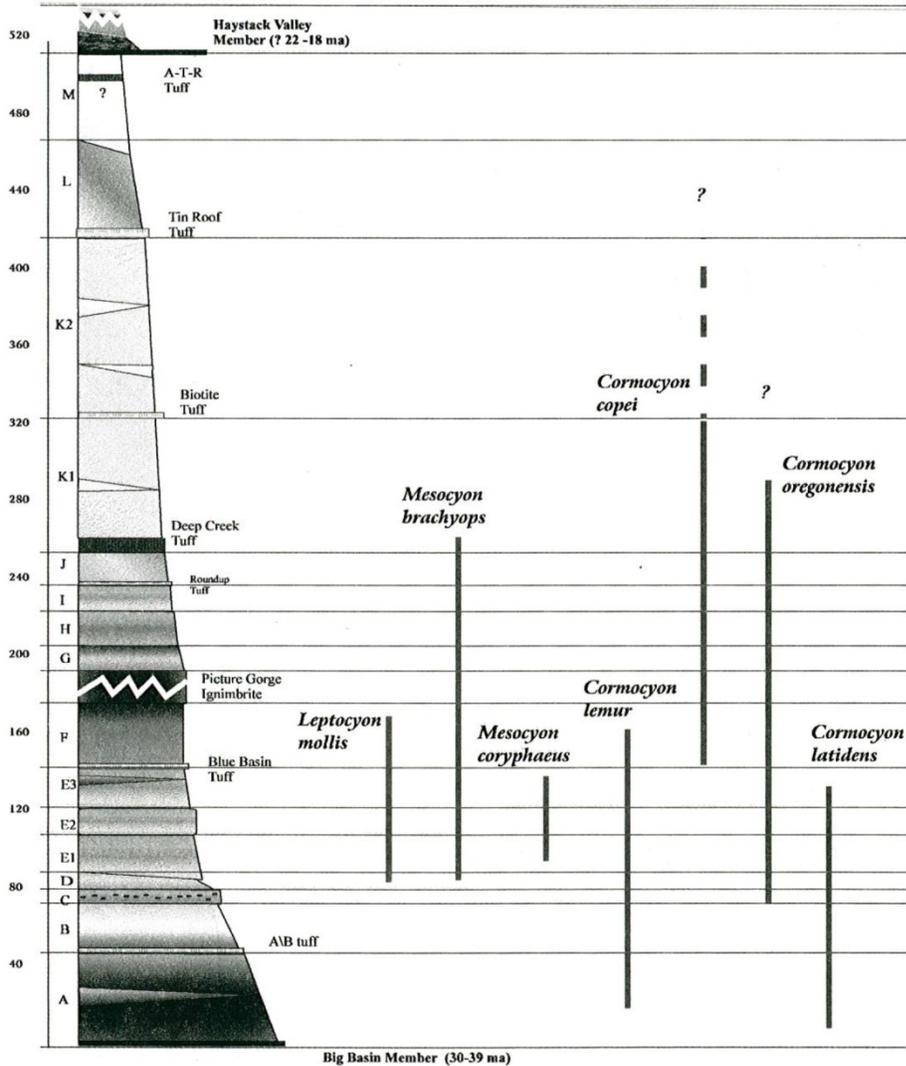


National Park Service Paleontological Research

Edited by Vincent L. Santucci and Lindsay McClelland

Technical Report NPS/NRPO/NRTR-95/16



United States Department of the Interior • National Park Service • Natural Resources Publication Office

U.S. NATIONAL PARK SERVICE
Natural Resource Program Center
Denver, CO

Geologic Resources Division

National Park Service Paleontological Research

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INTRODUCTION

Any student of science discovers early in his/her career that much remains to be understood. Endless hours of literature review reveal a history of human sacrifice in order to gain understanding of the natural and physical world. Sometimes scientists are rewarded with a profound discovery. However, more typically the devoted practitioner provides more modest contributions. Often the work of an individual may go unrecognized from some time.

In the early 1840's a young employee of the American Fur Company, named Alexander Culbertson, traversed the American plains in search of beaver. A keen eye and good sense prompted Culbertson to collect a few "petrifications" that he encountered in the Dakota badlands. The ancient remains were eventually turned over to another insightful individual named Hiram Prout. In 1846 Prout, a St. Louis physician published an account of the fossil jaw bone. This report quickly gained world-wide recognition and helped to initiate the first period of fossil exploration in the American west. Nearly 150 years later, we have come to realize the significance of Culbertson's actions as they relate to the early history of vertebrate paleontology in this country and the irony that ties Prout's specimen to the "badlands" that will later become a national park.

Fossils, synonymous with "paleontological resources" in government circles, are exceedingly common within units of the National Park System. To date, over 100 national parks containing significant paleontological resources have been identified. Collectively, fossil pollen, leaves, wood, bone, teeth, and tracks, preserved in the parks, provide a detailed record for the history of life in the same manner as the Civil War history is available in the Battlefield Parks.

The abundance of fossils in parks has provided tremendous challenges to the National Park Service (NPS) in terms of management and protection. The lack of adequate and specific federal legislation related to fossils has left Interior Department agencies with little guidance and limited sources of funding to support paleontological resource programs. The flourishing relationship that currently exists between the NPS and paleontologists was not always so well established.

Progress over the last decade, in defining the NPS role in management of paleontological resources, has rapidly evolved into an extremely ambitious program. This success can be attributed to a few specific factors including:

- (1) increased levels of communication and education that were initiated through the NPS Paleontological Resources Conferences at Dinosaur National Monument (1986), Petrified Forest National Park (1988), and Fossil Butte National Monument (1992). Additionally, specific symposia sessions organized at the North American Paleontological Convention in Chicago (1992) and at the Society of Vertebrate Paleontology Annual Meeting in Albuquerque (1993) have furthered the development of a communication network for park paleontology;

(2) establishment of the NPS Natural Resources Management Guidelines (NPS-77). This document, for the first time anywhere, provided guidelines for paleontological resources management (Chapter 2, p. 155-175). Not only are objectives and planning alternatives defined, but NPS-77 goes beyond to affirm that, "Paleontological research by the academic community will be encouraged and facilitated ...";

(3) support by the NPS with the publication of paleontological research in "Park Science" and within the NPS Natural Resources Technical Report Series;

(4) dedication and endurance of paleontologists conducting research projects within the parks. These are the individuals who intuitively understand the significance of park fossils and work, (often without NPS funding), to assist park management better understand their resources.

In an attempt to illustrate the diversity of paleontological research projects conducted within the national parks, the "NPS Paleontological Research Abstract Volume" (Technical Report NPS/NRPEFO/NRTR-93/11) was produced in 1993. In this publication over 75 research abstracts were presented reflecting projects in 27 different NPS units. This publication greatly increased awareness about the significant work being conducted in parks and has served as a catalyst to further research. Clearly, the opportunity to produce the first publication exclusively dedicated towards NPS paleontological research was extremely important. It provided an outlet for information exchange that may not have occurred otherwise and a format that would be suitable to both scientists and land managers.

The suggestion to produce a second paleontological research volume including short scientific research papers was repeated by many individuals receiving and contributing to the Abstract Volume. There were obviously many potential paleontological research papers that needed to find a home. Hence, a proposal to publish a volume of NPS Paleontological Research mini-papers was submitted and accepted.

This "National Park Service Paleontological Research Volume" has been produced as a companion volume to the, "National Park Service Paleontological Research Symposium", at the Geological Society of America, Rocky Mountain Section Annual Meeting, in Durango, Colorado (May, 1994).

I would like to extend my gratitude to Emmett Evanoff for originally suggesting the organization of the symposium in Durango and his efforts, along with Jack Ellingson, in ensuring the meetings success.

Thanks very much to Lindsay McClelland and Anne Frondorf for all of their guidance and energy in the proposal and preparation of this publication. The NPS Paleontology Program is well represented in Washington by Lindsay and Anne. Special thanks to Donna O'Leary and Jean

Matthews, from the National Park Service Publications, for their continuous support in producing publications highlighting paleontological research.

Gary Cummins (GRCA) and Dave McGinnis (FOBU) have both made tremendous contributions to promote the success of the NPS Paleontology Program. As superintendents of fossil parks, both Gary and Dave have transformed dreams into reality and plans into action through bold and creative management. They both share a contagious level of enthusiasm that sparks the teams around them. Although I have not worked directly with Dr. Robert Schiller (RMRO), I understand that he is another important supporter of the NPS Paleontology Program and his efforts are also greatly appreciated. As always, I am grateful to the support, patience and understanding from my wife Linda, and children Sarah, Bethany, Luke and Jacob.

It is to Stan Robins (BADL) that this volume is dedicated. Stan is about the nearest thing that I have come across that fits the definition of "hero". His efforts and sacrifices exhibited towards the protection of paleontological resources are unrivaled and unrecognized. His professionalism and dedication truly exemplifies the image of the NPS ranger. Someday, those who advocate and fight to achieve greater fossil protection legislation will learn about the contributions of a humble and caring ranger from Badlands National Park.

Finally, through the combined efforts of those men and women mentioned above, along with many others, a solid foundation has now been firmly established for the NPS Paleontological Program. Many research questions remain to be explored within the parks. Clues lie quietly buried within park sediments awaiting discovery. Clearly parks are not merely beautiful and scenic places to visit, but they can often provide tremendous research opportunities to scientists.

