common and *Notogoneus* was not collected. These findings parallel those of Grande (1984) and Grande and Buchheim (1994) for near-shore deposits. Sedimentological analyses of these deposits also indicate a near-shore site (Buchheim 1993, 1994). The composition of the fish community at site H-1 therefore appears to be characteristic of a relatively shallow-water, near-shore habitat.

Overall fish fossil density at site H-1 is approximately five times that of site A-1. Although this difference may be an artifact of differential preservation at the two sites, the overall excellent quality of specimens from both localities suggests that the difference in fossil density may be the result of an actual difference in fish density between the communities. This finding is consistent with observations from most extant lakes, where fish density in near-shore areas is considerably higher than off-shore, pelagic habitats.

The fish community structure of site A-2, although from a site geographically located near the center of the lake basin,

is very similar to that of near-shore site H-1. The sites contained similar percentages of *Knightia*, *Diplomystus* and *Mioplosus*, and nearly all *Diplomystus* were less than 150 mm SL. At site A-2 *Priscacara* was slightly more abundant than at site H-1 and *Phareodus* and several uncommon genera were not collected, but the overall structure of the fish communities at sites A-2 and H-1 were remarkably similar. Overall fish fossil density was also similar at the two sites. These findings strongly suggest that site A-2 contained a typical near-shore fish fauna, although perhaps slightly less diverse than site H-1.

Sedimentological studies of strata contemporaneous with site A-2 suggest that in the later lake stages, there may have been instability in both lake depth and salinity (Buchheim 1993, Grande and Buchheim 1994). The preliminary results of this study indicate that, in response to this instability, the fish community near the historic lake center shifted from a deep-water community to one typical of near-shore areas, but did not decline dramatically. Fish may have been able to survive in freshwater areas around the margins of the lake or the salinity may have been confined to the lower portions of the water column.

Ongoing work includes more refined data analyses to fully document the size distribution of each genus at each site, compare the fish faunal composition among sites with multivariate ordination techniques (e.g., see Gauch 1982), and investigate stratigraphic changes in fish community structure within each site. The objective of the latter analysis is to examine changes during the time period over which the targeted stratigraphic section at each site was deposited. The time involved in deposition is unknown, but is currently thought to be from a few hundred to a few thousand years (Grande and Buchheim 1994). Sampling is also underway at another locality approximately 8 km east-northeast of sample sites A-1 and A-2. This site encompasses the same sandwich bed strata as site H-1, and also appears to be a near-shore site.

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FOSSIL CYCAD NATIONAL MONUMENT: A CASE OF PALEONTOLOGICAL RESOURCE MISMANAGEMENT

VINCENT L. SANTUCCI¹ AND MARIKKA HUGHES²

¹National Park Service, P.O. Box 592, Kemmerer, WY 83101

²Peabody Museum of Natural History, Paleobotany Division, P.O. 208118, New Haven, CT 06520-2118

ABSTRACT—Through the power provided in the Antiquities Act (1906), on October 21, 1922, President Warren G. Harding created Fossil Cycad National Monument. Scientists recognized that the fossil locality preserved a significant exposure of a Cretaceous cycadeoid forest. Hundreds of fossilized cycad specimens, one of the world's greatest concentrations, were exposed at the surface of the 320 acre site during the early 1920s.

Years of negligent management at the monument resulted in adverse impacts on the fossil resource. The fossils on the surface disappeared faster than erosion could expose other specimens from beneath. The loss of the exposed petrified plant remains eventually left the site devoid of fossils and ultimately without a purpose to justify its existence as a unit of the National Park Service. On September 1, 1957, the United States Congress voted to deauthorize Fossil Cycad National Monument.

INTRODUCTION

AT THE turn of the century there was a growing awareness towards the country's hidden treasures. In 1906, Congress passed the Antiquities Act as a means to protect some of America's cultural and scientific resources. The Antiquities Act provides the President of the United States with the direct authority to set aside areas of significant scientific or scenic values as national monuments.

In 1916, the National Park Service was established under the Organic Act with the mission, "...to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." Originally the National Park Service was established to administer areas designated as national parks, monuments, and reservations. Today, the National Park System also administers historical/cultural parks, seashores, scenic riverways, recreation areas, and a variety of other federal land designations.

In 1922, Fossil Cycad National Monument was established as a unit of the National Park Service through the authority provided in the Antiquities Act. Hence, the monument and its resources were entitled to the same levels of protection and management provided through the National Park Service Organic Act.

By the 1930s, most of the fossilized plants called cycads were depleted from the surface at Fossil Cycad National Monument. Years of neglect, unauthorized fossil collecting, unchallenged research collecting and a general misunderstanding of paleontological resources, lead to the near complete loss of the resource in which the monument was named and designated. In the early 1950s, it had become apparent that the National Park Service failed to uphold the mission addressed in the Organic Act at Fossil Cycad National Monument. Therefore, in 1957, under the request of the National Park Service, one of America's important paleontological localities lost its status as a unit of the National Park System.

Figure 1 - Paleobotanist George Reber Wieland (used with permission from Yale University)

PRE-MONUMENT HISTORY

In 1892, F. H. Cole of Hot Springs, South Dakota discovered the fossilized cycad beds in the southern Black Hills, near Minnekahta. After the discovery, Cole sent photographs of the fossils he had found to Professor Henry Newton, a geologist at the Smithsonian Institution. The first description of the locality was published in 1893 by Professor Thomas MacBride of the University of Iowa.

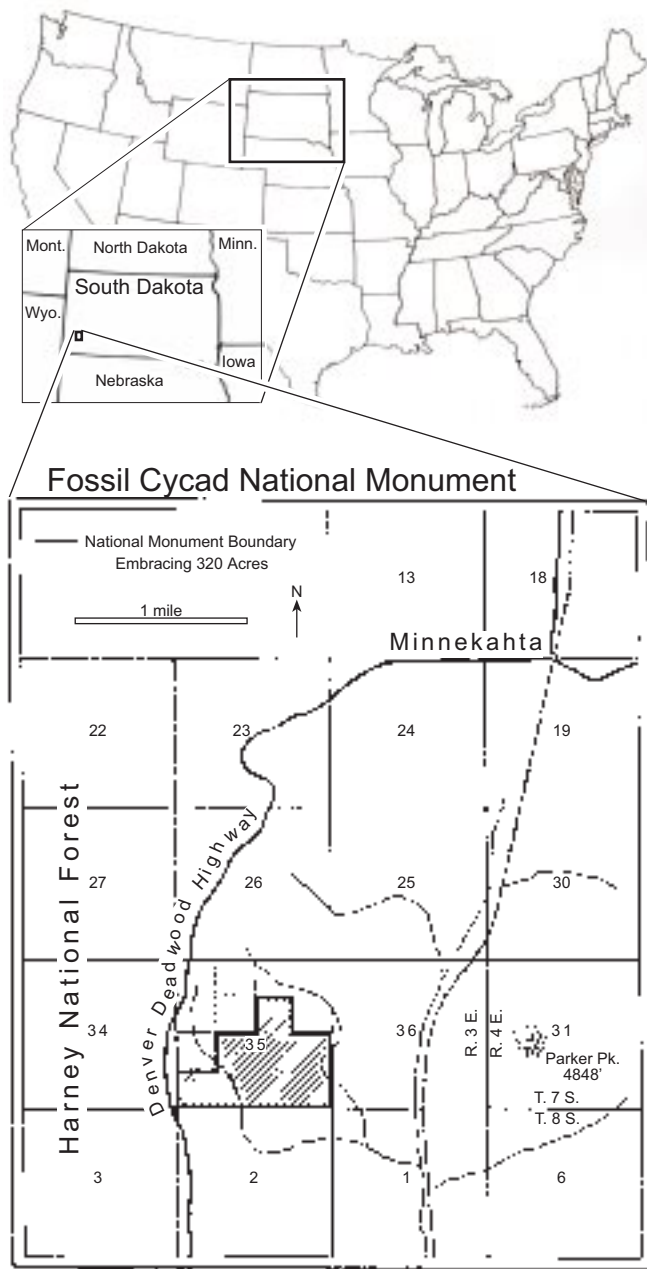


FIGURE 2—Location of Fossil Cycad National Monument (adapted from a 1922 Department of Interior map).

Also in 1893, Lester Ward of the United States Geological Survey started collecting the fossilized cycadeoids in the Black Hills. In 1897, an extreme interest in the cycad sites of South Dakota took hold in George Reber Wieland (Figure 1). While assisting O. C. Marsh, Professor of Paleontology at Yale University, Wieland traveled to South Dakota and met Ward. Through the encouragement of Ward and Marsh, Wieland's scientific interest in the cycads of South Dakota grew and he changed his focus from vertebrate paleontology to that of paleobotany. Wieland returned to Yale University and the Peabody Museum and continued to study the cycadeoids. He later had two volumes titled *American Fossil Cycads* published by the Carnegie Institution of Washington (Wieland,

1916).

In 1920, Wieland obtained the fossil cycad-rich land under the Homestead Act "in order that the cycads might not fall into unworthy hands" (Hot Springs Star, 1938). Two years later, he offered to return the land to the federal government, so that a national monument could be established to further protect the petrified plants.

The 320-acre site, located in the Dakota Sandstone Formation (120 million years old), contained immense quantities of the fossilized cycadeoids. "The area is probably one of the most interesting fossil plant localities and is known amongst scientific men the world over," wrote E. C. Finney to President Warren G. Harding before the establishment of the monument (Finney, 18 October 1922). Many of the fossil cycad specimens exhibited branching features that were not previously observed. The fossil cycads held the promise of helping to explain the origin of flowering plants.

ESTABLISHMENT OF FOSSIL CYCAD NATIONAL MONUMENT

With Wieland's offer to give the homesteaded land back to the government for the creation of a monument, the government sought insight from scientists. Charles D. Walcott of the U. S. Geological Survey and the Smithsonian Institution was asked to visit the site and assess its value. Without visiting the locality, Walcott concluded that although there were reports that all surficial cycads had been removed, "in the future, more specimens will be exposed by erosion, and at that time it would be well for the area to be under the jurisdiction of the Government" (Walcott, 15 April 1922). After reviewing the scientific reports, President Harding signed a proclamation on October 21, 1922, establishing the site as Fossil Cycad National Monument (Figure 2):

"Whereas, there are located in section thirty-five, township seven south, range three east of Black Hills Meridian, South Dakota, rich Mesozoic deposits of fossil cycads and other characteristic examples of paleobotany, which are of great scientific interest and value " (Presidential Proclamation 1641).

ADMINISTRATION OF FOSSIL CYCAD

The day to day surveillance of Fossil Cycad National Monument was entrusted to local ranchers. Although the superintendent of Wind Cave National Park was asked to look after the monument at the time of its establishment in 1922, there were only sporadic and brief visits to the site. Fossil Cycad does not appear in any of the superintendent's reports until 1933.

Regional Geologist Carrol Wegemann mapped the stratigraphy of the monument (Wegemann, 1936). He concluded that the cycad sand, which was six to eight feet thick, was either of the Dakota or possibly Morrison Formation. He commented that the lack of good exposures around the monument limited the view of the stratigraphic section. He also reported that the cycads occurred in stream deposits.

Research on the land resumed in October 1935, when Wieland and a crew of thirteen Civilian Conservation Corps workers opened six to eight excavation pits, according to the

FIGURE 3—Professor Wieland supervising a CCC crew during the 1935 fossil cycad test excavation (used with permission from Yale University).

superintendent of Wind Cave National Park Edward D. Freeland (Figure 3). Wieland reported that the excavation was a brilliant success with over a ton of uneroded specimens collected. Freeland stated that the excavation had “unquestionably proven that numerous cycads still remain on the monument and excellent specimens have been found.”

Development of the monument was not seriously discussed until around 1936, when Wieland started pressing the issue. The value of the monument, though, was already being questioned. In 1929, Acting Director of the National Park Service, Arno B. Cammerer, wrote to Dr. J. Volney Lewis and discussed the validity of the monument:

“It was considered worth conserving at the time, and the situation surely cannot have changed. It is similar to Dinosaur [National Monument], where there is nothing on the surface to show its scientific importance, but nevertheless it is there.” (Cammerer, 11 December 1929)

Similar discussions continued throughout the existence of the monument. Development of the monument proceeded slowly for two major reasons: the lack of surficial *in situ* specimens at the site and a dispute between Wieland and Wegemann.

The Wieland-Wegemann dispute started in 1935, when Wegemann accused Wieland of stealing fossils collected dur-

ing the November 1935 excavation. Wegemann stated that Wieland had removed all of the original surficial specimens and taken them to Yale University before donating the land to the government. This feud escalated when Wegemann shut down the 1935 excavation at Fossil Cycad. The issue culminated when Superintendent Freeland defended Wieland and at the same time criticized Wegemann. Freeland stated, “Wegemann has an unfortunate manner with other people, and he has been tactless enough to offend Dr. Wieland, by continual rudeness.” (Freeland, 18 November 35). At that point Wegemann engaged in direct communication with the Assistant Director of the National Park Service, Harold C. Bryant, regarding Fossil Cycad without the permission of Superintendent Freeland. In a letter to Wegemann, Bryant wrote that “Doctor Wilson has resigned and Doctor Wieland feels that your treatment of him was discourteous.” Bryant also mentioned that Wegemann “should first have communicated with Mr. Freeland so that orders for stopping the work of excavation could have been given by him.” (Bryant, 22 November 1935)

The lack of surficial *in situ* specimens emerged as an obstacle when Wieland insisted on the construction of a visitor center at the monument site, so that the uniqueness of the fossil resource could be explained to visitors at Fossil Cycad. Wieland’s persistence resulted in the Director of the Park Ser-



FIGURE 4—One of several architectural drawings of a proposed visitor center at Fossil Cycad National Monument prepared by a student at Yale University.

vice recommending the development of a display about fossil cycads at the Wind Cave visitor center. Wieland's response to this idea was negative. He wrote repeatedly on the value of an *in situ* display:

"Fossil Cycad Monument more than all others of its series is as we now see dependent on an absolutely *in situ* development and display. Without this it can mean but little, as a mere blurred shadow, all but lost again in the shuffle of time." (Wieland, 1937)

In order to expedite the creation of a visitor center, Wieland asked architecture students at Yale to submit proposals for a building design. These draft plans were sent to the Department of the Interior for review (Figure 4). The response from Washington was that the cost for construction of a building at the Minnekahta site was too expensive. In addition to the construction of the visitor center and the building maintenance, there would be a need to build roads into the monument. There was also the fact that the distinct value of Fossil Cycad National Monument eluded many people in the government:

"Developments of additional areas cannot be undertaken unless their justification is unimpeachable and their future maintenance is assured. The Fossil Cycad National Monument does not satisfy either of these requirements. It is realized that the area is of outstanding paleobotanical interest. But it is also realized that the subject of fossil cycads does not have a broad appeal and, therefore, extensive development of the monument would benefit only a limited group of people. This is particularly true since the area does not possess other outstanding attractions. The scenery is neither impressive nor is it unusual; the geological interest, other than its paleobotanic relations, is not phenomenal; the area is too small for wildlife preservation; the terrain does not lend itself well to recreational development, and there is little historic interest." (Slattery, 23 July 1937)

Wieland's insistence continued. His next step was to urge senators and congressmen to contact the Secretary of the Interior regarding the developmental plans for Fossil Cycad National Monument. When these supplications failed, Wieland asked the senators and congressmen from South Dakota and Connecticut to introduce an appropriations bill that would provide funding for a visitor center at Fossil Cycad. The De-

partment of the Interior contended that they did not have the funds to develop the monument, nor did they have a strong enough reason to seek funds:

"Naturally, the development of any exhibit of this type is dependent upon an allotment of funds and these funds can be obtained only if the proposal justified the expense and those making the allotment are convinced that the exhibit is equal to, or better than, many others now waiting development in the various national parks and monuments." (Slattery, 28 May 1937)

THE LOST SPECIMEN

In 1933, just before the opening of the "Century of Progress" Exposition at the World's Fair in Chicago, the National Park Service Director's Office wrote to Wind Cave requesting a specimen of fossil cycad to be used in a display at the Fair.

Wind Cave did not have a specimen and contacted Mr. W.E. Parks of Lincoln, Nebraska. Parks agreed to loan his cycad specimen to be placed on display at the Chicago World's Fair. The National Park Service later lost the fossilized cycad specimen loaned by Parks. Mr. Parks requested that the National Park Service either replace the specimen or provide some compensation for the lost specimen.

The National Park Service effectively avoided the issue for years. Since a receipt of property was never produced at the time the specimen was received on loan, Parks' persistent claims regarding the lost specimen did not receive appropriate attention. Parks' requests for \$75 as compensation for the lost specimen were challenged by the Regional Naturalist who recommended that only \$50 compensation be paid instead of the \$75 requested.

In a letter dated October 5, 1945, Mr. Trager, Regional Chief Naturalist described the lost specimen as, "a crushed cycad stump about 6 or 7 inches wide by 10 or 12 inches long. It was a very poor specimen and consequently was not exhibited at Chicago." (Trager, 5 October 1945). Because of a misunderstanding, this specimen was thought to be worthless and discarded.

Dr. Wieland suggested to Parks and the National Park Service that a specimen could be made available to replace the lost specimen. In June 1946, National Park Service staff traveled to Fossil Cycad National Monument to see if they could find a cycad to replace Parks' lost specimen. A replacement specimen could not be located.

The Interior Solicitor presented his opinion in a memo dated July 16, 1946, "Unless settlement can be made under the act of December 28, 1922 (42 Stat 1066, 31 US Code Sec 215) the only financial relief for Mr. Parks would be by Act of Congress on a Bill for his relief." (Interior Solicitor, 16 July 1946)

On January 27, 1947, the Solicitor wrote, "We realize that the settlement of Mr. Park's claim has been unduly drawn out. As yet, however, no logical solution has presented itself. A monetary settlement is not possible now since the statutory limitation of one year from presenting the claim has passed

long since.” (Interior Solicitor, 27 January 1947)

Parks responded to the National Park Service in a letter dated April 5, 1947, “From the past it looks as if I am a victim of government red tape.” (Parks, 5 April 1947) By the fall of 1947, Parks decided that his only option was to write to his congressman. (Parks, 28 October 1947)

On July 6, 1949, H.R. 3010 “A Bill for the Relief of Walter E. Parks” was passed by the House of Representatives. The Bill awarded Parks a settlement of \$125.

DEAUTHORIZATION OF THE MONUMENT

By the early 1950s, the principal advocates for Fossil Cycad National Monument, George Wieland and South Dakota Senator Peter Norbeck, had died. “The National Park Service thinks Fossil Cycad National Monument is a white elephant and wants to get it off its paper”, according to Secretary Will G. Robinson of the South Dakota Historical Society (Robinson, 18 January 55). Representative E.Y. Berry from South Dakota introduced legislation in January 1955 to abolish Fossil Cycad National Monument. The bill was introduced at the request of the National Park Service.

Robinson suggested that the site be transferred to the South Dakota Historical Society with the intent to preserve the fossil locality from any exploitation by private individuals. Robinson traveled to Fossil Cycad National Monument on May 28, 1956 with the Superintendent of Wind Cave. There was no evidence of fossil cycad material on the surface during their visit.

According to Dr. Bump, a professor at the South Dakota School of Mines, there are other cycads found in the Black Hills. Bump indicated, though, that other than a few specimens in the collections at his institution, Wieland apparently took all the cycads from the monument and set them up in a museum at Yale.

During the 84th Congress, Senate Bill 1161 was introduced to abolish Fossil Cycad National Monument as a unit of the National Park Service. The bill was supported by the Department of Interior and by the National Parks Association. The bill was signed into law on August 1, 1956 and became effective September 1, 1957. On December 6, 1957, Assistant Secretary of Interior Royce A. Hardy issued Public Order 1562 to carry out the directive of the public law. The land was turned over to the Bureau of Land Management.

POST-MONUMENT HISTORY

Between 1957 and 1998, the Bureau of Land Management (BLM) has maintained the 320 acre site previously designated as Fossil Cycad National Monument within the South Dakota Resource Area. In 1980, construction within a 300 foot highway right-of-way occurred within the boundaries of the revoked monument. During construction activities, fossil cycad material was unearthed.

In 1997, the BLM published an environmental assessment (EA) that analyzed the Fossil Cycad area relative to meeting the Area of Critical Environmental Concern (ACEC) criteria. The ACEC designation highlights areas where special management attention is needed to protect and prevent irreparable damage to resources. Members of the public nomi-

nated the Fossil Cycad area for ACEC designation.

In the Draft Amendment to the South Dakota Resource Management Plan prepared by the BLM, states, “BLM management objectives should involve the long-term conservation of the area’s geologic, and paleontologic values for future generations to study and enjoy.” The preferred alternative (Alternative C) indicates the following determinations: 1) retaining the area in public ownership would help make the scientific information available to the public; 2) restricting activity would help protect the area; 3) by allowing rights-of-way, important scientific information may be uncovered during surface disturbance; and 4) this information would be recovered by BLM and made available to the scientific community.

Fossil Cycad National Monument was never officially open to the public and never had a visitor center or public programs. According to paleontologist Dr. Theodore White, “No present areas of the National Park Service contain fossil cycads. Therefore it could be concluded that the area should have been retained in the system based on its merits in relation to the thematic evaluation.” The legislation abolishing the monument contains the following statement, “That if any excavations on such lands for the recovery of fissionable materials or any other minerals should be undertaken, such fossils remains discovered shall become property of the Federal government.” (S. 1161).

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MESOZOIC MOLLUSCAN FOSSILS FROM THE GOLDEN GATE NATIONAL RECREATION AREA AND THEIR SIGNIFICANCE TO FRANCISCAN COMPLEX TERRANE RECONSTRUCTIONS, SAN FRANCISCO BAY AREA, CALIFORNIA

WILLIAM P. ELDER

National Park Service, Fort Mason, Building 201, San Francisco, CA 94123

ABSTRACT—Macrofossils are extremely rare in the Franciscan Complex. Three important Franciscan macrofossil localities are on lands of the Golden Gate National Recreation Area (GOGA). Two of these localities contain age diagnostic ammonites and lie in the Marin Headlands terrane, adjacent to the Golden Gate. At one locality, just south of the Gate, *Douvilleiceras* cf. *D. mammillatum* (Schlotheim) indicates an Albian age. At the second locality, north of the Golden Gate in the Marin Headlands, *Mantelliceras* sp. provides a Cenomanian age. The third important area is on Alcatraz Island, where several sites provide bivalve collections made over the past 130 years. The earliest collections consist of molds of *Inoceramus* and other bivalves of uncertain age. More recently, the Valanginian bivalve, *Buchia pacifica*, was reported from Alcatraz. Most recently, a juvenile inoceramid bivalve suggestive of a Cenomanian age was found on the island.

Blake et al. (1984) assigned Alcatraz Island to a terrane separate from the nearby Marin Headlands terrane on the basis of apparent age and petrographic differences between graywackes of the two terranes. However, the inoceramid specimen recently found on Alcatraz, as well as others described by Gabb (1869) as *Inoceramus elliotii*, resemble Cenomanian species, implying a similar age for graywackes of the two terranes and diminishing the need for a separate Alcatraz terrane. However, minimal stratigraphic separation between the Cenomanian and Valanginian fossils on Alcatraz suggests a problem with one of the age calls. A reasonable alternative solution, therefore, is assignment of the inoceramids to the *Inoceramus neocomiensis* group of Neocomian age, thus, indicating that the Alcatraz terrane is indeed separate from the Marin Headlands terrane.

INTRODUCTION

THE FRANCISCAN Complex is comprised of a complexly deformed amalgamation of tectonostratigraphic terranes of differing depositional and deformational histories. The terranes are composed of oceanic blocks that may include both mafic basement and overlying sedimentary rocks. These blocks were shingled against the western margin of North America as the Pacific Plate was subducted under the North American Plate prior to formation of the San Andreas fault. In the San Francisco Bay area, the Franciscan Complex has been divided into numerous terranes contained within the Eastern and Central melange belts. The Eastern belt lies inboard and structurally higher than the Central belt and is of higher metamorphic grade. Blake et al. (1984) defined essentially eight terranes in the Central belt in the San Francisco Bay area (Figure 1) on the basis of differences in basement rock types and ages, in the ages and types of overlying sedimentary sequences, and in metamorphic grade. Of particular importance to this report are the Marin Headlands and the Alcatraz terranes, where the molluscan fossils discussed herein were found.

Sedimentary rocks of the Franciscan Complex are predominantly composed of continental margin sediments, primarily argillite and graywacke sandstone, but also are represented to a lesser extent by open-ocean facies, such as chert or limestone primarily composed of radiolaria or foraminifera, respectively. Where preserved, these microfossils provide age control for times of open-ocean deposition on Franciscan terrane blocks. However, the time of accretion of these oceanic blocks onto the western margin of North America is typically

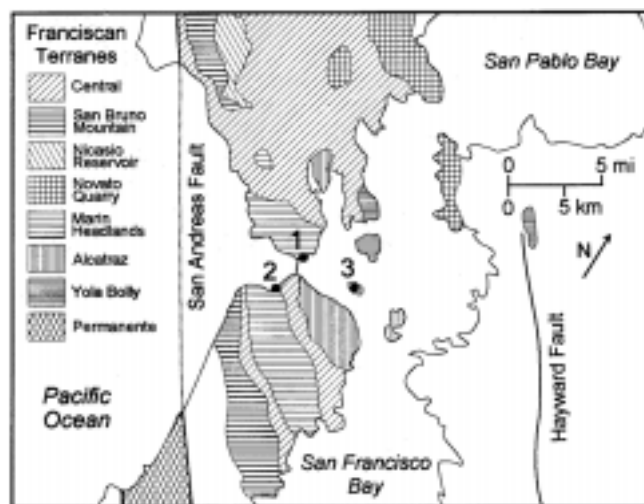


FIGURE 1—Location map showing terranes of the Franciscan Complex identified in the San Francisco Bay area by Blake et al. (1984), and the three GOGA molluscan localities discussed herein: 1) Marin Headlands locality where Cenomanian *Mantelliceras* was found; 2) Baker Beach locality with Albian *Douvilleiceras*; 3) Alcatraz localities where *Inoceramus*, *Buchia*, and other bivalves have been found. Modified from Blake et al. (1984).

poorly constrained, because the clastic facies deposited on the blocks when they neared the continental margin generally preserve no fossils. Therefore, the molluscan fossils found in the GOGA are highly significant because they provide critical control on the time when these oceanic blocks collided with

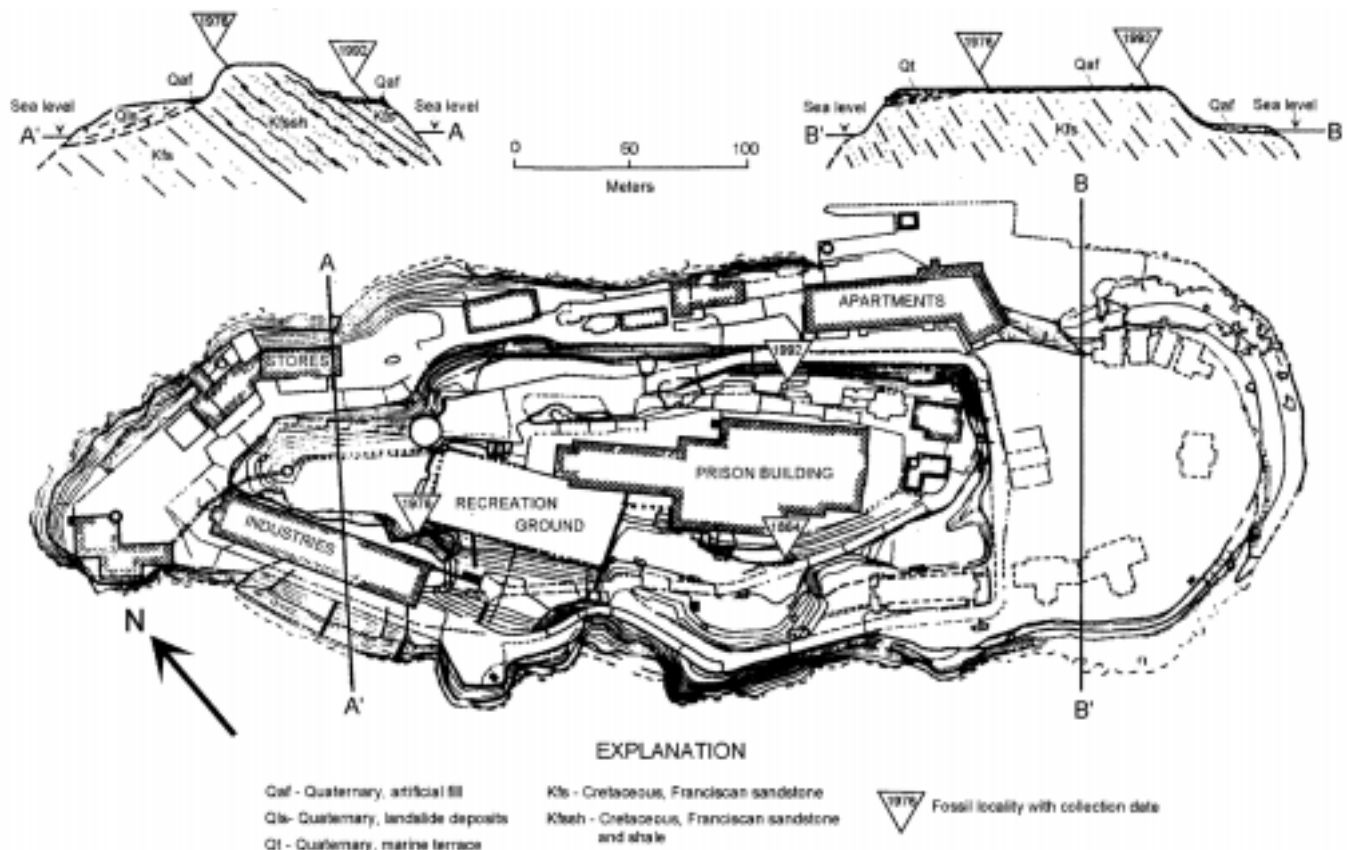


FIGURE 2—Map of Alcatraz Island showing fossil localities (triangles) and geologic cross sections with *Inoceramus* and *Buchia* localities projected onto them, indicating approximate stratigraphic separation. Modified from Armstrong and Gallagher (1977).

North America. In addition, the fossils help in defining and assigning rocks to the different terrane blocks.

FOSSILS

Molluscan fossils from the Franciscan Complex in lands that now lie in the GOGA have been known for over 130 years, with the earliest specimens being found in a barge containing sandstone blocks quarried from Alcatraz Island in the 1860s. These fossils were presented to paleontologist William M. Gabb by Major George H. Elliot. Gabb (1869, p. 193, pl. 31, fig. 90) subsequently described *Inoceramus elliotii* based on several internal and external molds of these specimens and additional material that he collected on the island in 1864 (Figures 2 and 3). No other specimens have been assigned to this species, however, due to the poor condition of the syntypes on which it is based, although Crame (1985, p. 483, text-fig. 4b) identified an *Inoceramus* aff. *I. elliotii* Gabb from the Lower Cretaceous of Antarctica.

Because of the significance of Alcatraz specimens on providing an age for the Franciscan Complex, they have been further discussed or illustrated by Stewart (1930, pl. 2, fig. 2), Anderson (1938, pl. 7, fig. 1), Matsumoto (1960), Bailey et al. (1964, p. 115), and Elder and Miller (1993, p. 8). Anderson (1938, p. 99) considered *Inoceramus elliotii* to be related to *I. ovatus* Stanton and thought it to be of Neocomian age. In

contrast, Matsumoto (1960) and Elder and Miller (1993) speculated that *I. elliotii* may be equivalent to *I. crippei* Mantell of Cenomanian age. Anderson (1938, p. 121) also described *Lucina alcatrazis* on the basis of three molds obtained from Gabb's Alcatraz material. Likewise, this species has not been identified elsewhere and is of little age significance.

In 1976, the next fossil find on Alcatraz (Figure 2) produced specimens identified as *Buchia pacifica* (Jeletzky) and *Pleuromya* sp. by David Jones in Armstrong and Gallagher (1977). *Buchia pacifica* is indicative of a latest Berriasian to early Valanginian age and *Pleuromya* is a genus typical of the Neocomian rocks of the west coast (Jones et al., 1969; Bralower et al., 1990; Anderson, 1938). The most recent fossil find on Alcatraz was in 1992, when Ranger Ted Stout found a juvenile inoceramid bivalve (Figures 2 and 3). Elder and Miller (1993) assigned this specimen to the *Inoceramus pictus* group of late Cenomanian age.

A Cenomanian age for the new inoceramid from Alcatraz Island is consistent with the age indicated by a specimen of the ammonite genus *Mantelliceras*, found at the north end of the Golden Gate Bridge and identified by Hertlein (1956) (Figure 1). The early Cenomanian age indicated by that ammonite is slightly younger than the early Albian age indicated by a *Douvilleiceras* cf. *D. mammillatum* (Schlotheim) specimen found just south of the Golden Gate (Figure 1), at the north

FIGURE 3—1, Scanned image of plaster cast of syntype of *Inoceramus elliotii* Gabb, 1869, from which Gabb's (1869; pl. 31, fig. 90) was drawn. Specimen also was illustrated by Stewart (1930; pl. 2, fig. 2) and is an internal mold; Accession No. ANSP# 4411, Cat. No. 28869. 2) Scanned image of plaster cast of syntype of *Inoceramus elliotii* from Gabb's collection but never before illustrated. Specimen is an internal mold; Accession No. ANSP# 4411, Cat. No. 28870. 3-4) Inoceramid found by Ted Stout in 1992 and identified as *Inoceramus* ex gr. *pictus* in Elder and Miller (1993). Accession # GOGA-1651, Cat. No. GOGA-18502a&b. 3 - Scanned image of latex pull of external mold. 4 - Scanned image of plaster cast of internal mold. 5-6) Scanned images of Woods' (1911) figures of *Inoceramus neocomiensis* d'Orbigny, 1846. 5 - Woods (1911, pl. XLV, fig. 1). 6 - Woods (1911, pl. XLV, fig. 2).

end of Baker Beach (Schlocker et al., 1954). Both of those ammonites were found in rocks assigned to the Marin Headlands terrane of the Franciscan Complex.

DISCUSSION

Blake et al. (1984) defined the Alcatraz terrane as separate from the Marin Headlands terrane on the basis of the former being primarily composed of a relatively thick sequence of turbidite sandstone with minor shale of Valanginian age, in contrast to the latter terrane, which includes oceanic volcanic basement overlain by pelagic chert that is as young as late Albian to early Cenomanian. The chert of the Marin Headlands terrane is overlain, however, by a thick turbiditic graywacke sequence from which the Cenomanian *Mantelliceras* and Albian *Douvilleiceras* ammonites have been

found. In addition to the apparent age differences in the graywackes of these two terranes, they also differ petrologically, with the Alcatraz sandstones containing a significantly lower lithic component (Jayko and Blake, 1984, figs. 4a-b). However, if the rocks on Alcatraz are Cenomanian rather than Valanginian in age, as suggested by the inoceramids, then designation of a separate Alcatraz terrane is less compelling, thus, somewhat simplifying Bay Area geology.