Vincent L. Santucci

THE MIOCENE CARNIVORE DENS OF AGATE FOSSIL BEDS NM, NEBRASKA: OLDEST KNOWN DENNIN BEHAVIOR OF LARGE MAMMALIAN CARNIVORES

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ABSTRACT

In 1981 University of Nebraska paleontologists discovered a concentration of mammalian carnivore dens at Agate National Monument, Sioux County, Nebraska, that contained fossil remains of extinct Early Miocene beardedogs, mustelids, and canids, dated at about 19.2 Ma. A decade of excavation (1981-1990) under National Park Service auspices produced six species of carnivores in association with bone fragments of probable prey (juvenile oreodonts, rhinoceros, and camel). Young, mature, and aged beardedogs of a single species were found in the dens, including an adult female and her juvenile male offspring. This age distribution and analysis of sediments in the burrows suggest a relatively sudden death event, possibly a prolonged drought, in which animals died in their burrows within an ephemeral stream valley. After the death event their partially scavenged skeletons were buried by fine volcanoclastic silt and sand carried into the dens by wind and water over an unknown amount of time, presumably several months to years.

Another older den complex was recently found near Agate National Monument in 1991 and preserves the largest vertebrate burrows yet reported in the fossil record. The 22 million year-old site includes 5-6 large cylindrical burrow fills to 10m in length and 1-2m in diameter, distributed over 450m². Bones of a wolf-sized beardedog, a small fox-sized canid, and a rodent were found in association with the burrows. These den sites occur in extensive paleosol horizons indicating flat regional geomorphic surfaces, interpreted as semiarid Miocene grasslands of the upper Arikaree Group in western Nebraska and southeastern Wyoming.

INTRODUCTION

Evidences in the fossil record of the ecology of extinct mammals are rare. Most often the remains of fossil vertebrates are preserved in stream, lake, or wind-deposited sediments with little or no information revealing the nature of their habitat, community associations, lifestyle, or other ecological relationships. Two Miocene sites discovered by the University of Nebraska in 1981 and 1991 proved an exception in that fossil remains of extinct carnivores were found within and in proximity to their dens. These den complexes were preserved intact, filled with fine-grained volcanoclastic sediments, and only revealed by recent erosion of Arikaree Group rocks in the Niobrara River valley, Sioux County, Nebraska. The carnivore dens occur in relationship to Early Miocene land surfaces (paleosols) within the Arikaree Group of western Nebraska. The

two sites have been radiometrically dated at about 19 Ma and 22 Ma, respectively. They represent the oldest evidence of denning behavior by large mammalian carnivores known anywhere in the world.

QUARRY 3 DEN SITE (19.2 Ma)

The den complex was exposed by recent erosion of the west face of Beardog Hill, about 200m southeast of the Carnegie Hill waterhole bonebed at Agate National Monument. The site was discovered by O.A. Peterson of the Carnegie Museum (Pittsburgh) in 1904, and initially excavated by him and his co-workers in 1905. They found partially articulated skeletons of the beardog *Daphoenodon superbus* and less complete remains of other carnivores, but were unaware they had stumbled upon a den complex despite the large amount of carnivoran skeletal material at the site. Peterson named the locality Carnegie Quarry 3.

Quarry 3 remained undisturbed until 1981 when a University of Nebraska party relocated and opened the site in an attempt to explain the predominance of carnivoran fossils. Relative to ungulates which comprise almost all bones found in the waterhole bonebed at Carnegie and University Hills, carnivore remains are never abundant in the various waterhole bonebeds found at this stratigraphic level in the region. When we first excavated at Quarry 3 in September 1981 we were immediately rewarded by not only the discovery of large burrows but also by partial skeletons of previously undiscovered carnivores within the burrow fills. As work progressed from 1981 to 1990 the extent of the dens occupying an area of about 125m² was defined and mapped (Fig. 1) and numerous carnivoran fossils were plotted and removed. Why Peterson and his men did not fully explore and excavate Quarry 3 remains a mystery: careful searches for field notes or diaries from the Carnegie excavations of 1904-1905 have proven fruitless, and we have only Peterson's brief comments in his publication of 1910 on the carnivores from Quarry 3.

Our census of the carnivores found in the dens, completed in 1994, includes our finds and Peterson's earlier material. There are two large beardogs (Family Amphicyonidae: *Daphoenodon* and a wolf-sized temnocyonine), two mustelids (Family Mustelidae: *Megalictis* and *Promartes*), and two small fox-sized canids (Family Canidae: *Phlaocyon* and *Tomarctus*). The carnivore present in greatest numbers in the burrows is *Daphoenodon superbus*, known from more than ten individuals ranging in age from juveniles to mature and aged adults. Among the most interesting discoveries during the excavation of Quarry 3 is evidence of marked sexual dimorphism in *Daphoenodon*. Males are large, robust, long-jawed with elongate premolars whereas females are much smaller, more gracile, and short-jawed with shorter premolars. Males display elaborate bony exostoses on the internal face of the distal radius which appear to be absent in the females.

A rare temnocyonine beardog is known from a skull and partial skeleton in Den 2 found less than 2m from a male *Daphoenodon* skeleton but segregated in its own burrow. The temnocyonine was a mature young adult, based on tooth wear: its death was surely premature as were the deaths of the juvenile *Daphoenodon* and its mother found nearby. In addition to these beardogs,

several individuals of *Megalictis*, a large wolverinelike mustelid, and scarce remains of the small marten-sized *Promartes* were discovered during excavation of the northern part of the den complex (Fig. 1). Multiple individuals of the small canid *Phlaocyon* are represented by dental remains, and a few isolated teeth record the somewhat larger canid *Tomarctus*.

Fossils of the small canids are so rare and fragmented that one cannot be certain they were not prey of the larger animals in the dens. Arguing against this, however, is the fact that the only noncarnivoran bone found in the dens is a small, well-defined sample of limb, foot, and dental fragments of ungulates that seems to be the primary prey residue left in the dens. Such incomplete and comminuted fragments differ from the more complete, often partially articulated carnivoran skeletons in the dens, and are found scattered throughout the various burrows. These ungulate skeletal fragments belong to a limited range of animals, chiefly juveniles of the small oreodont *Merychys*, the small rhinoceros *Menoceras*, and occasional rare camels. The small canids seem unlikely members of the prey suite recorded by the ungulate bone sample.

Carnivore bones in the dens bear the imprint of teeth and were scavenged by other mammals before sediment burial in the dens. Within the burrows the skeletons were covered by thinly-laminated, ash-rich, fine sand and silt carried into the dens by water and wind. Reexcavation of at least one burrow is evident after partial filling by such laminated sediments. Final burial of the den complex was accomplished by at least 10m of fine volcanoclastic sediment deposited over the site by a wide, shallow ephemeral stream that also buried the waterhole bonebed at Carnegie Hill. The stream valley was eventually filled by wind-deposited volcanoclastic loess that succeeded the local stream deposits, entombing the dens and their occupants until exposed by Quaternary erosion of the modern Niobrara River drainage.

HARRISON FORMATION DEN SITE (22 Ma)

Realizing that these dens were closely associated with fossil soils (paleosols) of the upper Arikaree Group in the vicinity of Agate National Monument, we began to search for additional evidence of burrows in the numerous paleosols of the region. In May 1991 we were fortunate to discover another den complex near Agate National Monument at a lower, hence older, stratigraphic level in the Harrison Formation (the Quarry 3 dens are in the base of the Upper Harrison beds). This new complex included the largest vertebrate burrows known to us, some measuring 10m in length and 1-2m in diameter (Fig. 2). These burrows differed from the Quarry 3 dens in their hardened outer rind of white siliceous rhizoliths (root casts) that formed a dense meshwork enclosing the burrow-fill. The siliceous encasing meshwork of roots creates a resistant capsule protecting the burrow-fill, hence these burrows are etched from the outcrop by erosion, creating a series of linear tubes standing in relief. In the vicinity of the burrows was a fully-articulated skeleton of a small canid and a partial skeleton of a rodent. Too small to have dug the dens, they probably explored and occupied them after they were developed by larger animals. Significantly, a few bones of a large bearded dog were found in place in one of the dens, suggesting the identity of the probable excavators of the tunnels. Our excavation of this site has been

preliminary; future work may reveal more details of the site occupants and the areal extent of the den complex.

Our study of the upper Arikaree paleosols in the region east of the Hartville Uplift in western Nebraska and adjacent southeastern Wyoming indicates abundant paleosol horizons, dense rhizolith networks, and frequent preservation of vertebrate and invertebrate burrows. These discoveries have alerted us to the existence of a rich reservoir of paleoecological information providing insights into Early Miocene land surfaces, vegetation, infauna, and climate. Arikaree sediments of the central Great Plains retain the record of a 10 million year interval (19 to 29 Ma) when enormous volumes of fine volcanic sand and silt were introduced into the region by wind, much of it reworked by wind and local streams, eventually building a thick blanket of volcanoclastic sediments hundreds of meters thick in northwest Nebraska. The well-defined and regionally widespread sequence of ancient land surfaces marked by paleosols indicates periodic pauses in deposition of the upper Arikaree Group during the interval from about 19 to 22 Ma. These ancient soils appear to have been entisols and inceptisols with minimal development due to a seasonally semiarid climate in the North American midcontinent in the Early Miocene. Thus the dens are preserved as the result of a fortuitous combination of geologic and climatic events: the influx of fine volcanically derived sediment into the Great Plains; the episodic nature of Arikaree deposition leading to soil development on regional land surfaces east of the Rocky Mountain front; the alkaline chemistry of Miocene ground water and sediments conducive to preservation of phosphatic vertebrate bone mineral; and a semiarid climate that conserved the mineralogy of the fine volcanoclastics, and created chemical conditions favorable to development of dense rhizolith horizons. This dry climate also retarded the breakdown of vertebrate bone exposed to the Miocene environment until burial could take place. We can predict that fine volcanoclastics deposited under semiarid to arid conditions elsewhere in the world during the Cenozoic may also retain important diagenetic features (paleosols, plant traces, burrows, vertebrate fossils) useful to understanding the paleoecology of these regions.