The main obstacle to declaring a Cenomanian in age for all the rocks on Alcatraz is the Valanginian *Buchia* specimens identified in Armstrong and Gallagher (1977). Unfortunately, those specimens have been lost and, therefore, cannot be restudied. Several recent attempts to recollect the locality have failed to yield identifiable fossils. A Valanginian age assignment for these specimens presents two problems.

First, the presence of Franciscan graywackes of that age requires establishment of a separate Alcatraz terrane; a requirement that is supported, however, by petrographic differences between the rocks on Alcatraz and those of the Marin Headlands terrane. Second, the stratigraphy on Alcatraz Island indicates that the Valanginian fossils lay only about 60 m stratigraphically below the inoceramids of apparent Cenomanian age (Figure 2). In the rapid depositional setting of turbidite environments, this is an insufficient stratigraphic separation to account for a 40 Myr age difference, and there are no obvious intervening faults or other structural features that can account for this missing time. In re-evaluating the age implications of the fossils reported on by Armstrong and Gallagher (1977), Elder and Miller (1993) suggested that the *Buchia pacifica* identified may actually be deformed *Inoceramus gradilis* Pergament, which looks very similar to *B. pacifica* and is of middle Cenomanian age. There are two problems with this interpretation, however. First, *Inoceramus gradilis* has not been found on the Pacific coast south of Alaska (Elder and Box, 1992). Second, the co-occurring genus *Pleuromya* is largely restricted to and typical of Neocomian age rocks on the west coast.

One solution to the above-noted age problem is that the Cenomanian inoceramid calls are wrong, and that the rocks on Alcatraz are all of Neocomian age. Neocomian inoceramids on the Pacific coast of North America are not diverse and are poorly documented. In addition, the rocks and fossils of Alcatraz are somewhat deformed, making identifications tenuous. However, inspection of plaster casts made from three of Gabb's inoceramid specimens, as well as the specimen found in 1992, provides a better idea of the morphology of the inoceramid species than was previously possible (Figure 3). The morphology of these specimens is not like that of typical west coast Neocomian inoceramids, such as *I. ovatooides* Anderson, but is compatible with them belonging to the *Inoceramus neocomiensis* d'Orbigny group (Figure 3.5, 3.6; also see Woods, 1911, pl. XLV, figs. 1-2). Specimens of this species group, which resemble *I. anglicus* Woods but have coarser concentric rugae, occur in Hauterivian age rocks of Oregon in association with *Pleuromya* (Imlay, 1960, p. 177). The *I. neocomiensis* group is typical of the Valanginian to Berranian interval (Dhondt, 1992).

In conclusion, until more definitive paleontologic evidence is unearthed on Alcatraz, the age of the rocks on the island, and the validity of the Alcatraz terrane, will remain in question. However, the bulk of the paleontologic data, coupled with the stratigraphic constraints on Alcatraz, argue for a Neocomian age for the Franciscan graywacke on the island. This age is significantly older than the Albion to Cenomanian graywacke of the Marin Headlands terrane, supporting a distinct Alcatraz terrane with petrologically different sandstone.

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TAXONOMY AND ICHNOFACIES OF PERMIAN TETRAPOD TRACKS FROM GRAND CANYON NATIONAL PARK, ARIZONA

ADRIAN P. HUNT¹ AND VINCENT L. SANTUCCI²

¹Mesalands Dinosaur Museum, Mesa Technical College, 911 South Tenth Street, Tucumcari, NM 88401

²National Park Service, PO Box 592, Kemmerer, WY 83101

ABSTRACT—A recent renaissance in the study of Permian tetrapod ichnofaunas has resulted in a reevaluation of the important specimens from Grand Canyon National Park. The ichnofauna of the Coconino Sandstone consists of *Chelichnus bucklandi*, *C. gigas* and *C. duncani* and represents the cosmopolitan *Chelichnus* ichnofacies. The ichnofauna of the Hermit Shale includes *Batrachichnus delicatulus*, *Parabaropus coloradensis*, *Hyloidichnus bifurcatus*, *Gilmoreichnus hermitanus*, *Limnopus* sp. and *Ichnoterium* sp. and represents an "inland" redbed facies.

INTRODUCTION

UNDOUBTEDLY the most significant collection of Paleozoic vertebrate tracks in North America was collected and described by Charles Gilmore of the United States National Museum (Smithsonian) in a series of classic works (Gilmore, 1926b, 1927b, 1928a). Gilmore collected these specimens from three formations in Grand Canyon National Park. During the last five years there has been a radical reappraisal of Permian tetrapod tracks and ichnofacies. The purpose of this paper is to briefly review the taxonomy of the Grand Canyon collections of tetrapod tracks and to comment on their ichnofacies significance in the light of these recent changes.

ICHNOTAXONOMY

History of study.—Schuchert (1918) first collected tetrapod tracks in Paleozoic strata on the South Rim of the Grand Canyon. Lull (1918) utilized this collection from the Permian Coconino Sandstone in the first scientific description of Paleozoic tetrapod tracks from Arizona. In 1924 the National Park Service invited Charles Gilmore to visit Schuchert's locality and to prepare an *in situ* exhibit on the now abandoned Hermit Trail (Spamer, 1984). Gilmore (1926b) described this new Coconino collection and was later funded by the Marsh Fund Committee of the National Academy of Sciences (1926) and the Grand Canyon Exhibit Committee of the National Academy of Sciences (1927) to make additional collections and exhibits (Spamer, 1984). These new collections came from the Hermit Shale (Permian) and Wescogame Formation of the Supai Group (Pennsylvanian) as well as the Coconino

and were described by Gilmore in additional monographs (Gilmore, 1927b, 1928a) and a short paper on the first tracks from the North Rim (Gilmore and Sturdevant, 1928). Gilmore also wrote three more popular papers describing his collecting efforts (Gilmore, 1926a, 1927a, 1928b).

For the next 70 years there was little reevaluation of Gilmore's work except by Don Baird of Princeton (Baird, 1952, Baird in Spamer, 1984). A renaissance of Paleozoic track studies took place in the mid 1990's. The Rosetta Stone for a new reevaluation of Permian tracks was provided by studies of the extensive ichnofaunas from the redbeds of southern New Mexico (Haubold et al., 1995, Hunt et al., 1995). The New Mexico tracksites provided large sample sizes of all the most significant Permian ichnotaxa and included a broad range of preservational variants. These samples provided a new perspective on the plethora of ichnotaxonomic names of tetrapod tracks from Permian redbeds, most of which had been described on the basis of small sample sizes. During the same timeframe there was a major reevaluation of the equally confused ichnotaxonomy of tetrapod tracks from Permian eolianites (Morales and Haubold, 1995; Haubold et al., 1995; McKeever and Haubold, 1996). Haubold (1996) reviewed the new ichnotaxonomy of Permian tracks that derived from these works. One of the main purposes of this work is to provide a new evaluation of the taxonomy of the Permian tetrapod tracks from the Grand Canyon (Tables 1-2).

Coconino Sandstone.—The first fossil footprints to be described came from Permian eolianites of Scotland (Grierson, 1828). Subsequently, important ichnofaunas were described

TABLE 1—Revised ichnotaxonomy of tetrapod ichnofauna of the Coconino Sandstone at Grand Canyon National Park (McKeever and Haubold, 1996).

<i>Chelichnus duncani</i> (Owen, 1842) (= <i>Baropezia arizonae</i> , <i>Allopus? arizonae</i> , <i>Baropezia eakini</i> , <i>Agostopus matheri</i> , <i>Agostopus medius</i> , <i>Palaeopus regularis</i> , <i>Barypodus tridactylus</i> , <i>Barypodus metzleri</i> , <i>Nanopus maximus</i> , <i>Laoporus noblei</i> in part of Gilmore, 1926b)
<i>Chelichnus gigas</i> Jardine, 1850 (= <i>Barypodus palmatus</i> , <i>Amblyopus pachypodus</i> , <i>Baropus coconinoensis</i>)
<i>Chelichnus bucklandi</i> (Jardine, 1850) (= <i>Dolichopodus tetradactylus</i> , <i>Laoporus schucherti</i> , <i>Laoporus coloradensis</i> , <i>Nanopus merriami</i> , <i>Laoporus noblei</i> of Lull, 1918)

by eolian strata of Germany (Cornberger Sandstein), Colorado (Lyons Sandstone) and Arizona (Coconino Sandstone, DeChelly Sandstone) as well as additional specimens from Scotland (Hopeman, Corncockle and Locharbriggs Sandstone Formations). A large literature described many ichnotaxa from these formations. However, recent work spearheaded by Hartmut Haubold has demonstrated that virtually all tetrapod tracks from Permian eolinaites represent three species of one genus, with only the rarest exceptions (Haubold et al., 1995b; McKeever and Haubold, 1996; Haubold, 1996). Certainly all the Coconino tracks fall within three species of *Chelichnus* (McKeever and Haubold, 1996). *Chelichnus* is characterized by rounded manual and pedal impressions that are of nearly equal size and which exhibit five short, rounded toe impressions (though less than five may be preserved). Trackways have a pace angulation of about 90° and the manual and pedal impressions are close together (McKeever and Haubold, 1996). The three valid species of *Chelichnus* are distinguished on the basis of size alone and are presumed to be the tracks of caseid-like animal (e. g. Haubold, 1971). *Chelichnus bucklandi* has pedal impression lengths of 10–25 mm, *C. duncani* of 25–75 mm and *C. gigas* of 75–125 mm (McKeever and Haubold, 1996). Thus, all Gilmore's (and Lull's) named ichnotaxa from the Coconino Sandstone of the Grand Canyon can be placed in one of these three species. Gilmore (1927b) was aware of the similarity of some of his specimens from the Grand Canyon to those from Scotland, but he persisted with his (and Lull's) distinct ichnotaxonomy (e. g., Gilmore, 1928a).

Size by itself is not the ideal criterion to distinguish between ichnospecies, but, the revised ichnotaxonomy presented here represent the current consensus. The low ichnotaxonomic diversity in Table 1 is in keeping with the low animal diversity that would be expected in a dunefield.

Hermit Shale.—The Hermit Shale tetrapod tracks occur in redbeds, in contrast to the eolian strata of the Coconino Sandstone. Recent work has indicated that Permian redbed ichnofaunas are of low diversity and cosmopolitan nature (Haubold et al., 1995a; Haubold, 1996; Hunt and Lucas, 1988b). A reevaluation of Gilmore's ichnotaxonomy indicates that he had overestimated the diversity of the Hermit Shale ichnofauna. Gilmore, in common with all pre-1990's ichnologists, was not sufficiently aware of the variable traces that could made by a single trackmaker given variations in substrate conditions and gait. Thus, Gilmore assumed that all

TABLE 2—Revised ichnotaxonomy of tetrapod ichnofauna of the Hermit Shale at Grand Canyon National Park (Haubold et al., 1995a; this paper).

<i>Batrachichnus delicatulus</i> (Lull, 1918) (= <i>Exocampe (?) delicatula</i> , <i>Batrachichnus delicatula</i> , <i>Batrachichnus obscurus</i> , <i>Dromillopus parvus</i>)
<i>Parabaropus coloradensis</i> (Lull, 1918) (= <i>Megapezia (?) coloradensis</i>)
<i>Hyloidichnus bifurcatus</i> Gilmore, 1927b (= <i>Hyloidichnus whitei</i>)
<i>Gilmoreichnus hermitanus</i> (Gilmore, 1927b) (= <i>Palaeosauropus hermitanus</i> , <i>Hylopus hermitanus</i> , <i>Colletosaurus pentadactylus</i> , <i>Cursipes</i> sp.)
<i>Limnopus</i> sp. (= <i>Parabaropus coloradensis</i> of Gilmore, 1927b in part)
<i>Ichniotherium</i> sp. (= <i>Parabaropus coloradensis</i> of Gilmore 1928a in part)

differences in footprint morphology or trackway pattern reflected the presence of different trackmakers. A reevaluation of the tetrapod ichnotaxa from the Hermit Shale of the Grand Canyon reveals a lower ichnodiversity than was previously recognized (Table 2).

The Hermit Shale ichnofauna includes the nearly ubiquitous temnospondyl track *Batrachichnus delicatulus*. Reptile tracks include *Parabaropus coloradensis* and *Hyloidichnus bifurcatus* (seymouriamorph or diadectid tracks) and the small pelycosaur track *Gilmoreichnus hermitanus*. Two other more problematical ichnotaxa are present in the Hermit Shale collections. Haubold (1971) named *Ichniotherium gilmorei* for a specimen (USNM 11707) originally described by Gilmore (1928a, pl. 1). Unfortunately the holotype of this specimen is now lost (Haubold et al., 1995a). *Ichniotherium* is common in Europe but very rare in North America (Haubold et al., 1995a; Hunt et al., 1995; Hunt and Lucas, 1998b). A second problematic specimen is USNM 11598, a specimen that Gilmore (1927b, pl. 17, no. 1; Haubold et al., 1995a, fig. 24B) assigned to *Parabaropus coloradensis*. Haubold et al. (1995a) noted that this specimen is different from *P. coloradensis* in possessing distinct plantigrade impressions, elongate pedal imprints and less diverging digit impressions. They concluded that this trackway represents undertracks of either a *Dimetropus* specimen that preserves prominent pads and reduced digit impressions or a large *Limnopus* specimen (e. g., *Limnopus zeilleri*). We prefer the second interpretation because of the large manual pad impressions and because the long axis of the manual imprints is inclined at a high angle to the direction of travel.

ICHNOFACIES

History of study.—Gilmore was aware that the Coconino Sandstone and Hermit Shale were deposited in different sedimentary environments but Baird (1965) was the first to emphasize that the differences between the Permian ichnofaunas of the redbeds of the American West and those of eolinaites might be a result of facies differences. There has been a long tradition of recognizing ichnofacies in invertebrate traces, but the concept has only recently been applied to vertebrate tracks (Lockley et al., 1994). Tetrapod ichnofacies have been defined as “multiple ichnocoenoses that are similar in ichnotaxonomic composition and show recurrent association in particular environments (Lockley et al., 1994, p. 242). Lockley et al. (1994), Hunt et al. (1995), Haubold (1996) and Hunt and Lucas (1998a) have all discussed Permian tetrapod ichnofacies.

Coconino Sandstone.—The low-diversity tetrapod ichnofauna of the Coconino Sandstone clearly represents the *Chelichnus* ichnofacies (= *Laoporus* ichnofacies of Lockley et al., 1994) that is known from the DeChelly and Coconino Sandstone of Arizona, the Lyons Sandstone of Colorado, the Hopeman, Corncockle and Locharbriggs Sandstone Formations of Scotland, the Cornberger Sandstein of Germany and the Los Reynos Formation of Argentina (Hunt and Lucas, 1988a,b).

Hermit Shale.—Permian tetrapod ichnofaunas from redbeds are cosmopolitan in nature, but a number of ichnofacies can be recognized (Hunt et al., 1995; Hunt and Lucas, 1988a). Hunt and coworkers (Hunt et al., 1995; Hunt and Lucas, 1988a) have suggested that the Hermit Shale ichnofauna shows similarities with track assemblages from “inland” environments that were not in close proximity to a marine shoreline. This hypothesis is supported by the following features of the Hermit Shale ichnofauna (Hunt et al., 1995; Hunt and Lucas, 1988a):

- Presence of *Ichniotherium* and *Parabaropus* that are “inland” facies fossils;
- Absence of *Dromopus* that is abundant in coastal ichnofaunas;
- Presence of *Limnopus* that is uncommon in coastal ichnofaunas.

The Hermit Shale ichnofauna shows several similarities with the “inland” ichnofauna of the Sangre de Cristo Formation in New Mexico (*Ichniotherium*, *Parabaropus*), but is distinct in lacking *Dromopus* and *Dimetropus*.

CONCLUSIONS

Recent work has resulted in a major reevaluation of the ichnotaxonomy and ichnofacies context of the Permian tetrapod tracks of the Grand Canyon. Hopefully this renaissance of knowledge about Paleozoic tracks will spur further study of the important ichnofaunas of Grand Canyon National Park.

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AN IDENTIFICATION KEY TO PERMIAN TETRAPOD TRACKS FROM GRAND CANYON NATIONAL PARK

ADRIAN P. HUNT¹ AND VINCENT L. SANTUCCI²

¹Mesalands Dinosaur Museum, Mesa Technical College, 911 South Tenth Street, Tucumcari, NM 88401

²National Park Service, PO Box 592, Kemmerer, WY 83101

ABSTRACT—Abundant Permian vertebrate tracks from Grand Canyon National Park are preserved in the Coconino Sandstone and Hermit Shale. Most of these tracks were studied and described by Charles Gilmore of the Smithsonian Institution during the 1920s. A recent renaissance in the study of Permian tetrapod ichnofaunas in North America has resulted in a reevaluation of their ichnotaxonomy. A key to the identification of the Permian tracks from Grand Canyon has been developed utilizing the revised nomenclature.

INTRODUCTION

THE MOST significant early collections of Permian tracks to be described from North America came from Grand Canyon National Park. Charles Gilmore of the Smithsonian Institution described most of these footprints in a series of classic monographs (Gilmore, 1926, 1927, 1928). During the last five years there has been a renaissance of the study of Permian tracks that has led to a new understanding of the significance of the Grand Canyon specimens (e. g., Haubold, 1996). These studies have led to a reevaluation of the correct nomenclature for these tracks and of their true diversity (Hunt and Santucci, 1998). The purpose of this paper is to provide a brief identification key to the Permian tracks from the Grand Canyon utilizing the revised nomenclature. Lucas and Hunt (1998) provide a complimentary key to identifying some Permian tracks from New Mexico. Note that this key is only for Permian tracks (Coconino Sandstone and Hermit Shale) and should not be used for tracks from the Supai Group.

Hunt and Santucci (1998) recognize the following Permian footprint types from the Grand Canyon:

- Coconino Sandstone—*Chelichnus bucklandi*, *Chelichnus gigas*, *Chelichnus duncani*;
- Hermit Shale—*Batrachichnus delicatulus*, *Parabaropus coloradensis*, *Hyloidichnus bifurcatus*, *Gilmoreichnus hermitanus*, *Limnopus* sp., *Ichniotherium* sp.

IDENTIFICATION KEY

1. Four-toe impressions on hand print.

Yes - Go to 2.

No - Go to 3.

[Note that unusual preservation conditions may result in the preservation of less than the actual number of digit impressions. Be particularly wary of tracks that appear indistinct. If your specimen is from the Coconino and only has four apparent toe impressions you are probably dealing with a poorly preserved specimen of *Chelichnus* - see no. 4]

2. Foot print is less than 5 cm long.

Yes - *Batrachichnus delicatulus* (Figure 1A)

[This is the most common small track in the Hermit Shale and is widespread in redbeds of Permian age

throughout the world and represents a small amphibian]

No - *Limnopus* sp. (Figure 1B)

[This track is only known from one example from the Hermit Shale - see Hunt and Santucci (1998) and represents a larger amphibian]

3. Hand and foot prints are about the same size and have short toe impressions.

Yes - Go to 4

No - Go to 5

4. Foot print has a length of (Figure 1D).

1-1.5 cm - *Chelichnus bucklandi*

2.5-7.5 cm - *Chelichnus duncani*

7.5-150 cm - *Chelichnus gigas*

[These are the only three track species that you should find in the Coconino Sandstone. If you found these tracks in the Hermit Shale then you have probably made a mistake. *Chelichnus* tracks are locally very common in the Coconino and they display a tremendous range of preservational variants that can give very different looking footprints. These tracks may represent a herbivorous caseid reptile]

5. Foot print is greater than 50 cm long with wide toe impressions.

Yes - Go to 6

No - Go to 7

6. Footprints are placed almost in front of each other (narrow trackway) and the footprint has a very long heel impression relative to the hand.

Yes - *Parabaropus coloradensis* (Figure 1E)

[This is one of the largest tracks in the Hermit Shale and probably represents a primitive tetrapod such as a seymouriamorph or a diadectid]

No - *Ichniotherium* sp. (Figure 1C)

[This is a very rare Hermit Shale fossil, very common in Europe, that probably represents an edaphosaurian reptile]

7. Foot length is less than 50 cm with narrow toe impressions. Well developed heels and curved digit impressions.

Yes - *Gilmoreichnus hermitanus* (Figure 1F)

[This is most easily confused with *Hyloidichnus bifurcatus*. This track was made by a small

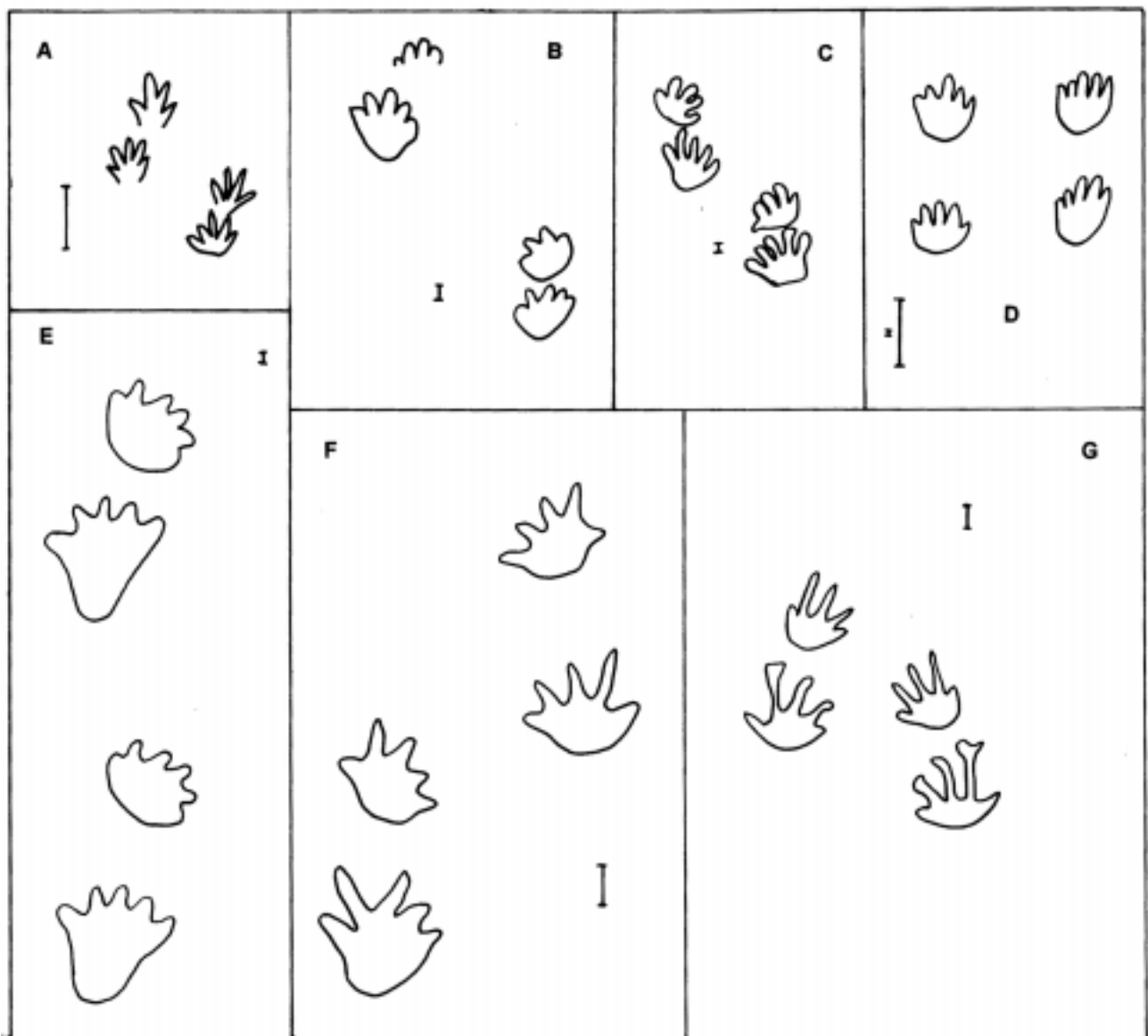


FIGURE 1—Types of animal footprints from the Permian of the Grand Canyon National Park. A, *Batrachichnus delicatulus*. B, *Limnopus* sp. C, *Ichniotherium* sp. D, *Chelichnus* spp. E, *Parabaropus coloradensis*. F, *Gilmoreichnus hermitanus*. G, *Hyloidichnus bifurcatus*. Scale bars are 1 cm. The two scale bars in D indicate the size range of this ichnogenus.

pelycosaurian reptile]

No - *Hyloidichnus bifurcatus* (Figure 1G)

[Some specimens have split tips to their toe impressions which is the result of a primitive way of walking, not toes that actually divide into two parts. This type of track was made by a seymouriamorph or a diadectid]

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INVENTORY OF PALEOZOIC FOSSILS IN CADES COVE, GREAT SMOKY MOUNTAINS NATIONAL PARK, TENNESSEE

JOHN E. REPETSKI

U.S. Geological Survey, MS 926A National Center, Reston, VA 20192;

ABSTRACT—Carbonate rocks of marine origin form the bedrock of Cades Cove, in the western part of Great Smoky Mountains National Park. Some of these limestones and dolostones contain fossils. All of the faunas known to date indicate a medial Early Ordovician age and correlation with the middle part of the upper Knox Group and with the Jonesboro Limestone in eastern Tennessee outside of the Park. An inventory of known Paleozoic fossils from Cades Cove is presented herein; the faunas include conodonts, brachiopods, mollusks, and trilobites.

INTRODUCTION

NEARLY ALL of the bedrock in Great Smoky Mountains National Park, North Carolina and Tennessee, is barren of fossils. However, the bedrock in Cades Cove, in the western part of the Park (Figure 1), consists chiefly of fossiliferous carbonate sedimentary rock of marine origin. These lower Paleozoic carbonate rocks, assigned to the Jonesboro Limestone of the Knox Group (Upper Cambrian and Lower Ordovician), contain the fossilized remains of several groups of marine animals. Fossils are common in these rocks; however, they are either small and easily overlooked or so small that they require a microscope for examination. The limestones and dolostones of Cades Cove have received very little paleontological study. Most of the previous collecting was related to earlier mapping in the Park and to studies related to regional geologic structure and Appalachian basin geologic history. Current geologic research in the Park includes additional paleontological studies in Cades Cove. This report is a preliminary summary of the fossils currently known from Cades Cove.

As with artifacts and living plants and animals, the fossils of this and all other National Parks can be collected only with formal permission from the appropriate Park Superintendent.

MICROFOSSILS

Conodonts are tiny (generally 0.1 to 1 mm), calcium phosphate, tooth-shaped microfossils that were the only hard parts of a group of extinct marine animals. These animals, also called conodonts, were common to abundant in most marine environments from the Late Cambrian through the Triassic Periods, that is from about 510 million to about 205 million years ago. Conodonts are known from five samples of the Jonesboro Limestone in Cades Cove.

Sample SOCC-25 [USGS fossil locality 10448-CO].—Collected by A.P. Schultz & R.C. Orndorff; locality published in Orndorff and others (1988). This sample, as well as SOCC-26 and SOCC-27, were processed and the faunas initially analyzed by Orndorff and A.G. Harris in USGS internal report (E & R) O&G-86-4; the faunas were re-analyzed for the present report.

FIGURE 1—Map showing the location of Cades Cove in the Great Smoky Mountains.

- Colaptoconus quadraplicatus* (Branson & Mehl) (Figure 2C–D)
- 3 quadraplicatiform elements
- 46 triplicatiform els.
- 29 *Drepanoistodus concavus* (Branson & Mehl)
- 6 *Eucharodus parallelus* (Branson & Mehl)
- 1 *E. toomeyi* (Ethington & Clark)
- 5 aff. *E. parallelus*
- 9 cf. *Laurentoscandodus triangularis* (Furnish) (Figure 2A)
- 16 *Macerodus diana*e Fahraeus & Nowlan (Figure 2A)
- Rossodus?* n. sp. (Figure 2B)
- 38 coniform elements
- 9 oistodontiform els.
- 1 “*Scolopodus*” *acontiodiformis* Repetski
- 5 “*S.*” *filosus* Ethington & Clark

FIGURE 2—Scanning electron microscope (SEM) photomicrographs of some representative conodont elements from Cades Cove, Great Smoky Mountains National Park, Tennessee. All are from USGS fossil collection locality 10448-CO. These specimens are repositied in the type collections of the Paleobiology Department, U.S. National Museum (USNM), Washington, D.C. 20560. A, cf. *Laurentoscandodus triangularis* (Furnish); inner lateral view of tall-based drepanodontiform element, X80, USNM 498189. B, *Rossodus*? new species; inner lateral view of oistodontiform element, X120, USNM 498190. C–D, *Colaptoconus quadraplicatus* (Branson and Mehl); posterolateral views of quadraplicatiform and triplicatiform elements, respectively, X150, USNM 498191 and 498192. E–G, *Striatodontus*? *prolificus* Ji and Barnes; posterolateral views, X150 (E, F) and X120 (G), USNM 498193–195. H, *Macerodus diana*e F&Ehrens and Nowlan; lateral view, X 160, USNM 498196.

- 88 *Striatodontus*? *prolificus* Ji & Barnes (Figure 2E–G)
- 1 *Ulrichodina abnormalis* (Branson & Mehl)
- 18 Genus & species undetermined
- 1 unassigned oistodontiform element
- 11 indeterminate coniform elements

Age.—Early Ordovician; early middle Ibexian; *Macerodus diana*e Zone.

Sample SOCC-26 [USGS foss. loc. no. 10449-CO].—Collected by A.P. Schultz & R.C. Orndorff; locality published in Orndorff and others (1988).

- 1 *Colaptoconus quadraplicatus* (Branson & Mehl) (Fig-

ure 2C–D)

- 1 *Striatodontus*? *prolificus* Ji & Barnes (Figure 2E–G)
- 1 indeterminate fragment

Age.—Early Ordovician; early middle Ibexian; “Low Diversity Interval” to *Macerodus diana*e Zone.

Sample SOCC-27 [USGS foss. loc. no. 10450-CO].—Collected by A.P. Schultz & R.C. Orndorff.

- 1 *Colaptoconus quadraplicatus* (Branson & Mehl); triplicatiform element
- 1 cf. *Eucharodus parallelus* (Branson & Mehl)
- 5 indeterminate fragments

Age.—Early Ordovician; middle or late Ibexian; “Low Diversity Interval” to *Reutterodus andinus* Zone.

Sample RBN-1941-1 [USGS fossil locality number 11493-CO].—Collected by R.B. Neuman, in 1941. Sample represents matrix from sample collected for macrofossils; processed by Repetski.

- Colaptoconus quadraplicatus* (Branson & Mehl)
- 6 quadraplicatiform elements
- 5 triplicatiform elements
- 4 *Drepanoistodus concavus* (Branson & Mehl); drepanodontiform els.
- 3 cf. *Eucharodus toomeyi* (Ethington & Clark)
- Rossodus*? aff. *R. manitouensis* Repetski & Ethington
- 1 coniform element
- 3 “*Scolopodus*” *filosus* Ethington & Clark
- 1 *Striatodontus*? *prolificus* Ji & Barnes
- 1 *Ulrichodina deflexa* Furnish
- 1 unassigned drepanodontiform element
- 2 unassigned scandodontiform els.

Age.—Early Ordovician; early middle Ibexian; *Macerodus diana*e to lower part of *Acodus deltatus*-*Oneotodus costatus* Zone.

Sample Cades Cove block 97-1 [USGS fossil locality number 11494-CO].—Collected by C.S. Southworth (USGS), 1997; sample was a block of silicified-brachiopod-rich lime wackestone. Sample was processed by Repetski in acetic acid as a single block to recover the brachiopods, as well as the acid-insoluble conodonts and possibly other microfossils. About one-third to one-half of the block was dissolved before neutralization of the acid bath, so that many of the brachiopods are partially exposed from the etched block. Conodonts are listed below.

- Colaptoconus quadraplicatus* (Branson & Mehl)
- 15 quadraplicatiform elements
- 24 triplicatiform elements
- 2 *Drepanodus* sp. cf. *D. arcuatus* Pander; drepanodontiform element
- 7 *Drepanoistodus* sp., aff. *D. concavus* (Branson & Mehl)
- 11 *Eucharodus parallelus* (Branson & Mehl)
- 2 *Eucharodus* sp.
- 2 *Eucharodus*? sp.
- 2 *Paroistodus*? n. sp.
- 4 *Scalpellodus*? sp.
- Utahconus*? n. sp.
- 9 coniform elements

ity 1 in Neuman, 1947). *Lecanospira* sp. (gastropod); ((locality 2 and at several other sites, presumably in several stratigraphic horizons, according to Neuman, 1947)

Trilobites.—*Hystericurus*(?) sp.; (locality 1 in Neuman, 1947)

The three species of brachiopod reported by Neuman (1947) are represented by approximately ten valves of each species. These are loose silicified specimens and are reposit in the collections of the Paleobiology Department of the U.S. National Museum of Natural History, Washington, D.C. They are small and extremely delicate. There is no record of any of the cephalopods or gastropods being reposit in the collections. According to Neuman's recollections (oral commun., 1997), some of the identifications of the mollusks were field identifications, with the specimens not collected. This is the case with the trilobite as well; apparently this record is based on one specimen exposed on a pinnacle of limestone, which was not collected.

Additional brachiopods were freed from the block (97-1) collected by Southworth (mentioned above in conodont section). Several dozen specimens were recovered in the acidizing process. These also are small and fragile; preservational quality varies widely. These specimens most likely represent the same species identified by Cooper for Neuman. More could be extracted rather routinely from the appropriately silicified horizon(s).

BIOSTRATIGRAPHY AND CORRELATION

The macro- and microfossils are consistent in indicating a lower middle Ibexian (Lower Ordovician) stratigraphic assignment for their host rocks. The fossils and rocks are totally consistent with their deposition on the carbonate continental shelf or ramp in tropical or semi-tropical latitudes on the Iapetus (proto-Atlantic) Ocean-facing edge of the Laurentian (including present North America) paleocontinent (Figure 3). The best correlation with Knox Group rocks in eastern Tennessee, which comprise shallower paleoenvironments on this part of the continental shelf, is with the uppermost part of the Chepultepec Dolomite, the Kingsport Formation, to the lower, probably lowermost, part of the Mascot Dolomite in sections west of the Saltville fault (e.g., see Repetski, 1985). This interval is approximately equivalent to that of the Longview-Kingsport interval of the Knox Group of older literature. To the northeast of the Great Smoky Mountains National Park, and in the eastern thrust belts of East Tennessee, the equivalent interval would be at some level in the Jonesboro Limestone. Systematically collected fossils from the Jonesboro are needed for precise correlation. Figure 4 shows the total possible stratigraphic ranges in the Ordovician of all of the fossil collections treated in this report.

ACKNOWLEDGEMENTS

A.P. Schultz and R.C. Orndorff provided helpful reviews of this manuscript, and D.J. Weary, USGS, kindly helped with the graphics. R.B. Neuman, USGS-Emeritus, discussed and helped locate his early macrofossil collections.

FIGURE 3—Paleogeographic reconstruction of North America for Early Ordovician time, showing relative location of Cades Cove.

- 4 scandodontiform els.
- 5 *Ulrichodina deflexa* Furnish
- 1 unassigned drepanodontiform element
- 1 Genus & species indeterminate
- 14 indeterminate coniform elements

Age.—Early Ordovician; early middle Ibexian; *Macerodus diana* to lower part of *Acodus deltatus*-*Oneotodus costatus* Zone.

MACROFOSSILS

Brachiopods are the most common of the known shelly macrofossils in the Jonesboro Limestone of Cades Cove, followed by rare mollusks (including gastropods and nautiloid cephalopods) and trilobites. Neuman (1947) collected the only known published macrofauna; the identifications were made by G.A. Cooper of the Smithsonian Institution, Washington, D.C.

Brachiopods.—*Diaphelasma pennsylvanicum* Ulrich & Cooper; (locality 1 in Neuman, 1947). *Finkelburgia virginica* Ulrich & Cooper; (locality 1 in Neuman, 1947). *Xenelasma syntrophoides* Ulrich & Cooper; (locality 3 and several other exposures perhaps of one bed, spottily exposed over about a mile, in Neuman, 1947).

Mollusks.—cf. *Orthoceras* (nautiloid cephalopod); (locality 2 in Neuman, 1947). *Hormotoma* sp. (gastropod); (local-

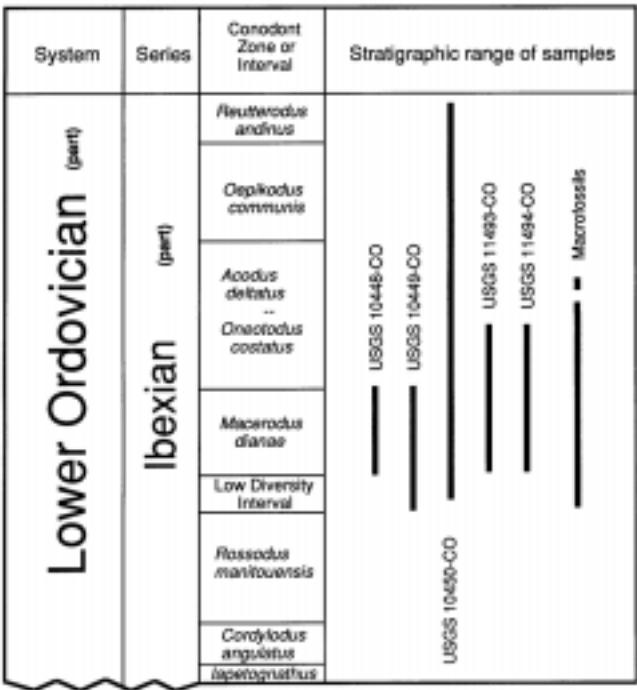


FIGURE 4—Diagram showing stratigraphic range in the Lower Ordovician of fossils known from Cades Cove.

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THE HAGERMAN HORSE QUARRY: DEATH AND DEPOSITION

DEAN R. RICHMOND AND H. GREGORY MCDONALD

Hagerman Fossil Beds National Monument, P.O. Box 570, Hagerman, ID 83332

ABSTRACT—Previous studies at the Hagerman Horse Quarry, Hagerman Fossil Beds National Monument, Twin Falls County, Idaho have focused on the remains of the horses and how they contribute towards our understanding of horse evolution and systematics. The context in which the horse remains have been preserved has not received as much attention. Recent work in the Horse Quarry by Hagerman Fossil Beds National Monument has been directed towards developing a better understanding the origin and taphonomy of this important concentration of horse fossils and how this site can aid in better understanding the paleoecology of the earliest species of *Equus*.

INTRODUCTION

THE MOST diverse Blancan vertebrate assemblage in North America has been collected from the Glenss Ferry Formation within Hagerman Fossil Beds National Monument. The Glenss Ferry Formation has also produced the single largest sample of the earliest species of *Equus*, *E. simplicidens* (MacFadden, 1992). Although horse is the dominant large species from the quarry (over 200 individuals of all ages); camel, mastodon, peccary and antelope have been recovered. A diverse microvertebrate fauna including fish, frog, turtle, snake, bird, rabbit, gopher, vole and shrew has also been found. Invertebrates recovered from the quarry include both gastropods and pelecypods.

There has previously only been a cursory examination of the causes for this large accumulation of horse remains and previous explanations for the large number of individuals has been based on minimal data. Hagerman Fossil Beds National Monument received a grant from Canon U.S.A. to conduct an excavation at the quarry to specifically collect data on the depositional environment. The study permitted a more complete understanding of this assemblage and its origin.

DISCUSSION

The Horse Quarry fossil assemblage was deposited within a fine-grained, poorly sorted sandstone bed that is lithostratigraphically in the lower portion of the Glenss Ferry Formation (Pliocene, Blancan). The quarry is located 9.5 meters below the unconformable contact with the overlying Pleistocene Tuana Gravel. Chronostratigraphically the Glenss Ferry Formation at Hagerman Fossil Beds ranges from about 3.7 to 3.0 mya. Magnetostratigraphy suggests that the quarry is younger than 3.4 mya and its position above the Shoestring Basalt places it younger than 3.2 mya. During excavation of the quarry a siliceous ash directly overlying the quarry sandstone bed was uncovered and is currently being dated using Ar-Ar techniques.

The fluvial system in which the fossil accumulation was deposited had a high width/depth ratio ($F=56.6$) and low sinuosity ($P=1.17$) indicating that the channel was a relatively straight bedload system. Lateral accretion sets resulting from point bar migration of a meandering fluvial system are not evident in the quarry. A longitudinal bar present in the

western portion of the 1997 excavation consists of a large accumulation of poorly sorted (1.95 phi) medium-grained (2.0 phi) sandstone, intraformational mudstone rip-up clasts and bones. The mean grain size for the quarry sandstone is fine (.25 - .125 mm). The sandstone is poorly sorted (mean of 1.47 phi) lithic arenite containing subangular grains larger than 2 mm in diameter with a few (>5 mm) pebble-sized grains.

Considering the .25 mm grain size and dune bedforms, the paleoflow velocity can be bracketed between 60 and 100 cm/sec. Flow depth was less than half a meter. Measurement of thirty trough cross-sets of the fluvial channel exposed during excavation of the quarry indicates a south-southwest (mean 226° azimuth) transport direction (Figure 1). The majority of bones are aligned transverse to fluid flow, supporting the sedimentological evidence for a low flow velocity and a shallow water depth. The channel sediments fine upward and represent a single waning flood event.

The historical Hagerman Horse Quarry consisted of three informal quarries: the original main quarry of the Smithsonian also known as the red sandstone quarry, the white sandstone quarry, and the green sandstone quarry. The Smithsonian red sandstone quarry, excavated in 1929, 1930 and 1931 yielded the highest percentage of excavated Smithsonian fossil material. The white and green sandstone quarries were excavated in 1934 by the Smithsonian and were enlarged by later excavations by the Los Angeles County Museum and Idaho Museum of Natural History. The location of the 1997 excavation was positioned to connect these separate quarries and determine their spatial relationships to each other. The red sandstone quarry is topographically lower than the other quarries and differences in elevation reflect the topography of the bottom of the paleochannel. The red sandstone quarry is interpreted to be a paleochannel that was infilled by sediment and bones during deposition of the overlying braided channel. At present, due to subsequent erosion, only a small portion of the red sand quarry sediments are exposed. The white sandstone quarry is well-cemented, intraformational rip-up conglomerate at the base of the braided channel. The green sandstone quarry consists of the overlying friable trough cross-bedded sandstone portion of the braided channel. The entire package of sediments represents a fining upward sequence deposited during a waning flood

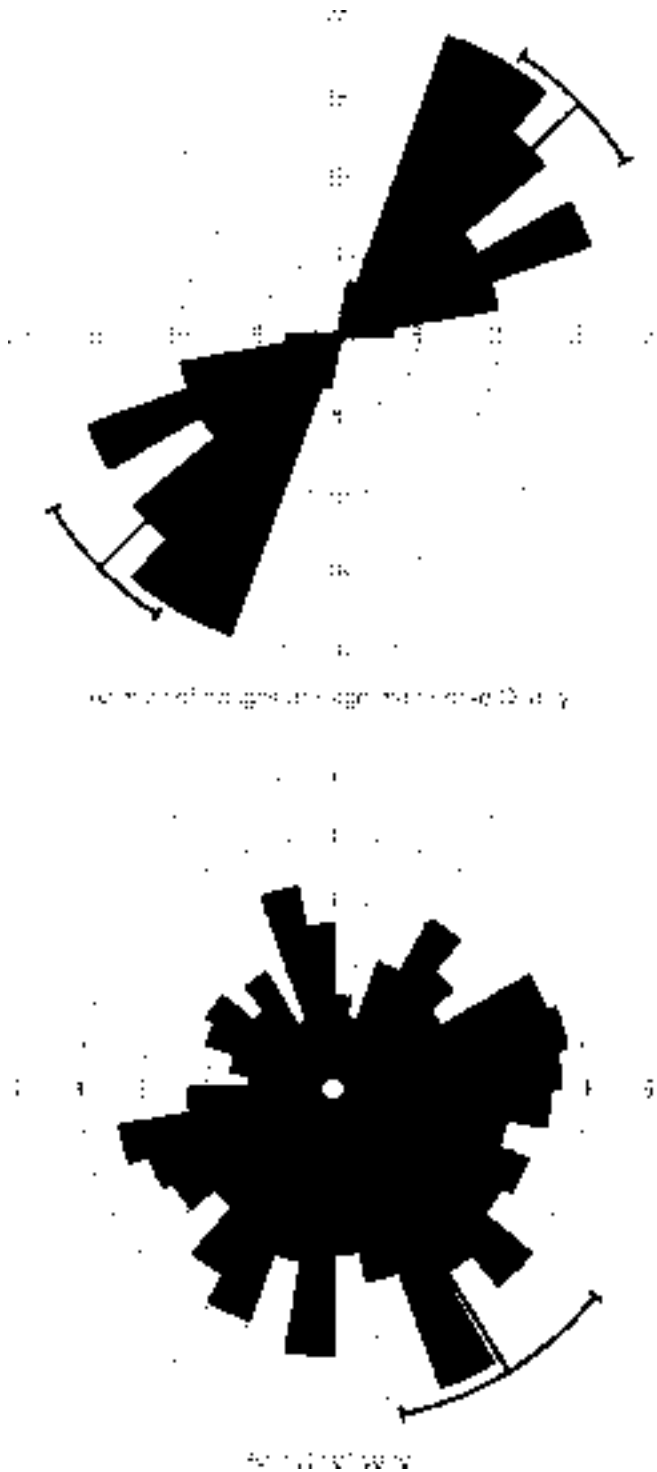


FIGURE 1—Rose diagrams showing azimuth of trough cross sets and of long bones of *Equus simplicidens* from the Hagerman Horse Quarry.

event. Bones were recovered from all three sedimentary packages during the 1997 field season.

CONCLUSIONS

Historical explanations for the large accumulation of horse bones have ranged from long term accumulation around a water hole (Gazin, 1936) to a single catastrophic accumulation during a flood event in a deep river (McDonald, 1996). As a result of our recent study of the quarry we interpret the accumulation, consisting of thousands of bones, to have resulted from a Phase II drought followed by a seasonal flash flood. The moderate drought resulted in the mass mortality of *Equus simplicidens* and other members of the fauna, including the microvertebrates in the area of what is now the Hagerman Horse Quarry. The horses and other animals were attracted to remnant water holes in low areas of the shallow river bed where they died of starvation and dehydration. This mass mortality produced a considerable accumulation of disarticulated horse remains of individuals of all ages (2-3 weeks old to > 20 years) scattered on the dry river bed. The lack of weathering on most bones indicates only a short interval of time of exposure prior to a short-lived flash flood that refilled the river channel and transported, entrained, deposited and buried the bones. No obvious modification of bones by scavengers has been observed suggesting that the surplus of carcasses minimized the need for scavengers to extract nourishment from the bones. Geologic and taphonomic characteristics suggest the bones traveled a very short distance prior to burial. A general inventory of bones indicates all three Voorhies Groups are present, indicating an autochthonous fossil concentration.

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CURRENT PALEONTOLOGICAL INVENTORY EFFORTS IN THE CAVES OF MAMMOTH CAVE NATIONAL PARK, KENTUCKY

RICKARD S. TOOMEY, III¹, MONA L. COLBURN¹, AND RICK OLSON²

¹Geology Section, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62702

²Division of Science and Resources Management, Mammoth Cave National Park
Mammoth Cave, KY 42259

ABSTRACT—Mammoth Cave National Park and the Illinois State Museum are cooperating on a three-year inventory of paleontological resources in selected park caves. The project focuses on paleontological resources associated with the sediments in the caves. The overall purpose of the project is to provide the park with information needed to properly manage its paleontological resources. The inventory will also provide important information needed to manage non-paleontological resources, because some of the resources provide information on cave conditions prior to intensive modification associated with tourist activities. The project involves detailed mapping and inventory of a variety of paleontological resources by personnel of the Illinois State Museum, Mammoth Cave National Park, and the Cave Research Foundation.

INTRODUCTION

IN LATE 1997 the Illinois State Museum (ISM) and the National Park Service entered into a cooperative agreement to begin an inventory of paleontological resources in caves within Mammoth Cave National Park. Field work under this three-year project has only been in progress for three months, so it is premature to begin discussing the results of the work. This paper will therefore focus on the goals of the project and the procedures being used to inventory paleontological remains within the park.

The goals of the Mammoth Cave National Park cave paleontological inventory are as follows:

- Identify paleontological resources within selected caves in the park.
- Determine the significance of the paleontological resources.
- Evaluate the present condition of paleontological resources.
- Map the location of paleontological resources and link them to cave resource databases and Geographic Information Systems currently in use and being developed at the park.
- Identify and evaluate current and potential factors (natural and management related) that will negatively impact paleontological resources within the park.
- Recommend actions that will prevent or mitigate the loss of paleontological resources or information caused by either natural or management-related activities.
- Use information from Holocene paleontological resources to provide information on cave environmental conditions before modification of the caves caused by historical use.
- Provide information for predictive modeling of the likelihood of significant paleontological resources for different types of caves or different areas of a single cave.
- Provide information on past use of some park caves by the Indiana bat (*Myotis sodalis*) and gray bat (*Myotis grisescens*), both of which are federally endangered.

- Provide information for reconstructing the past biota, environment, and climate of south-central Kentucky.
- Provide information on the paleontological resources of park caves to Division of Interpretation and Visitor Services personnel for use in programs.

Caves, including those found in Mammoth Cave National Park, provide access to two different classes of paleontological resources: autochthonous and allochthonous resources. Autochthonous resources are those remains associated with the original rock(s) in which the cave is formed and subsequently exposed for study by the processes of cave formation. Allochthonous resources are those remains that are deposited in the cave after the cave has formed. This type of resource includes the remains (and trace fossils) of plants and animals that either entered the cave or were deposited in the cave after death. Allochthonous resources include bones and mummified remains of animals that frequented the cave, scat of those animals (including guano, paleofeces, and coprolites), scratches and staining on cave walls and ceilings from animal activities, footprints, and remains of plants and animals that either washed in, fell in, or were brought into the cave as food items or nesting material by other animals. Although the park's caves have significant allochthonous and autochthonous paleontological resources, the current inventory focuses on their allochthonous resources. However, when unusual autochthonous fossils are encountered, they are noted for later study.

The caves of Mammoth Cave National Park are extremely variable in many ways, including extent, entrance and passage types, ecology, and history. Even within a single cave these factors vary in important ways. For example, the cave for which the park is named, Mammoth Cave, is part of the largest cave system in the world, containing over 350 miles of passages. Some of the passages are large (tens of feet wide and high); others are very small with heights and/or widths of less than one foot. Some passages are readily accessible from current or past entrances; others are several miles from known entrances. Some passages have been visited by millions of people in the past 200 years the cave; others have been entered by only three or four people. Some portions of the cave

were utilized by Native Americans approximately 2000 years ago and contain prehistoric archeological resources intermingled with paleontological resources. All of these factors contribute to differences in the paleontological resources between caves or between different areas within the same cave (or cave system). These differences in both the potential for and the type of paleontological resources are a key reason it is important to inventory these caves in detail.

Previous work clearly indicates that the caves in the park contain significant paleontological resources. Published records include an important Pleistocene bat guano deposit (Davies and Chao, 1959; Jegla and Hall, 1962; Rubin and Alexander, 1960), notable deposits of extinct Pleistocene megafauna (Wilson, 1981, 1985), and deposits of bones of recent bats (Jegla, 1963). In addition to these published records, files of the Cave Research Foundation (CRF), discussions with CRF personnel, and NPS files at the park all indicate that caves in the park contain significant paleontological materials that have not been adequately located, inventoried, and evaluated. The current project is the beginning of our attempt to address this situation.

In the current inventory, personnel from the ISM and Mammoth Cave National Park are being assisted by personnel from the CRF, which has been working with Mammoth Cave National Park for the past forty years. CRF is actively engaged in many avenues of research within the caves of the park including mapping the Mammoth Cave System; identifying, mapping and inventorying smaller caves in the park; and performing on-going biological, hydrological, geological, and archeological investigations of many of the park's caves. CRF personnel are assisting the paleontological inventory effort in many ways. Some are participating on crews that are locating resources. Others have provided important information on paleontological resources and the potential for resources in remote portions of the Mammoth Cave System and other park caves that ISM and NPS personnel had not yet visited. CRF personnel also act as guides and caving advisors to assist project personnel in reaching areas with paleontological materials (especially remote areas) and in mapping resources in those areas. In addition, CRF personnel are producing and providing the base maps and working maps onto which the paleontological remains are plotted. In some areas CRF crews are specifically surveying and mapping areas in conjunction with the paleontology inventory project. This is especially important in areas where previous maps do not exist or in areas where existing maps are inadequate to represent the resources. CRF is also working with the park on the development of the cave GIS and resource databases.

The current cooperative paleontological inventory will be accomplished in several phases. The first phase is examining the portions of the cave between the Historic Entrance and Violet City Entrance of Mammoth Cave. The paleontological inventory of this area is the highest priority portion of the inventory for several reasons. This area has been the focus of saltpetre mining and tourist activity in the cave during the past 200 years; it continues to be the focus of tourist activities today. Cave management associated with tourist activities can

impact paleontological resources. Significant paleontological resources have been previously identified in this area of the cave (Davies and Chao, 1959; Jegla and Hall, 1962; Rubin and Alexander, 1960). Remains from this area provide important information about the ecosystem of the Historic area of Mammoth Cave prior to the last 200 years of human modification of the cave. Information on the pre-historic cave ecosystem will help support cave management decisions that are designed to mitigate the effects of 200 years of intensive human modifications. The later phases of the project will focus on the past and present bat roosts in park caves and on a variety of more remote sites with known or suspected paleontological resources.

The paleontological inventory is being accomplished as follows. First, trained personnel of the ISM, NPS, and CRF carefully examine an area of cave and mark all potential paleontological materials with pin flags or flagging tape. Following this flagging, ISM paleontologists revisit each location and identify the resources at each flag. The material is recorded on data sheets, and remains are photographed with a digital camera. The location of each point is recorded in at least one of several ways. Where possible the points are plotted on maps of the cave produced by CRF. If maps have not yet been produced, points are recorded on the preliminary survey sketch made during the CRF mapping of the cave. Where convenient the points are also mapped using a total station theodolite. Information from the data sheets is entered into several databases, including a location, collection, and photographic database that are compatible with NPS software. Limited numbers of specimens are being collected as either vouchers for identifications or for age-dating. Management concerns that might impact the remains are also noted.

Because the Mammoth Cave System contains over 350 miles of passages and because the park contains numerous other caves (several over one mile in length), this three-year paleontological inventory will only serve as a beginning point for paleontology at Mammoth Cave National Park. The inventory will identify threats to paleontological resources, so that the impact of those threats can be avoided or mitigated, provide information to assist park personnel in making cave management decisions, and identify paleontological resources that should receive further study. In addition, it will provide information important in guiding further inventory efforts in the caves of the park.

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PERMIAN ROOT TRACES FROM NATURAL BRIDGES NATIONAL MONUMENT

SHAWN DUFFY

Natural Bridges National Monument, Box 1, Lake Powell, UT 84533

ABSTRACT—Original interpretations of the Cedar Mesa Member of the Cutler Formation in and adjacent to Natural Bridges National Monument in southeastern Utah concluded it to be a near shore marine deposit (Barrs, 1972, 1989). Other studies concluded an aeolian origin (Stanescu & Campbell, 1989). The recent discovery of *in situ* root traces in the Cedar Mesa Member provide supporting evidence for the latter interpretation.

INTRODUCTION

THE CEDAR Mesa Member of the Cutler Formation in southeastern Utah dominates the canyons in and adjacent to Natural Bridges National Monument. Primarily composed of white sandstone with pink arkosic shale and limestone lenses, the member displays strong cross bedding suggesting an aeolian origin. Because of the presence of fragmentary marine creatures within the sandstone, other interpretations concluded a marine origin (Barrs, 1972, 1989). This latter interpretation does not fully take into account the abundant root casts and traces found throughout the member. Originally, the casts and traces were believed to have been transported to their present position from regional streams, however, the orientation of the roots suggest an insitu origin.

THE ROOTS

The roots occur as casts, molds, and traces staining the surrounding host rock. Most roots are an average of 2.5 to 5 centimeters thick and roughly 30 centimeters long. Several roots were discovered to be over 3 meters in length and exhibit a branching or radiating pattern which suggest connecting either to each other or to a centralized point like a tree trunk. The sandstone within the Cedar Mesa Member is primarily white, however, most localities in which the roots occur display strong pink and brown mottled patterns suggesting a paleosol (Stanescu & Campbell, 1989).

During the spring of 1997, a site was discovered in Natural Bridges National Monument in which the root casts were over 2 meters in length (Figure 1). The most interesting feature about the site was the fact that the roots did not follow the bedding planes within the sandstone as in most sites, but rather cut across the bedding planes. This pattern suggest

FIGURE 1—Detail of rootsite. Only the larger roots are of Permian age. The smaller roots appear to be calcification of recent roots.

that the roots were growing down through the sand before lithification. Along with the larger roots were masses of smaller intertwining roots covering the sandstone surface. It has been determined thus far that these smaller roots are not connected to the larger ones and most likely represent recent calcification of park flora.

CONCLUSION

Taken as a whole, the random orientation, definite spacing, and the cutting across of bedding planes along with the association of mottled patterns strongly suggest that we are dealing with an insitu origin for the roots. This in turn supports the interpretation that the Cedar Mesa Member of the

Cutler Formation represents a series of terrestrial dunes containing islands of vegetation similar to today's coastal sabkhas.

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CONODONTS AND BIOSTRATIGRAPHY OF THE LOWER ORDOVICIAN ROUBIDOUX FORMATION IN AND NEAR THE OZARK NATIONAL SCENIC RIVERWAYS, SOUTHEASTERN MISSOURI

JOHN E. REPETSKI¹, JAMES D. LOCH², AND RAYMOND L. ETHINGTON³

¹U.S. Geological Survey, MS 926A National Center, Reston, VA 20192;

²Earth Sciences Department, Central Missouri State University, Warrensburg, MO 64093; and

³Geological Sciences Department, University of Missouri-Columbia, Columbia, MO 65211

ABSTRACT—Conodonts from exposures in and near the Ozark National Scenic Riverways, southeastern Missouri, clarify the biostratigraphic setting of the Lower Ordovician Roubidoux Formation. The underlying Gasconade Dolomite ranges from at least as low as the *Rossodus manitouensis* Zone in its lower and middle parts to the "Low Diversity Interval" in its upper member. Conodonts of the "Low Diversity Interval" continue through the lower part of the Roubidoux. *Macrodus diana* Zone conodonts appear approximately one-third to halfway through the Roubidoux and the biozone is represented through most or all of the remainder of the formation. Faunas characteristic of the *Aodus deltatus* - *Oneotodus costatus* Zone first occur either in the uppermost part of the Roubidoux or in the lowermost part of the overlying Jefferson City Dolomite.

INTRODUCTION

THE OZARK Plateau region (Figure 1), comprising basically that part of Missouri south of the Missouri River and the part of Arkansas north of the Buffalo and White Rivers, contains one of the largest areas of exposed Lower Ordovician, or Ibexian Series, rocks in the United States. Due to its inboard location on the trailing margin of Laurentia, in tropical to subtropical latitudes during that time of deposition, this area accumulated chiefly shallow-marine carbonate sediments. Most of this section is now dolostone, much of it primary or early diagenetic. However, much of it also is coarsely-grained dolostone, often chert-rich, reflecting one or more periods of subsequent diagenetic episodes, such as the periods of massive diagenesis related to subsurface hydrothermal fluids that moved through the section in the Pennsylvanian and Permian associated with the Ouachita orogeny (e.g., see Leach and Rowan, 1986; Leach and others, 1997).

The section also contains many sandstones; nearly all are quartz sands, and most of them probably are multiply-re-worked, as the region was hundreds of miles from the low-

FIGURE 1—Map showing location of Ozark National Scenic Riverways and the watershed areas of the Current and Jacks Fork Rivers in southeastern Missouri. Triangle indicates location of Jacks Fork crossing section.

Figure 2—Scanning electron microscope (SEM) photomicrographs of some representative conodont elements from the Gasconade, Roubidoux, and Jefferson City formations in southeastern Missouri. Illustrated specimens are repositied in the type collections of the Paleobiology Department, U.S. National Museum (USNM), Washington, D.C. 20560. A–B, *Juanognathus? felicitii* (Ji and Barnes); posterolateral views of two specimens from sample RC-149 at Roubidoux Creek section, X 85, USNM 498496 and 498497. C, *Drepanodus* sp., inner lateral view of drepanodontiform element, from sample RC-149, Roubidoux Creek section, X 85, USNM 498498. D–E, *Colaptoconus quadraplicatus* (Branson and Mehl); posterolateral (D) and lateral (E) views of triplicatiform and quadraplicatiform elements, respectively; D, from sample JF-H, Jacks Fork section, X 110, USNM 498499; E, from sample JC-J, lower part of Jefferson City Dolomite at Jim's Creek section, X 64, USNM 498500. F, cf. *Colaptoconus quadraplicatus* (Branson and Mehl); shallowly grooved specimen, from sample JF-J at Jacks Fork section, X 90, USNM 498501. G, *Ulrichodina deflexa* Furnish; posterolateral view of immature(?) specimen from lower part of Jefferson City Dolomite at Jim's Creek section, sample JC-J, X 110, USNM 498502. H, *Paroistodus? sp.*; inner lateral view of scandodontiform element, same sample and location as G, X 110, USNM 498503. I–L, *Histiodela donnae* Repetski; posterior views of blade-like elements (I, K, L) and inner lateral view of coniform element (J), from samples JF-H (K) and JF-J (I, K, L) at Jacks Fork section, I and J -X 90, K -X 170, L -X 110, USNM 498504–507. M, *Laurentoscandodus? n. sp.*; inner posterolateral view of short-based element, from sample JF-J at Jacks Fork section, X 70, USNM 498508. N, *Drepanoistodus* sp.; inner lateral view of drepanodontiform element, from sample JF-J at Jacks Fork section, X 90, USNM 498509. O, *Juanognathus? n. sp.*; posterior view of nearly symmetrical element, from sample JF-J at Jacks Fork section, X 90, USNM 498510. P–Q, *Striatodontus? prolificus* Ji and Barnes; posterolateral

views, P from sample JF-J at Jacks Fork section, X 90; Q from upper part of Gasconade Dolomite (sample RC-02) at Roubidoux Creek section, X 95, USNM 498511 and 498512. R-S, *Oneotodus* aff. *O. simplex* (Furnish); posterior and lateral views of two specimens from lower part of upper Gasconade Dol. at Phillips Quarry, Bartlett 7-1/2 minute quadrangle, Shannon Co., MO, X 65, USNM 498513 and 498514. T, *Chosonodina herfurthi* Müller; posterior view of specimen from upper part of middle Gasconade Dol. at Phillips Quarry, X 75, USNM 498515. U, *Rossodus manitouensis* Repetski and Ethington; inner lateral view of coniform element; same sample as T, X 50, USNM 498516. V, *Loxodus bransoni* Furnish; inner lateral view; specimen broke during preparation; from upper part of middle Gasconade Dol. at a section near Rolla, MO, X 45, USNM 498517. W, *Acanthodus uncinatus* Furnish; lateral view of non-serrate subrectiform element, from same sample as T, X 50, USNM 498518. X, *Variabiloconus bassleri* (Furnish); inner lateral view, X 60, same sample as T, USNM 498519. Y, *Oneotodus simplex* (Furnish); lateral view, X 75, USNM 498520. Z, *Scolopodus sulcatus* Furnish; inner lateral view of scandodontiform element, X 75, same sample as T, USNM 498521.

lying exposed sources of Precambrian and Cambrian rocks in the upper Midwest. Most of these Ozarks sands are thin lenses, stringers, and channels, with only local lateral extent, but some horizons or intervals contain apparently laterally-persistent sands that have been used for both subdividing the section into formations and for local and long-distance correlations. Numerous hills and pinnacles of Precambrian volcanic rocks of the St. Francois Mountains complex apparently were emergent periodically during the Late Cambrian and Early Ordovician, and these certainly affected the local sediment distribution patterns. However, these Ozarks volcanics did not contribute significant volumes of sand to the Ibexian units. Some of the sand intervals have been incorporated into sequence stratigraphic schemes of various scales, but without rigorous control of their positions in a stratigraphic framework. Our work on conodonts (Figure 2) and trilobites in the Ibexian of the Ozarks is only in its early stages, but we are able to make some refinements in the age control in some of the stratigraphic marker horizons.

Very little biostratigraphic control exists for this succession of rock, especially considering its areal extent. The depositional environments for most of the units were probably somewhat hypersaline and with restricted circulation, and were not conducive for development of diverse faunas. In addition, the pervasive secondary dolomitization wiped out much of the original shelly record. Most of the macrofauna known from the Ibexian of the Ozarks is preserved in chert. Presumably, local replacement of the carbonate rocks by secondary chert took place before pervasive dolomitization had destroyed the invertebrates, as must have happened where chert did not form. Because much of the record is from chert float blocks, precise occurrence and stratigraphic range data are seriously lacking. Mollusks are the most abundant and diverse of these macrofossils; trilobites are known from relatively few intervals. Most of these faunas were described in a very few works, in the 1930's to 1950's (e.g., Bridge, 1930; Heller, 1954). This study is part of a cooperative U.S. Geological Survey-National Park Service project of bedrock mapping in the Ozarks of Missouri.

The Ozark National Scenic Riverways is a National Park Service unit along the Current and Jacks Fork Rivers (Figure 1). Large tracts in the Ozarks are part of the Mark Twain National Forest. Fort Leonard Wood, a major U.S. Army reservation, is nearby. Associated with these public lands, and the region as a whole, are a variety of land-use issues for which accurate geologic maps are vital. This is a world-famous karst region, with vast cave systems, thousands of sinkholes and springs, and all the hydrogeological problems associated with those regions. This region also is host to the world's largest known lead deposits, hosted mainly in Upper Cambrian carbonate rocks. Lead sulfide exploration is continuing, and accurate knowledge of the geologic framework is needed, especially as it pertains to the public lands tracts, for the permitting process.

From a few preliminary studies (Kurtz, 1981) conodonts were known to occur, at least sparsely, in some of the formations of the Ozarks. We therefore began a systematic examination of these dolostones, involving sampling of key mea-

sured sections for conodonts as well as other fossils, to try to establish a refined biostratigraphic framework that can be applied to the mapping and other studies in these units and to better correlate the Ozark succession with other regions.

The Ibexian section in the south-central Missouri Ozarks is up to more than a thousand feet thick. The units are, in ascending order: the Eminence Dolomite, only the upper part of which is Ibexian; the Gasconade Dolomite, about 300 feet thick; the Roubidoux Formation, 100 to 300 feet thick; Jefferson City Dolomite, 125 to 350 feet thick; and the Cotter/Powell formations, about 100 to more than 300 feet thick (Thompson, 1991). Because of mapping needs, we began our biostratigraphic work with the Roubidoux Formation, including its position relative to the underlying Gasconade Dolomite and to the lower part of the overlying Jefferson City Dolomite.

We located and measured several sections of the Roubidoux, including the type section, and concentrated on sections which contain formational boundaries and other marker horizons. For this work we collect and process samples of 4- to 6-kilograms from the estimated best lithologies, and concentrate on bracketing these boundaries and markers. The large samples have proven necessary, as our productive samples average only a few conodont elements per kg. A fine sieve size also is necessary; we use a 200-mesh bottom sieve. In most samples there are few accessory minerals in the heavy residues; following magnetic separation, the heavy residue is almost exclusively snowy-white diagenetic dolomite rhombs. The color alteration index (CAI) of the conodonts is 1 to 1-1/2, indicating only low levels of long-term post-burial heating, in the range of less than 50° to about 90° C. Preservation of the conodont elements tends to be quite good.

As with artifacts and living plants and animals, the fossils of this and all other National Parks can be collected only with formal permission from the appropriate Park Superintendent.

GASCONADE DOLOMITE

Previously, Kurtz (1981) showed, from a few samples near Camdenton, MO, some tens of miles north-northwest of our study area, that the lower part of the Gasconade Dolomite is lower Ibexian, rather than Upper Cambrian as earlier studies and maps had assumed. Our initial sampling from the middle Gasconade near Rolla, MO (Repetski and others, 1993; Repetski and others, in press) yielded species typical of the *Rossodus manitouensis* Zone, including the diagnostic species *Loxodus bransoni* (Figure 2:V) Furnish, *Scolopodus sulcatus* (Figure 2:Z), and *R. manitouensis* itself (Figure 2:U). Subsequently we have sampled several additional sections that expose the upper part of the Gasconade.

Somewhat surprising was finding that the uppermost Gasconade has the fauna of the so-called "Low Diversity Interval" of Ethington and Clark (1981). This interval, characterized by presence of only a few coniform taxa of rather simple morphologies, mostly assignable to species of *Oneotodus*, *Teridontus*, *Striatodontus*?, and *Eucharodus* (e.g., Figure 2:P-S), follows the abrupt disappearance of most of the taxa of the

FIGURE 3—Top surface of a large chert float block from middle part of the Roubidoux Formation, preserving molds of the gastropod *Lecanospira*. This moldic mode of preservation is typical for mollusks found in the Roubidoux. Block collected in steep slope immediately east of Pike Creek; SW 1/4 of section 22, T. 27N., R. 3W., Low Wassie 7-1/2 minute quadrangle, Shannon Co., MO; USGS fossil locality number 11527-CO; USNM 498495. Scale bar is 2 inches long.

subjacent *R. manitouensis* Zone. This abrupt faunal changeover was documented by Ethington, Engel, and Elliott (1987) to occur almost precisely at the Mackenzie Hill - Cool Creek formation contact in Oklahoma, and similarly at the House - Fillmore formation boundary in Utah. Recently, Ji and Barnes (1993) also discussed this same turnover within the Boat Harbour Formation of the St. George Group of western Newfoundland, Canada. What surprised us is that this faunal changeover in the Ozarks does not coincide with the Gasconade - Roubidoux contact, which is recognized at a regionally significant influx of sand, but it occurs somewhat lower, at a level near or at the boundary between the cherty middle part and the non-cherty upper part of the Gasconade.