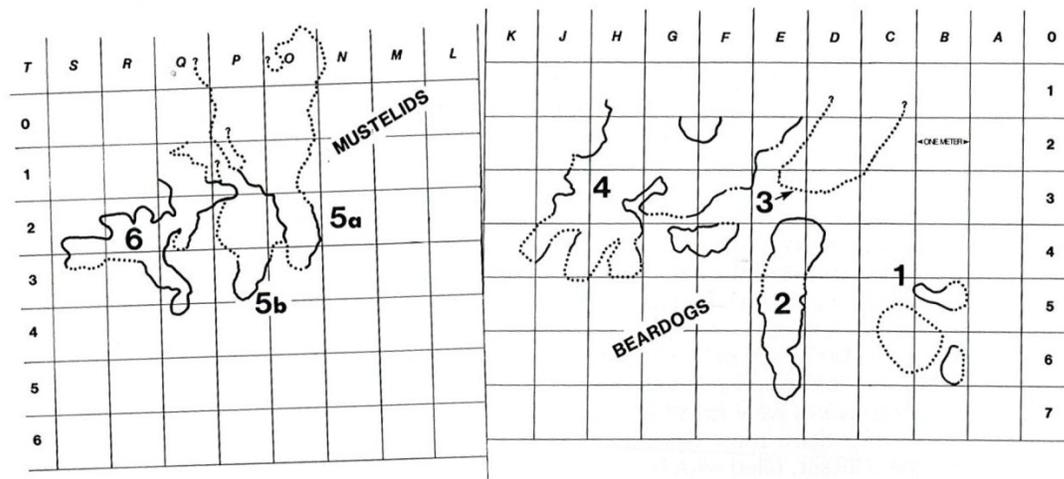


Figure 1. The Quarry 3 den complex at Bearddog Hill, Agate Fossil Beds National Monument, Nebraska. Mammal bones occur in every den, and partial skeletons were found in Dens #1, 2, 3, and 5. Bearddogs were common in the south part of the quarry (meters B to K, 1 to 7) and both mustelids and bearddogs were found in the north part of the site (meters O to S, rows 0 to 4). The three distal terminations of den 4 seen in row 4, H, J, and K, appear to be pupping chambers for young bearddogs. Peterson's best *Daphoenodon* skeletons belonging to an adult female and her male offspring are believed to have come from den 1.

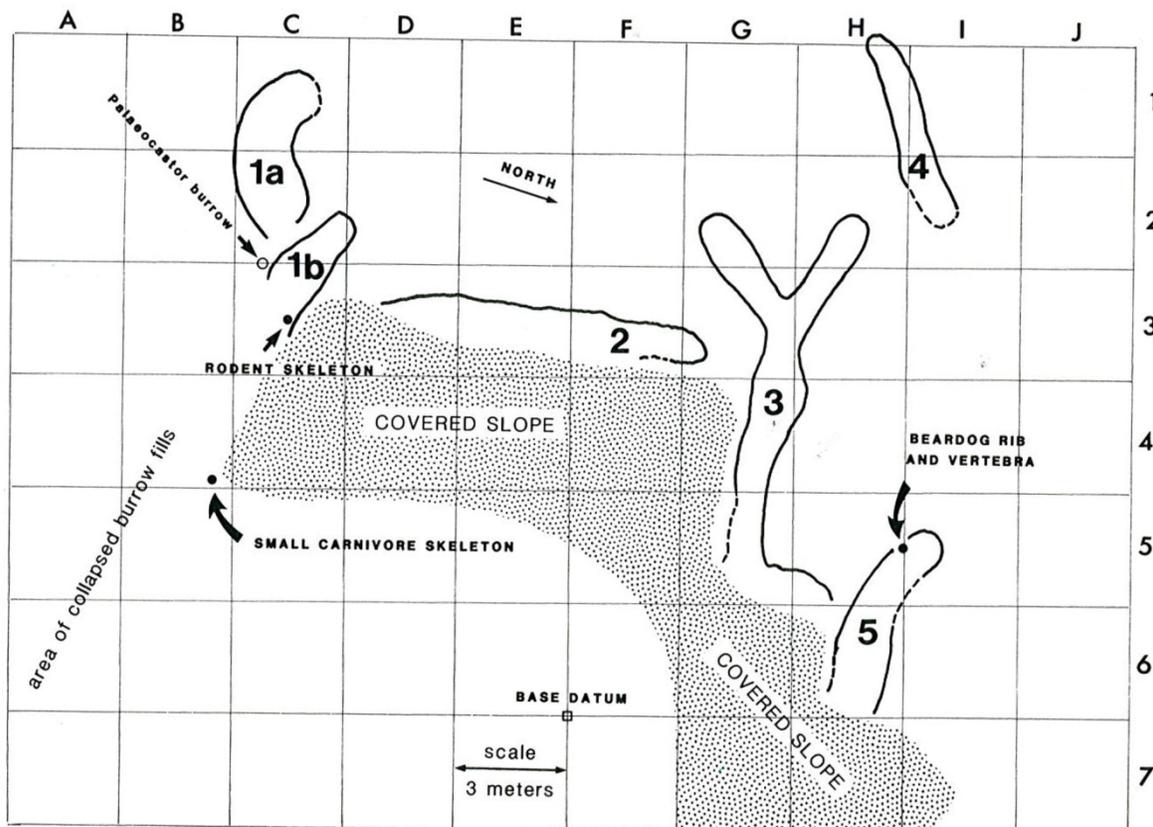


Figure 2. The Harrison Formation den complex contains enormous burrows, some with bearddog bones in situ. Five major burrows have been identified: only preliminary excavation of den 5 has taken place. The small carnivore skeleton in square B4 may occur within a burrow but its perimeter cannot be reliably defined at present. Den 3 is the largest vertebrate burrow presently known, at least 10m in length, and over 1m in diameter.

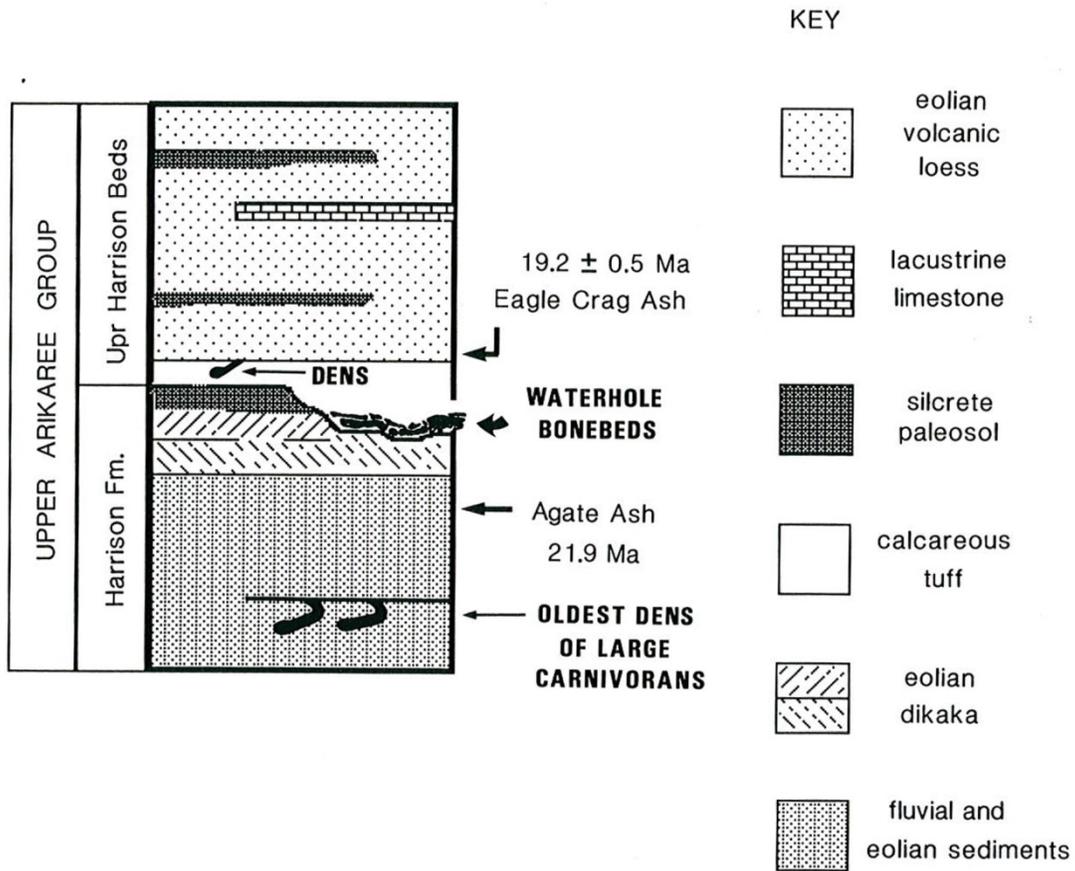


Figure 3. Stratigraphic placement of the carnivore den complexes at and in the vicinity of Agate Fossil Beds National Monument, Nebraska. The Quarry 3 den complex occurs as burrows excavated into calcareous tuff that contains the Carnegie Hill waterhole bonebed. This level at the base of the Upper Harrison beds is dated by the Eagle Crag Ash at about 19.2 Ma (fission track, zircon). A paleosol above the dens represents the Early Miocene land surface burrowed by these carnivores. The Harrison Formation den complex occurs below the Agate Ash (21.9 Ma, potassium-argon, biotite) and is presumed to date to about 22 Ma. This is the oldest den complex of large carnivorans currently reported in the fossil record.

A PRELIMINARY SURVEY OF PALEONTOLOGICAL RESOURCES FROM THE ALASKA REGION NATIONAL PARKS

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INTRODUCTION

The National Park Service manages extensive areas within Alaska. Stratigraphically, sedimentary rocks range from the Proterozoic through the recent. Isolated reports suggest a wealth of paleontological resources occurring in some of the Alaskan National Parks. Comprehensive paleontological surveys are difficult due to the vast acreage and limited access. To date, the scope and distribution of paleontological resources in the Alaska Region parks is poorly understood.

This preliminary report is an attempt to summarize the available data for known paleontological resources in the Alaskan National Parks. Information will continue to be compiled in order to produce a more complete final published report documenting paleontological resources.

A Research Proposal has been submitted along with this report. The proposal is directed towards the establishment of a pilot paleontological resource survey that will initiate in conjunction with the ongoing Alaskan Coastline Resource Surveys.

The objective is to compile paleontological resource baseline data to facilitate both resource management and protection. This information will be valuable in providing baseline fossil resource data for park and regional office staff, as well as for future researchers.

A brief summary of available information is provided for each Alaska Region unit. Lack of available data does not necessarily indicate the lack of significant paleontological resources in any of these units. Our hope is to promote greater research interests and expand the understanding of a paleontological resource that will almost certainly prove to be extensive.

ANIACHAK NATIONAL MONUMENT

The only known paleontological resources include paleobotanical material discovered in cores of Lake Idavain.

BERING LAND BRIDGE NATIONAL PRESERVE

The preserve contains 2.69 million acres of land. The northern Seward Peninsula has not been glaciated for over 100,000 years and has a high potential for paleontological resources. Pleistocene mammal remains, insects, leaves, pollen and coalified wood has been reported from the preserve. Mammoth material has been found including a reference of a juvenile mammoth in the collections at the Colorado School of Mines. Mammoth and walrus ivory is scattered throughout the preserve and is occasionally collected by Native Americans. A Pleistocene beaver dam is reported from the preserve (Newman, 1978).

Cape Deceit - coastal locality just east of preserve boundary that contains some of the earliest North American records of certain species of animals.

Cape Espenberg - coastal site with Pleistocene flora and fauna including marine fossils preserved during glacial cycles.

Goodhope River - late Pleistocene faunal remains found on gravel bars along the river including mammoth teeth, tusks, etc.

Imuruk Lake - rich fossil pollen record from core samples extend back 100,000 years. The record provides valuable data regarding vegetational changes during glacial cycles.

Inmachuk & Kugruk Rivers - fossil plant material found in river gravel below a Pliocene lava provide information on a warm climate vegetation. Late Tertiary beetles are abundant at these sites.

Kuzitrin Flats - a gravel deposit spans Miocene through Pleistocene in age. Older deposits contain fossil pollen and wood suggesting a temperate forest of hardwoods and conifers. Younger Pleistocene deposits include mammoth, bison and horse. Fossil plant associations demonstrate cold and warm climatic cycles in the late Pleistocene.

Trail Creek - mammoth scapula excavated from cave and radio-carbon dated at $11,360 \pm 100$ years B.P.

DENALI NATIONAL PARK

The current knowledge of paleontological resources at Denali is limited. A collection of Paleozoic marine invertebrates and late tertiary plant remains have been curated by park staff. A mammoth tooth was discovered west of Teklanika Ridge. Plant impressions include deciduous leaves such as birch and conifer stems and needles similar to *Sequoia*. Sites with marine invertebrates have been also reported from areas in the southern portion of the park.

GATES OF THE ARCTIC NATIONAL PARK & PRESERVE

Numerous fossil deposits occur within this unit. Fossil rich deposits range in age from the Devonian through the Cretaceous. Pleistocene deposits have yielded the remains of fossil bison and mammoth along the Middle Fork Koyukuk River. Devonian invertebrates including coral are located throughout the central Brooks Range and in the center of the park. The Lisburne Limestone (Mississippian/Pennsylvanian) contain brachiopods, corals, crinoids, blastoids, conodonts and occasional trilobites. This limestone is prevalent in the northern part of the park and fossils found along river cuts such as North and Middle Forks of the Koyukuk River. Cretaceous plant fossils have been found in the Fortress Mountain Formation in outcrops of the Castle/Fortress Mountain Unit of the park.

Bombardment Creek - Triassic marine fossils including *Monotis* and *Halobia* occur in the Shublik/Otuk Formation at the base of Mount Doonerak. Very fossiliferous exposures. Also found along Monotis Creek.

Karupa Lake - thin layer of Cretaceous limestone with the round shelled pelecypods *Buchia subclaveous* are found in the Okpikruak Formation.

Nigu River - Permian fossils including marine brachiopods, pelecypods and shark's teeth found in the Siksikpuk Formation along the river.

GLACIER BAY NATIONAL PARK

Information regarding paleontological resources is limited. Curated specimens include mainly marine invertebrates and a few paleobotanical specimens.

Cenotaph Island - numerous marine invertebrate specimens collected from this island in Lituya Bay.

KATMAI NATIONAL PARK

Reports of paleontological resources at Katmai are limited, however, there are curated fossils in the park collection. These specimens include invertebrates from Kagayuk Point and from the Valley of Ten Thousand Smokes. Most of the invertebrates are from Late Jurassic (Naknek Formation) and Cretaceous (Kaguyak Formation) exposures.

Kagayuk Point - Upper Cretaceous fossil invertebrates including *Pachydiscus* sp. and *Inoceramus* sp. collected from this site.

Naknek Lake - leaf imprints and petrified wood have been collected from the lake beach near Brooks Camp.

KENAI FJORDS NATIONAL PARK

The only record of paleontological resources at Kenai Fjords National Park include accounts of ancient trees preserved in glacial ice.

LAKE CLARK NATIONAL PARK & PRESERVE

The park contains approximately 2.6 million acres and the preserve contains about 1.4 million acres. A paleontological survey of this unit has not been conducted. A significant Jurassic site is located along the coast called Fossil Point. The site has potential for both marine fossils and Pleistocene remains inland.

Fossil Point Jurassic Section - site on west side of Cook Inlet about 56 miles southwest of Kenai. The type locality of the Tuxedni Group begins at Fossil Point with the Red Glacier Formation. Many fossils are present including *Grammatodon* sp., *Inoceramus lucifer*, *Oxytoma* sp., *Comptonectes* sp., *Thracia* sp., and many others. This faunal assemblage can be correlated with northwest European assemblages (Bajocian through Bathonian). The site is impacted by illegal fossil collecting. Proposed as a National Natural Landmark.

WRANGELL-ST. ELIAS NATIONAL PARK & PRESERVE

Devonian through Tertiary sediments are present in the park. The more significant fossil units include: the Permian Mankomen Group limestone with ammonites and brachiopods; the Permian Hansen Creek Limestone with horn corals; the early Cretaceous Chisana Formation with pelecypods; and tertiary coal deposits and plant fossil localities.

YUKON-CHARLEY RIVERS NATIONAL PRESERVE

This unit contains a remarkably rich and extensive fossil record ranging from the Proterozoic through the Pleistocene. Vertebrate fossils include ice age mammoth, bison and sheep. Invertebrates and paleobotanical fossils are abundant.

MIDDLETON ISLAND NATIONAL NATURAL LANDMARK

This island consists of approximately five square miles and is located in the Gulf of Alaska about 155 miles southwest of Anchorage. Important Plio-Pleistocene fossils occur at this locality. Incorporated into the National Natural Landmark Program.

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THE BIG PIG DIG OF 1993: DISCOVERY, LOGISTICS, AND EXCAVATION OF EARLY OLIGOCENE MAMMALS IN BADLANDS NATIONAL PARK

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Early in the summer of 1993 a routine visitor report resulted in the largest paleontological dig ever undertaken by Badlands National Park. The report of a large articulated vertebral column, two large long bones, and scattered material, eroding out of the ground was taken seriously by park rangers, but although Badlands National Park is one of the largest sources of mammalian fossils in the world, the management was initially unprepared for such a large paleontological find. Professional knowledge, leadership, supplies, coordination by all park managers and supervisors, and many hours of labor were required in order to adequately address the situation. The park staff, assisted by South Dakota School of Mines and Technology paleontologists, the Badlands Natural History Association, the regional office of the National Park Service, and many skilled volunteers were able to successfully undertake the excavation of the many mammalian vertebrate fossils, which include *Archaeotherium*, *Subhyracodon*, and *Mesohippus*.

DISCOVERY

On Thursday, June 10, 1993, Stephen Gassman, a photographer from Elkader, Iowa, and Jim Carney, of Manchester, Iowa, were photographing the Badlands scenery when they serendipitously came upon a large assemblage of fossil bones eroding out of a wash. After taking many photographs, they made note of the location of the bones and reported the find to park rangers. The conduct of Mr. Gassman and Mr. Carney should be noted because they were able to relay this important information with a clear description and location without disturbing the fossils in any way, thereby preserving the scientific integrity of the site.

Park rangers investigated the find shortly after receiving the report. Photographs were taken and notes were made, but the find was still not disrupted. The park, which did not have a paleontologist at the time, relied on the expertise and leadership of two volunteer Paleontologist-interns to investigate the scientific potential of the find and to recommend and initiate further action. Normally, a salvage collection is within the scope of an intern's experience and ability, but it soon became evident that this site was to outgrow the designation of salvage.

LOGISTICS

From the onset, there were considerations that made this site unique. First, it was located in a drainage directly adjacent to a country road, which had been redirected recently and the drainage contoured. The work had uncovered the fossils without actually damaging them which resulted

in newly exposed vertebrate fossils that didn't show the damage of slow weathering. The fossils were in unusually good condition, but were only five meters from a well-traveled country road. The initial concern was to find out who had immediate jurisdiction over the removal of the fossils. They were within the right-of-way of a Pennington County road that intersects the park. Additionally, the Road-and-Trails Division of Badlands National Park is interested in any project that may affect water flow within a constructed drainage. A further concern was that the entire site was adjacent to a designated wilderness area. The success of the excavation was contingent on the cooperation of all parties involved. Pennington County, which has jurisdiction over the road, but not the fossils, indicated that there would be no foreseeable problems with the excavation, and in fact often stopped to survey progress and offer assistance or suggestions. The Badlands Road-and-Trails foreman, after inspecting the site, took interest in the project and offered assistance in the form of personnel and equipment on many occasions as the summer progressed. After checking maps, the site was found to be outside of the nearby wilderness area. Another consideration was that of security, including protection of the site from both intentional and unintentional vandalism and ensuring the safety of visitors who stopped to observe the excavation. This included an increased law enforcement presence as well as enclosure of the area by snow fence to keep a safe distance between fossils and visitors.