The rather diverse fauna that is typical for the *R. manitouensis* Zone occurs, in low numbers of specimens per kg of rock, beginning low in the Gasconade (Kurtz, 1981). It contains mostly shallow-water Laurentian species such as *Loxodus bransoni*, *Scolopodus sulcatus*, and *Variabiloconus bassleri* (Figure 2:V,Z,X). Uncommonly, cosmopolitan species such as *Chosonodina herfurthi* (Figure 2:T) also occur in this part of the Gasconade.

The uppermost member of the Gasconade contains mostly morphologically "simple" coniform elements of species simi-

lar to, and presumed related to, *Oneotodus simplex* (Figure 2:Y), which occurs in the underlying *R. manitouensis* Zone. The most significant appearance in this interval is that of *Striatodontus? prolificus* Ji and Barnes (Figure 2:P,Q), which continues upward as one of the numerically dominant species of the Roubidoux Formation.

ROUBIDOUX FORMATION

The Roubidoux Formation is separated from the Gasconade by its higher content of quartz sand, including numerous sandstone beds especially in the upper half, and generally thinner bedding (see Thompson, 1991, for history of nomenclature and usage). The quartz sand content also serves to distinguish the Roubidoux from the overlying Jefferson City Dolomite. Partly because of the increased permeability due to the sandstones and partly due to the thin- to medium-bedded nature of its carbonate beds, the Roubidoux weathers back rapidly and the resulting slopes are characterized by loose blocks of sandstone. Chert float blocks from the middle part of the formation are common in some areas; sometimes they preserve the molds of gastropods (Figure 3), nautiloid cephalopods, and, rarely, of trilobites. Significant exposed thicknesses of the Roubidoux are extremely rare, leading to difficulties in studying the actual succession of rocks and fossils within the formation, and thereby hindering attempts to biostratigraphically subdivide the unit.

The designated type section of the Roubidoux (Heller, 1954) is a cut-bank cliff along Roubidoux Creek, Texas County, MO. It affords reasonably good exposure of the entire formation, including both lower and upper contacts. Conodont samples from the Roubidoux type section confirm again that the Low Diversity Interval begins well below the base of the Roubidoux (Figure 4). We can document here that the base of the next biozone, the *Macerodus diana* Zone, falls in the lower part of the middle Roubidoux, indicated by the appearance of *Histiodellella donna* (Figure 2I-L) and *Ulrichodina* n. sp. 1 of Repetski (1982). The few samples near the top were not diagnostic of a zonal call near the base of the Jefferson City.

Figure 4 also shows the distribution of conodonts and some trilobites that we collected from Heller's (1954) section at Ava, Douglas Co., approximately 50 miles west of the National Park. This section does not expose either base or top of the Roubidoux, but it preserves the interval from the Low Diversity Interval to the *M. diana* Zone and it allows some calibration of the conodont and trilobite ranges for this region.

JACKS FORK CROSSING SECTION

We sampled another section that exposes most of the Roubidoux and more than 50 feet of the upper Gasconade, where Highway 17 crosses the Jacks Fork River, within the boundary of the Ozark National Scenic Riverways. From the level of the river below the bridge to approximately the level of the highway at the north end of the bridge, the thick-bedded dolomite of the uppermost part of the Gasconade forms a cliffy exposure. The Roubidoux drops back in profile because of weathering of the sandy dolostone beds. The sandstone beds

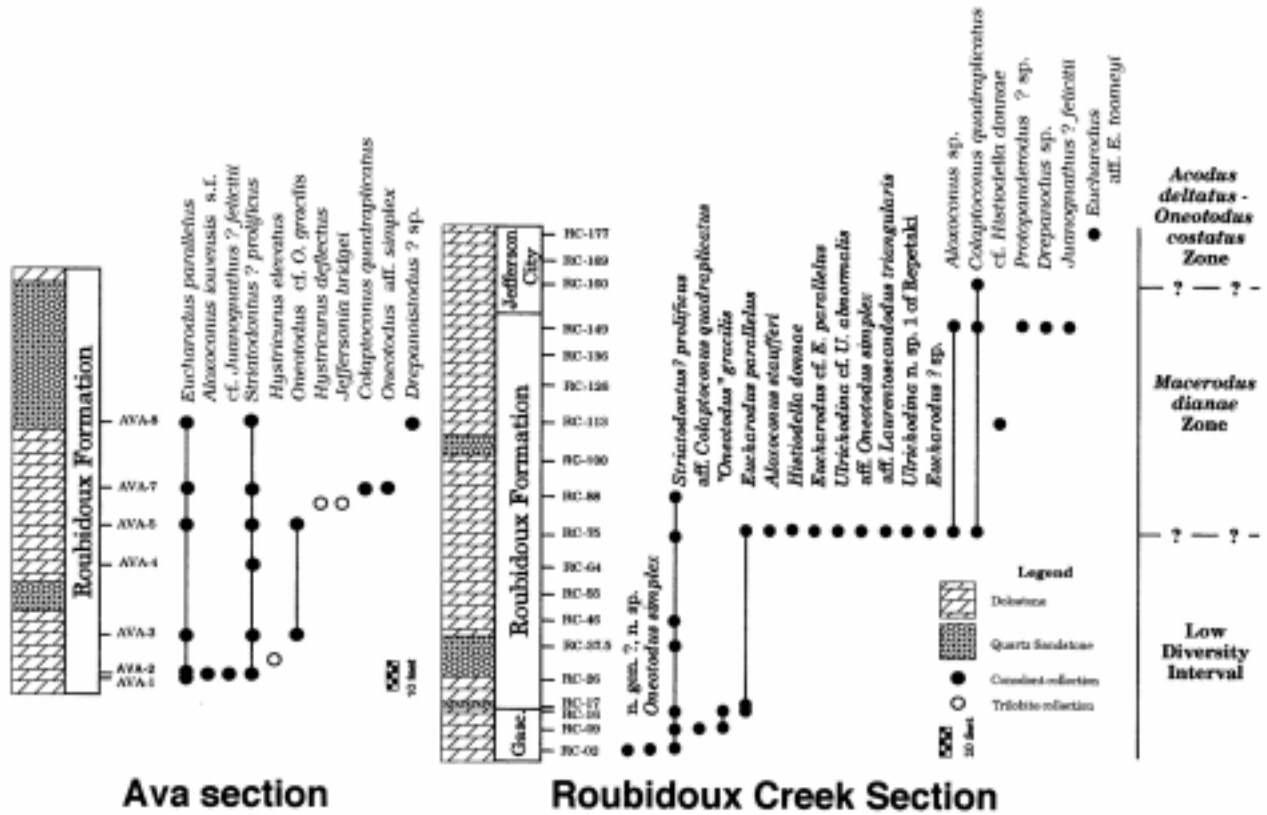


FIGURE 4—Conodont and trilobite faunal distribution charts for the Ava and Roubidoux Creek sections.

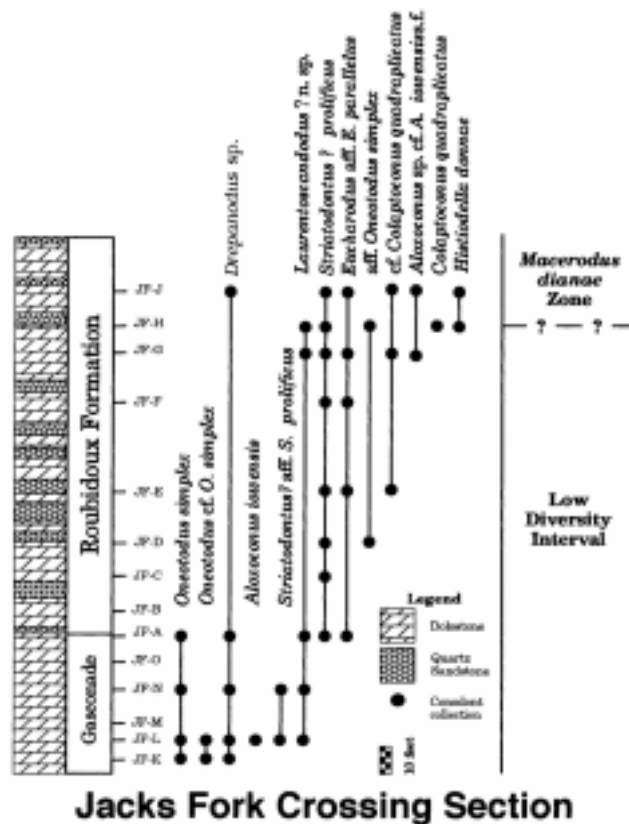


FIGURE 5.—Conodont faunal distribution chart for the section at Jacks Fork crossing section.

ORDOVICIAN SYSTEM (part)	IBEXIAN SERIES	<i>Reutterodus andinus</i>
		<i>Oepihodus communis</i>
		<i>Acodus deltatus - Oneotodus costatus</i>
		<i>Macerodus dianae</i>
		"Low Diversity Interval"
		<i>Rossodus manitouensis</i>
		<i>Cordylodus angulatus - lapetognathus</i> n. sp.
		<i>Cordylodus lindstromi - Cordylodus intermedius</i>
		<i>Cordylodus proavus</i>

ROUBIDOUX CONODONTS

FIGURE 6—Conodont zonation for the Ibexian Series (Lower Ordovician) of the North American Midcontinent faunal realm, following Ross and others (1997), and showing the biostratigraphic range of conodonts recovered from the Roubidoux Formation in southeastern Missouri.

tend to stand out and they become more prominent higher in the section. This section was described in detail by Muilenberg and Beveridge (1954), and their section description is repeated in Thompson (1991)

Figure 5 shows the conodont distribution for the Jacks Fork crossing section. A little more than 100 feet of the Roubidoux is exposed here; we estimate that about 50 feet is covered above. All of the exposed Gasconade is in the "Low Diversity Interval." *Histiodelpha donnae* (Figure 2:I-L), and probably also *Ulrichodina* n. sp. 1 of Repetski (1982), appearing in the middle Roubidoux marks the *Macerodus diana* Zone. It is clear now that the widespread influx of sand marking the base of the Roubidoux does not coincide with any notable change in the conodont fauna. However, the thicker and more prominent sandstone beds that begin in the middle part of the Roubidoux do grossly coincide with the base of the *M. diana* Zone within the current resolution of our faunal control.

Lithologic and biostratigraphic relations at the boundary between the Roubidoux and overlying Jefferson City Dolomite are difficult to assess because that contact is so rarely exposed. For mapping purposes, that contact is usually drawn at 25 to 35 feet below the base of the "Quarry Ledge" of the Jefferson City, a 12- to 15-foot thick widespread marker bed that is more often exposed than the beds beneath it, due to its characteristic thick to massive bedding.

The Quarry Ledge also is significant because its top and immediately overlying beds have produced most of the trilobites known from the lower Jefferson City. We sampled a short section in the lower part of the Jefferson City Dolomite near Vichy, MO, about 40 miles north of the National Park, that yielded both trilobites and conodonts. This interval not only yielded a number of trilobite taxa, essentially marking the Jeffersonian Stage assemblage, but the conodonts allow recognition of the *Acodus deltatus* - *Oneotodus costatus* Biozone at this level, from the appearance of *Ulrichodina deflexa* (Figure 2:G) and *Eucharodus toomeyi*.

Another of our Jefferson City sections, Jim's Creek, yields conodont data that suggest that the boundary between the *Macerodus diana* Zone and the *Acodus deltatus*-*Oneotodus costatus* Zone may well fall near or at the base of the "Quarry Ledge."

CONCLUSIONS

Even though much more work remains to be done in refining the Ibexian framework for the Ozark region, the work thus far shows that the conodonts, especially, are both present and biostratigraphically useful in these strata. They are already allowing a firming up of some of the formational and marker bed age constraints. Figure 6 represents our latest age assignment for the Roubidoux Formation against the current Ibexian conodont biozonal framework for the North American Midcontinent faunal realm (Ross *et al.*, 1997).

On a broader scale, some recent sequence stratigraphic interpretations within this interval have been made assuming age-equivalency for certain levels essentially based only on physical stratigraphic grounds. For example, some workers

have correlated the coeval stratigraphic break at the House-Fillmore contact in Utah and the McKenzie Hill-Cool Creek in Oklahoma with the base of the Rockdale Run Formation and Nittany Dolomite in the central Appalachians (Goldhammer and others, 1993). Conodonts show that the Stonehenge-Rockdale Run and Stonehenge-Nittany contacts in Maryland and central Pennsylvania, respectively, occur within the *Rossodus manitouensis* Zone, and thus are demonstrably older than either the base of the Roubidoux, base of the Fillmore, or base of the Cool Creek. Likewise, the fossils demonstrate that the influx of sand at the base of the Roubidoux is younger than the House-Fillmore and McKenzie Hill-Cool Creek contacts. Biostratigraphy can be a powerful ally to sequence stratigraphers; certainly it should not be ignored.

Ongoing and planned paleontological work in the Ozark National Scenic Riverways includes: 1) continued biostratigraphic support for the geologic mapping efforts; 2) refinement of the placement of the individual biozonal bases within the Ibexian formations relative to formation contacts and other marker beds or intervals; 3) testing of the lateral continuity, i.e., the reliability to mapping, of these marker beds; and 4) documentation of the fossil successions through the other formations in this region.

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RESEARCH UPDATE ON HYMENOPTERAN NESTS AND COCOONS, UPPER TRIASSIC CHINLE FORMATION, PETRIFIED FOREST NATIONAL PARK, ARIZONA

STEPHEN T. HASIOTIS¹, RUSSELL F. DUBIEL², PAUL T. KAY³, TIMOTHY M. DEMKO⁴,
KRYSTYNA KOWALSKA¹, AND DOUGLAS MCDANIEL¹

¹Department of Geological Sciences, University of Colorado, Campus Box 399, Boulder, CO 80309-0399

²U.S. Geological Survey, Box 25046, Denver, CO 80225

³P.O. Box 18848, Denver, CO 80218

⁴Department of Earth Resources, Colorado State University, Fort Collins, CO 80523

ABSTRACT—This paper updates our work-to-date on the bee and wasp (Hymenoptera: Aculeata) nest ichnofossils first discovered in Petrified Forest National Park (PEFO), Arizona, in 1993. Recent work includes the collection and the identification of new localities of bee nests and wasp cocoons (these are not elaborated on here to protect the sites). These hymenopteran ichnofossils were compared to other insect traces of nests and cocoons to demonstrate the differences in their architectures. The Triassic material was also compared to other bee and wasp nest and cocoons ichnofossils to illustrate their similar architecture. This is important because the ichnofossil evidence suggests that hymenopteran behavior has changed very little over 220 million years and that they were pollinators of plants in Triassic terrestrial ecosystems.

INTRODUCTION

AFTER THE initial discovery of Triassic bee and wasp (Hymenoptera: Aculeata) nest ichnofossils in Petrified Forest National Park (Hasiotis and Dubiel, 1993), additional specimens have been collected in the northern and southern portions of the Park (Figure 1, 2; Hasiotis *et al.*, 1995, 1996; Hasiotis, 1997). The new specimens include the first known Triassic nests of bees in petrified wood and in paleosols from the Monitor Butte and Petrified Forest Members, and previously unknown casts of wasp cocoons in immature paleosols from the lowerpart of the Petrified Forest Member (Figure 1). In order to accurately define the ichnologic characters of fossil hymenopteran nests, the Triassic fossil material is compared to other bee and wasp ichnofossils from Mesozoic and Cenozoic continental deposits in North America (e.g., Brown, 1934; Retallack, 1984; Hasiotis and Demko, 1996; Bown *et al.*, 1997; Hasiotis unpublished data). This overview updates on-going research on these new ichnofossils and emphasizes their significance to paleoecosystem analysis in continental deposits. The new ichnofossils serve as proxies for the presence of bees and wasps in the Triassic and preserved the interactions of these insects with the environment.

HYMENOPTERAN ICHNOFOSSIL EVIDENCE

Several types of ichnofossil hymenopteran (Aculeate) nests and cocoons occur as clusters of molds and casts in paleosols and silicified fossil logs in the Monitor Butte and Petrified Forest Members of the Upper Triassic Chinle Formation (Hasiotis *et al.*, 1995, 1996; Hasiotis, 1997). All are nearly identical in size, shape, and micro-morphology to nests of extant primitively-social bees and gregarious wasps. These Triassic nests predate the earliest evidence of the aculeates from body fossils by more than 100 million years. Here we report new evidence of hymenopteran ichnofossils from new localities with members mentioned above in the Painted Desert

and in Rainbow Forest of PEFO.

Bee nests.—Flask-shaped, smooth-walled cells approximately 20 mm long occur as circular and linear clusters that form multi-tiers of cells. Nests in paleosols exhibit at least three distinct configurations: (1) linear strings of up to ten cells; (2) radial clusters of up to 100 cells in groups of three or four; and (3) tightly constructed clusters of up to twelve cells with shared walls (Figure 3A, 4A). Nests within silicified logs were constructed in areas below the bark in the heartwood, including areas with knots formed by fallen tree limbs (Figure 5A-B, 4B). Some of these cells have caps that are sometimes woven and spiral, like those of extant bee nests, and contain black, spherical balls or pellets about 4 mm in diameter that appear to contain plant matter, pollen, and other unidentifiable material. The complex, highly organized clusters of cells suggests cooperation between numerous constructors working together to make a large nest with a repetitive bauplan. The comparison of Triassic nest architecture and contents to extant bee nests suggest that Triassic hymenopterans probably foraged for gymnosperm and cycadeoid pollen, resins, ascomycete and rust spores, and other plant fluids for nutrients and cell provisioning. Modern hymenopteran (Halictidae and Anthophoridae) nests of similar construction often reflect some degree of social interaction between the egg producer (queen) and the workers, in which the offspring of the founding female become workers and assist with nest construction and provisioning (Michener, 1974). Triassic hymenopterans may also have scavenged carrion (flesh and fluid), as do some modern species of halictid, anthophorid, trigoniid, and meliponine bees (Michener, 1974).

Since modern bees line the cells of their nests with organic compounds produced from their Dufour's gland, we analyzed the ichnofossil nest cells for chemical evidence that bees constructed the nests. Organic chemical analysis of the wall linings of the cells in the bee nests (Kay *et al.*, 1997) yielded

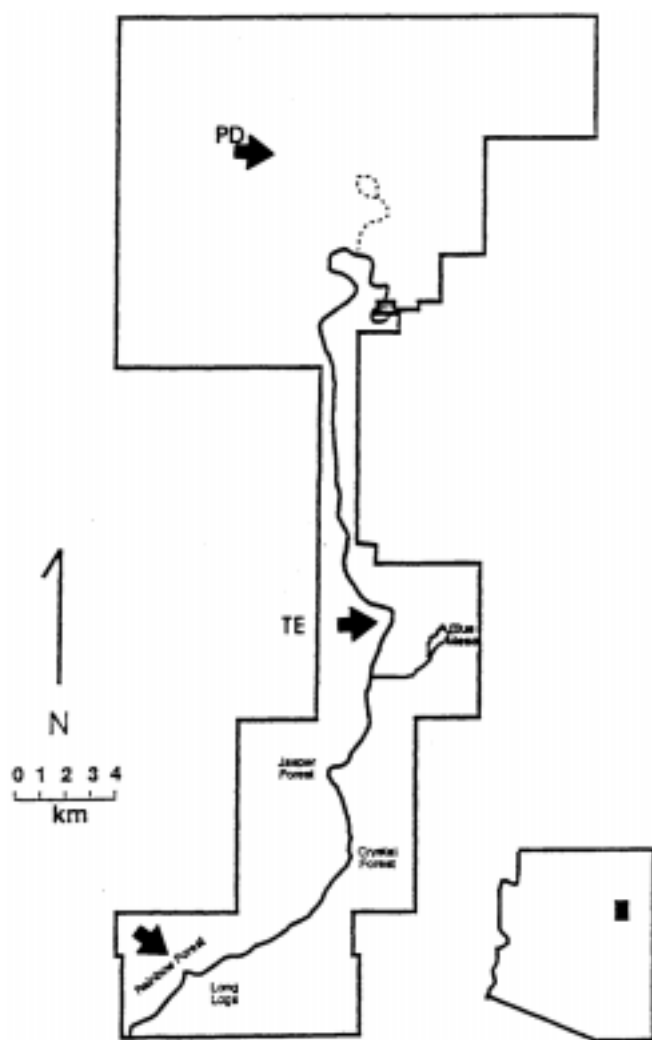


FIGURE 1—Study area map with approximate positions of bee and wasp nests in Petrified Forest National Park, Arizona. Abbreviations: (PD) Painted Desert, (TE) Tepees.

biochemical evidence of a phylogenetic link to modern bees in the Anthophoridae and Colletidae. Gas chromatography-mass spectrometry/mass spectrometry techniques released straight-chain carbon molecules from the bee nest cell walls. This organic material today is only found in socially varied bees and is produced from the Dufour's gland (Michener, 1974). The chemical analysis also demonstrates that despite the silicification of the wood, organic carbon is preserved in forms that can be identified to particular organisms.

Wasp nests.—Spindle-shaped casts and molds interpreted to be cocoons about 10–35 mm long are also found in paleosols (Figure 3B). These occur in clusters of four to ten individuals, each showing a woven, thread-like surficial morphology. The cocoon morphology, nest configuration, and nesting site distribution strongly resemble constructions of modern gregarious sphecoid wasps (Evans, 1963), which nest in close proximity to one another, construct nests with of four to twenty cells, and whose larvae spin cocoons with a sturdy silken weave. The cells of these Triassic nests were probably provisioned

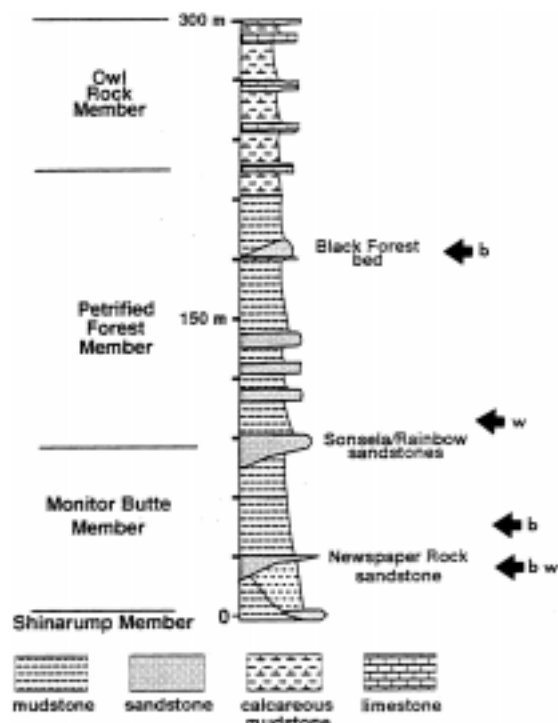


FIGURE 2—Composite stratigraphic section of Triassic rocks within Petrified Forest National Park, Arizona. Arrows denote the stratigraphic positions of bee and wasp nest ichnofossils. Abbreviations: (b) bee nests, (w) wasp nests (cocoons).

with insects and other carrion materials in a fashion similar to modern wasp provisioning (Hasiotis, 1997).

COMPARISON WITH OTHER REPRODUCTIVE INSECT BEHAVIOR

When reproductive structures of xyelid wasps (Symphyta, sawflies), various beetles (Coleoptera), and moths (Lepidoptera) (Essig, 1926; Keen, 1939) are compared to the Triassic nest and cocoon ichnofossils, all of these insects are ruled out as the constructors of the Triassic structures based on the morphology of their nests and borings. Although modern xyelid and other symphytid wasp larvae bore into coniferous wood, they construct relatively simple borings, with primitive hollowed-out structures for pupation, and are relatively dispersed rather than tightly clustered in the heartwood. Like their Mesozoic representatives, modern Cupedoidea beetles (e.g., Scolytidae, Cupedidae, and Platypodidae) construct reproductive structures that contain radially-arranged galleries from central tunnels that are poorly-organized in plan and loosely-connected as a series of short galleries extending from central galleries. These radiating galleries are subsequently expanded by the growing larvae and become wider as they are excavated away from the central tunnel (Essig, 1926). Cocoons of modern moths and butterflies are commonly either very large (>30 mm), or slender (4:1 length to width), or have the form and size of the pupa (Essig, 1926). They do not exhibit a delicate weave pattern, but rather show delicate masses of silken strands. However grossly similar, these and other reproductive puparia of sawflies, beetles, and moths are

FIGURE 3—A, Plan view of a portion of a bee nest in an immature paleosol, Monitor Butte Member, Tepees. B, Wasp cocoon molds (and casts-removed in photo) in an immature paleosol, Monitor Butte Member, Tepees.

not as complex, organized, or crafted as are the Triassic ichnofossils that are clearly more structurally similar to the constructions of bees and wasps.

NEW COMPARATIVE EVIDENCE OF HYMENOPTERAN ICHOFOSSIL NESTS

The morphology of Triassic bee and wasp ichnofossils compare favorably with hynemopteran ichnofossils collected from the Upper Jurassic Morrison Formation (Utah), the Lower Cretaceous Dakota Formation, the Upper Cretaceous Two

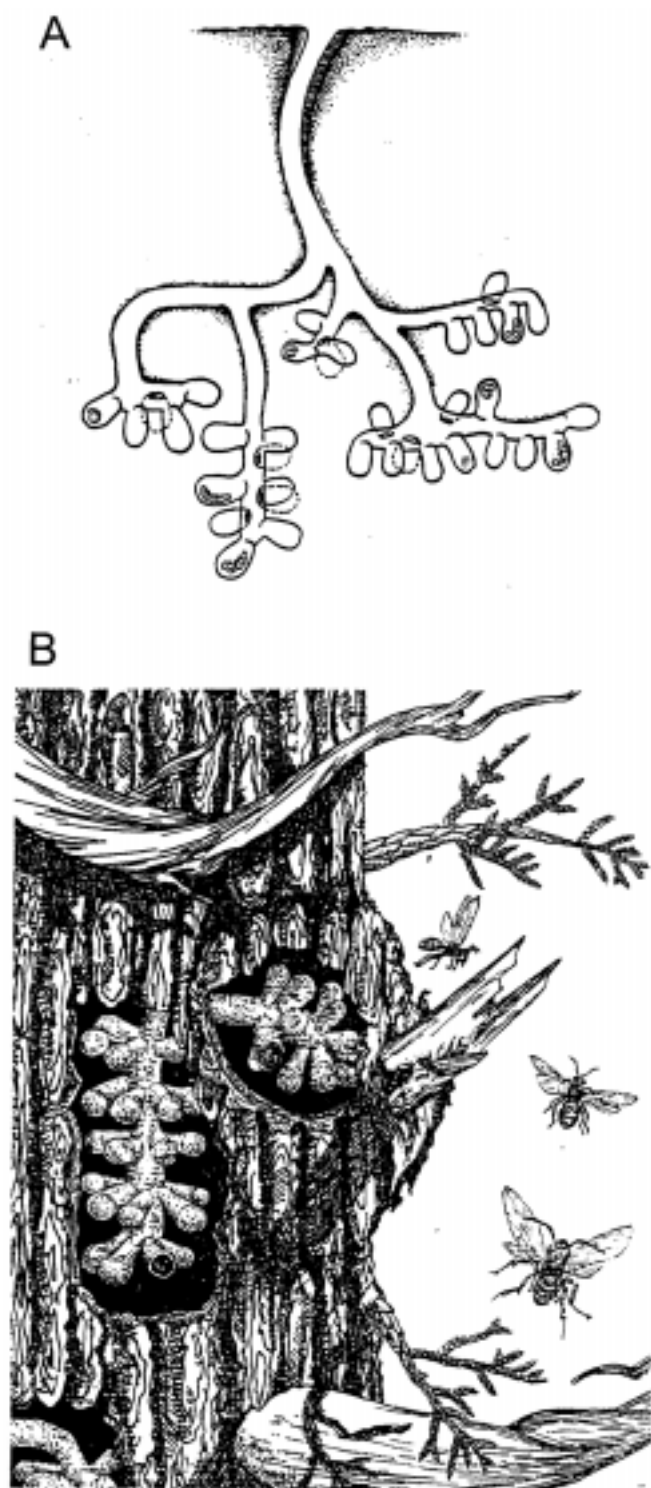


FIGURE 4—Triassic life-reconstructions of bee nests (A) a soil and (B) a conifer, *Araucarioxylon arizonicum*.

Medicine Formation (Montana), the Paleocene-Eocene Claron Formation (Utah), the Eocene Brian Head Formation (Utah), the Eocene Bridger Formation (Wyoming), the Miocene of Greece (Santorini), and the Holocene dunes in Great Sand Dunes National Monument (Colorado) (Hasiotis *et al.*, in

preparation). Nearly 200 bee cells and over 1000 wasp cocoons have been collected from these units. Preliminary measurements of the cells collected from nests in paleosols share strikingly similar proportions between the cell length and the widest and narrowest segments of the cell with those proportions found in Triassic bee cells in xylic substrates and paleosols. Preliminary measurements of well-preserved cocoons collected from paleosols also share corresponding proportions between cocoon length and width with those proportions found in Triassic cocoons. All the Mesozoic and Cenozoic cells and cocoons preserve at least three size ranges of both wasp cocoons and bee cells. Two other size ranges are also being discriminated quantitatively from the deposits mentioned above and probably represent puparia of moths (Lepidoptera) and beetles (Coleoptera). These moth and beetle insect traces are clearly different from the hymenopteran cocoons: moth cocoons are typically barrel-shaped, and occur in paleosols rather than in xylic substrates; beetle traces are spherical to hemispherical in morphology and also occur in paleosols. The additional information from the beetle and moth cocoons further strengthens our argument that we can discriminate between hymenopteran and non-hymenopteran ichnofossils.

SIGNIFICANCE

Late Triassic ichnofossil insect nests record very early, yet advanced behavioral and morphological characteristics of the Hymenoptera. These trace fossils shed new light on hypotheses regarding the timing of insect diversification and its co-evolution with plants in terrestrial ecosystems. Insect ichnofossils better constrain the age of origination of numerous groups because they have a greater preservation potential than do body fossils, which are typically much rarer. Triassic ichnofossils of derived hymenopteran insects extend the ages of these insects by more than 100 million years (Hasiotis *et al.*, 1995, 1996). Hymenopteran ichnofossils reveal more information about behavior than do body fossils, which can be used to interpret behavior solely through functional morphology. The highly organized nest configurations of Triassic hymenopteran ichnofossils imply that complex behavior reflecting primitive socialization and pollenization, was established long before the advent of angiosperms; these organisms were acting as pollinators in the Triassic terrestrial ecosystems. The pre-established plant foraging and feeding strategies of early Mesozoic hymenopterans constitute a pre-adaptation for a later origin of pollination mechanisms in early angiosperms, thus favoring rapid angiosperm radiation and diversification. Through time, these and other insects probably switched plant resources (from gymnosperm-cycadeoid to angiosperm) as they co-evolved with the rapidly diversifying angiosperms to form the intricate ecological relationships exhibited by insects and angiosperms today.

ACKNOWLEDGMENTS

We thank the park superintendents, rangers, resource managers, paleontologists, administrative and field personal, interns, and colleagues who have assisted our research over

FIGURE 5—A, Plan view of a circular portion of a bee nest in a petrified log, Black Forest bed, Petrified Forest Member, Painted Desert. B, Plan view of a linear portion of a bee nest in a petrified log (continuation of nest above), Black Forest bed, Petrified Forest Member, Painted Desert.

the years at Petrified Forest National Park, Arizona. Without their support and foresight, this work would not be possible. We also thank Adolf Coors and the Colorado School of mines for use of their SEM and Gas Chromatograph. This work is part of a dissertation conducted by STH at the University of Colorado, Boulder and is also paleontology research projects

by KK and DM at the Museum at the University of Colorado, Boulder.

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A HOLISTIC APPROACH TO RECONSTRUCTING TRIASSIC PALEOECOSYSTEMS: USING ICHNOFOSSILS AND PALEOSOLS AS A BASIC FRAMEWORK

STEPHEN T. HASIOTIS¹, RUSSELL F. DUBIEL², AND TIMOTHY M. DEMKO³

¹Department of Geological Sciences, University of Colorado, Campus Box 399, Boulder, CO 80309-0399

²U.S. Geological Survey, Box 25046, Denver, CO 80225

³Department of Earth Resources, Colorado State University, Fort Collins, CO 80523

ABSTRACT—*In situ* indicators of inhabitants and indicators of environmental settings used for reconstructing paleoecosystems are typically not used, and often are secondarily considered compared to the use of plant and vertebrate fossils to characterize paleoecosystems. Environmental and climatic interpretations are formulated from the gross sedimentology, palynomorph composition, and faunal and floral taxonomic components. Much of the paleontological evidence used for the reconstructions and climatic interpretations are often reworked, time-averaged, and out of ecological context.

We propose that paleosols and ichnofossils, in conjunction with the sedimentology and stratigraphy of a unit, be used as a basic framework from which to build on with other paleontological evidence for reconstructing paleoecosystems. Ichnofossils preserve *in situ* organism behavior that record interactions with other organisms and their environment. Paleosols record the effects of environment, ecologic interactions, and climate. Ichnofossils record the lower portions of the food web, the infaunal components of ecosystems, and the locations and ranges the mobile herbivores and carnivores. When paleosols and ichnofossils are evaluated together the environmental and climatic trends of paleoecosystems can be reconstructed and detailed by other sedimentological, paleontological, and geochemical evidence.

INTRODUCTION

PALEOECOSYSTEM RECONSTRUCTIONS are typically based on plant and vertebrate body fossils that are often reworked and interpreted out of ecological context. The plant and vertebrate fossils also represent primary producers and secondary consumers, respectively. Many invertebrates and their ecologic roles as secondary and tertiary consumers and detrital recyclers go undetected because they are rarely preserved as body fossils. Trace fossils of invertebrates are frequently preserved in many different environments, occur *in situ*, and are not subject to reworking. The recent recognition of invertebrate ichnofossils in continental settings and their ecological importance provides information about previously unrecorded biodiversity and ecological interactions (Hasiotis and Dubiel, 1993a,b; Hasiotis, 1997).

Ichnofossils are the result of organism-substrate interactions that record in their structure both morphological and behavioral data. Thus, they are valuable sedimentologic and paleontologic interpretational tools for geologists (Hasiotis and Bown, 1992). Ancient and modern animal burrowing and plant-root penetrations also modify substrates in which they occur. The interaction of different suites of organisms with various types of substrates result in different types and stages of soil (paleosol) formation. Invertebrate and plant traces are sensitive indicators of depositional energy, temperature, precipitation, water chemistry (i.e., salinity and alkalinity), oxygenation, substrate consistency, hydrology, biological competition, and nutrient availability; all organisms are physiologically constrained by these environmental parameters. Together, these physical, biological, and chemical components define an ecosystem and provide insight into the paleogeography and paleoclimate (Jenny, 1941; Aber and Melillo, 1991; Hasiotis

and Bown, 1992; Hasiotis, 1997).

Based on our research in the Upper Triassic Chinle Formation in and around Petrified Forest National Park, Arizona, we are strong proponents for the use of ichnofossils and paleosols as a basic framework for reconstructing paleoecosystems. We feel that this framework, when combined with body fossil evidence, will provide a more detailed, holistic, and accurate description of Late Triassic paleoecosystems.