Visitor interpretation was a critical component of the fossil excavation. Because of its proximity to a well-traveled road, many people stopped to view the dig. It was necessary to address the many inquiries by distributing handouts that outlined the direction of the dig and its importance. Initially, the excavation process was slow because workers were spending large portions of their time answering visitor questions. The Assistant Chief of Interpretation Division, Valerie Naylor, responded by adjusting schedules to provide a professional interpreter to aid with on-site interpretation. In addition to facilitating effective use of time for excavation workers, this schedule change provided the visitors with friendly, up-to-date information about the dig and the importance of paleontology at Badlands National Park.

The office staff of the park played an important role in the administration of the site. Funds were secured to cover the ever-growing expenses of supplies and equipment. They also wrote funding requests and purchase orders, tracked accounts, and saw to it that supplies were delivered. In addition, countless hours were spent administering the site by both staff and volunteers. It was the responsibility of Paleontologist-inter Scott Foss to manage the site for the park and provide much of the leadership required to catalyze the above-mentioned logistics. Paleontologist-intern Kimberlee Stevens took charge of actual excavation activities and, after preparing the fossils, plans to work out the taphonomy of the site.

EXCAVATION

Shortly after the start of the excavation, it became apparent that outside advice and assistance would be necessary. The advice and presence of Rachel Benton, Park Service Paleontologist for Fossil Butte National Monument, allowed for an easy transition from the intern-run salvage

collection to a fully controlled excavation to be directed by Dr. Phil Bjork of the South Dakota School of Mines and Technology. Dr. Bjork implemented a new mapping technique which included the accession of vertical as well as horizontal information. The results, collected with new surveying equipment provided by the School of Mines, should provide useful insight into the relative positions of all the fossil bones.

The day-to-day progress of the excavation was maintained by volunteers who engaged in the actual work of digging, mapping, jacketing, and fossil removal. Many of the park staff took an active interest in the site and offered hundreds of volunteer hours. Special projects, including the removal of larger jackets, were facilitated by equipment and personnel loaned to the dig by other divisions of the park. This enthusiastic response by all of the park managers and supervisors facilitated the success of the dig.

The placement of the drainage culvert was a dramatic display of inter-division as well as inter-agency cooperation. After consecutive days of damaging rain, a drainage culvert was deemed necessary to route rain runoff around the site. With the assistance of Park Superintendent, Irv Mortenson, and Chief of Maintenance, Ted Haliday, large culvert sections and sandbags were purchased and delivered. A civil engineer was brought in for consultation, while the Road-and-Trails foreman, Lylle Amiotte, provided sand and personnel. Additional personnel and equipment were provided by the Buildings-and-Utilities foreman, Terry Saunders, as well as by the divisions of Resource Management, Interpretation, and Visitor and Resource Protection. For a few hours, the full park staff turned to the needs of the site. Virtually all park activity was suspended save visitor interpretation, fee collection, and visitor safety. Within a couple of hours, the drainage had been levied with sandbags, and water was routed around the site via the new culvert.

The South Dakota School of Mines and Technology (SDSM&T) provided many qualified volunteers, professional staff, equipment, and supplies. The fossils were carefully uncovered, field jacketed, removed, and transported to the SDSM&T vertebrate fossil preparation laboratory. Once prepared and catalogued, the fossils will be studied. Although the fossils remain the property of the U.S. Government, they will be housed at the SDSM&T where they will be available for research and inquiry.

RESULTS

The excavated fauna includes at least two relatively complete *Archaeotherium*, a nearly complete *Subhyracodon*, and many cranial and post-cranial elements of *Archaeotherium*, *Subhyracodon*, *Mesohippus*, and many as yet unidentified postcranial sections of Oligocene mammals.

Vertically, the site is only a few meters above the Chadron - Brule intersection and so is assumed to be earliest Oligocene in age. The taphonomy of the site has only begun to be interpreted and much of the site has yet to be uncovered; new and exciting insights into the fauna and paleoecology of the Badlands can certainly be expected.

The Dig also became a high profile paleontological event in the media with coverage in many

states including South Dakota, Iowa, and Colorado. The coverage always portrayed a positive message when describing the role of the Park Service and the South Dakota School of Mines and Technology and their ability to manage such a large and complex paleontological find. This is in contrast to the negative publicity afforded the institutions, especially the Federal Government, as a result of their roles in other recent paleontological events in South Dakota.

Badlands National Park benefitted from the "Big Pig Dig" in many ways. The Division of Interpretation was given a challenging concept to relay to visitors, while the Resource Management Division was enticed to further embrace paleontology in its present and long term resource management plans. The Ranger Operations Division was challenged to respond to new facets of resource protection, and the Badlands Natural History Association, which funded the paleontology-interns, found a new way to fulfill its charter goal of enhancing research and education in Badlands National Park. Overall, the dig heightened both the public's and the park staff's awareness of paleontology first hand during the summer of Jurassic Park.

A BIOMECHANICAL ANALYSIS OF MASTICATION IN THE FOSSIL RODENT *ISCHYROMYS* AND ITS BEARING ON THE ORIGIN OF SCIUROMORPHS

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ABSTRACT

A biomechanical analysis of mastication in the protrogomorphous Oligocene rodent, *Ischyromys* is presented. *Ischyromys* jaw muscles are reconstructed based on comparison with various modern rodents, particularly *Sciurus*. Detailed dissections of the temporalis, masseter lateralis, masseter medialis, and masseter superficialis in *Sciurus*, *Rattus*, and *Cavia* provided baseline data for the sciromorph, myomorph, and hystricomorph jaw muscle patterns. Analysis of muscle vectors and dental wear patterns indicate *Ischyromys* had a single phase chewing cycle centered around grinding at the cheek teeth. This information is compared to mastication in modern rodents which exhibit an anterior shift of some parts of the masseter muscle and a more posterior orientation for the temporalis. This muscle arrangement allows advanced rodents to utilize a two phase chewing cycle, an ingestive phase when the incisors are in proper occlusion and a grinding phase when the cheek teeth line up. We believe the reason for the expansion of the masseter muscle onto the rostrum is for increased efficiency in gnawing. The posterior orientation of the temporalis is interpreted as an adaptation to resist extrinsic forces at the incisors and for positioning the jaw properly for the grinding phase. Increased efficiency of gnawing is viewed as the major reason for the success of rodents by opening up additional feeding niches, i.e. nuts and other hard shelled vegetation.

INTRODUCTION

Rodents are the most successful, diverse group of mammals alive today. There are 29 families, 426 living genera, and 1,814 living species of rodents (Nowak, 1991). They are found in a wide variety of habitats: deserts, tundra, mountains; some are burrowers and some are aquatic. They are a remarkably complicated group with respect to morphological diversity, lines of descent, and parallel evolution of similar features in different groups (Vaughan, 1986).

Three jaw muscle patterns, sciromorph, myomorph, and hystricomorph are often used to designate major taxonomic divisions of the rodents. Not every rodent can readily be placed into one of these groups, however, nor do experts agree on how the morphologic types evolved (Eisenberg, 1981). Specifically these groups represent important differences in the structure of the skull and masseter muscles. Sciromorphs typically do not have an enlarged infraorbital

foramen and the lateral masseter attaches to both the zygomatic arch and rostrum via the zygomatic plate. Myomorphs have a slightly enlarged infraorbital foramen and the medial masseter attaches to the zygomatic arch and rostrum via the infraorbital foramen. Myomorphs also have a zygomatic plate which allows the lateral masseter to expand onto the rostrum. Hystricomorphs have a greatly enlarged infraorbital foramen and the medial masseter attaches to the zygomatic arch and the rostrum via the infraorbital foramen. The most primitive rodents were protrogomorphous, a masseter condition lacking the specializations described above.

The oldest rodent, *Acritoparamys*, appeared in the late Paleocene. By the late Eocene some rodents had abandoned the primitive arrangement of jaw musculature in which all three parts of the masseter were attached to the zygomatic arch. The time between the late Eocene and middle Oligocene was a period of important diversification (Wilson, 1972).

The phylogenetic relationships between rodent groups are complex. Different rodent lineages may have evolved similar jaw muscle patterns independently. Since rodent evolution is so equivocal, we decided to avoid this massive complexity and look at the radiation of rodents not from an ancestor-descendant viewpoint, but from a biomechanical or functional viewpoint. A particular focus of our research was to determine what morphological changes gave rise to sciuriforms and why these changes occurred.

MATERIALS AND METHODS

The jaw musculature from a typical example of each of the major rodent groups was examined in detail. All recent specimens used in this study are housed in the Georgia College Mammal Collection (GCM). A tree squirrel, *Sciurus carolinensis*, was chosen for the sciuriform; GCM 594, 595, 596, 597, 598, 850, 851, and 852; a laboratory rat, *Rattus norvegicus*, was selected for the myomorph; GCM 599, 600, and 853; and a guinea pig, *Cavia porcellus*, provided the hystricomorph, GCM 601, 602, and 854.

Each rodent was preserved in 10% formalin and then dissected. The points of origin and insertion for the temporalis and each component of the masseter muscle: the masseter superficialis, masseter medialis, and masseter lateralis were identified. The fiber pattern for each muscle was described in order to determine the line of action of the muscle. We arbitrarily decided not to include the pterygoideus in this study to simplify our analysis.

Individual muscles from both the right and left side were removed and weighed on an Ainsworth balance to the nearest 0.01 gram in order to determine the relative mass of each muscle. Based on these muscle weights we determined the relative percent of the total muscle mass for each muscle to use in a vector analysis (see Hiiemae, 1971 for technique).