ICHOFOSSILS AND PALEOSOL EVIDENCE

In modern, as well as in ancient, continental settings, the distribution of vegetation types, biodiversity patterns, and soil types constituting the major terrestrial biomes closely corresponds to latitudinal variation in climatic regimes (Aber and Melillo, 1991). In the Upper Triassic Chinle Formation, trace fossils and paleosols (serving as proxies for organisms and soils, respectively) are preserved in nearly every depositional environment. They are not as subject to dissolution as body fossils, and are rarely reworked by subsequent depositional processes as body fossils. Thus, these ichnologic and pedogenic features provide essential information to fully reconstruct the in-place, original faunal, floral, and edaphic components of Late Triassic Chinle ecosystems.

Ichnofossils.—Insects and other arthropods constitute the majority of ichnofossil constructors recovered from the Chinle Formation. Today, insects and other continental arthropods constitute 90% of the biodiversity in the world. Chinle trace fossils of millipedes, horseshoe crabs, crayfish, gastropods, mollusks, nematodes, aquatic and terrestrial earthworms, caddisflies, flies, moths, beetles (semi-aquatic, terrestrial, and wood-boring), termites, soil bugs, bees, and wasps provide evidence for the occurrence and interactions of arthropods in

the Triassic paleocommunities (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1993a,b; Hasiotis, 1997). These ichnofossils are important indicators of the arthropods' ecologic roles as herbivores, carnivores, omnivores, and detritivores within primary, secondary, and tertiary levels of the food web.

The depth, tiering, and distribution of trace fossils illustrate the differences of soil moisture and water table levels in different environments (Hasiotis and Bown, 1992; Hasiotis, 1997). For example, extant crayfish burrow to the depth of the water table, soil bugs prefer the intermediate vadose zone, and bees and wasps prefer the upper vadose zone (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1993a, b; Hasiotis, 1997). Shallow and surface traces of terrestrial beetles abound in point-bar, levee, and overbank floodplain deposits with high soil moisture and water table levels. Termite nests dominate intermediate depths of distal overbank floodplain deposits with low soil moisture and modified by mature soils. Bees and wasps nests also occur with termite and beetle traces, but dominate shallow and intermediate depths of proximal floodplain deposits with moderate soil moisture levels. Shallow to deep crayfish burrows primarily occur in levee and proximal floodplain deposits that are imperfectly drained with highly fluctuating water tables. Surface and very shallow horseshoe crab crawling trails are found mainly on the wet, firm substrates (bedding planes) of point-bar and levee deposits and feeding traces are just below the surface. Flow regime, turbidity, and substrate consistency controlled the distribution of snail, gastropod, oligochaete, and nematode burrows and trails in lentic and lotic water bodies. The occurrence and distribution of these and other organism-substrate interactions were controlled by 1) the depth and fluctuation of the water table, 2) soil moisture levels, 3) depositional energy, 4) substrate texture and consistency, and 5) food web interactions.

Vertebrate ichnofossils, including tracks and trails of small aquatic reptiles, metaposaurs, phytosaurs, and dicynodonts, complement the invertebrate trace fossils. Metapsaur and phytosaur tracks dominate channel and point-bar deposits. Dicynodont tracks occur in levee deposits. Small reptile tracks are found in point-bar and levee deposits. These tracks demonstrate exactly where these organisms spent their time in the environment and the activities in which they may have been involved (herbivory, carnivory, breeding, feeding, etc.), whereas body fossils mainly demonstrate where they died or were carried away and accumulated after death.

Further ecologic information is obtained from rooting patterns and rhizomes of plants preserved in immature to mature paleosols (discussed below). The depth and configuration of roots and rhizomes reflect the amount of soil moisture and depth of the water table in a particular setting. The size of the roots also reflect the stratification of vegetation above the soil surface; canopy trees have large root systems, ground-cover plants have shallow and fine roots, intermediate plant cover has root dimensions intermediate between the other plants.

Paleosols.—Variations in Chinle alluvial, lacustrine, and eolian paleosols reflect lateral and temporal changes in Trias-

sic climate, paleogeography, paleohydrology, infaunal biota, and vegetation. As in modern soil-forming processes, parent material, topography, biota, climate, and time constitute the factors that determine what type of soils develop (Jenny, 1941). Major types of paleosols present in the Chinle include Gleysols, Alfisols, Vertisols, Calcisols, and Aridisols, all of which also range in stages of maturity based on the amount of time in their formation (e.g., Mack *et al.*, 1993).

Gleysols are abundant in the basal Chinle (Shinarump Member/"mottled strata"), where they are characterized by extensive purple, yellow, and white mottled horizons, contain deep crayfish burrows and roots, and indicate deep though fluctuating water tables. Alfisols are common in floodplain mudrocks in the lower and middle Chinle (Monitor Butte and Petrified Forest Members), consisting of thick red, clay-rich horizons, locally exhibiting small carbonate nodules. These soils contain red-purple mottles, abundant beetle burrows (*Scoyenia*) and small rhizoliths, and indicate predominantly moist soils and persistently high water tables. Vertisols (Monitor Butte and Petrified Forest Members) are characterized by clay-rich horizons, deep mudcracks, slickensides, gilgai micro-relief, carbonate nodules, crayfish burrows and extensive rhizoliths, and are indicative of periods of wetting and drying. Calcisols (Owl Rock and Church Rock Members) with carbonate accumulations in their upper portions, contain rhizotubules and rhizcretions, and occur predominantly in siltstone deposits. Aridisols (Church Rock Member) contain varying stages of carbonate nodule development, few rhizoliths, rare bioturbation, and indicate decreased precipitation coupled with persistently deeper water tables.

SIGNIFICANCE

The integration of ichnologic, sedimentologic, and paleopedologic information allows for a more complete reconstruction of paleoecosystems, including interpretation of their hydrologic and climatic settings. The sequences of sedimentary facies, paleosols, and associated ichnofossils provide hierarchical criteria to interpret long-term and short-term trends in the evolution and succession of Chinle ecosystems and climates. These criteria also comprise the internal framework that plant, invertebrate, and vertebrate fossils can be placed in to reconstruct various paleocommunities with distinct biological, environmental, and climatic attributes.

Based on all the physical, biological, and chemical evidence collected to date, the Petrified Forest monsoonal (wetter periods with higher humidity) climate became increasingly arid during the Late Triassic (Carnian to Norian). During the deposition of the Shinarump and Monitor Butte Members, the early Chinle (Carnian) climate was warm and humid with ample rainfall. During deposition of the Petrified Forest and Owl Rock Members (Norian), climate became strongly monsoonal with strongly seasonal rainfall and high temperatures. Climate during the deposition of the latest Chinle, represented by the Church Rock Member (latest Norian), became increasingly arid with less precipitation and greater temperature extremes due to lower humidity.

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We thank the park superintendents, rangers, resource managers, paleontologists, administrative and field personal, interns, and colleagues who have assisted our research over the years at Petrified Forest National Park, Arizona. Without their support and foresight, this work would not be possible. We also thank the many people who volunteered their time with us in the field to collect sedimentologic, paleontologic, and paleopedologic data. This work is part of a dissertation conducted by STH at the University of Colorado, Boulder.

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STRATIGRAPHIC DISTRIBUTION AND AGE OF PETRIFIED WOOD IN PETRIFIED FOREST NATIONAL PARK, ARIZONA

ANDREW B. HECKERT¹ AND SPENCER G. LUCAS²

¹Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, NM 87131

²New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104

ABSTRACT—We present detailed stratigraphic and sedimentologic evidence that supports the conclusion that two stratigraphic units in the Upper Triassic Chinle Group contain almost all of the petrified wood in the Petrified Forest National Park. Although incidental deposits of petrified wood occur throughout the stratigraphic section, the Sonsela Member of the Petrified Forest Formation hosts almost all of the brightly colored, large trunks and logs for which the park is known. The Black Forest Bed in the Painted Desert Member of the Petrified Forest Formation contains another large deposit of petrified logs. Incidental petrified wood deposits occur primarily in sandstone beds within the Painted Desert Member, although some are also known in the Blue Mesa Member. Available biochronological evidence, including tetrapods, megafossil plants, pollen, and calcareous microfossils, indicates that both the Sonsela Member and the Black Forest Bed are of early- to mid-Norian (220–215 Ma) age.

INTRODUCTION

ALL THE petrified wood in the Petrified Forest National Park (PEFO) occurs in deposits of the nonmarine Upper Triassic Chinle Group. Geologic investigations of the Chinle in PEFO include Gregory (1917), Cooley (1957), Roadifer (1966), Stewart et al. (1972), Billingsley (1985a,b), Ash (1987a), Murry (1990), Ash (1992), and Lucas (1993, 1995). These studies, combined with our own, have resulted in an extensive database of detailed measured sections throughout PEFO and vicinity (Figure 1). In PEFO, the following previously named Chinle Group units are exposed (ascending order): the Bluewater Creek Formation, the Blue Mesa, Sonsela, and Painted Desert Members of the Petrified Forest Formation, and the Owl Rock Formation (Figure 2). The bulk of the petrified wood in PEFO, including the spectacular deposits (“forests”) of large, highly colorful, trunks, occurs in the Sonsela Member of the Petrified Forest Formation. The gray-black logs of the Black Forest occur in the Black Forest Bed of the Painted Desert Member. Isolated logs also occur in bench-forming sandstones of the Painted Desert Member, and in deposits of the Blue Mesa Member.

Published studies on the systematics and stratigraphic occurrence of petrified wood in PEFO include Blake (1856) Goepfert (1858), Knowlton (1889), Jeffrey (1910), Daugherty (1934, 1941), and Gould (1971). Almost all of the petrified wood in PEFO was transported prior to deposition, as evidenced by a lack of limbs, bark, or roots preserved with most specimens. A few *in situ* stumps have been recorded, predominantly in the Blue Mesa Member or in the Black Forest Bed (Ash and Creber, 1992). In general, the spectacularly colored logs in the Sonsela Member are typically referred to the genus *Araucarioxylon*, and most are probably representatives of the species *A. arizonicum* (Daugherty, 1941). The Black Forest logs, so named because of their dark gray to black color, also include *A. arizonicum* and most of the area’s specimens of *Woodworthia* and *Schilderia* (Ash, 1992).

Historically, most workers have agreed that the bulk of the petrified wood in PEFO is concentrated in a few horizons.

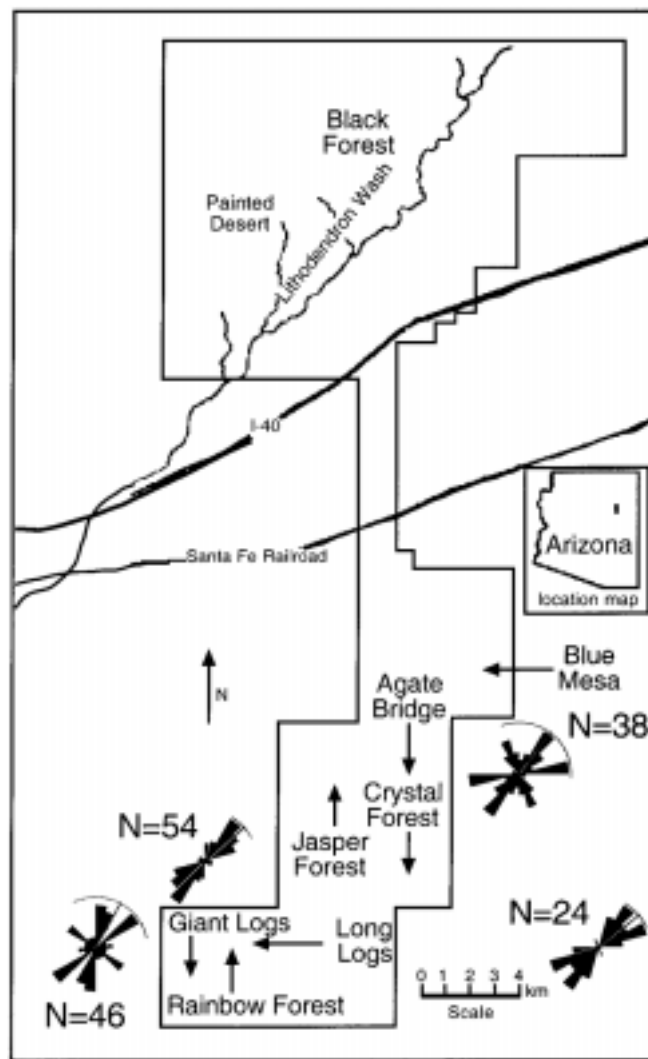


FIGURE 1—Map of the Petrified Forest National Park. Arrows show locations of measured sections used in Figure 3. Rose diagrams show paleocurrent measurements from logs in the Sonsela Member outside park boundaries, indicating a predominantly south-west-northeast channel trend of Sonsela Member sediments.

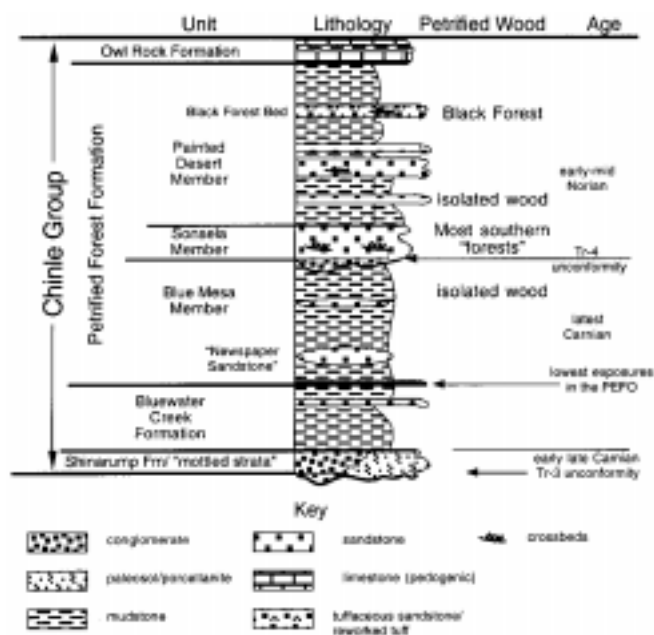


FIGURE 2—Schematic stratigraphic section showing the Chinle Group stratigraphy of the Petrified Forest National Park and the stratigraphic distribution of major petrified wood accumulations in the park.

Some, including Cooley (1957, 1959), Billingsley (1985a,b), and Ash (1987a, 1992), argued that three highly fossiliferous horizons were present, the informal “Rainbow Sandstone,” Sonsela Member, and the Black Forest Bed. Others, including Roadifer (1966) and Deacon (1990) considered the “Rainbow Sandstone” and the Sonsela Member homotaxial, and thus

thought that only two principal horizons were present, namely the Sonsela Member and the Black Forest Bed. Here we present stratigraphic and paleocurrent information that supports the conclusions of Roadifer (1966) and Deacon (1990) and demonstrates that most petrified wood deposits in PEFO are in either the Sonsela Member or the Black Forest Bed (Figure 2).

Sonsela Member forests.—The vast majority of the fossil wood in PEFO occurs in trough crossbedded sandstones and conglomerates of the Sonsela Member of the Petrified Forest Formation. Almost all of the famous localities in the southern portion of the park, including the spectacular “forests” of trunks preserved in Giant Logs, Rainbow Forest, Long Logs, Crystal Forest, Jasper Forest, Agate Bridge, and Blue Mesa, are in the Sonsela Member, as are several “forests” on adjacent private and state lands. The Sonsela Member typically consists of gray, grayish brown, and grayish green sandstones and conglomerates. Conglomerate clasts include pebble- to cobble-sized chert and quartzite clasts and rip-ups of underlying Blue Mesa Member mudstones, some of which approach boulder size. Deacon (1990) thoroughly investigated the sedimentology of the Sonsela Member and concluded that it represented a low sinuosity fluvial system consisting of northerly to northeasterly draining braided channels. Lucas (1993) demonstrated that the Sonsela disconformably overlies an erosional surface on the Blue Mesa Member that represents his Tr-4 unconformity, and Heckert and Lucas (1996) examined the details of this relationship in PEFO and vicinity.

In the past, numerous workers, including Cooley (1957, 1959), Billingsley (1985a,b), and Ash (1987a), have referred to an informal unit called the “Rainbow Sandstone” and considered it the sandstone unit that contained the “forests” at

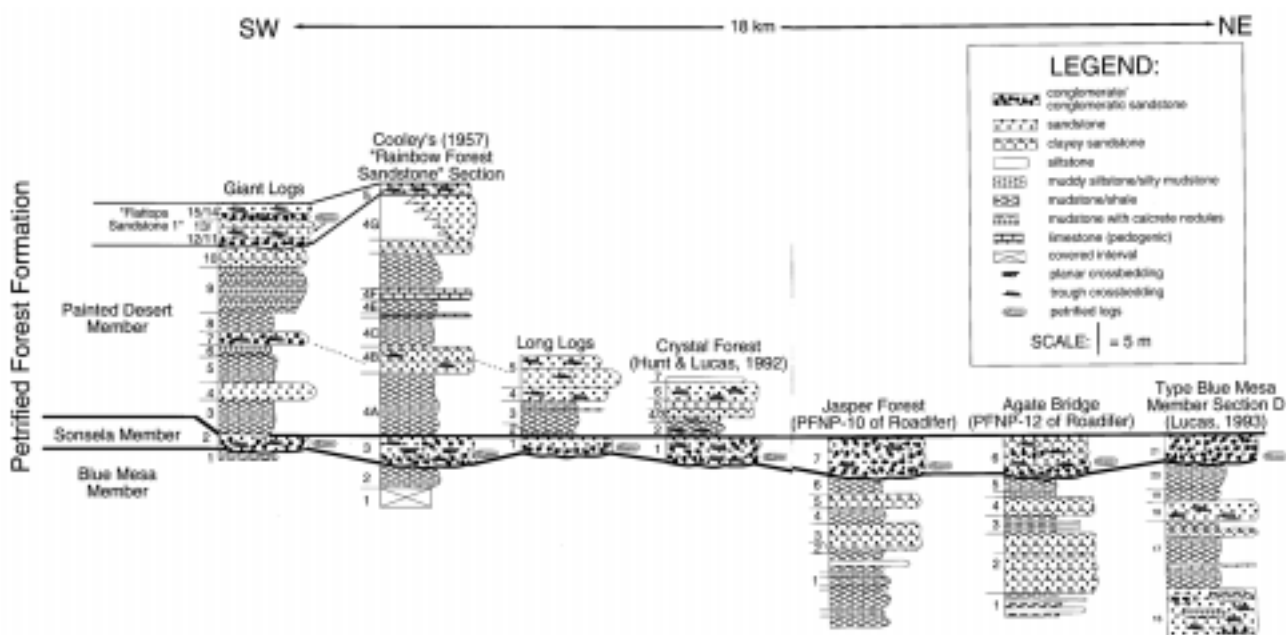


FIGURE 3—Correlated measured sections showing the stratigraphic distribution of the major “forests” of petrified wood in the southern portion of the park. Location of measured sections given in Figure 1. Sections credited to original author as appropriate, sections not credited are our own.

Giant Logs, Rainbow Forest, and Long Logs. However, we agree with Roadifer (1966) and Deacon (1990) that this interval actually represents the same stratigraphic interval as the Sonsela Member. Recently, one of us (ABH) conducted extensive stratigraphic work on the private lands adjoining PEFO and determined that all the trough-crossbedded, wood-bearing, extrabasinal conglomerate and conglomeratic sandstone is at a single horizon (Figure 3). Paleocurrent data, both our own and those of Deacon (1990) corroborate this stratigraphic hypothesis, and show an overall channel trend toward approximately N30E. This channel can be traced from the extreme southwestern portion of the park into the subsurface, re-emerging at the Crystal Forest, where it is readily traced to Jasper Forest, Agate Bridge, and Blue Mesa (Figure 1). *Araucarioxylon* is by far the most common genus of tree preserved in these forests (Ash and Creber, 1992).

Painted Desert Member.—The Painted Desert Member contains much less petrified wood than the underlying Sonsela Member. Scattered petrified wood occurs in the bench-forming sandstones in the Painted Desert, usually referred to as “Flattops Sandstones” in the southern portion of the park and as “Painted Desert Sandstones” in the northern portion (e.g., Billingsley, 1985a,b). Most logs are found in Jim Camp Wash, and are typically less colorful and smaller than those in the Sonsela Member. None of the major forests in PEFO are composed of this wood, and most of these deposits appear to represent more typical, isolated wood deposition in fluvial systems. Because of its scattered and fragmentary nature, this wood is not well-studied, but *Araucarioxylon* dominates the identifiable specimens (Daugherty, 1941; Ash and Creber, 1992).

Black Forest Bed.—Ash (1992) named the Black Forest Bed for the extensive deposits of limestone-pebble conglomerate and reworked tuff in the Painted Desert Member in the northern portion of the park. These deposits occur approximately 60–65 m above the top of the Sonsela and range from 0 to 12.6 m in thickness in the park (Ash, 1992; Lucas, 1993). Ash (1992) described the Black Forest Bed as a basal, well-indurated calcrete pebble conglomerate overlain by reworked, andesitic tuff with thin interbeds of mudstone and siltstone. The petrified logs here are gray-black and most abundant in the Black Forest itself, roughly 2.5 km (1.5 miles) north of the Painted Desert overlooks, although numerous logs derived from the Black Forest Bed can be found as float on the slopes below those overlooks. The Black Forest Bed wood, like the Sonsela, includes abundant specimens of *Araucarioxylon*, but also includes rarer *Woodworthia* and *Schilderia* (Ash, 1992). Most of the wood is concentrated in the upper, tuffaceous portion of the unit, which is the highest stratigraphic occurrence of petrified wood within the park.

Biostratigraphy, biochronology, and numerical ages.—The superposition of the petrified forests clearly demonstrates that the oldest extensive wood deposits are those in the Sonsela Member, with scattered wood deposition occurring in the various Painted Desert Member sandstone beds until another major depositional event resulted in the preservation of the fossil logs in the Black Forest Bed. Unfortunately, the petrified logs

are not themselves age diagnostic, as is well demonstrated by the universal occurrence of *Araucarioxylon* in petrified wood deposits throughout the park. Extensive work on tetrapod vertebrates (summarized in Hunt and Lucas, 1995), megafossil plants (Ash, 1980, 1987b), pollen (Litwin et al., 1991), and calcareous microfossils (Lucas and Kietzke, 1995) indicates that both the Sonsela and the Painted Desert Members are early-mid Norian in age. Lucas (1997) summarized this biostratigraphic evidence and noted that the available biochronologic evidence indicated that the absolute age for these strata probably ranges between 215 and 220 Ma.

Two numerical ages have been reported from PEFO, both from the Black Forest Bed. Ash (1992) suggested that a K-Ar age on a biotite of 239 ± 9 Ma is the age of a Middle Triassic tuff that was subsequently reworked during Late Triassic time to form the Black Forest bed. Riggs et al. (1994a) reported a U-Pb age on zircons from the Black Forest Bed of 207 ± 2 Ma and suggested that this is the syndepositional age of the unit. Riggs et al. (1994b) went further to conclude that the Black Forest Bed represents the fluvial deposition of a Plinian ash fall that disrupted stream flow, causing avulsion and crevasse splay formation.

This sedimentological interpretation seems unlikely because: (1) the tuff of the Black Forest Bed is extremely localized and only known from one location outside of PEFO (Ash, 1992), which would not be the case in a Plinian ash fall; and (2) geometry and sedimentary structures of the Black Forest Bed differ little from those of other Painted Desert Member channel deposits, which suggests an ash fall was not needed to produce this type of facies architecture. Furthermore, an age of 207 Ma for the early Norian Black Forest Bed seems unlikely, unless all previous calibration of the Late Triassic timescale is incorrect (Lucas, 1994, 1997). Therefore, neither of the published numerical ages of the Black Forest Bed is a reliable syndepositional age, and abundant biostratigraphic evidence constrains deposition of both the Sonsela Member and the Black Forest Bed to the early- to mid-Norian.

CONCLUSIONS

Two horizons, the Sonsela Member and the Black Forest Bed, contain the vast majority of the petrified wood in PEFO. Sonsela Member deposits are the oldest widespread deposits in the park and include the spectacular logs associated with Giant Logs, Rainbow Forest, Long Logs, Crystal Forest, Jasper Forest, Agate Bridge, and Blue Mesa in the southern portion of the park. The most extensive deposits in the Painted Desert Member are those in the Black Forest Bed in the northern portion of the park, although scattered petrified wood also occurs in other sandstone beds within the Painted Desert Member. Available stratigraphic and sedimentologic evidence suggests that deposits termed the “Rainbow Sandstone” by some authors are actually basal Sonsela Member deposits. These are the oldest major deposits of petrified wood in PEFO, and are early Norian in age. The Black Forest Bed is also well-constrained biochronologically to the early-mid Norian, in spite of isotopic data that suggest other ages.

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The Petrified Forest Museum Association generously supported this research. Additional support was provided by the New Mexico Museum of Natural History. Numerous personnel have facilitated field work involved with this project, including P. Bircheff, C. Davis, P. Huber, A. Hunt, K. Kietzke, P. Reser and park employees L. Bolich, D. Humphries, and M. Schmitt. Personnel of PEFO, especially Carl Bowman, Mark DePoy, David Dewitt, Pat Quinn, and Vince Santucci facilitated logistics of our study. We are also indebted to the New Mexico and Arizona Land Company, especially J.D. Sphar, for allowing access to lands adjacent to the park and allowing us to publish data collected there.

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THE OLDEST TRIASSIC STRATA EXPOSED IN THE PETRIFIED FOREST NATIONAL PARK, ARIZONA

ANDREW B. HECKERT¹ AND SPENCER G. LUCAS²

¹Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, NM 87131

²New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104

ABSTRACT—All Triassic rocks in the Petrified Forest National Park pertain to the Upper Triassic Chinle Group. We identify localized, topographically low exposures of siliciclastic redbeds and purple mudstones near Newspaper Rock as the Bluewater Creek Formation, the oldest unit exposed in the park. Mudstone and sandstone of the Blue Mesa Member of the Petrified Forest Formation are the oldest widely exposed strata in the park, and are overlain disconformably by sandstone and conglomerate of the Sonsela Member. The Sonsela Member is overlain conformably by mudstone and sandstone of the Painted Desert Member. In the extreme northern portion of the park, pedogenic limestones of the Owl Rock Formation conformably overlie the Painted Desert Member. Surface and subsurface stratigraphic evidence indicates that the Bluewater Creek Formation is the oldest unit exposed in the park—not the mottled strata, Shinarump Formation, or Moenkopi Formation, as claimed by some recent workers. Lithologic and tetrapod biostratigraphic evidence indicates that Chinle strata encompass a single major unconformity at the base of the Sonsela Member, with strata below the Sonsela bearing tetrapod fossils of Adamanian (latest Carnian) age and the Sonsela and overlying units containing Revueltian (Norian) tetrapod fossils.

INTRODUCTION

CHINLE GROUP deposits dominate the outcrops of the Petrified Forest National Park (PEFO), and the park contains several type sections of Chinle Group units. Geologic investigations of PEFO include Gregory (1917), Cooley (1957), Roadifer (1966), Stewart et al. (1972), Billingsley (1985a,b), Ash (1987a), Murry (1990), and Lucas (1993, 1995). In PEFO, the following previously named Chinle Group units are exposed (ascending order): the Bluewater Creek Formation, the Blue Mesa, Sonsela, and Painted Desert Members of the Petrified Forest Formation, and the Owl Rock Formation. Recently, some workers (Dubiel et al., 1995; Hasiotis and Dubiel, 1995) have proposed that the oldest outcrops in PEFO pertain to the Moenkopi Formation, although descriptions in these works indicate that they actually mean “mottled strata,” a name given to pedogenically reworked strata at the base of the Chinle Group by Stewart et al. (1972). This hypothesis is at odds with the available stratigraphic and paleontologic data. Here we use detailed surface stratigraphy, subsurface lithologic information, and tetrapod biostratigraphy to demonstrate that the oldest strata in PEFO are no lower stratigraphically than

the top of the Bluewater Creek Formation and thus are of latest Carnian (Adamanian) age.

SURFACE STRATIGRAPHY

The Petrified Forest National Park is well-known for its extensive badlands, which afford numerous opportunities to measure detailed stratigraphic sections. In the course of various studies, we have developed an extensive database of more than fifty measured sections. Of these, several are pertinent to discussion here. In particular, we have measured detailed sections near Newspaper Rock, from the Haystacks to Blue Mesa, and in the vicinity of the Rainbow Forest Museum.

The Blue Mesa Member has long been thought to be the stratigraphically lowest unit exposed in the park (Roadifer, 1966; Billingsley, 1985a,b; Ash, 1987; Lucas, 1993). However, we follow Cooley (1957) in identifying the Bluewater Creek Formation (“lower red member” of Cooley) as the lowest unit exposed in the park, based on our Newspaper Rock section and the type Blue Mesa Member section of Lucas (1993, 1995) (Figure 1). This effectively constrains the oldest beds in the park to a latest Carnian age (Lucas, 1993).

Unit 3 of the Newspaper Rock section (Figure 1) is a bed

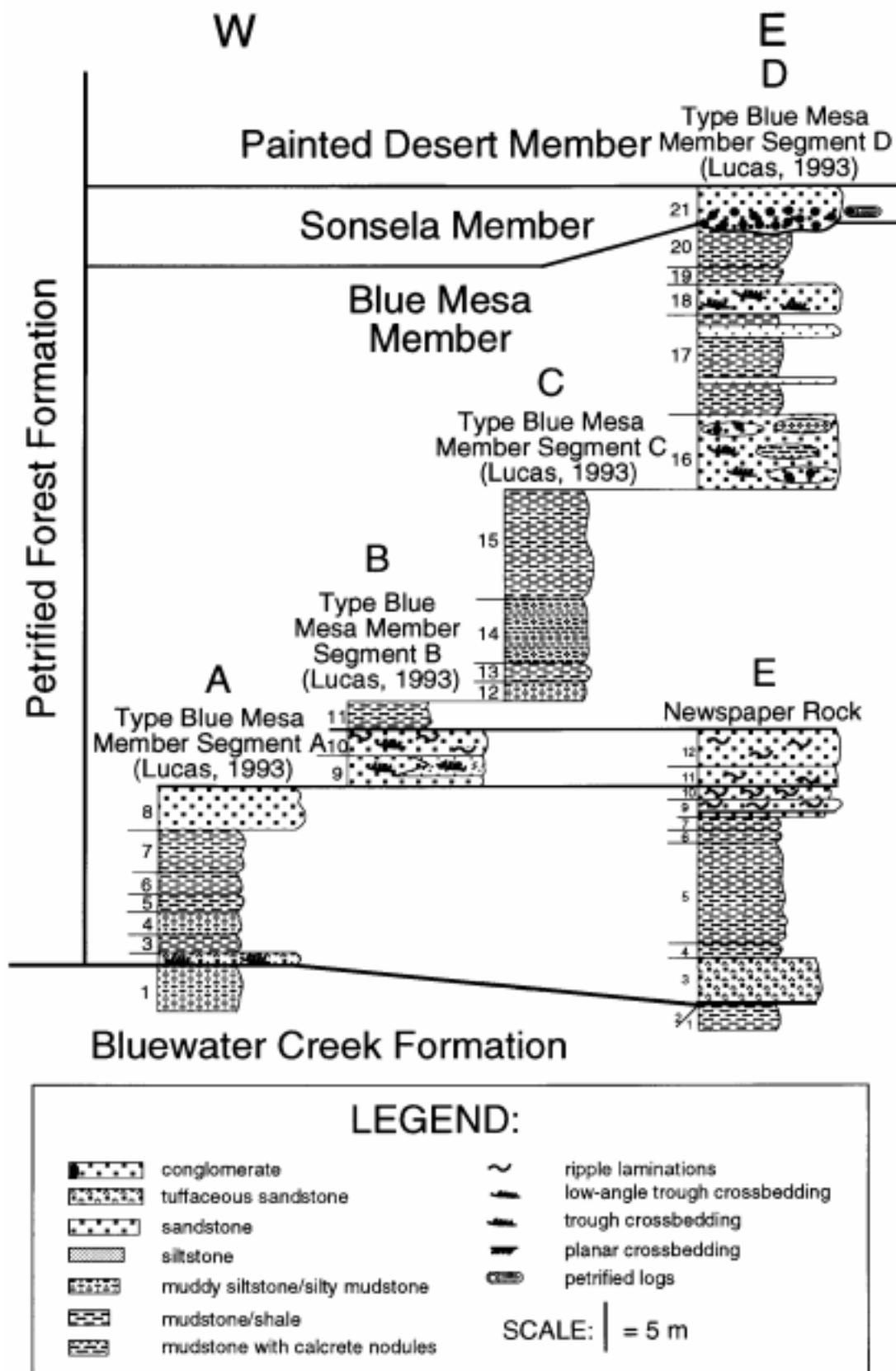


FIGURE 1—Correlated measured sections in the vicinity of Blue Mesa, the Teepees, and Newspaper Rock in PEFO. Note that the lowest exposures are of the uppermost Bluewater Creek Formation. Sections are located as follows: (A) SW1/4 SW1/4 SE1/4 sec. 21; (B) SW1/4 NW1/4 SW1/4 NE1/4 sec. 22; (C) SE1/4 NW1/4 SW1/4 sec. 23; (D) E1/2 SE1/4 SE1/4 SW1/4 sec. 23; (E) SE1/4 SE1/4 NW1/4 sec. 6; all in T18N, R24E.

of tuffaceous, highly micaceous sandstone 4.6 m thick (equivalent to unit 2 of Lucas [1993] type Blue Mesa Member type section) at the base of the Blue Mesa Member. This arenite/wacke interval is lithologically similar to the basal Blue Mesa Member in the vicinity of Fort Wingate, New Mexico, where approximately 5 m of ashy sandstone lie conformably on bentonitic mudstone “red beds” of the Bluewater Creek Formation (Lucas and Hayden, 1989; Heckert and Lucas, 1996; Lucas et al., 1997; Anderson et al., 1997). In both cases, this sandstone is muddy and/or ashy, micaceous, and poorly sorted. Near Fort Wingate, the basal Blue Mesa sandstones display more bedforms, particularly very low-angle trough crossbeds (see Chapter 4), but the bed in PEFO is similar to this in the vicinity of the Teepees, where it is approximately 12.9 m below the Newspaper Rock Bed.

Based on overall lithologic similarity to basal Blue Mesa Member outcrops elsewhere, we interpret this bed as the base of the Blue Mesa Member in PEFO. This lithology is unlike any found in units that underlie the Blue Mesa anywhere else in eastern Arizona or western New Mexico (Heckert, 1997). The pale purple and grayish red purple bentonitic mudstones below it belong to a different stratigraphic unit, either the Mesa Redondo Formation (Cooley, 1958, 1959) or the Bluewater Creek Formation (Lucas and Hayden, 1989). Lithologically, the red (grayish red purple and grayish red) mudstones below this sandstone suggest that the Blue Mesa Member is underlain here by the Bluewater Creek Formation, as the Mesa Redondo Formation is generally much sandier (Cooley, 1958; Stewart et al., 1972). Preliminary clay mineral analysis indicates that these strata also closely resemble the slightly bentonitic (proportionately less mixed layer smectite/illite) mudstones typical of the Bluewater Creek Formation and are unlike the highly bentonitic mudstones that typify the Blue Mesa Member in this outcrop belt (Heckert, 1997). These deposits more closely resemble the colors and lithologies of the Bluewater Creek Formation and represent, together with similar deposits immediately to the south and west of the park, the westernmost outcrops of this unit.

However, Dubiel et al. (1995) and Hasiotis and Dubiel (1995) identify some of these same strata as pertaining to the “Moenkopi Formation,” by which they mean the “mottled strata.” Dubiel et al. (1995) and Hasiotis and Dubiel (1995) however, represent an anomalous usage of this informal unit, that runs contrary to the description of either the “mottled strata” or the Moenkopi Formation as designated and utilized by Stewart et al. (1972) and used by most subsequent workers. The term “mottled strata” is used by most to refer to color-mottled paleosols and other deposits that represent isolated deposition and paleosol formation during the development of the pre-Chinle Tr-3 unconformity of Pípiringos and O’Sullivan (1978). As such, it is used exclusive of the term Moenkopi Formation, even though it is possible that some mottled strata may represent pedogenically modified Moenkopi Formation sediments.

In PEFO, the bioturbated mudstones near the base of the section are lithologically distinct from “mottled strata” on the rest of the Colorado Plateau. True “mottled strata” are gener-

ally limy to siliceous and form distinct porcellanite beds such as those at Fort Wingate and Bluewater, New Mexico (Stewart et al., 1972; Lucas and Hayden, 1989; Heckert and Lucas, 1996). Many outcrops of the mottled strata clearly represent pedogenically modified conglomerates, with numerous pebble and cobbles of quartzite and chert and occasional relict trough crossbedding. We have not observed these lithologies anywhere in the park. Rather, in the vicinity of the Teepees, and indeed, throughout exposures of the Blue Mesa Member in the southern portion of the park, bentonitic mudstones locally display a variety of reduction spots, color-mottling and vertical coloration changes long interpreted as representing paleosol development on floodplains associated with fluvial systems in the Blue Mesa Member (Cooley, 1959; Kraus and Middleton, 1987). However, this alteration is limited to fine-grained sediments of the Blue Mesa Member. Thus, we do see some paleosol development in the Blue Mesa Member, but no evidence of the extensive bioturbation, color mottling, and silicification characteristic of the “mottled strata” and the presence of tuffaceous sandstones and bentonitic mudstones throughout PEFO demonstrates that all of the strata contain abundant volcanic detritus, which is absent in the “mottled strata” (Stewart et al., 1972; Lucas and Hayden, 1989; Hasiotis and Dubiel, 1993) and uncommon in the upper Moenkopi Formation (McKee, 1954; Lucas and Hayden, 1989).

A cursory look at any large-scale geologic map of the region surrounding PEFO (e.g., Wilson et al. 1960) indicates that the Moenkopi-Chinle contact must lie between PEFO and the town of Holbrook approximately 20 miles (32 km) to the west. Therefore, we investigated this issue by examining outcrops of the Chinle Group west of the southern entrance of the park. Here we observed several outcrops of lower Chinle Group strata and attempted to extrapolate our interpretations into subsurface of the southern PEFO, where there is additional well control (Harrell and Eckel, 1938).

Approximately 9.6 km WNW of the southern PEFO headquarters a series of low outcrops consists of (ascending) Moenkopi, “mottled strata,” Shinarump, and Bluewater Creek Formations. Just to the ESE and slightly higher topographically are outcrops of the Blue Mesa Member of the Petrified Forest Formation. All beds are essentially flat-lying. Moenkopi strata at point A (Figure 2) consist of grayish red siltstones and sandstones. Overlying “mottled strata” are thin (1.5 m), limy to siliceous, pedogenically modified silt- and sandstones. Above the “mottled strata” are 1.6 m of well-indurated, trough-crossbedded, quartzose sandstones with pebble- to cobble-sized, siliceous conglomerate typical of the Shinarump Formation. At point B are greenish-gray and blue bentonitic mudstones typical of the lower Bluewater Creek Formation as described by Lucas and Hayden (1989) and Heckert and Lucas (1996). Outcrops between B and C are mostly covered, but at point C, bentonitic, pedoturbated mudstones and ash-rich silty sandstones typical of the Blue Mesa Member crop out, thus demonstrating the superposition of the Moenkopi, mottled strata, Shinarump, Bluewater Creek, and Petrified Forest Formations typical of these strata in western New Mexico (Lucas and Hayden, 1989; Heckert and Lucas, 1996).

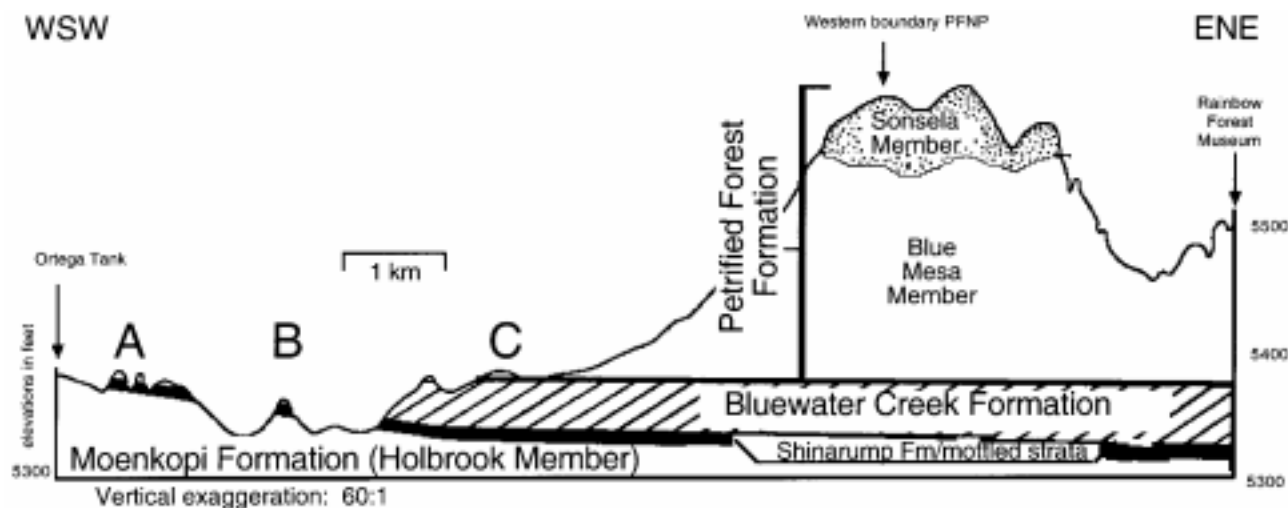


FIGURE 2—Cross-section of Triassic strata near the southern edge of PEFO. The Petrified Forest well reported by Harrell and Eckel (1938) provides stratigraphic control at the east (right) edge of the cross section. Note that mottled strata and the Moenkopi Formation are at least 120 ft (35 m) below the surface of PEFO. All outcrop control points surface checked. Synclinal structure probably the result of dissolution collapse in underlying (Permian) rocks.

Local subsurface information from the two wells discussed below indicates that perhaps 35 m of additional Chinle strata underlie the lowest mudstone unit exposed in the park before contact with the Shinarump Formation (Harrell and Eckel, 1939). Therefore, we consider the lowest grayish red and reddish purple mudstones exposed in PEFO to belong to the Bluewater Creek Formation.

SUBSURFACE STRATIGRAPHY

No recent subsurface stratigraphic information is known from within the park, so we draw principally on water-well logs published by Harrell and Eckel (1939). Two wells drilled near the rail lines at Adamana west of PEFO indicate that, after drilling through approximately 15 m of alluvium and fine-grained Chinle sediments, sandstones and conglomerates pertaining to the Shinarump Formation were encountered

(Harrell and Eckel, 1939, p. 100). Adamana is approximately 10-20 m lower in elevation than the base of our Newspaper Rock Bed type section. This yields a minimum of 25-30 m of Chinle strata below the Blue Mesa Member (Figure 3), a number more consistent with the Mesa Redondo Formation at its type locality (Cooley, 1958) than the Bluewater Creek Formation. However, the dominance of fine-grained lithologies in this region indicates that this may just be a relatively thin section of the Bluewater Creek Formation, which is normally 60 m thick (Lucas and Hayden, 1989; Heckert and Lucas, 1996). One of the wells may have encountered mottled strata ("blue shale") 10 m below the top of the Shinarump Formation.

A well drilled at the south park headquarters penetrates the Sonsela Member and approximately 90 m of fine-grained strata before the logger, park naturalist M.V. Walker, interpreted a Shinarump contact (Harrell and Eckel, 1939, p. 94). This figure and the fine-grained nature of the strata penetrated – "shales" and "sandy shales" – are consistent with a similar interpretation of a thick Blue Mesa Member with an underlying thin Bluewater Creek Formation (Figure 2). It is not clear on what grounds Walker identified the Shinarump. Perhaps he did so because at this level the well produced water, and the Shinarump is the first likely aquifer to be encountered (Harrell and Eckel, 1939). Therefore, we present these data much more tentatively than those of the Adamana wells.

TETRAPOD BIOCHRONOLOGY

Two distinct vertebrate fossil assemblages have long been recognized in PEFO: a late Carnian assemblage and a younger, Norian assemblage (Gregory, 1957; Long and Padian, 1986; Murry and Long, 1989; Murry, 1990; Lucas, 1993, 1995; Lucas and Hunt, 1993; Hunt and Lucas, 1995; Long and Murry, 1995). These assemblages were collected from narrow stratigraphic intervals below and above the Sonsela Member. Other fossils from PEFO used for biochronology include

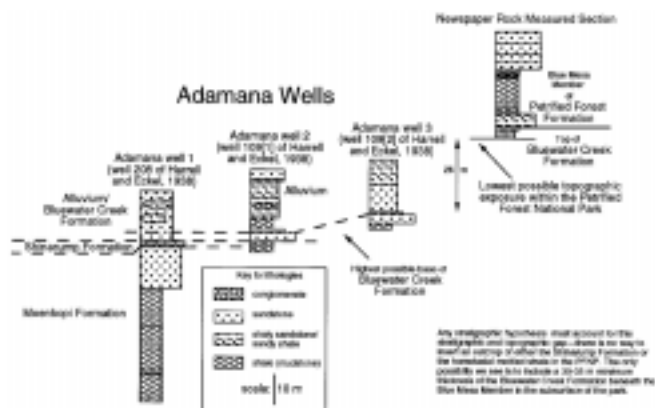


FIGURE 3—Correlation of well information of Harrell and Eckel (1938) with the Newspaper Rock section. Note that mottled strata and Moenkopi Formation sediments are well below the surface of the PFNP.

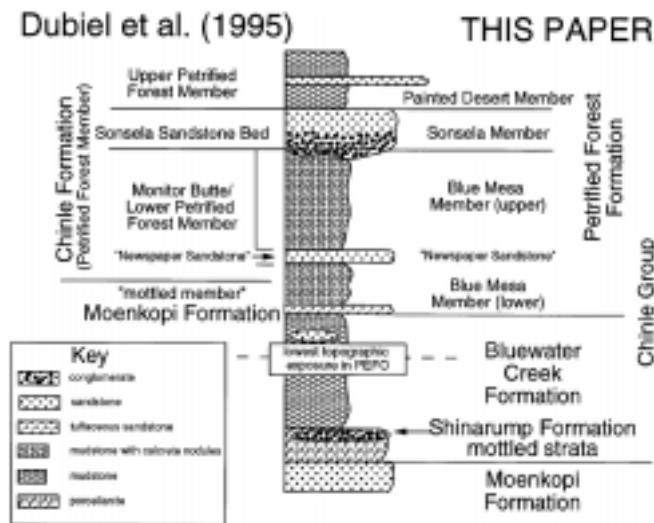


FIGURE 4—Comparison of the stratigraphic interpretations of Dubiel et al. (1995) and this paper in a schematic stratigraphic column. Subsurface information follows that in Figures 2 and 3.

palynomorphs, megafossil plants, and calcareous microfossils (Lucas, 1993).

Gregory (1957) differentiated two vertebrate fossil assemblages in PEFO but was unable to assign either to a stage within the Late Triassic. Murry and Long (1989), Lucas (1993, 1995), and Long and Murry (1995) noted that a Norian vertebrate assemblage is present above the Sonsela, whereas a Carnian assemblage has been found below. Palynology (Litwin et al., 1991), plant megafossils (Ash, 1980, 1987b), and calcareous microfossils (Kietzke, 1989; Lucas and Kietzke, 1993) indicate that the unconformity between the Sonsela and its correlatives and the underlying units approximates the Carnian-Norian boundary. Further biochronological studies by Lucas and Hunt (1993) and Hunt and Lucas (1995) assigned these faunas to the Adamanian and Revueltian land-vertebrate faunachrons, of latest Carnian and early- to mid-Norian age, respectively.

CONCLUSIONS

We use lithologic, stratigraphic, subsurface, and biochronologic information to demonstrate that there are no outcrops of the Moenkopi Formation, Shinarump Formation, or "mottled strata" in PEFO, contrary to the arguments made by some earlier workers. Figure 4 shows our interpretation of the available evidence, and how this interpretation differs from the stratigraphic interpretations advocated by Dubiel et al. (1995). Abundant surface, subsurface, and biochronologic evidence indicates that the stratigraphically lowest exposed strata in PEFO pertain to the top of the Bluewater Creek Formation, which crops out at the base of mudstone-dominated slopes in the vicinity of Newspaper Rock, the Teepees, and the Haystacks. Biochronologic evidence indicates that these strata are of latest Carnian age. Correlation from nearby outcrops to wells in and near PEFO demonstrates that at least 25-30 m of Chinle Group sediments underlie the park (Figure 4).

Therefore, we reaffirm that the oldest strata in the park are latest Carnian.

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PRELIMINARY RESULTS OF THE DAWN OF THE DINOSAURS PROJECT AT PETRIFIED FOREST NATIONAL PARK, ARIZONA

ADRIAN P. HUNT

Mesalands Dinosaur Museum, Mesa Technical College
911 South Tenth Street, Tucumcari, NM 88401

ABSTRACT—The Dawn of the Dinosaurs Project is a multi-year project to understand the pattern and ecological context of early dinosaur evolution in western North America with a special emphasis on Petrified Forest National Park (PEFO). This work has resulted in the discovery of a new dinosaur locality and numerous specimens at other locations. All dinosaur localities at PEFO are in paleosols. Dinosaur Ridge is in the upper Blue Mesa Member of the Petrified Forest Formation and all other dinosaur localities are in the lower portion of the Painted Desert Member. Late Triassic dinosaurs were dryland facies fossils and their apparent rise to dominance before the end of the Triassic in Europe and South America reflects local drying events.

INTRODUCTION

THE MESALANDS Dinosaur Museum is conducting a multi-year study of the Late Triassic faunas of Petrified Forest National Park (Dawn of the Dinosaurs Project). The goal of this project is to understand the pattern and ecological context of early dinosaur evolution in western North America with a special emphasis on Petrified Forest National Park.

Two hundred and thirty million years ago there were no dinosaurs. By 200 million years ago, every terrestrial animal, larger than a modern house cat, was a dinosaur. How did dinosaurs become the dominant terrestrial vertebrates on Earth? The fossil record in Western Europe and South America suggests that dinosaurs took over rapidly in the middle of the Late Triassic (Hunt, 1991). What does the North American fossil record indicate? Dinosaurs are rare components of Late Triassic vertebrate faunas in western North America and more than 90% of specimens have been recovered from one quarry at Ghost Ranch in north-central New Mexico. Dinosaurs usually constitute less than 5% of vertebrate fossils in any fauna in Upper Triassic strata of this area. Petrified Forest National Park (PEFO) preserves a sequence of highly fossiliferous Upper Triassic strata that include important dinosaur localities. The Dawn of the Dinosaurs Project is a multi-year study of the context and composition of Late Triassic dinosaur faunas at PEFO to help elucidate the rise of the dinosaurs.

The Dawn of the Dinosaurs Project at PEFO has three principal goals: (1) to locate all dinosaur localities in the park; (2) to study taphonomic, paleoecologic and stratigraphic context of all dinosaur localities; and (3) to compare and contrast vertebrate-fossil-bearing localities that produce dinosaur fossils with those that do not. The results of this project will facilitate the understanding of the temporal and ecologic context of early dinosaurs. This paper presents some preliminary results of the project gathered during 1996, 1997 and early 1998.

GEOLOGICAL SETTING

Two formations of the Upper Triassic Chinle Group (sensu Lucas, 1993) are present at Petrified Forest National Park (PEFO). These are the lower Petrified Forest Formation,

which is divided in ascending order into the Blue Mesa, Sonsela and Painted Desert Members and the upper Owl Rock Formation. Vertebrate fossils at PEFO are restricted to the Petrified Forest Formation. Most fossils occur in the upper portion of the Blue Mesa and the lower portion of the Painted Desert Members (Lucas, 1993; Hunt and Lucas, 1995). These faunas are respectively, Adamanian (late Carnian: late Tuvalian) and early Revueltian (early Norian), in age (Lucas and Hunt, 1993; Hunt and Lucas, 1995).

NEW DINOSAUR LOCALITY

Our surveys have resulted in the discovery of a significant new dinosaur locality named Dinosaur Ridge. This locality lies at approximately the same stratigraphic level as the Dying Grounds area in the upper portion of the Blue Mesa Member of the Petrified Forest Formation (late Carnian). Specifically it is 29.6 m below the Sonsela Sandstone Member in a sequence dominated by mudstone, siltstone and silty- and sandy-mudstone. The vertebrate assemblage derives from a sandy mudstone that is grayish purple (5P 4/2) with yellowish gray (5Y 8/1) mottles and contains thin, interbedded pebble lenses.

Dinosaur Ridge represents the only locality at PEFO of late Carnian age to produce a diverse accumulation of terrestrial vertebrates (including dinosaurs). The dinosaur specimens represent at least two species. The larger species is only known at present from a proximal tibia that represents an animal comparable in size to the specimen described from Norian strata in PEFO by Padian (1986). A smaller species is represented by several specimens including phalanges, vertebrae and tooth-bearing cranial and dentary fragments. This site is only the sixth known latest Carnian (Adamanian) dinosaur locality in western North America and only the second to yield two kinds of theropod dinosaurs.

The associated fauna is dominated by small tetrapods including several osteoderms of the small aetosaur *Acaenosuchus geoffreyi* and sphenosuchian vertebrae. Larger vertebrates are represented by fragmental bones and teeth of phytosaurs. Vertebrate coprolites are common.

Dinosaur Ridge represents a overbank mudstone, subject to a fluctuating watertable, that has been pedogenically modified. Color-mottling, carbonate concretions and permineralized roots attest to the paleosol origin of this bed.

This locality is laterally equivalent to channel avulsion facies (Hunt et al., 1996)

OTHER DINOSAUR LOCALITIES

Introduction.—Apart from Dinosaur Ridge, all dinosaur localities at PEFO are in the Painted Desert area of the northern portion of the park. The first specimens were collected in the 1980's from the most productive locality that is known as Dinosaur Hill (= Lacey Point = Bolt Quarry of some authors). The second most important locality is Dinosaur Hollow which yielded the holotype of *Chindesaurus bryansmalli* (Long and Murry, 1995).

These dinosaur localities occur in the lower portion of the Painted Desert Member of the Petrified Forest Formation (Hunt, 1995; Hunt et al., 1996). These localities are from 10-30 m below the Black Forest Bed and occur in mottled mudrocks (Hunt et al., 1995; Hunt, 1995).

The Painted Desert localities are characterized by mottled mudrocks, reduction haloes and calcrete nodules indicative of paleosol formation (Hunt et al., 1995). Dinosaur Hill represents an abandoned channel deposit that was subject to seasonal ponding and pedogenic alteration. The productive interval overlies a fine- to medium-grained, well-sorted channel sandstone.

Dinosaur Hill.—The fauna of the Dinosaur Hill locality is dominated by small, terrestrial tetrapods. Significant specimens include a partial skeleton of a theropod assigned by Padian (1986) to *Coelophysis* that is repositated at the University of California Museum of Paleontology (UCMP). This specimen (UCMP 129618) differs from the neotype of *Coelophysis bauri* in having (Hunt and Lucas, 1988): (1) femoral head more offset from the femoral shaft, with a deep groove on the proximal face of the head and a concave distal margin to the head so that the medioventral corner of the head forms a ventrally directed point; (2) a tibia with a more robust cnemial crest and very large crest for attachment of the flexor muscle and ligaments on the anterior face; (3) a larger ascending process of astragalus; (4) an ilium with larger supra-acetabular crest and proportionally shorter posterior blade; and (5) proximal tarsals that are more flared.

Other described specimens from Dinosaur Hill include a partial skeleton of the sphenosuchian *?Hesperosuchus* (cf. *Sphenosuchus* of Parrish [1991]) and teeth of an ornithischian identified by Padian (1990) as *Revueltosaurus* (Anchisaurid of Murry and Long, 1989). Other specimens included a skull and postcrania of the small metoposaurid *Apachesaurus* and undescribed specimens of a smaller theropod dinosaur.

Our collecting has yielded specimens of a third, smaller, ?ceratosaurian dinosaur including a complete femur and numerous vertebra as well as several more teeth of *Revueltosaurus*. In addition, we have collected the most complete known vertebral column of the small amphibian *Apachesaurus*. Other specimens included vertebrae of a very small archosaur and armor plates of a new aetosaur-like crurotarsan previously only known from New Mexico.

The Dinosaur Hill specimens also include a partial skeleton (vertebrae from all portions of body, limb bones,

armor plates and miscellaneous other elements) of a very small (dorsal centrum length 6 mm) terrestrial reptile. This animal is a new species and is characterized by a short, stout neck (and presumably large head) and armor that is the shape of a pitched roof with a pitted ornamentation.

Dinosaur Hollow.—The Dinosaur Hollow locality contains only the holotype of *Chindesaurus* and fragmentary specimens of a rauisuchian. This locality represents a very small fossiliferous pocket that has only yielded a few fragmentary vertebrae in recent years.

Other localities.—Fragmentary theropod specimens have been collected from other localities in the Painted Desert. These specimens all come from paleosol sites in the same stratigraphic interval as Dinosaur Hill and Dinosaur Hollow.

NON-DINOSAURIAN LOCALITIES

The Dawn of the Dinosaurs project has also involved examining localities that yield vertebrate fossils but no dinosaur remains. Prospecting for non-dinosaurian sites has yielded some significant specimens. One of the other new localities less than 200 m from Dinosaur Wash contains the partial skeleton of a new aetosaur. This taxon is distinguished by being narrow-bodied with paramedian osteoderms with a weak pattern of random pits and a ventral bar. Recovered specimens include portions of the carapace, vertebral column and limbs. This aetosaur is related to an undescribed taxon represented by a partial skeleton at the Mesalands Dinosaur Museum from the Santa Rosa Formation of Santa Fe County, New Mexico.

TAPHONOMY OF DINOSAUR LOCALITIES

Taphonomic investigations of Late Triassic vertebrate localities throughout the American Southwest have recognized three principal taphofacies in fluvial environments. Hunt et al. (1995) identified these three taphofacies in the Upper Triassic strata of PEFO: (1) channel-sandbody-hosted assemblages; (2) floodplain mudrock assemblages; and (3) paleosol-hosted assemblages. Vertebrate specimens in channelform sandstones are dominantly the isolated and abraded fragments of phytosaurs, aetosaurs and metoposaurs, which represent channel-lags. Floodplain assemblages represent the majority of fossil vertebrate specimens and include articulated specimens of larger (dorsal centra > 3 cm in length) tetrapods. These specimens occur in mudrocks formed on proximal floodplains. Paleosol assemblages are depauperate in aquatic/semiaquatic taxa and include articulated specimens of small tetrapods (dorsal centra < 6 cm in length). These assemblages occur in mottled mudrocks that contain carbonate (calcrete) nodules.

Dinosaur Ridge and all the other dinosaur localities at PEFO occur in the paleosol taphofacies. This has provided a good search model for identifying additional localities and utilization of this model led to the discovery of Dinosaur Ridge.

It appears that the stratigraphic distribution of taphofacies is not random (Table 1: Hunt and Lucas, 1993; Hunt et al., 1995). Vertebrate accumulations of the paleosol taphofacies are better known from the Painted Desert

TABLE 1—Some of the principal vertebrate localities at Petrified Forest National Park characterized by taphofacies. Note that none occur in the channel-sandbody-hosted assemblage. Locality names are those used historically, in the paleontological files at PEFO and in recent publications (modified after Hunt et al., 1995).

Floodplain taphofacies	Paleosol taphofacies	Stratigraphic unit (Member)
Dying Grounds		Blue Mesa
Crocodile Hill		Blue Mesa
Jasper Forest		Blue Mesa
Crystal Forest		Blue Mesa
Devil's Playground		Blue Mesa
Phytosaur Basin		Blue Mesa
	Dinosaur Ridge	Blue Mesa
Flattops		Painted Desert
Black Forest		Painted Desert
Billings Gap		Painted Desert
	Lungfish Locality	Painted Desert
	Dinosaur Hill	Painted Desert
	Dinosaur Hollow	Painted Desert

Member. However, this may be in part a collecting bias. Previous collectors have tended to concentrate on the collection of larger specimens and the small, fragmentary specimens from paleosols have been overlooked. We predict that future dinosaur localities will be found in the Blue Mesa Member utilizing the paleosol search model.

IMPLICATIONS FOR DINOSAURIAN EVOLUTION

Preliminary results from PEFO indicate that Late Triassic dinosaurs inhabited dryland environments where calcretes were forming and that they were absent from wetter ecosystems. In essence, Late Triassic dinosaurs were dryland facies fossils. This suggests that the apparently rapid rise to dominance of dinosaurs in the Norian as evidenced in Western Europe and South America may indicate a localized drying events. In North America, where the climate remained moist, dinosaurs remained a minor part of the overall ecosystem until the end of the Triassic. At the very end of the Triassic in western North America the eolian facies of the Wingate Sandstone indicate a drying trend (Lucas et al., 1997) that coincided with the rise to dominance of the dinosaurs on this continent.

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VERTEBRATE TRACKS AND THEIR SIGNIFICANCE IN THE CHINLE FORMATION (LATE TRIASSIC), PETRIFIED FOREST NATIONAL PARK, ARIZONA

ANTHONY J. MARTIN¹ AND STEPHEN T. HASIOTIS²

¹Geosciences Program, Emory University, Atlanta, GA 30322.

²Department of Geological Sciences, University of Colorado, Boulder, CO 80309.

ABSTRACT—Previous research in the Upper Triassic Chinle Formation in Petrified Forest National Park (PEFO) has only yielded two isolated footprints, which is in stark contrast to the comparatively large number of vertebrate body fossils found there. We report here the discovery of a numerous reptilian tracks, including two dinosaur tracks, in the Chinle Formation in PEFO, considerably expanding the paleontological database for vertebrates in PEFO.

Tracks of phytosaurs, small-sized reptiles, and dinosaurs occur in ripple-laminated sandstones of the Monitor Butte Member, whereas other small- and intermediate-sized reptile tracks occur in cross-bedded sandstones of the Petrified Forest Member. A phytosaur trackway is discontinuous but consists of 12 footprints having a total length of 2.2 m and was likely made by a juvenile animal with a walking movement that turned slightly to the right. One small reptile trackway (comprised of *Rhynchosauroides* isp.) represents lateral movement by the tracemaker, rather than straight, forward locomotion. One isolated print that we are attributing to a large theropod and a smaller partial print formed by either a theropod or ornithomimid supplement skeletal evidence of dinosaurs in the area. Tracks in the Petrified Forest Member are numerous in places, most show claw marks, and are smaller than phytosaur tracks, suggesting intermediate-sized reptilian tracemakers. Most of these tracks apparently are not parts of continuous trackways, although some show manus-pes pairings, and they are relatively consistent in size and shape, pointing toward a probable adult animal of the same species as a tracemaker.

Vertebrate tracks and trackways in the Chinle Formation of PEFO affirm that sedimentological conditions were sufficient in this area for footprint preservation, although most tracks likely represent undertracks. Further investigation of Chinle strata should yield more information regarding the identity of tracemakers, further reconciling the vertebrate body fossil and trace fossil records in this area.

INTRODUCTION

VERTEBRATE BODY fossils are common in the Upper Triassic Chinle Formation of the southwestern U.S. and have been the subject of much research (Camp, 1930; Camp and Welles, 1956; Colbert, 1972; Padian, 1986; Long and Padian, 1986; Lucas and Hunt, 1993). Reports of vertebrate trace fossils of the Chinle, especially tracks and trackways, are also well known from the upper part of the Chinle (Hunt et al., 1989; Lockley et al., 1992; Lockley and Hunt, 1993; Lockley et al., 1993; Lockley and Hunt, 1995, p. 99, 103-104). However, tracks from the lower part of the Chinle throughout the southwestern U.S. are apparently uncommon (Lockley and Hunt, 1995, p. 103-104), and the Chinle of Petrified Forest National Park (PEFO) of northeastern Arizona has had only two isolated footprints reported, both of *Rhynchosauroides* isp. (Santucci and Hunt, 1993; Santucci et al., 1995). The apparent lack of tracks and trackways in PEFO has been interpreted as a result of wet conditions during deposition of some Chinle sediments in the region (M. G. Lockley and A. P. Hunt, personal communication with Hasiotis, 1994; Lockley and Hunt, 1995, p. 103-104). Phytosaurs, the most common vertebrates represented by body fossils in PEFO, have had none of their tracks reported. Other animals in PEFO, such as metoposaurs, rauisuchians, aetosaurs, theropods, dicynodonts, and various other reptiles and amphibians, also seemingly left no trackway evidence, despite their presence indicated by body fossils in parts of the Chinle (Long and Padian, 1986).

We propose that because invertebrate trace fossils are exceedingly common and diverse in the Chinle of PEFO, despite the lack of corresponding body fossils (Dubiel and Hasiotis, 1995; Hasiotis and Dubiel, 1993a, b, 1995), then preservational conditions conducive for invertebrate traces should also apply to vertebrate traces. This observation, combined with the presence of vertebrate tracks in the Chinle outside of PEFO, implies that tracks should be present. Confirmation of their presence is the purpose of this report, where we document the discovery of tracks and trackways made by unknown reptilian tracemakers, phytosaurs, and dinosaurs in PEFO; the phytosaur and dinosaur tracks are the first ever interpreted from this area.

STUDY AREA AND STRATIGRAPHY

PEFO, in northeastern Arizona, has one of the best exposures of the Chinle in that region. Sediments composing the Chinle Formation were deposited in fluvial, palustrine, and lacustrine environments of conterminous continental depositional basins and modified by various stages of pedogenesis during the Late Triassic (Dubiel, 1989; Hasiotis and Dubiel, 1993b). Tracks described here occur in the southern part of PEFO in the Monitor Butte and Petrified Forest Members of the Chinle. Tracks in the Monitor Butte occur in the region of "The Tepees" and tracks in the Petrified Forest Member occur in the region of "Rainbow Forest" and "The Flattops." The geology of these areas has been well documented in previous studies (Ash, 1986; Dubiel et al., 1994; Demko, 1995; Hasiotis

FIGURE 1—*Rhynchosauroides* trackway from Monitor Butte Member, Chinle Formation, PEFO, showing lateral movement of tracemaker (from right to left).

and Dubiel, 1995).

Tracks and trackways in the Monitor Butte Member primarily occur on the tops of ripple-laminated and plane-bedded, fine-grained sandstones in the upper part of the Newspaper Sandstone fluvial complex in the area of The Tepees, mostly at Lone Tepee. Tracks in the Petrified Forest Member occur in the base of a trough cross-bedded, medium-grained sandstone in a thick sandstone (Flattop #1) above the Sonsela/Rainbow Forest sandstone complex, which is near the base of the Petrified Forest Member, in the south end of PEFO (Rainbow Forest).

DESCRIPTION AND INTERPRETATION OF VERTEBRATE TRACKS

Tracks in PEFO represent at least four distinctive groups of tracemakers and can be broadly categorized on the basis of track size and shape. These groups of tracemakers are: (1) small reptiles, possibly rhynchocephalians; (2) intermediate-sized reptiles; (3) phytosaurs; and (4) dinosaurs.

Small Reptiles.—The smallest tracks in PEFO are assignable to the ichnogenus *Rhynchosauroides*. Specimens of *Rhynchosauroides* consist of five- or four-toed prints, foot-print lengths and widths of about 1 cm, and individual toe widths and lengths of 2 mm and 5–7 mm, respectively. These tracks occur in both the Monitor Butte and Petrified Forest Members, although a trackway is preserved in the Monitor Butte. This trackway is unique in its evidence of lateral movement by the tracemaker. Manus prints, preserved as negative-relief epichnia (molds) are parallel to one another, whereas pes prints are apparently absent from the same bedding plane (Figure 1). Some of the prints overlap one another, showing a sequence of lateral movement of the tracemaker from right to left. Other tracks that more-or-less parallel the lateral trackway may or may not have been made by the same individual tracemaker, although slight differences in size and orienta-

FIGURE 2—Bedding plane exposure of tracks used for track census in Table 1; float block from Petrified Forest Member, Chinle Formation, PEFO.

tion argue more for multiple individuals. If made by the same individual, different preservation modes and lack of preservation of manus prints are responsible for gaps between tracks.

Claw marks without pedal impressions are clearly undertracks, pointing to subtle differences in substrate conditions in the original preservational medium. Close-up views of some tracks also reveal some evidence of foot rotation where sand was pushed up behind the foot as the tracemaker moved. Such details are indicators of a firm, cohesive substrate in places, sufficient to preserve the effects of movement by a rather small vertebrate.

Rhynchosauroides tracemakers left abundant tracks in some Late Triassic deposits (Lockley and Hunt, 1995, p.95) and the most probable tracemakers for *Rhynchosauroides* were rhynchocephalians (Lockley and Hunt, 1995, p. 87). A few specimens of *Rhynchosauroides* were also found in the Petrified Forest Member, although trackways were lacking. We anticipate that the abundance of this ichnogenus in the Chinle of PEFO will be better established through future investigations.

Intermediate-Sized Reptiles.—Numerous tracks in the Petrified Forest Member indicate an abundant and active small- and medium-sized tetrapodal fauna in this region. Tracks are preserved as positive-relief hypichnia (casts); the majority of tracks observed were in float blocks but were easily traceable to adjacent outcrops of Flattop Sandstone Bed #1. Some in-situ tracks were found on the underside of a bed within the middle of this thick sandstone unit, thus supporting our correlation of the tracks with their stratigraphic position.

Most tracks in the Petrified Forest Member were apparently made by similar tracemakers, based on consistencies in size and shape of the prints. One bedding plane yielded 15 identifiable prints that showed little variation in size parameters, although not all toe prints were preserved (Figure 2; Table 1). Some manus-pes pairs are evident on this bedding plane, indicating quadrupedal tracemakers, but we could not discern any continuous trackways. Tracks are not distinctive

TABLE 1—Track census and descriptive statistics from bedding plane in Flattop Sandstone Bed #1, Petrified Forest Member (n = 15). Prints are presumed pes impressions.