We chose *Ischyromys*, a common fossil protrogomorph from the Oligocene of Badlands National

Park, South Dakota, to represent the ancestral rodent jaw muscle pattern. The origin and insertion for each jaw muscle was determined by comparing muscle scars on the recent rodents to the corresponding muscle scars on *Ischyromys*. All of the *Ischyromys* specimens used in this study are housed in the Georgia College Vertebrate Paleontology Collection (GCVP). Cranial material included GCVP 275, 276, 277, 279, 290, and 295. We estimated the mass for each muscle in *Ischyromys* by determining its surface area and comparing that to *Sciurus*.

To eliminate size differences we measured the diameter of the foramen magnum of each species, then standardized the size of each rodent to the taxon with the largest foramen magnum. A vector length of 10cm=100% was chosen for *Sciurus*, the largest rodent. Individual vector length was based on its percentage of the total muscle mass. Vector direction was a line drawn from the point of insertion through the center of mass of the muscle. Individual lever arms were measured for each muscle using the jaw joint, cheek teeth, and incisors as alternate fulcra (Bramble, 1978). To test the accuracy of our biomechanical analysis of *Ischyromys* we examined cheek teeth using a Bausch and Lomb dissecting scope at 30X magnification to determine wear facet patterns. Dental wear patterns are a good indicator of the relative importance of each part of the chewing cycle which ultimately is dictated by muscle activity (Butler, 1972). The following specimens were examined: GCVP 28, 45, 47, 49, 50, 60, 79, 80, 81, 86, 276, 279, 289, 291, 292, 293, 522, 766, 1133, 1138, and 1793.

RESULTS

Masticatory Musculature of Recent Rodents (Table 1)

M. Masseter Lateralis - In *Rattus norvegicus* this muscle originates on the anterior zygomatic arch and on the rostrum via the zygomatic plate; it inserts on the border of the masseteric fossa and the edge of the jaw. The lateralis was the largest component of the masseter muscle. In *Sciurus carolinensis* the muscle originates on all of the zygomatic arch and onto the rostrum via the zygomatic plate; it inserts on the jaw from the anterior border of the cheek teeth through to the posterior border of the masseteric fossa and edge of jaw. The lateralis is the largest jaw muscle in the squirrel. In *Cavia porcellus* the lateralis originates only on the zygomatic arch; it inserts on the posterior region of the jaw and angle of the jaw. The lateralis is the smallest of the masseter muscles in the guinea pig.

M. Masseter Medialis - In *Rattus norvegicus* the medial masseter originates on the anterior portion of the zygomatic arch and onto the rostrum via the infraorbital foramen; it inserts onto the masseteric fossa. The medial masseter is the smallest component of the masseter muscle in the myomorph. In *Sciurus carolinensis* the medial masseter originates on the ventral surface of the zygomatic arch via the zygomatic plate and inserts onto the masseteric fossa. It is larger than the superficial masseter but smaller than the lateral masseter. In *Cavia porcellus* the medial masseter originates on the rostrum via the enlarged infraorbital foramen; it inserts onto the masseteric fossa. It is larger than the lateralis but smaller than the superficialis.

M. Masseter Superficialis - In *Rattus norvegicus* the masseter superficialis originates on the pit on the rostrum; it inserts on the angle of the jaw. It is the second largest of the masseter muscles in the rat. In *Sciurus carolinensis* the masseter superficialis originates on the anterior base of the zygomatic arch; it inserts on the angle of the jaw. It is the smallest of the masseter muscles in the squirrel. In *Cavia porcellus* the masseter superficialis originates on the anterior portion of the zygomatic arch and it inserts on the angle of the jaw. It is the largest jaw muscle in the guinea pig.

Temporalis - In *Rattus norvegicus* the temporalis originates on the temporal fossa; it inserts on the coronoid process. It is the largest jaw muscle in the rat. In *Sciurus carolinensis* the temporalis originates on the temporal fossa and inserts on the coronoid process. It constitutes next to the smallest amount of the skull musculature in the squirrel. In *Cavia porcellus* the temporalis is the smallest of the jaw muscles studied and originates in a small temporal fossa; it inserts on the coronoid process.

Table 1. Wet Weights and Percentages of Rodent Jaw Muscles		
Rodent	Weight	Percentage
<i>Rattus norvegicus</i> (Myomorphous)		
M. Masseter Lateralis	1.68g	29.7%
M. Masseter Medialis	0.99g	17.5%
M. Masseter Superficialis	1.23g	21.7%
Sum of Masseter	3.90g	68.9%
Temporalis	1.76g	31.1%
Sum of Masseter + Temporalis	5.66g	100%
<i>Sciurus carolinensis</i> (Sciurormorphous)		
M. Masseter Lateralis	2.66g	40.8%
M. Masseter Medialis	1.49g	22.9%
M. Masseter Superficialis	0.96g	14.7%
Sum of Masseter	5.11g	78.4%
Temporalis	1.41g	21.6%
Sum of Masseter + Temporalis	6.52g	100%
<i>Cavia porcellus</i> (Hystricomorphous)		
M. Masseter Lateralis	0.16g	7.5%
M. Masseter Medialis	0.66g	30.8%
M. Masseter Superficialis	1.25g	58.4%
Sum of Masseter	2.07g	96.7%
Temporalis	0.07g	3.3%
Sum of Masseter + Temporalis	2.14g	100%

BIOMECHANICAL ANALYSIS

Our reconstruction of the jaw musculature of *Ischyromys* is shown in Figure 1. The masseter lateralis originated only on the zygomatic arch and inserted on the edge of the jaw. The masseter medialis originated on the zygomatic arch and inserted onto the masseteric fossa. The masseter superficialis originated on a pit on the rostrum and inserted along the angle of the jaw. The temporalis originated on the temporal fossa and inserted on the coronoid process. *Ischyromys* is advanced compared to other protrogomorphous rodents

(such as *Ischyrotomus* reconstructed by Wood, 1965) in having the origin of the superficial masseter on the rostrum instead of on the zygomatic arch.

Figure 2 illustrates our vector analysis of jaw muscles in *Cavia*, *Rattus*, *Ischyromys*, and *Sciurus*. Note in particular the dominance of the temporalis and medial masseter in *Ischyromys*, and the more vertical orientation of these muscles compared to the other rodents. Our analysis of jaw muscle action implies that the lingual phase has become more important than the buccal phase in modern rodent mastication.

Examination of dental wear patterns supports our findings. Primitive rodent occlusion was ectental with the lingual phase possessing a more anterior component than the buccal phase which approaches the horizontal (Butler, 1972). The hypocone and protocone are similar in size and shape in *Ischyromys*. The hypocone occludes with the protoconid and the protocone occludes with the hypoconid. On the lower molars, the entoconid is high and connects with the hypoconid via a transverse ridge. Here a facet is present resulting from occlusion with the protocone; similarly, there is a facet on the metaconid resulting from its occlusion with the hypocone and a facet on the entoconid also resulting from occlusion with the hypocone. In *Ischyromys*, lingual phase wear facets cover a larger area of the tooth, but distinct buccal phase wear facets are present. In *Sciurus*, lingual and buccal phase facets are almost continuous forming a single oblique grinding surface. Note for example, that the path of the hypoconid, during the buccal and lingual phase, develops a more anterior and longitudinal orientation in *Sciurus* than in *Ischyromys*. This wear pattern is almost certainly due to the anterior shift in orientation of the masseter in sciuriforms.

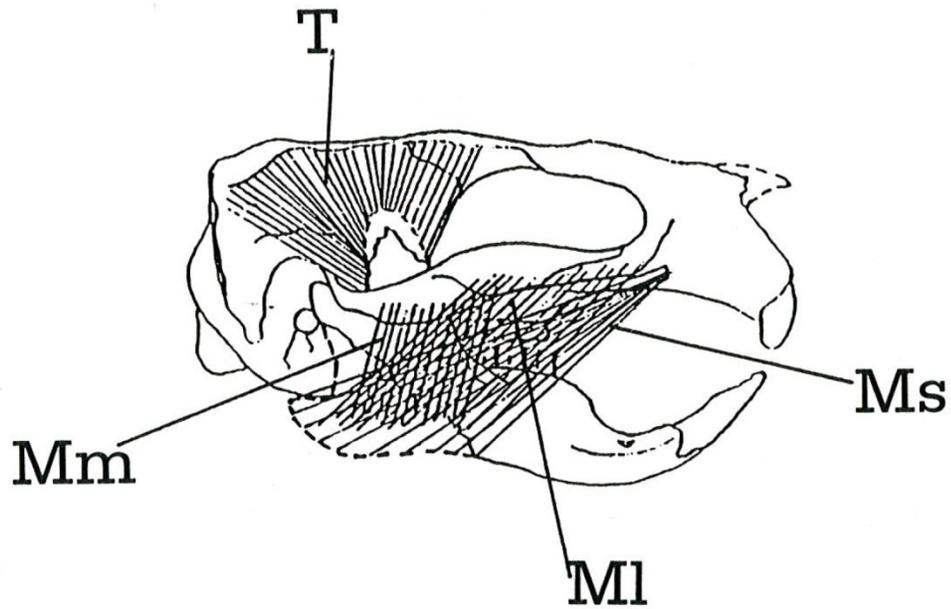


Figure 1. Muscle reconstruction of *Ischyromys*. Abbreviations: Ml, masseter lateralis; Mm, masseter medialis; Ms, masseter superficialis; and T, temporalis.

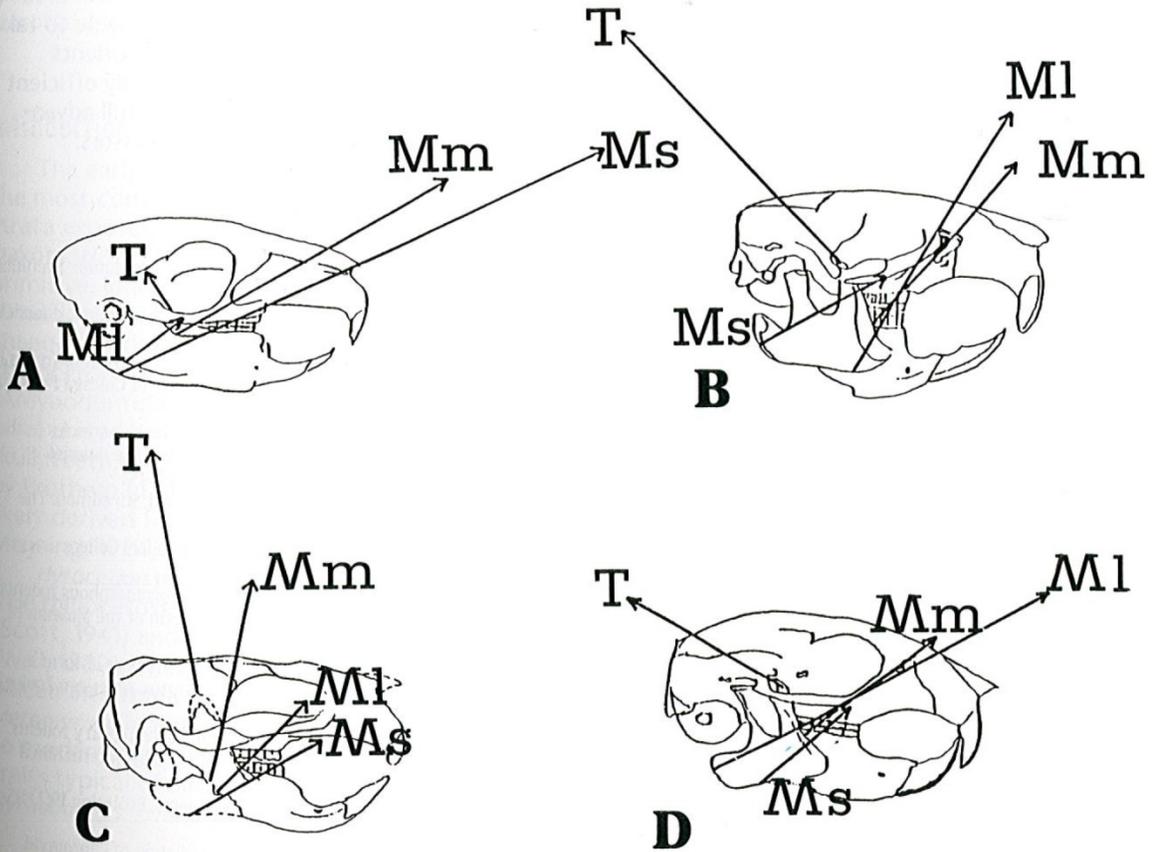


Figure 2. Vector diagrams illustrating relative magnitude and direction of Ml, masseter lateralis; Mm, masseter medialis; Ms, masseter superficialis; and T, temporalis. A, *Cavia porcellus*; B, *Rattus norvegicus*; C, *Ischyromys* sp.; and D, *Sciurus carolinensis*.

DISCUSSION

Rodent classification is based primarily on the structure of the jaw muscles, infraorbital foramen, characteristics of the lower jaw, and the cheek teeth (Weijs, 1980). These characters are all part of the food acquisition system, and when traced through time, their observed modifications reveal a complex phylogeny. Gaps in the sequence, however, cannot always be filled. Whole families of rodents stand in uncertain relations to proposed phylogenies. This situation is not surprising; in a phase of rapid evolution a gap of a few million years is enough to permit a discrete group to appear full-blown in the fossil record. The ancestry of such a group is often unclear because of parallelism among the earlier lineages from which it could have descended (Wahlert, 1974). Since definitive ancestor-descendant relations are difficult to determine, questions regarding the origin of modern groups are still problematic. Functional analysis of the feeding mechanism should add to our knowledge of rodent evolution. Woods and Howland (1979) examined the radiation of recent capromyid rodents in a similar way with moderate success.

The aim of this study was to construct a biomechanical model which could explain what changes took place in the evolution of sciuriforms from protrogomorphs. Modern rodents have a two phase chewing cycle, one when the cheek teeth are in occlusion, the masticatory cycle, and the other when the incisors are in occlusion, the ingestive cycle (Hiimae, 1971). The masseter and pterygoideus are responsible for side to side movement during mastication. The anterior segments of the masseter are responsible for rapid jaw closing, which is demonstrated when the incisors are in occlusion.

The evolution of sciurid mastication from a protrogomorph like *Ischyromys* is due primarily to a shift in the orientation and relative importance of the jaw muscles. *Ischyromys* had a more vertical orientation for all of the jaw musculature and the vector lengths for each muscle were not significantly different. In *Sciurus*, all components of the masseter have a noticeable anterior orientation with the masseter lateralis being greatly enlarged. The temporalis is also enlarged and displays a posterior orientation. A similar dichotomy between the masseter and temporalis is seen in myomorphs and hystricomorphs. The vertical orientation of the jaw muscles in *Ischyromys* implies that protrogomorphs had only a single phase chewing cycle centered around the cheek teeth. We believe the anterior migration of the masseter muscle in advanced rodents increased efficiency in the ingestive phase of the chewing cycle. Expanding the masseter onto the rostrum adds a second phase to the chewing cycle, resulting in increased speed of jaw closure while the incisors are in occlusion. The posterior orientation of the temporalis allows it to act as a stabilizer during the ingestive phase, resisting extrinsic forces at the incisors and as a jaw retractor to correctly align the cheek teeth during the grinding phase.

Our interpretation of the importance of incisor gnawing in the evolution of sciuriforms is supported by a comparison of the lever systems for each muscle using the jaw joint, bite point, and incisors as possible fulcra. *Sciurus* exhibits increased efficiency compared to *Ischyromys*

when viewing the incisors or jaw joint as the fulcrum but the two genera are similar when the cheek teeth are interpreted as the fulcrum.

Increased efficiency in the ingestive phase allowed the advanced rodents to occupy additional niches by making available a new food source: nuts and other hard shelled vegetation, a food source that protrogomorphs were probably unable to take advantage of. The success of modern rodents therefore seems to be due to their highly efficient two phase chewing cycle which takes full advantage of the chisel-like, ever-growing incisors.

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A BIOMECHANICAL ANALYSIS OF LOCOMOTION IN THE OLIGOCENERHINOCEROTOID, *HYRACODON*

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ABSTRACT

The Oligocene rhino *Hyracodon* is generally regarded as cursorial primarily because it is smaller than other rhinocerotoids. However, the cursorial abilities of this animal have never been tested biomechanically. The appendicular skeleton of *Hyracodon* is described and compared to *Ceratotherium* (white rhinoceros). The relative development of significant locomotor muscles is interpreted from muscle scars on specimens of *Hyracodon*. Relative lengths of each segment of the limb in *Hyracodon* are compared to a variety of modern ungulates ranging in locomotor habits from graviportal to cursorial. *Hyracodon* limb indices do not compare favorably with modern cursorial mammals. The following indices provide typical examples. The MCIII/radius index for *Hyracodon* (54.56) compared more favorably with *Hippopotamus* (56.30) than with the cursor *Antilocapra* (105.45). The tibia/femur index for *Hyracodon* (83.72) is very similar to the index for *Sus* (86.69) but falls far below that for *Antilocapra* (123.81). The data suggests a different lifestyle for *Hyracodon* than was earlier believed. Wild pigs or peccaries would be a more accurate modern locomotor analog for *Hyracodon* than cursorial ungulates.

INTRODUCTION

The early rhinocerotoid *Hyracodon* is one of the most common fossils found in the Oligocene strata exposed in Badlands National Park, South Dakota. *Hyracodon* (family Hyracodontidae) is a primitive, long lived taxon that survived for nearly 10 million years in North America with very little change (Prothero et al, 1986). The superfamily Rhinoceroidea is made up of three families (Amyndontidae, Hyracodontidae, Rhinocerotidae) united by derived characteristics of the skull, teeth, and post cranial skeleton as described by Prothero et al (1986). Rhinocerotoids are most likely derived from hyrachyid tapiroids (Wall and Manning, 1986).

Hyracodon lived contemporaneously with the true rhinoceroses, *Trigonius* and *Subhyracodon* (Scott, 1941) and the amyndontid *Metamynodon* (Wall, 1989). These animals are traditionally placed into three very different ecologic roles. *Metamynodon* probably filled a niche comparable to modern hippopotami. The rhinocerotids exhibit traits typical of large terrestrial herbivores. *Hyracodon* is invariably called the "running rhino" because of its smaller size and lighter build compared to other rhinocerotoids. The actual locomotor abilities of *Hyracodon* have never been examined biomechanically.

Limb structure and proportions are closely tied to an animal's body size and life habits. Biomechanical analysis of limb/locomotor systems can be used to assign an animal to one of four traditional locomotor groups - graviportal, mediportal, subcursorial, and cursorial. Strict definition of these groups is not possible since they represent a continuum from one extreme (graviportal - limbs primarily designed for weight bearing) to another (cursorial - extreme development of cursorial adaptations as seen in most long distance runners; see Coombs, 1978 for a detailed discussion of these terms).

This paper presents the results of a comparative biomechanical investigation of *Hyracodon* and the modern white rhino, *Ceratotherium*, to a variety of modern ungulates.

MATERIALS AND METHODS

This work is divided into two parts: first, a description of relevant portions of the limb anatomy of *Hyracodon* and *Ceratotherium*; and second, an interpretation of the locomotor abilities of *Hyracodon* based on a comparison of limb bone indices to a variety of modern ungulates. Muscle reconstructions of *Hyracodon* were based on specimens housed in the American Museum of Natural History, New York City, NY (AMNH 1168, 1176), Frick Collection (FAM 0-21-549, also housed at the American Museum), Georgia College Vertebrate Paleontology Collection, Milledgeville, GA (GCVP 4756, 4928), and South Dakota School of Mines and Technology, Rapid City, SD (SDSM 9789). Muscle origins and insertions were determined from identification of muscle scars and comparison to literature on recent mammalian anatomy (Beddard and Treves, 1889; Davis, 1964; Gregory, 1929; Howard 1973, 1975; Osborn, 1929; Sisson and Grossman, 1975; Windle and Parsons, 1901, 1903).