	Mean	Median
Track Width	6.3 ± 1.6 cm	5.8 cm
Track Length	4.3 ± 1.3 cm	4.0 cm
Width/Length Ratio	1.5 ± 0.5	1.4
Number of Toes	2 (1 specimen); 3 (9 specimens); 4 (5 specimens) Mode = 3	3

enough to assign to a specific ichnogenus and their variable preservation, probably as undertracks, argues against applying such designations. Nevertheless, claw impressions are clearly represented by most specimens, thus reflecting reptilian tracemakers.

The considerably larger size of these tracks, in comparison to specimens of *Rhynchosauioides*, clearly indicates larger tracemakers than rhynchocephalians. However, their consid-

erably smaller dimensions relative to foot sizes of larger quadrupedal tracemakers represented by body fossils in the region, such as aetosaurs, phytosaurs, or dicynodonts (Long and Padian, 1986), precluding adults of these animals as sources of the larger tracks. Although these tracks could be from juvenile animals of larger quadrupeds, the size consistency of most tracks suggests that they are more likely from adult reptiles of an unknown but similar species.

Phytosaurs.—Individual tracks and a trackway in the Monitor Butte Member provide the first compelling trace fossil evidence in PEFO of phytosaurs, commonly represented by body fossils in the Chinle there. One individual track (Figure 3a) displays four well-defined claw marks (6-11 cm long) that curve backward from their initial penetration of the sediment; overall track width is about 14 cm. This same curving of four claw marks is also observable in the clearest print in a trackway from the same unit (Figure 3b). Claw marks are similar in length to the previously described footprint (6-12 cm long), although the track width is slightly less (10 cm). A third footprint (not associated with a trackway) shows five foot pads without claw marks; width is 10.8 cm and length is 15.0 cm. This track, interpreted as a pes print, also has a mediolateral pad impression associated with the fifth metatarsal impression.

The trackway (Figure 4) is 2.2 meters long, 37-38 cm wide, and has 12 total prints, although it is missing some impressions in the sequence. The overall trend of the trackway turns slightly to the right of the tracemaker. The trackway shows a similarity in spacing between manus and pes impressions (24-28 cm, out of four manus-pes pairs), although stride measurements are uncertain because of the incompleteness of the trackway and partial preservation of tracks. Nevertheless, right pes-pes stride is about 35 cm at the beginning of the trackway and this measurement served as a predictive indicator for other impressions. Variability in measurements can be attributed to changes in surface topography, the turning motion of the tracemaker, substrate conditions, measurement of only partial prints, and their probable preservation as undertracks.

Based on previous assessments of phytosaur body fossils, their functional morphology, and presumed pedal morphology, our evidence points toward phytosaurian tracemakers for the tracks we have described here. The curving of the claw marks indicate a rotational aspect to the tracemaker's movement, which is consistent with interpreted movement for phytosaurs (Parrish, 1986). The obscured impressions of digits (which are not visible in most tracks of the trackway) are also consistent with this rotation of the pes. Footprint sizes are within the range of known phytosaur sizes, although some tracks described here could be from juvenile animals. The trackway width, manus-pes spacings, and stride length could be attributed to other large vertebrate tracemakers (i.e., rauisuchians, aetosaurs) but when viewed in combination with the preceding evidence are not inconsistent with a juvenile phytosaurian tracemaker. Additionally, the sheer abundance of phytosaur body fossils in PEFO in comparison to other quadrupedal vertebrates argues that any relatively large tracks

Figure 3—Tracks interpreted as made by phytosaurian tracemakers in Monitor Butte Member, Chinle Formation, PEFO. *Top*, individual track not associated with a trackway. *Bottom*, track (presumed pes impression) from beginning of trackway shown in Figure 4.

gion and parts of two toes proximal to the heel. Track form is tridactyl and a medial toe pad distal from the heel is also evident. Overall track length is 26 cm and outside toes are 19–20 cm long, presumably representing minimum size of the track owing to its incompleteness. Pressure ridges are evident in the heel, lower part of the middle toe, and distal toe pad impressions and all three ridges reflect the animal's shifting of weight and subsequent movement in the same direction. Assuming bipedalism and forward movement, the track is from a left pes. We are attributing the track to a large theropod, although without better preservation we cannot make a more precise designation.

A smaller partial print (Figure 5b), also a positive-relief hypichnion, shows a clear impression of one toe (with accompanying clawmark) and a partial impression of the middle toe; the presumed third toe is missing from the print. This track, similar in impression to the other track, is also interpreted as a left pes print. The size and shape of the partial print is comparable to pes impressions of *Aetripus*, a dinosaur track described from the Chinle outside of PEFO (Lockley and Hunt, 1995, p. 85). The interpreted tracemaker for *Aetripus* has been a subject of contention but has been most persuasively attributed to ornithischians (Olsen and Baird, 1986). However, *Aetripus* is, by definition, a track associated with a quadrupedal trackway (Olsen and Baird, 1986), thus until further evidence of quadrupedalism is seen with similar tracks in the Chinle of PEFO, we hesitate to assign this ichnogenus name (or any other) to this partial track.

Both tracks provide independent evidence of a dinosaurian presence in the region of PEFO at the time of Monitor Butte deposition and support body fossil evidence of dinosaurs, although a large enough tracemaker for the first described dinosaurian track has not yet been found here. Indeed, the size of this track is a notable exception to smaller dinosaur tracks found in age-equivalent strata of the region and a discerned gradual increase in dinosaur footprint size toward the Triassic–Jurassic boundary, as postulated by Lockley and Hunt (1995, p. 104–105).

SUMMARY OF RESULTS AND CONCLUSIONS

Tracks and trackways discovered in the Chinle Formation of Petrified Forest National Park (PEFO), northeastern Arizona, are locally abundant and reflect at least four distinctive tracemakers. A list of possible tracemakers for any vertebrate tracks found in the Park, based on skeletal data, would include the following animals: metoposaurs, phytosaurs, aetosaurs, rauisuchids, poposaurs, trilophosaurs, rhynchosaurs, spheodontids, and theropods. Interpretation of tracemakers from tracks reported here are difficult owing to the incomplete preservation of most tracks. Thus, our interpretations are limited to small reptiles, intermediate-sized reptiles, phytosaurs, and dinosaurs. We have excluded rauisuchians and aetosaurs as tracemakers for what we interpret as phytosaur tracks for reasons explained previously, but other tracks made by intermediate-sized reptilian tracemakers may relate to poposaurs, trilophosaurs, and spheodontids. Rhynchocephalians are most likely represented by the smallest footprints,

FIGURE 4—Dislodged block in Monitor Butte Member, Chinle Formation, PEFO, showing trackway interpreted as made by phytosaurian tracemaker (chalk outlines around tracks). Snowflakes and *S. Hasiotis* for scale.

found in the area showing quadrupedalism likely belong to phytosaurs, if track abundance is at all correlative with body fossil abundance.

Tracks indicative of phytosaurian behavior do not seem as common in the Petrified Forest Member as in the Monitor Butte. However, one large four-toed track found there might have been made by a phytosaur, although the absence of identifiable claw marks allows for other tracemaker interpretations, such as metoposaurs. Nevertheless, this track hints at the presence of a larger tetrapodal fauna at the same time and place as the smaller tracemakers, which may lead to more discoveries of larger tracks in the Petrified Forest Member.

Dinosaurs.—Two individual tracks from the Monitor Butte Member suggest the presence of dinosaurian tracemakers. One print, although incomplete, shows dimensions consistent with large theropod tracks in the Chinle from outside of PEFO (Figure 5a). The track is preserved as a positive-relief hypichnion with well-defined relief in the heel re-

FIGURE 5—Individual tracks interpreted as made by dinosaurian tracemakers, Monitor Butte Member, Chinle Formation, PEFO. *Left*, Large partial track, presumed theropod tracemaker. *Right*, Small partial track showing claw mark on far right toe, presumed theropod or ornithischian tracemaker. Lens cap = 5.5 cm in both pictures.

such as *Rhynchosauroides*.

Significant aspects of the our study include the following:

- Tracks and trackways represent the first substantial record of such vertebrate trace fossils in strata from PEFO.
- Most tracks simply indicate walking behavior, although the *Rhynchosauroides* trackway in the Monitor Butte apparently represents lateral movement, which is unusual for fossil vertebrate tracks.
- The phytosaur trackway in Monitor Butte is one of the few interpreted from the geologic record; some workers have postulated that their preservation was unlikely because of phytosaur locomotion.
- The dinosaur tracks are the first interpreted from the confines of PEFO and they help to confirm body fossil evidence of dinosaur presence in the area during the Late

Triassic.

- The sheer abundance of tracks in the Petrified Forest Member and preservation of other tracks show that substrate conditions were conducive for track preservation within the area represented by PEFO.
- The large theropod track in the Monitor Butte is an apparent exception to stratigraphic trends postulated for theropod footprint size during the Late Triassic.

In conclusion, we anticipate that our findings will encourage future exploration of Chinle strata within PEFO for similar and different tracks, as well as better correlation between the traces and the tracemakers through a combination of ichnology and paleontology of vertebrate skeletal material.

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VERTEBRATE COPROLITES AND COPROPHAGY TRACES, CHINLE FORMATION (LATE TRIASSIC), PETRIFIED FOREST NATIONAL PARK, ARIZONA

ALLISON M. WAHL¹, ANTHONY J. MARTIN², AND STEPHEN T. HASIOTIS³

¹Department of Biology, Emory University, Atlanta, GA 30322.

²Geosciences Program, Emory University, Atlanta, GA 30322.

³Department of Geological Sciences, University of Colorado, Boulder, CO 80309.

ABSTRACT—Although vertebrate coprolites have been noted by previous workers in parts of the Late Triassic Chinle Formation, Petrified Forest National Park (PEFO), little attempt has been made to better assess the paleontological significance of these trace fossils. This study represents the first such attempt to describe and interpret coprolites from the Chinle in the PEFO by using both qualitative and quantitative methods. Coprolites also contain traces of coprophagy (consumption of the original feces), which provides further information about coprolite taphonomy and nutrient cycling during the Late Triassic in this region.

Coprolites occur in the Petrified Forest Member in association with a bone bed known in PEFO as “The Dying Grounds;” the environment is interpreted as a perennial swamp or watering hole. Coprolites are primarily ellipsoidal and cylindrical; specimens examined have an average of 1.4 ± 0.4 cm diameter ($n = 45$) and lengths range from 1–6 cm, although most specimens are incomplete. Digestive tract morphology of tracemakers is revealed by coprolite size, surface markings (vertical parallel and horizontal heteropolar striations), and pinched or tapered ends. Bone fragments and concentrations of calcium and phosphorus, evident in some samples through macroscopic and SEM examinations, reflect a carnivorous feeding habit for at least some tracemakers. Likely candidates for tracemakers, estimated through the vertebrate body fossil record for this region, are aetosaurs, metoposaurs, phytosaurs, rauisuchians, or theropods.

About a third of examined coprolites have minute-diameter holes (0.7 ± 0.3 mm; $n = 16$, measured through SEM), some of which show interconnections through tunnels parallel to coprolite surfaces. We interpret these features as coprophagy traces made by insects, such as dipteran larvae, which may be among the oldest reported such traces in the geologic record. These traces demonstrate cycling of organic material from vertebrate feces occurred soon after fecal formation and represent time preceding early diagenesis, exhumation, transportation, and final burial of feces.

INTRODUCTION

ALTHOUGH COPROLITES (fossilized feces) have gained some popular recognition in recent years, particularly as related to dinosaurs (Hunt et al., 1994; Wright, 1996), they remain comparatively less studied than trace fossils such as tracks, trails, and burrows. Although unpopular, coprolites are nevertheless valuable trace fossils because of their direct relation to paleodiet. These trace fossils can be used to determine the existence of certain food types, such as plants or animals, during the time of fecal formation (Walderman and Hopkins, 1970; Sohn and Chatterjee, 1979; Chin 1990; Chin et al., 1991a,b) and digestive tract morphology (Thulborn, 1991). Traces within coprolites, such as burrows by organisms consuming organic material in the original feces, are also instructive for understanding nutrient cycling in the context of the tracemakers’ environments (Chin and Gill, 1996).

Trace fossils in strata of the Chinle Formation (Late Triassic) of Petrified Forest National Park (PEFO) are very common, interpreted as originating from both invertebrate and vertebrate tracemakers in a variety of continental settings (Dubiel and Hasiotis, 1995; Hasiotis and Dubiel, 1993a,b, 1995; Martin et al., 1997). Although Late Triassic coprolites in nearby New Mexico were investigated by Ash (1978) and Weber and Lawler (1978), vertebrate coprolites in the Chinle of PEFO have not been thoroughly described or interpreted in terms of their taphonomic and paleoecologic significance. Here

we provide a preliminary description of vertebrate coprolites and their accompanying trace fossils. The latter may be the oldest interpreted evidence of feeding on vertebrate fecal remains (coprophagy) in the geologic record.

STUDY AREA AND STRATIGRAPHY

The 45 specimens in this study were collected in PEFO from a smectitic purple-gray mudstone in the Petrified Forest Member of the Late Triassic Chinle Formation (Figure 1). The bone bed containing the coprolites is referred to as the “Dying Grounds” by some workers in this region because of its abundance of skeletal material. This area was formed mainly through deposition in low-sinuosity streams (Kraus and Middleton, 1987), as represented by channel sandstones, floodplain-paleosol mudstones, and locally evident organics-rich pond and bog mudstones (Parrish, 1989). The depositional environment for final coprolite burial is interpreted as a pond or floodplain.

METHODS

The 45 specimens were initially assessed through qualitative and quantitative analysis. Each specimen was examined for specific morphology. The samples exhibited most standard morphological characteristics for coprolites, as outlined by Thulborn (1991) and Hunt et al. (1994), and thus proved capable of categorization. Sizes were assessed through measurement and calculation of circumference, diameter, radius, and length. Circumferences were taken from the three

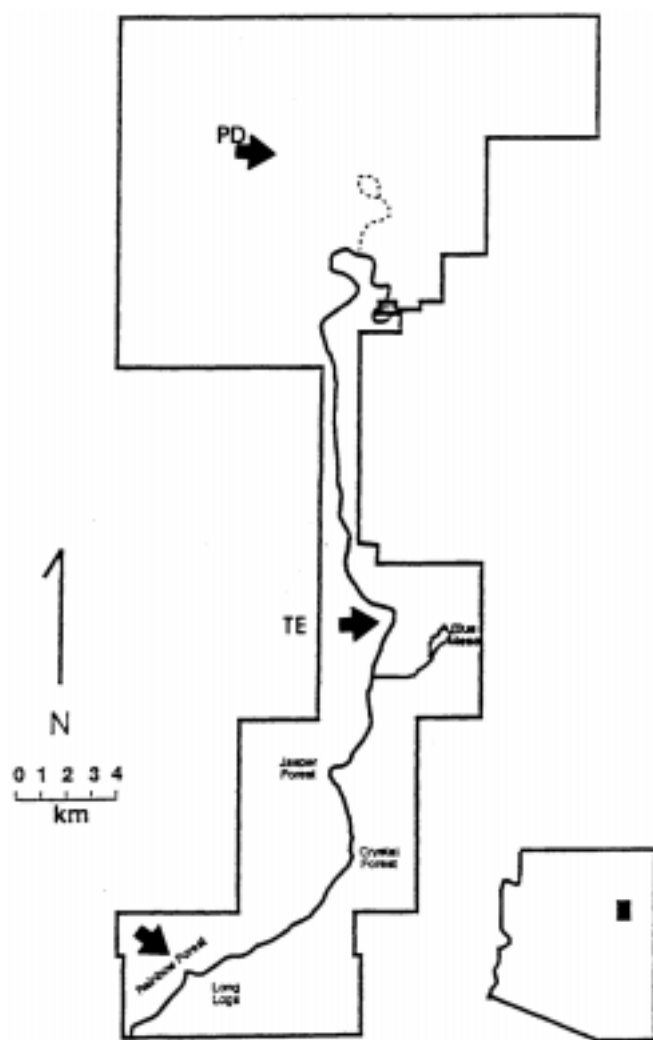


FIGURE 1—Location of coprolite samples in Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona; “D.G.” indicates “Dying Grounds.”

thickest zones on coprolites and averaged to give the approximate circumference. Diameter and radii were then calculated from circumference data. Length was incomplete in nearly all specimens but measurements were taken for the sake of comparison.

About one-third of specimens showed regularly shaped holes and connections between holes, hence scanning electron microscopy (SEM) was employed to better describe and measure these features. Samples for SEM investigation were washed with acetone, then vacuum-pumped dry and gold coated with a Denton Vacuum DESK II Cold Sputter/Etch Unit. Once samples were coated with gold, they were placed on the mounting stage in the SEM. The SEM, a Zeiss DSM-962, was furnished by Fernbank Natural History Museum in Atlanta, Georgia, for this portion of the study. The SEM allowed examination of microstructures and accurate measurements of diameters of the suspected burrows within the coprolites. Carbon-coated coprolites were also examined for elemental analysis on the same unit.

TABLE 1—Percentages of morphological categories or features for coprolites from Petrified Forest Member, Chinle Formation, PEFO (n = 45).

Amphipolar = 0%	Bend = 26%
Heteropolar = 0%	Radial = 0%
Cylindrical = 93.3%	Concentric = 42%
Pellet = 0%	Parallel Striations = 28%
Pinched End = 24%	Regular Pits = 13%
Tapered End = 55%	Irregular Pits = 35%
Constriction = 22%	

RESULTS

Coprolite morphological terms include 15 types commonly used in the coprolite literature. Neumayer (1904) coined the terms amphipolar and heteropolar; Thulborn (1991) subsequently initiated the use of isopolar and anisopolar as descriptive terms for coprolite morphology. Of these 15 descriptive terms, at least one of nine could be applied to the examined Chinle specimens (Table 1). Most of the samples are incomplete and broken on one end, which makes some of the morphological types difficult to distinguish. For example, determination of isopolar and anisopolar requires two complete ends, but because the entire length of the coprolites did not always remain intact, these types could not be interpreted. Weathering also may have broken down surface morphology, therefore this feature also could not be documented in some samples.

Coprolite sizes varied to some degree (Table 2) but with more sampling a normal distribution might become more apparent. Because the coprolites were mostly ellipsoidal and cylindrical, circumference, diameter, radius, and length were the most useful measurements to quantify. Specimens examined have an average of 1.4 ± 0.4 cm diameter, and lengths range from 1–6 cm, although because most specimens are incomplete, these lengths represent minimum values.

Regularly-sized holes and connections between holes on some coprolites, examined through SEM, showed evidence of probable coprophagy traces. Sample PEFO-14 (Figure 2a-b) proved to be the best sample for the study of these regularly shaped holes. With the SEM, 16 well-defined holes were measured and analyzed. From these measurements diameters ranged from 0.28 to 1.32 mm, with a mean of 0.7 ± 0.3 mm. Proportionately, 38% of the holes are in the 0.7 mm range, which demonstrates a regularity in size that is probably attributable to a similar-sized tracemaker. Analysis of the holes with the SEM also showed tunneling and interconnections parallel to the coprolite surface, which suggest a trace made by a living organism, as opposed to gas bubbles that might be associated with decay of fecal material.

TAPHONOMIC AND PALEOECOLOGIC SIGNIFICANCE OF CHINLE COPROLITES

Because fossilization occurred in a wetland environment, the tracemakers were probably carnivores or omnivores because digestion of animals with skeletons would leave bone residues in the fecal matter (Thulborn, 1991). Bone matrix is

Table 2 - Size data for coprolites from Petrified Forest Member, Chinle Formation, PEFO, Arizona (n = 45). All sizes in centimeters. Radius values calculated from diameter data (based on circular cross-sections from specimens).

	Range	Mean	Standard deviation
Circumference	2.4-8.27	4.4	1.3
Diameter	0.76-2.63	1.4	0.4
Radius	0.4-1.3	0.7	0.2
Length	1.0-6.1	2.7	1.2

very useful in fossilization because it provides minerals and structure from which apatite can form. Herbivore scat tends to contain larger quantities of undigested plant matter which will decay instead of fossilize (Chin et al., 1996), hence most coprolites are likely from carnivore tracemakers. Bone fragments in Chinle coprolites are evident, as well as localized high concentrations of calcium and phosphorus (indicated by elemental analysis on the SEM), which also indicates a carnivorous diet for most tracemakers. Furthermore, cylindrical morphology, observed in 93% of Chinle specimens, is also suggestive of meat-eating tracemakers. In modern terrestrial vertebrates, pellet-shaped scat is typically formed by herbivores, whereas cylindrical scat is more commonly left by carnivores (Halfpenny and Biesot, 1986).

End morphology can also suggest other aspects of digestion, such as how the anal sphincter of an animal may have worked. Feces with pinched ends may have been excreted from an animal with a stronger or faster-closing sphincter muscle than those that produce feces with tapered ends. Constrictions and bends could be incurred after exiting the body but otherwise they suggest periodicity of peristalsis of the large intestine. Parallel striations also characterize the large intestine but they imply striations on the internal surface of the intestine. Because none of the coprolites exhibit heteropolar striations, they can not be attributed to fish (Thulborn, 1991). Irregular pits, as opposed to regularly shaped holes attributable to coprophagy, may be a product of transportation of coprolitic material before final burial or holes produced when bone fragments dislodged from the exterior of the coprolite.

Coprophagy traces have been rarely evaluated. Grooves discovered in an Eocene coprolite might be attributed to dung beetles (Bradley, 1946). Chin and Gill (1996) evaluated coprophagy traces from Late Cretaceous coprolites and attributed them to dung beetles, but no coprophagy traces of any kind have been reported from coprolites as old as Late Triassic. Dung beetles are clearly too large as possible tracemakers for burrows in the Chinle coprolites, but possible tracemakers may have been dipteran larvae, such as those exemplified by modern dung-eating flies (Petersen and Wiegert, 1982; Nilsson, 1983; Iwasa, 1984; Stevenson and Dindal, 1987; Zhemchuzhina and Zvereva, 1989; Stoffolano et al., 1995). Fungal microrhizae are an alternative hypothesis for the traces, but the regularity in size and interconnectiveness of the traces are contrary to the size variation and randomness exhibited by microrhizal structures.

Coprolite makers most likely would have been represented

by any or all of four possible carnivorous tracemakers, indicated by body fossils found in PEFO: phytosaurs, metoposaurs, theropods, and rauisuchians (Parrish, 1989). An absence of flattening that normally occurs with impact upon the open-air ground suggests that these coprolites were probably excreted into water (Waldman and Hopkins, 1970), favoring an aquatic habitat for the trace makers. The floodplain region could have accommodated each of these inhabitants; metoposaurs and phytosaurs were especially likely candidates because of their aquatic life habits and the presumed deposition of fecal material in water (interpreted from the nonflattened specimens). Aetosaurs or other herbivore tracemakers may have been responsible for the 7% of non-cylindrical coprolites, but no other evidence other than shape reflects a herbivore origin.

CONCLUSIONS

From this study we show that it is possible to classify the PEFO coprolites into descriptive categories. Specifically, because the coprolites in this study showed many similar and consistent morphological attributes, they were possibly left by similar types of animals. The overwhelming percentage of cylindrical coprolites at least suggests similar intestinal workings and diet, and other evidence, such as bone fragments and high concentrations of calcium and phosphorus in some specimens, reflect carnivorous tracemakers. None of the examined coprolites was left by fish because none of them have heteropolar markings, typical of fish feces; correlation with known body fossils in PEFO thus points toward theropods, rauisuchians, metoposaurs and phytosaurs as possible tracemakers, with herbivorous aetosaurs as less likely candidates. Further study of Chinle coprolites in PEFO should better define tracemakers.

Evidence of coprophagy in Chinle coprolites is reasonably conclusive because of the overall morphology and regularity of holes and tunnels evident in some specimens. More research is necessary to better delineate possible tracemakers but insects, such as dipteran larvae, are a possibility. Fungal coprophages, which would be evident through microrhizae, represent an alternative explanation for tracemakers but the regularity and size of the traces argue against this interpretation. If these traces are more persuasively shown as related to insect activity in vertebrate feces, they would be the oldest reported such traces in the geologic record.

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FIGURE 2—Coprolite sample PEFO-14. *Top*, Macroscopic view, showing overall cylindrical morphology of coprolite and burrows in coprolite; millimeter scale. *Bottom*, Composite SEM image of coprolite with view of numerous holes and tunnels between holes, representing burrows (coprophagy traces) in sample.

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DINOSAUR FOOTPRINTS IN THE BASAL NAVAJO SANDSTONE (LOWER JURASSIC) AT PIPE SPRING NATIONAL MONUMENT, NORTHWESTERN ARIZONA

ROGER J. CUFFEY, MARIA J. DI NARDO-MAGILTON, AND BRYAN J. HERZING

Department of Geosciences, 412 Deike Building
Pennsylvania State University, University Park, PA 16802

ABSTRACT—Three dinosaur footprints, representing a single trackway, were recently discovered on the mesa immediately west from the visitor center at Pipe Spring National Monument, in the basal part of the thick Navajo Sandstone, dated previously as Early Jurassic (Toarcian). Imperfect preservation and ichnotaxonomic splitting complicate their identification; they seem closest to several species of *Eubrontes* (moderately large theropods) known from correlative parts of the East Coast Newark Supergroup.

INTRODUCTION

DINOSAUR FOOTPRINTS have long been known from early Mesozoic sandstones across the Colorado Plateau, frequently mentioned, but seldom fully documented. An early photograph was provided by Gregory (1917), a partial listing of later finds by Stokes (1978).

Until recently, fossils of this kind had not been reported from Pipe Spring National Monument. Then, Stokes (1988) published a photograph showing a detached or float cast of a footprint on display there. That picture attracted attention (Santucci, 1991), and R. J. Cuffey visited Pipe Spring in 1995. Park Service personnel on duty told him of a couple of footprints along the hiking trail. Cuffey located those, side by side, and found a third out in front of them; a preliminary note announced these footprints (Cuffey, Di Nardo, and Herzing, 1997), which are illustrated in the present paper.

Pipe Spring National Monument is primarily a memorial to late-19th-century cattle ranching, but also includes significant geologic resources, including the newly discovered dinosaur footprints.

LOCATION

Pipe Spring National Monument is located in Mohave County, on the

Kaibab-Paiute Indian Reservation, 13.4 mi (21.4 km) west of Fredonia. Its visitor center is about a third of a mile north of the east-west paved highway (Arizona 389). The footprints are along the foot trail up onto the mesa's top, at 5080 feet elevation, above and behind the visitor center, 0.2 mi (0.4 km) N35°W from that center. The footprints are in the NW1/4 SE1/4 SE1/4 sec. 17, T.40 N., R.4 W., Pipe Spring 7.5¢ quadrangle.

STRATIGRAPHY

The southern face (Figure 1) of the mesa west of the visitor center consists of a lower red covered slope (presumably Moenave), a thin middle dark red sandstone cliff (Kayenta), and a high-standing thick cap of light orange to tan sandstone (Navajo). These sandstones are part of the widespread Glen Canyon Group. The low flat plain on which the highway runs is apparently underlain by the Chinle (Upper Triassic).

FIGURE 1—South face of the mesa at Pipe Spring National Monument, west of the visitor center. The dinosaur footprints are on top of the low bench extending eastward from the high mass of the mesa. Upper half of the mesa is light-colored Navajo Sandstone, the dark-colored thinner sandstone cliff in the middle of the mesa is the Kayenta, and the covered slope forming the lower half of the mesa buries various lower stratigraphic units (particularly within the Moenave).

The footprints are preserved in orange-red or light orange, concave-upward cross-bedded, medium to coarse, quartz sandstone, 6 ft (2 m) above the base of the Navajo Sandstone, of which roughly 500 ft (160 m) more is exposed higher on the mesa to the west. The Navajo is a classic eolian dune or erg sandstone, and previous investigations nearby have dated it as comparatively high in the Lower Jurassic, specifically Toarcian or about 180-185 million years old.

The base of the Navajo is easily recognized by the color contrast with the underlying dark red or red-brown, flat or horizontal-bedded, medium to coarse, quartz sandstone, of which only about 10 ft (3 m) is exposed along the trail but up to 100 ft (30 m) is visible in the mesa face to the west.

Originally thought (as shown on one of the trailside plaques) to be part of the Chinle Formation, this dark red sand-

FIGURE 2—Overview of the footprint site on the Pipe Spring mesa; the pair of footprints are on the gently right-dipping bedrock surface immediately to the left of the solitary bush in the center of the photograph; facing north from the steps and bend in the trail as it comes up on top of the mesa (see text).

stone is instead the Kayenta. Carefully considering the observed dips and flexures in the mesa face, coupled with published thicknesses and regional stratigraphic variations, permitted clarification of the Pipe Spring units. Particularly helpful were papers by Blakey (1994), Clark and Fastovsky (1986), Peterson (1994), and Wilson (1967).

FOOTPRINTS

The foot trail switchbacks up the steep slope forming the south face of the mesa behind the visitors' center and the 19th-century buildings. It ascends through dark red sandstones (topmost Kayenta), and then climbs, via several rock-cut steps, up a small vertical cliff in light orange sandstones (basal Navajo), comes up onto the mesa's upper surface, and turns sharply left or west. The footprints lie directly ahead or north of those steps, 10-12 ft (3-4 m), off on the side of the trail's turn (Figure 2).

Two of the footprints are side by side (Figure 3A), about half a meter apart, with the heel of the left one (Figure 3C) even with the tip of the middle toe of the right one (Figure 3D). The third (Figure 3B) is isolated, 8 ft (2.7 m) ahead, and approximately on line enough to be part of the same trackway.

All are shallow depressions on the exposed bedding-plane surfaces in the sandstone bedrock. The right footprint (Figure 3D) is the best preserved of the three, is three-toed (tridactyl), 30 cm long from toe-tip to heel, and as wide between the two lateral toes' tips. More details would be desirable, but are not preserved clearly.

The float cast specimen (Stokes, 1988) appears much the same, from his published photograph.

IDENTIFICATION

As evident in the accompanying photographs, the exact outlines of the footprints are obscure, difficult to determine,

and thus prevent precise identification. Moreover, previous ichnotaxonomists have finely split footprint species elsewhere, with only the most subtle differences discriminating them.

Several species (possibly all synonymous) of *Eubrontes* known from Early Jurassic parts of the Newark Supergroup on the East Coast (Haubold, 1986) could be reasonable possibilities for the Pipe Spring footprints: *E. approximatus*, *E. divaricatus*, *E. giganteus*, *E. platypus*, or *E. tuberatus*. And, *Eubrontes* has now been reported from the Colorado Plateau sandstones generally (Lockley and Hunt, 1994).

Eubrontes was the track of a moderately large theropod dinosaur, a bipedal carnivore, probably a carnosaur and perhaps a megalosaurid more specifically, although other taxonomic affinities might be suggested. It is known from fossilized footprints only (i.e., is an ichnogenus), rather than skeletal remains.

RECOMMENDATIONS

Several steps should be taken to protect the Pipe Spring footprints and enhance their value to the visiting public. An appropriate exhibit could be constructed in the visitor center, including the detached specimen photographed by Stokes (1988), and featuring photographs of the in-place footprints up along the hiking trail, as well as drawings of the dinosaurs reconstructed as in life. The actual footprints can be marked with a suitable plaque and surrounded by a protective fence or railing, which would permit viewing but prevent trampling. A one-page handout or map might be passed out at the center to help guide hikers to the footprints themselves. The trailside plaque en route up should be corrected to read "Kayenta" instead of "Chinle" formation terminology. Finally, the bedrock bedding-plane surfaces around the three in-place footprints should be carefully searched for additional dinosaur tracks, which — if any more are found — should be incorporated into the site as well.

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FIGURE 3—Dinosaur footprints (probably a species of *Eubrontes*) in place in Pipe Spring National Monument (see text for exact location); pen is 15 cm long. A, left and right footprints together. B, isolated footprint. C, left footprint. D, right footprint.

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EARLY DISCOVERIES OF DINOSAURS FROM NORTH AMERICA AND THE SIGNIFICANCE OF THE SPRINGFIELD ARMORY DINOSAUR SITE

VINCENT L. SANTUCCI

National Park Service, P.O. Box 592, Kemmerer, WY 83101

ABSTRACT—Prior to the “Great American Dinosaur Rush” during the late 1800s, there were relatively few dinosaur sites recorded in North America. *Hadrosaurus foulkii* is recognized as the first articulated dinosaur collected, described and displayed in the New World. Most of the early discoveries consist of the fossil trackways from the Connecticut Valley and few partial dinosaur skeletons. The type specimen of the prosauropod dinosaur *Anchisaurus polyzelus* is recognized as one of the earliest dinosaur discoveries in North America. The fossil bones of *Anchisaurus* were uncovered during a blasting operation at the armory in Springfield, Massachusetts in the early 1800s. The excavation at this site is an important record in the early history of the science of dinosaur paleontology in North America.

INTRODUCTION

PRIOR to the 1870s and the “Great Era of Dinosaur Discoveries” there is a limited history for dinosaur paleontology in North America. Relatively few dinosaur specimens were recovered prior to the American Civil War. There appeared to be a general lack of interest in the petrifications of ancient life during the first half of the 19th century. The description and naming of the dinosaur remains often came long after their discovery.

EARLY DISCOVERIES OF DINOSAURS IN NORTH AMERICA

1802—Dinosaur footprints.—In 1802, Pliny Moody, a student at Williams College, found the footprint impressions near Moody’s Corner, his South Hadley, Massachusetts, farmstead. During this time these trackways were referred to as being made by “Noah’s Raven” and were generally regarded as associated with gigantic birds. The tracks were not recognized as dinosaurian until after 1860.

The high concentration of fossil tracks were later discovered throughout the Connecticut Valley and studied by Amherst College Professor Edward Hitchcock. Extensive descriptions of the tracks were published in “A report on the Sandstone of the Connecticut Valley especially its Fossil Footmarks.”, (Hitchcock, 1858). Subsequent work by other paleontologists associated the tracks with dinosaurs.

1818—Dinosaur bones from Connecticut.—The earliest discovery and collection of dinosaurian remains in North America occurred in 1818 (Galton, 1976). During the blasting of a well near Ketch’s Mills, in East Windsor, Connecticut, fossilized bone fragments were discovered by Solomon Ellsworth, Jr. in the Late Triassic red sandstones. Ellsworth gave the bones to Professors Smith, Ives and Knight, of the Medical Institution of Yale College, who all admitted, “the possibility that they might be human bones, but did not consider the specimens as sufficiently distinct to form the basis of a certain conclusion.”, (Smith, 1820).

The Ketch’s Mills bone material was recognized as reptilian by Professor Jeffries Wyman in 1855. Wyman described one of the fossil bones as, “... a caudal vertebrae of a Saurian reptile, to which it corresponds in the shape of the body, and

the transverse processes, and more nearly to those of the crocodiles than any other.” (Wyman, 1855). The specimen was later identified as dinosaurian and named *Anchisaurus colurus* (Lull, 1912). The latest reference to the Ketch’s Mills specimen, by Peter Galton (1976), recognizes the remains as prosauropod and reassigns the taxonomic identity as *Anchisaurus polyzelus*.

1830—A skeleton from New Jersey.—In the late 1830s, a partially articulated dinosaur skeleton was uncovered in a marl pit near West Haddonfield, New Jersey. These fossil bones were later excavated during 1858 under the direction of Professor Joseph Leidy from the Academy of Natural Sciences in Philadelphia. The specimen, preserved in the Late Cretaceous Woodbury Formation, was described by Leidy and assigned the name *Hadrosaurus foulkii* (Leidy, 1858). This type specimen was assembled as a free-standing mount at the Philadelphia Academy of Sciences and represents the first time that a dinosaur had been portrayed standing upright in a bipedal stance.

1855—Dinosaurs from the west.—In 1855, members of a government survey in the western territories, under Dr. Ferdinand Hayden, discovered a number of fossilized bones and teeth. In Nebraska Territory, the Hayden party found a fossil toe bone and some vertebrae. In Montana Territory, near the confluence of the Judith and Missouri rivers, a few fossil reptile teeth were collected by the survey team. The specimens were sent to Leidy and his descriptions of this material represent the first dinosaurs named in North America (Leidy, 1856).

THE SPRINGFIELD ARMORY DINOSAUR SITE

Despite the abundance of fossilized tracks in the Connecticut Valley, there is a relative rarity of fossil bones within the same deposits. In addition to the dinosaur bones collected at Ketch’s Mills, fossilized bones of an early Jurassic dinosaur were also collected, during the early nineteenth century, from a site located in the National Armory in Springfield, Massachusetts. This site is now administered by the National Park Service as Springfield Armory National Historic Site.

The Springfield bones were discovered by William Smith

during blasting related to some improvements at the “water shops” of the United States armory (Figure 1). The fossils were found at Mill Pond during the construction project. The actual date on which the bones were collected remains unknown, but the earliest reports indicate a date prior to 1856. A large portion of the fossilized remains were taken away by the workmen before Smith intervened. Armory superintendent General Whitney ordered the fossil specimens to be re-examined. Smith recovered as much material as possible and presented it to Professor Edward Hitchcock. According to Hitchcock (1858), the fossil remains from Springfield Armory were entirely replaced by a “carbonate of lime”.

Hitchcock eventually sent the fossil bones to Professor Jeffries Wyman for examination. Wyman provided the following reply dated January 21, 1857:

“With regard to the bones, I think that there can be no question that they are those of a reptile. This is shown by the configuration of the head, small trochanter, and a part of the shaft of a thigh bone, as well as by the imperfect caudal vertebrae; these last, however, are deficient in the concavo-convex bodies which are found in all scaly reptiles except the Enaliosaurians. Those from the sandstone are flat, or nearly so, on the ends, as in the Mammalia. The most remarkable feature, however, of the whole collection, is that of hollowness. This is carried so far, that but for the indications referred to, they might be referred to birds. Every bone except the vertebrae, and perhaps the small phalanges, is hollow. Nothing of the kind is known in Mammalia. Among reptiles the Pterodactyle had hollow bones, and some of them were referred, by Professor (Richard) Owen, to birds; but he subsequently corrected his opinion. . .”.

According to paleontologist Walter Coombs, “the discovery of the Springfield Armory bones seemed to have aroused little or no public interest and it is doubtful there are more detailed accounts of the circumstances of their discovery in contemporary local newspapers.” During the mid-1800s the concept “dinosaur” was in its infancy. There is no indication from Hitchcock’s writings that he associated this skeleton or any of the tracks he studied with dinosaurs. Likewise, it remains uncertain whether Hitchcock ever read about or even knew the word “dinosaur” (Coombs, pers.comm., 1998).

THE SPRINGFIELD DINOSAUR SPECIMEN

The fossil remains from Springfield Armory were originally described by Wyman (in Hitchcock, 1858) but he did not name the specimen. Hitchcock (1865) later named the specimen *Megadactylus polyzelus* based on comments given by Richard Owen. Taxonomic revisions led to the specimen being reassigned as the type specimen of *Anchisaurus polyzelus* (Marsh, 1885).

The *Anchisaurus polyzelus* specimen from Springfield Armory was collected from the early Jurassic Newark Series, Longmeadow Sandstone. The specimen is curated into the Vertebrate Paleontology Collection of the Pratt Museum of Natural History at Amherst College (catalog number is ACM 41109). The most recent and detailed description of the Springfield Armory *Anchisaurus polyzelus* type specimen is presented

FIGURE 1—Late 1800s magazine illustration of the Springfield Armory Watershop main gate. Dinosaur bones were discovered during the construction of this building.

by Galton (1976). The Springfield Armory specimen consists of the following elements:

- 11 vertebrae (including dorsal and caudal);
- right manus;
- distal ends of right radius & ulna;
- left femur & proximal end of left tibia;
- left fibula & pes;
- 2 ischia.

OSTROM’S REPORT TO THE NPS

In 1971, Dr. John Ostrom from Yale University was contracted by the National Park Service to produce a publication titled, “Report to the National Park Service on Mesozoic Vertebrate Paleontological Sites for Possible Inclusion in the Registry of Natural Landmarks” (Ostrom, 1971).

The objectives of Ostrom’s study included: 1) Compilation of an inventory of important Mesozoic paleontological sites, particularly of dinosaurs and Mesozoic mammals; 2) Analyses of those sites that are considered of unusual significance and potentially eligible for designation as a Natural Landmark; and, 3) Recommendation of sites for inclusion in the National Register of Natural Landmarks.

In his report, Ostrom recognized the historic and scientific significance of the Springfield Armory dinosaur site and identified the remains of *Anchisaurus polyzelus* as one of the earliest recognized fossil vertebrate remains from the Mesozoic of New England. This specimen also represents one of the earliest dinosaurs collected and reported in the New World.

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TRILOBITE MASS EXTINCTION EVENT AT THE BOUNDARY OF THE *ELVINIA* AND *TAENICEPHALUS* BIOZONES, YELLOWSTONE NATIONAL PARK

MATTHEW R. SALTZMAN

Department of Earth and Space Sciences, University of California,
Los Angeles, California 90095-1567

ABSTRACT—Evidence for placement of an Upper Cambrian extinction horizon in the southern Gallatin Range, northwestern corner of Yellowstone National Park, provides a datum that can be used to correlate mixed carbonate-siliciclastic strata with other fossiliferous sections in Wyoming and throughout North America. The extinction event is defined biostratigraphically by the transition between the *Elvinia* and *Taenicephalus* Zones of the standard North American trilobite zonation. It is also marked chemostratigraphically by a shift in carbon-isotope ($^{13}\text{C}/^{12}\text{C}$) ratios. Thus, both biostratigraphic horizons and carbon-isotopic data have been utilized to constrain the position of the bioterminal boundary in Yellowstone. Correlation with exposures of similar-age strata on the Buffalo Plateau in north-central Yellowstone and the northeast corner of the park reveal that major changes in paleogeography in Wyoming accompanied the world-wide extinction event. In particular, a healthy shallow-water carbonate factory during *Elvinia* Zone time is drowned and replaced by a lower-sedimentation-rate regime that characterized early *Taenicephalus* Zone time, likely reflecting a rise in sea levels across the extinction event. Further work aimed at better paleontologic characterization of these fossiliferous carbonate rocks in Yellowstone will provide a clearer picture of the significance of these results.

INTRODUCTION

THE UPPER Cambrian of North America is punctuated by three sharply defined mass extinction horizons which appear to represent isochronous surfaces (Palmer, 1984). They separate iterative evolutionary sequences in the history of non-agnostid trilobites and are known as bioterminals (which are essentially stages; see Palmer, 1984; and Westrop and Ludvigsen, 1987, for discussion). At least two of the trilobite mass extinctions can be recognized in exposures in Yellowstone National Park. Current hypotheses put forth to explain the extinctions include marine cooling, anoxia (Palmer, 1984), marine regression (Lochman-Balk, 1971), and biofacies shifts during transgression (Westrop and Ludvigsen, 1987). Previous hypotheses that lack supporting evidence include extra-

terrestrial heating and extraterrestrial impact (Palmer, 1984) and thus some combination of earth-bound causes seems most plausible.

Significant changes in the pattern of sedimentation across bioterminal boundaries provide important clues that may be used to falsify hypotheses of the extinctions. This is because facies changes observed in vertical stratigraphic sections must reflect local or regional changes in climate, sea level, subsidence and sediment supply. The focus of this paper is the nature of sedimentation patterns across the extinction events that mark the boundaries of the Pteroccephaliid bioterminal in Yellowstone and immediately surrounding areas. Saltzman et al. (1995) revealed significant facies changes across the Pteroccephaliid-Ptychaspid bioterminal boundary in northwestern Wyoming. Deiss (1936), Grant (1965), and Ruppel (1972)

FIGURE 1—Upper Cambrian locality map in the northwestern Wyoming area. Localities mentioned in the text include: CF = Clark Fork; SL = Swamp Lake; FX = Fox Creek; YO = Wyoming Creek; BP = Buffalo Plateau; MC = Mill Creek; TR = Three Rivers Peak. Inset showing generalized Late Cambrian facies map after Saltzman et al.(1995).

have also studied these deposits at various levels of resolution. The primary objectives of this contribution are to: (1) develop a paleogeographic framework for strata deposited in Yellowstone National Park; and (2) integrate newly acquired biostratigraphic and chemostratigraphic data to better constrain the timing of significant stratal surfaces.

GEOLOGIC FRAMEWORK

The Sauk transgression reached northwest Wyoming by Middle Cambrian time in response to a combination of eustatic sea-level rise and flexural bending of the cratonal edge. This initial transgression was marked by deposition of coarse clastic sediments of the Flathead Sandstone over Precambrian basement rocks. Subsequent deposition is characterized by large-scale alternations of fine-grained siliciclastic and carbonate strata. In Yellowstone National Park, the base of the Pterocephaliid biomere is within the uppermost beds of the massive cliff-forming Pilgrim Limestone (Deiss, 1936; Grant,

1965; Ruppel, 1972). This unit is abruptly overlain by the recessive Dry Creek Shale which grades into the carbonates of the Snowy Range (Open Door) Formation. The Pterocephaliid-Ptychaspid biomere boundary, corresponding to the transition between the *Elvinia* and *Taenicephalus* Zones, occurs within the Snowy Range (Open Door) Formation. Upper Cambrian strata are unconformably overlain by Middle Ordovician strata in Yellowstone.

LITHOFACIES ASSOCIATIONS

Two sections of mixed carbonate-siliciclastic strata were logged for this study in Yellowstone National Park (Figure 1) at Three Rivers Peak and on the Buffalo Plateau. The sections represent two distinct mappable units: (1) a succession of thrombolite boundstone, shale and flat-pebble conglomerate on the Buffalo Plateau which is similar to the Snowy Range Formation recognized by Grant (1965) in the Cooke City region; and (2) a succession of calcarenite, shale and lime mud-

at Three Rivers Peak is interpreted to reflect a relative rise in sea level. This is consistent with the pattern observed during this time period elsewhere (Osleger and Read, 1993; Saltzman et al., 1995). The section is however, unique in the presence of a brecciated olistostrome bed between the quartz sandstone and cherty wackestone. This bed may have formed as a result of a short-term, rapid sea-level fall that exposed the carbonate platform or, alternatively, may have formed in response to a seismic event that fractured the platform. The evidence for the drowning of the carbonate platform at the Buffalo Plateau locality is consistent with a tectonic event associated with a eustatic rise in sea levels rather than exposure of the carbonate platform in northwestern Wyoming. Nonetheless, the paleogeographic and bathymetric significance of the Three Rivers Peak breccia remains unclear at this time and future field and petrographic work is planned.

PALEONTOLOGY

At Three Rivers Peak, trilobites assigned as cf. *Pterocephalia* sp. occur at the top of the brecciated olistostrome bed. This species marks the presence of the *Elvinia* Zone. Grant (1965) found specimens of *Linnarssonella girtyi* and *Dellea suada* which mark the presence of the *Elvinia* Zone several kilometers away at Crowfoot Ridge. Two meters above the *Pterocephalia* sp. horizon at Three Rivers Peak, trilobites assigned to *Taenicephalus shumardi* mark the *Taenicephalus* Zone. Grant (1965) collected specimens of *Taenicephalus shumardi* one meter above *Elvinia* Zone trilobites at Crowfoot Ridge. No trilobites have yet been found on the Buffalo Plateau, although trilobite taxa found at similar sections in the nearby Cooke City area (Fox Creek, Swamp Lake, Wyoming Creek, Mill Creek and Clark Fork) indicate the presence of the *Elvinia* and *Taenicephalus* Zones.

CARBON-ISOTOPE STRATIGRAPHY

Changes in the $\delta^{13}\text{C}$ of limestones across the Pterocephaliid-Ptychaspid biomere boundary potentially provide a means of correlation, independent of biostratigraphy. Carbonate samples from Three Rivers Peak were analyzed for stable-isotope ratios. Homogeneous micrite identified in thin section was microsampled from polished slabs by using a microscope-mounted drill assembly. Care was taken to sample micrite with no visible cements or skeletal grains, although ~15% of the samples contain sparry calcite or skeletal material. Sample preparation procedures and analytical error are discussed further in Saltzman et al. (1995).

The $\delta^{13}\text{C}$ stratigraphic profile for sections in the Gros Ventre and Wind River Ranges were presented in Saltzman et al. (1995), along with profiles from two sections in the Great Basin. These profiles reveal a positive shift in $\delta^{13}\text{C}$ across the Pterocephaliid-Ptychaspid biomere boundary. The $\delta^{13}\text{C}$ stratigraphic profiles for the Three Rivers Peak section is presented in Figure 2. The highest $\delta^{13}\text{C}$ ratios recorded at Three Rivers Peak are in the *Taenicephalus* Zone, consistent with earlier studies of this trilobite zone. In addition, the most negative values occur at the biomere boundary (*Irvingella* major zone).

FIGURE 2—Measured section of Upper Cambrian rocks from Three Rivers Peak section in Yellowstone National Park (TR in Fig. 1). Stages and trilobite zones indicated. $\delta^{13}\text{C}$ data measured in per mil relative to PDB scale.

stone at Three Rivers Peak which is similar to the Open Door Formation studied by Shaw and Deland (1955) further to the south in the Gros Ventre, Teton and Wind River Ranges. The Snowy Range Formation is generally poorly exposed on the flanks of the Beartooth uplift, where it overlies the cliff-forming Pilgrim Limestone of *Crepicephalus* and early *Aphelaspis* Zone age. In marked contrast, deposits of the Open Door Formation are spectacularly exposed in the Gallatin Range. It should be noted however, that the Three Rivers Peak strata, although grouped with the Open Door succession, does differ from the general pattern in that it contains anomalous beds of quartz sandstone at the base, a ~1-meter-thick brecciated olistostrome bed in the middle and abundant chert in the upper wackestone unit (Figure 2).

SEQUENCE STRATIGRAPHY

The change from quartz sandstone to a cherty wackestone

These results are consistent with the biostratigraphic controls at Three Rivers Peak and suggest that the extinction event was associated with changes in carbon cycling (Saltzman et al., 1995). In particular, it seems that the burial ratio of organic carbon to carbonate carbon was increased following the extinction. This may have occurred as a result of increased nutrient fluxes to the surface oceans during sea level rise and subsequent increases in primary production. The significance of the minima at or near the extinction event is unclear. Either there was a sudden decrease in primary productivity related to initial toxicity of upwelling waters, or a sea-level change led to increased erosion of isotopically light organic carbon compared to its preservation before and after the event.

CONCLUSIONS

This study provides additional chemostratigraphic and sequence stratigraphic analyses from a section in Yellowstone National Park, consistent with the notion of a significant paleoceanographic event across the Pteroccephaliid-Ptychaspid biomere boundary. Future studies in this area focused on better constraining the paleontologic, sedimentologic and chemostratigraphic contexts of this extinction event will be useful in testing hypotheses of extinction. In particular, investigation should focus on the nature of the unique brecciated beds at Three Rivers Peak.

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LATE JURASSIC ECOSYSTEM RECONSTRUCTION IN THE WESTERN INTERIOR OF THE UNITED STATES

CHRISTINE E. TURNER AND FRED PETERSON

U.S. Geological Survey, Box 25046, MS-939, Denver, CO 80225.

And the Morrison Research Team (contact through above address):

D.J. Chure, T.M. Demko, S.P. Dunagan, D.D. Ekart, G.F. Engelmann,
E. Evanoff, A. Fiorillo, S.C. Good, S.T. Hasiotis, B.J. Kowallis, R.J. Litwin,
D.L. Newell, M.E. Schudack, and G.L. Skipp.

ABSTRACT—Interdisciplinary studies of the Late Jurassic Morrison Formation throughout the Western Interior have resulted in reconstruction of the extinct ecosystem inhabited by the largest herbivores that ever roamed the earth. The ecosystem within the Morrison depositional basin was governed in large part by a rain shadow that developed in the lee of the mountainous uplands to the west, which greatly influenced the availability of fresh surface and near-surface water in the depositional basin. Isotopic analyses of fossil soil nodules in the Morrison depositional basin confirm the rain-shadow effect of the uplands to the west. The upland regions captured moisture from the westerly winds and some of this precipitation fed streams that flowed eastward across the alluvial plain and also fed underground aquifers that controlled the water table beneath the alluvial plain. Wind-blown sand, evaporites, development of a large saline, alkaline lake, together with evidence from the flora, fauna, and trace fossils suggest that fresh surface water may have been scarce during Morrison deposition.

Local presence of unionid clams in some stream beds indicate that at least these streams were perennial in nature because the larval stage of unionid clams attaches onto the gills of fish, which only live in perennial streams. Crayfish burrows that occur in beds adjacent to stream channels offer clues to the nature of some of the streams as well, because crayfish must burrow down to the water table to survive. Crayfish burrows that extend downward into sandstone near the stream channels in the Morrison indicate that the water table was below the level of the stream, a condition consistent with effluent streams where the streams are feeding the water table. This situation is consistent with streams that develop in a semi-arid to arid climate.

Taken together, the evidence from the sedimentology, isotopic studies, body fossils, and trace fossils suggests that some of the Morrison streams were probably perennial but that many were probably ephemeral and may have experienced substream flow, resulting in the availability of surface water in the form of water holes much of the time. Streams that were perennial in nature, such as the deposits that contain the abundant dinosaur remains in the quarry sandstone bed at Dinosaur National Monument, Utah, may thus have been the exception rather than the rule, accounting for the concentration of dinosaur skeletons. The dinosaurs may have been congregating close to the last reliable stream during a major drought.

INTRODUCTION

THE MORRISON Extinct Ecosystem Project is a joint NPS-USGS-funded interdisciplinary study to reconstruct the Late Jurassic predominantly terrestrial ecosystem throughout the Western Interior during deposition of the Morrison Formation. This colorful formation is known worldwide for the skeletons of large dinosaurs, especially the giant sauropods, that have been recovered from it and displayed in many museums throughout the world. The formation is exposed in many NPS units including Arches NP, Bighorn Canyon NRA, Black Canyon of the Gunnison NM, Capitol Reef NP, Colorado NM, Curecanti NRA, Devils Tower NM, Dinosaur NM, Glacier NP, Glen Canyon NRA, Hovenweep NM, Wind Cave NP, and Yellowstone NP, as well as the newly designated Grand Staircase-Escalante NM managed by the BLM.

The goals of the project were to (1) apply modern research techniques that would yield an improved understanding of the habitat that existed when the Late Jurassic dinosaurs roamed the western U.S., which, in turn, would (2) help land managers make science-based decisions in resource management, and (3) improve NPS interpretive programs. Most of the results are included in technical reports published in the scientific literature and in administrative reports submitted to the NPS. In addition, under the auspices of the NPS-GIP (Geolo-

gist-in-the-Park) program, one of the principal investigators (Fred Peterson) will distill the scientific findings and prepare a less technical publication for the lay public.

The multidisciplinary approach allowed us to study various aspects of the rock and biostratigraphic record for the Morrison Formation, with various lines of evidence leading to an integrated picture. The investigations included studies of regional tectonics, regional stratigraphic framework, radiometric and paleontologic dating, sedimentology, paleosols (fossil soils), dinosaur biostratigraphy, trace fossils, taphonomy (processes that occur between the death of an organism and discovery as a fossil or trace fossil), microfossils, invertebrates, smaller vertebrates, and isotopic analysis of teeth and paleosol nodules. Integration of data from the various studies is resulting in one of the most complete understandings of an ancient continental ecosystem.

GEOLOGICAL SETTING

Eleven named members are currently recognized in the Morrison (Szigeti and Fox, 1981; Peterson, 1994; O'Sullivan, 1997), and all but two are restricted to the Colorado Plateau. Another closely related formation that correlates with the lower part of the Morrison is the Ralston Creek Formation in the Front Range foothills west of Denver (Peterson and Turner, in press). For simplicity the formation is here divided into up-

per and lower parts that are separated by a conspicuous difference in clay mineralogy, although other lithologies are also present and may predominate in each part. Clay minerals in the lower part consist dominantly of non-swelling types whereas clay minerals in the upper part consist dominantly of swelling (smectitic) types. The change in clay mineralogy reflects the dramatic increase in altered volcanic ash that was incorporated in the sediments (Turner and Fishman, 1991). The increased volcanic component indicates increased volcanism in the volcanic arc that lay off to the west. The change in clay mineralogy occurs as far north as northern Wyoming but is not present in Montana or the Black Hills of northeastern Wyoming and western South Dakota where all the clays in the formation are of the non-swelling type. Where present, the change in clay mineralogy constitutes a convenient marker horizon that is of considerable value for correlation purposes.

About 6-15 m (20-50 ft) below the clay change is a fairly persistent paleosol (or closely spaced series of paleosols) that also is fairly widespread and ultimately may prove to be another excellent marker horizon near the middle of the formation (Demko and others, 1996). Interestingly, although dinosaur bones and skeletons have been recovered in many parts of the Western Interior and from much of the vertical thickness of the formation, notable changes in the dinosaur fauna occurred near the middle of the formation and correlate with the distinct paleosol zone and the change in clay mineralogy (Turner and Peterson, in preparation).

Radiometric dating shows that the Morrison was deposited 155-147 million years ago (Kowallis and others, in press). Deposition stopped some 6 million years before the close of the Jurassic Period, which ended approximately 141 million years ago.

Because of continental drift, the Western Interior depositional basin was about 650 km (400 mi) farther south than today. This places the present-day Four Corners near the latitude of the southern border of Arizona (Parrish and others, 1982). Data from other workers who deal with climate on a global scale suggest that the Earth was warmer than today (for example, polar ice caps probably were absent; Hallam, 1982). Stable isotopes in carbonate nodules from Morrison paleosols indicate a significantly higher carbon dioxide content in the atmosphere than at present (Cerling and others, 1996; Ekart and Cerling, 1997). Because carbon dioxide is a significant "greenhouse" gas, this, as well as the more southerly latitude of the region, suggests that the climate in the Western Interior was appreciably warmer than today.

During the Late Jurassic, a volcanic mountain chain similar to the present-day Andes existed along the west coast of North America more or less along California's border with Arizona and Nevada. Another highland or possibly mountainous range lay farther inland roughly along the Nevada-Utah state line. The nature of the terrain between these two areas is unclear but it probably included a small number of scattered volcanoes.

Farther east lay the vast Western Interior lowland plain on which the Morrison Formation was deposited. The inland plain extended from Arizona and New Mexico northward to

Montana and on into Alberta, Canada, and it may have originally extended much farther east, as some beds of possible Late Jurassic age in Iowa (Cody and others, 1996) and Michigan suggest. Streams originating in the highlands flowed eastward, carrying their bedload of sand and gravel onto the aggrading Morrison alluvial plain (Turner-Peterson, 1986; Peterson, 1994).

Westerly to southwesterly winds (Peterson, 1988) impinged on the mountain range that lay to the west of the Morrison depositional basin, which left much of the basin in a rain shadow, as shown by isotopic analyses of carbonate soil nodules (Ekart and Cerling, 1997). The rain-shadow effect was responsible for the dry climate that prevailed throughout most of Morrison deposition. For most of the time, the climate in this area was semiarid or perhaps even arid in places, as indicated by deposits of bedded gypsum, which forms under highly evaporative conditions; windblown sandstone deposits; magadi-type chert (indicative of highly alkaline lake waters; Dunagan and others, 1997); and saline, alkaline lake beds (Turner and Fishman, 1991). There may have been somewhat wetter time intervals that occurred seasonally or intermittently.

DEPOSITION OF THE MORRISON FORMATION

During the earliest stages of deposition of the lower Morrison (Windy Hill Member and correlative strata), a seaway that was an arm of the ancestral Pacific Ocean extended east across Wyoming and into adjacent parts of Montana, the Dakotas, Nebraska, northern Colorado and northern Utah. Farther south in southeastern Utah and in western and eastern Colorado, gypsum in the Tidwell Member and correlative Ralston Creek Formation was precipitated as evaporite deposits in hypersaline lagoons at the margin of the seaway (Peterson and Turner, in press).

Subsequently, the seaway retreated to the northwest into Canada and streams that drained upland regions west of the Western Interior carried gravel, sand, and mud (represented largely by the Salt Wash Member) into the depositional basin, building up an extensive alluvial plain. In central Colorado, scattered low hills that were remnants of the ancestral Rockies were sufficiently high to support small streams that furnished local stream deposits unrelated to the Salt Wash fluvial system. Small lakes and ponds also developed locally on the alluvial plain as well as in the most distal regions in eastern Colorado and eastern Wyoming. The more distal lake deposits yield charophytes, stromatolites, oncolites, sponge spicules, mollusks, and rare fish remains (Dunagan, 1997; Dunagan and others, 1996).

During times when the streams dried up in the Colorado Plateau region, winds from the west and southwest removed sand-sized material from the dry stream beds and deposited it farther downwind in extensive dune fields that covered large parts of the Four Corners area. These deposits are represented today by the Bluff Sandstone and Junction Creek Sandstone Members as well as the eolian sandstone facies of the Recapture Member. Smaller dune fields also were established farther north in northern Utah, northwestern Colorado, Wyo-

ming, and South Dakota (Unkpapa Sandstone Member) by deflation of previously deposited shallow marine sands.

During deposition of the upper part of the Morrison Formation, a large stream complex in the Colorado Plateau region (Westwater Canyon and Fifty Mile Members) gave way to a large shallow saline, alkaline lake called Lake T'oo'dichi' that covered parts of northwestern New Mexico, northeastern Arizona, southeastern Utah, and southwestern Colorado during deposition of much of the Brushy Basin Member and, although much shallower, had about the same areal extent as Lake Michigan (Turner and Fishman, 1991). Judging from similar modern saline, alkaline lakes, the alkalinity of the water would have been high enough to cause alkaline burns to human skin. Development of the lake attests to the aridity of the time, as evaporation must greatly exceed precipitation and runoff to achieve the alkalinities and salinities recorded in the deposits of the ancient lake. The lake was fed by surface water from intermittent and perennial streams, but ground water was also an important component of lake hydrology. At times when the lake dried out to form a large pan or salina, flash floods carried sand well out into the lake basin. Throughout most of Morrison time, shallow carbonate-dominated lakes developed east and north of the present-day Front Range of the Rocky Mountains (Dunagan and others, 1996, 1997).

Toward the end of Morrison deposition, large fluvial complexes including the Jackpile Sandstone Member were locally established because of renewed uplift in the highlands west and southwest of the Western Interior. Increased precipitation, especially in the highlands (Bassett and Busby, 1997), probably was responsible for the renewed stream activity at this time.

Wetter conditions toward the end of Morrison deposition is supported by scattered black mudstone beds near the top of the formation in scattered localities from the Colorado Front Range foothills to Montana. Abundant carbonaceous mudstone and extensive coal beds in the upper part of the Morrison in central Montana suggest greater precipitation and a temperate climate in the northern part of the Western Interior plain. The northward or latitudinal temperature gradient is also supported by a northward increase in charophytes (lacustrine green algae) that prefer cool waters and a corresponding decrease in charophytes that prefer warm waters (Schudack, 1996).

Morrison deposition ended with thick soil development although the soil was partly or entirely removed in many places during the succeeding erosion event or by scour that accompanied deposition of lowermost Cretaceous fluvial strata (T.M. Demko, oral commun., 1996).

PALEOECOLOGY

A variety of life forms lived in the Morrison ecosystem, from the giant herbivorous sauropods to small lacustrine algae. These include dinosaurs, small mammals, reptiles, amphibians, fish, sponges, arthropods, mollusks, and a variety of vegetation from large trees to algae. The diversity of life forms at first suggests that an equable climate prevailed during Morrison time, but reconstruction of the ecosystem suggests

that, instead, the life forms were well adapted to a relatively dry and perhaps somewhat hostile environment.

The ecosystem of the Morrison depositional system was governed in large part by the rain shadow that developed in the lee of the highland areas to the west and was largely influenced by the availability of fresh surface and near-surface water. Wind-blown dunes, evaporites, the nature of the stream and lake deposits, together with evidence from the flora, fauna, and trace fossils suggest that fresh surface water may have been scarce during Morrison deposition.

Mountainous uplands to the west captured moisture from the westerly winds and some of this precipitation fed streams that flowed eastward across the alluvial plain and also fed underground aquifers that controlled the water table beneath the alluvial plain. Large alluvial complexes in the Morrison (Westwater Canyon and Salt Wash Members) attest to the development of major eastward-flowing streams. Subsequently (after burial), these alluvial complexes probably also served as major aquifers within the depositional basin. Whether these streams and other more isolated stream channels in the Morrison were perennial or ephemeral is an important aspect of ecosystem reconstruction. Local presence of unionid clams in some stream beds indicate that at least these streams were perennial in nature because the larval stage of unionid clams attaches onto the gills of fish, which only live in perennial streams (S.C. Good, oral commun., 1997). Crayfish burrows that occur in beds adjacent to stream channels offer clues to the nature of the streams as well, because crayfish must burrow down to the water table to survive. Crayfish burrows that extend downward into sandstone near the stream channels in the Morrison indicate that the water table was below the level of the stream, a condition consistent with effluent streams where the streams are feeding the water table (S.T. Hasiotis, oral commun., 1998). This situation is consistent with streams that develop in a semi-arid to arid climate.

Another indication of the semi-arid to arid climate is the association of large dune fields adjacent to the Salt Wash fluvial complex. The interfingering of fluvial and eolian deposits suggests that at times the streams were dry, and winds carried the sand from the exposed stream beds and deposited it in adjacent dune fields. Locally, termite nests occur in the eolian deposits. Because termites burrow down to the down to capillary fringe above the water table, the vertical extent of the nests is an indicator of the depth to the water table. Some of these nests extend as much as 40 m (130 ft) below the paleoland surface in the lower part of the formation in the southern San Juan Basin of northwestern New Mexico (Hasiotis, 1997). This observation requires that the water table there was at least 40 m (130 ft) beneath the surface.

Another clue to the nature of the streams derives from the nature of lake deposits in the Morrison. Development of Lake T'oo'dichi' (Turner and Fishman, 1991), an extensive saline, alkaline lake, required that evaporation far exceeded precipitation and runoff. This suggests that fresh-water replenishment of the lake by streams (either perennial and/or ephemeral) was not enough to dilute the lake brines. Lack of diversity but high abundance of trace fossils in these lake sedi-

ments (S.T. Hasiotis, oral commun., 1998), which is typical of a harsh or highly stressed environment, confirms the harsh conditions implied by the high salinities and alkalinities of Lake T'oo'dichi'.

Taken together, the evidence from the sedimentology; saline, alkaline lake geochemistry; isotopic data; body fossils; and trace fossils suggests that some of the Morrison streams were probably perennial but that many were probably ephemeral and may have experienced substream flow, resulting in the availability of surface water in the form of water holes much of the time. Streams that were perennial in nature, such as the deposits that contain the abundant dinosaur remains in the quarry sandstone bed at Dinosaur National Monument, Utah, may thus have been the exception rather than the rule, accounting for the concentration of dinosaur skeletons. The dinosaurs may have been congregating close to the last reliable stream during a major drought.

CONCLUSIONS

The Morrison landscape was a reflection of the interaction of surface water, subsurface water, and the moisture content of the overlying air mass. All of these were dramatically affected by creation of a rain shadow in the lee of mountainous highlands that lay to the west of the depositional basin. The Morrison fauna and flora adapted to the availability of moisture (or lack thereof).

We envision an environment similar in some respects to the depositional plain that contains Lake Eyre in Australia. The Lake Eyre basin may be more extreme than what we envision for the Morrison basin, but interesting parallels exist. In southern Australia, a coastal mountainous upland captures much of the moisture from winds that derive their moisture from the ocean, leaving the Lake Eyre basin in a severe rain-shadow region, where surface water is scarce and only furnished by infrequent storms that enter the region several years to several decades apart. The life forms in Lake Eyre are well adapted to the dryness and proliferate during times when moisture is temporarily abundant. Some surface and subsurface water did enter the Late Jurassic Western Interior basin, in the form surface runoff from precipitation in the highlands farther west and through underground aquifers that were recharged from source areas in the highlands. Surface runoff fed some perennial streams, but many of the streams may only have flowed intermittently.

We suspect that life concentrated around perennial streams and near water holes in streams where substream flow occurred. This may explain the concentration of dinosaur bones in the quarry sandstone bed at Dinosaur National Monument, a stream deposit that we interpret as perennial in nature. Wind blown sands; evaporite deposits; saline, alkaline lake deposits; and evidence from the trace and body fossils are consistent with a much drier interpretation than previously envisioned for the Morrison ecosystem. This raises questions about the amount of vegetation available for the large herbivores, and we can only surmise that they were able to range the basin and find enough vegetation to satisfy their food requirements. The vegetation was probably mostly, but not entirely

riparian. The death assemblages of the dinosaurs probably tell us more about the conditions of stress and drought than about the normal course of events, but in our new interpretation, drought may not have been that uncommon.

PLANNED RESEARCH AND REMAINING QUESTIONS

A popular publication is planned that attempts to capture and bring to life for the general public the extinct ecosystems of the giant herbivorous dinosaurs in the Late Jurassic. This will be prepared from the scientific synthesis in preparation for the Morrison Extinct Ecosystems Project. The scientific synthesis is underway and the popular publication will be prepared by Fred Peterson, one of the Principal Investigators of the project, under the auspices of the NPS GIP (Geologist-in-the-Park) Program in Dinosaur National Monument. Work on the popular publication will begin this summer. Preparation of a geologic history interpretive trail, and recommendations to improve exhibits at the Monument are also planned. In the future, it will be possible to prepare the information for other parks in the study area that have Morrison exposures. Additional summary scientific papers are in preparation by project members for publication in the technical literature, in addition to the ones already published by project members.

Remaining research areas that need to be addressed in the Morrison Formation include the plant taphonomy, and a better understanding about the distribution of vegetation. Preliminary studies of the plant taphonomy will begin this summer by Judy Parrish, a professor of paleoclimatology at the University of Arizona. Additional detailed work on the paleosols would also contribute to our understanding of the paleoclimate, especially when tied to the regional sedimentology and trace fossil data. We also discovered in the course of our studies that the beginning and end of some range zones of the dinosaurs as well as of the microfossils (charophytes, ostracodes, spores and pollen) correspond with significant changes in the sedimentary rock record, such as major hiatuses or changes in depositional style. It is possible that both the rock record and the biota were changing in response to climatic signals, but further work would be needed to refine these ideas. Additional age determinations (both radiometric and paleontologic) of the Morrison in Wyoming would contribute considerably toward our correlations. Paleoclimatic interpretations of the spores and pollen would also be an important contribution to constraining the climatic interpretations for the ecosystems studies.

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