All recent mammals cited, except *Elephas*, are housed in the Georgia College Mammal Collection (GCM). Modern mammals used for comparison included *Dama* (fallow deer, Artiodactyla: GCM 576), *Tragelaphus* (bush buck, Artiodactyla: GCM 577), *Lama* (llama, Artiodactyla: GCM 1587), *Antilocapra* (pronghorn, Artiodactyla: GCM 1229) as cursorial examples; *Sus* (pig, Artiodactyla: GCM 885) as a subcursorial example; *Ceratotherium* (white rhino, Perissodactyla: GCM 575) as a mediportal example; and *Elephas* (elephant, Proboscidea: from Osborn, 1929) as the graviportal example. Limb bone indices were calculated from measurements using Helios Vernier dial calipers for small elements, and a meter stick for larger elements.

The following standard limb ratios were used (each is multiplied by 100): Radius/Humerus; Olecranon/Propodium; metacarpal (MC) III/Humerus; MC III/Radius; Tibia/Femur; Calcaneum/metatarsal (MT) III; MT III/Femur; and MT III/Tibia. Measurements and indices are given in Table 1. Lever arms for selected locomotor muscles were also calculated (see Hildebrand, 1982, for an introduction to locomotor biomechanics).

RESULTS

The following description of *Hyracodon* skeletal elements supplements and reinterprets the detailed description by Scott (1941).

Scapula

The glenoid fossa of AMNH 1176 is more oval in shape than previously described and what Scott calls the coracoid appears to actually be the supraglenoid tubercle. Therefore the coracobrachialis either had a different origin or was absent. In either case it appears that the biceps brachii was the better developed of the two muscles.

Humerus

The humerus of *Hyracodon* is lightly built and relatively short compared to the ulna. Proximally the humerus is medio-laterally flattened. The greater tubercle is prominent and forms a deep bicipital groove with the lesser tubercle. A narrow deltoid tuberosity extends approximately half the length of the humeral shaft. Distinct muscle scars on the tubercles and tuberosity are not visible. Inferences about muscle development can be made based on the relative size of their sites of attachment. The supraspinatous and infraspinatous that insert onto the tubercles; and the deltoid that inserts onto the deltoid tuberosity were all well developed in *Hyracodon*. The lateral head of the triceps and the brachialis anticus both had large areas for attachment due to the flattening of the proximal humerus.

The teres major tuberosity is very small but does provide a point of reference and site of attachment for the teres major and latisimus dorsi. Behind this tuberosity the medial head of the triceps had only a small area for its origin while the lateral head had much more area behind the large deltoid tuberosity. No evidence of an anconeus can be determined on the specimens studied.

Distally, Scott (1941) describes an intercondylar ridge that is not present in either AMNH 1176 or AMNH 9789. The ridge on the lateral condyle where the extensor carpi radialis originates is well developed. Just distal to this is a triangular area for the origin of the extensor digitorum lateralis and the extensor carpi ulnaris. There is also a prominence for the origin of the extensor communis digitorum. On the median condyle are origin sites for the flexor carpi ulnaris, flexor digitorum profundus and the flexor carpi radialis.

Radius

The radius of *Hyracodon* is about equal in length to the humerus in AMNH 1176 (right radius). The shaft is compressed in an anterior-posterior fashion and is curved anteriorly. A roughened area for the biceps brachii is present. On the anterior-medial surface another

roughened area is visible for the attachment of the brachialis anticus. This second area is about equal in size to the scar left by the biceps. No evidence of an extensor metacarpi obliquus is present, but this might be an artifact of preservation in the specimens studied.

Ulna

The ulna is closely associated with the radius its entire length. It has a laterally compressed, curved shaft, and a well developed, rugose olecranon process. The semilunar notch has a curve of about 120 degrees (Scott, 1941). The area for insertion of the triceps is prominent and the olecranon is posteriorly deflected. The surface from which the olecranon portion of the flexor digitorum profundus and flexor carpi ulnaris arise is concave in shape to increase surface for attachment. The distal end does not articulate with the lunar, and the cuneiform facet lacks a saddle.

Manus

The proximal phalanx of metacarpal III is long but compressed palmo-dorsally. The second phalanx is shorter than the proximal one by about one-half, but similarly shaped. The ungal is long and broad.

Innominate Bone

The pelvis of *Hyracodon* is long and lightly built with a long compressed iliac body that expands into the wing. The acetabulum is large, deeply concave and with an almost circular outline. The ischium is short and has a prominent tuberosity posteriorly on the ischial plate. The pubis is short, slender, rod-like and somewhat broad at the symphysis. The obturator foramen is a large elongate oval.

Femur

The femur of *Hyracodon* has a flattened posterior surface. It has a well developed, rugose greater and third trochanter. The free border of the third trochanter is rugose and anteriorly deflected. The lesser trochanter is marked by a low, rugose ridge on the posterior-medial surface. The trochanteric fossa is appreciable in size due to the size of the greater trochanter. The shaft is broad proximally, narrows at the third trochanter and widens again distally. Just above the medial and lateral condyles are large rugosities for the gastrocnemius. The large greater trochanter provides insertion for a well developed gluteus medius and gluteus minimus. Likewise the long third trochanter provides a large attachment site for the gluteus maximus. The large concave trochanteric fossa allows for insertion of a well developed obturator internus. The origin sites for the gastrocnemius are prominent above the condyles indicating the muscle was large. In the middle 1/3 of the posterior surface is a long, thin rugose area for the attachment of the adductors. No

distinction between the brevis, magnus or longus can be made. Just above the internal condyle is a prominence for the insertion of the semimembranosus. Based on the size of this condyle the semimembranosus would have been a well developed muscle. No rugosities for the vastus internus and vastus externus are visible, however, there was ample space on the femur for their attachment.

Table 1. Limb bone measurements (in mm) and indices. Data for *Elephas* from Osborn (1929)

MEASUREMENT	HYRACODON	CERATOTHERIUM	SUS	DAMA	TRAGELAPHUS	ANTILOCAPRA	ELEPHAS
	AMNH 1176	GMC 575	GMC 885	GMC 576	GMC 577	GMC 1229	
Humerus	209.5	374.5	208.0	185.5	153.0	164.0	810.0
Radius	208.5	367.5	168.0	210.5	171.0	202.0	685.0
Epipodium	208.5	367.0	168.0	210.5	171.0	202.0	685.0
Olecranon	59.3	122.2		52.8	35.0		
MC III	113.7	179.0	77.0	199.5	169.5	213.0	183.0
Femur	258.0	511.5	248.0	237.5	213.5	210.0	1020.0
Tibia	216.0	348.5	215.0	277.5	242.5	260.0	618.0
Calcaneum	74.0	125.5		87.2	70.0		
MT III	113.0	163.5	77.0	224.5	177.5	218.0	138.0
Radius/Humerus	99.52	98.13	80.77	113.48	111.76	123.17	84.5
Olecranon/ Epipodium	28.46	33.31	25.08	20.48			
MC III/Humerus	54.3	47.8	37.02	107.55	110.78	129.88	22.59
MC III/Radius	54.56	48.71	45.83	94.77	99.12	105.45	26.72
Tibia/Femur	83.72	68.13	86.69	116.84	113.58	123.81	60.59
Calcaneum/MT III	65.49	76.81	38.86	39.44			
MT III/Femur	43.8	31.96	31.05	94.53	83.14	103.81	13.53
MT III/Tibia	52.31	46.92	35.81	80.9	73.2	83.85	22.33

Tibia

The tibia of *Hyracodon* (AMNH 1480) is shorter than the femur of the same specimen. Scott (1941) states that the tibia is almost equal in length to the radius. The proximal end is large and triangular shaped, with a deep pit anterior for the insertion of the patellar ligament. Medial to the tibial crest is a roughened area for the insertion of the gracilis and sartorius. Lateral to the tibial crest is a fossa for the tibial origin of the tibialis anticus.

Fibula

Scott (1941) described the fibula as being reduced and slender in size, and forming a narrow external malleolus. There is no tendency for the fibula to co-ossify with the tibia. There is, however, a long, close connection between the two.

Pes

The tarsus is high and lightly built like the carpus. The astragalus is short and has a relatively wide trochlea, and an open median groove. The two condyles do not rise sharply from the groove. The navicular facet has the typical Perrisodactyl saddle shape. The calcaneum tuber is laterally compressed but well developed. The cuboid is high

proximo-distally. It articulates with the astragalus and calcaneum proximally, and with metatarsal IV distally. The entocuneiform is almost equal in size to the navicular and articulates proximally with it. Distally the entocuneiform articulates with metatarsals II and III. Metatarsal III is the longest of the three found in *Hyracodon* (II, III, and IV). Metatarsal III is not quite as long as metacarpal III. Scott (1941), states that the phalanges of the pes are somewhat longer than those of the manus, but otherwise very similar.

COMPARATIVE OSTEOLOGY

The scapula of *Ceratotherium* is broad and well developed while the scapula of *Hyracodon* is more lightly built. Both genera can rotate the scapula as part of the forelimb, however, this is more likely a result of their lineage rather than a specific cursorial adaptation. The humeri of *Ceratotherium* and *Hyracodon* both provide a large area for the origin of the lateral head of the triceps. The medial head of the triceps has a small origin site in *Hyracodon* but a relatively larger site in *Ceratotherium*. The lateral condyle of *Ceratotherium* provides a relatively larger site for the origin of the extensor carpi ulnaris than is found in *Hyracodon*. This important flexor seems to be better developed in *Ceratotherium* than in *Hyracodon*. The proximal radii of both genera are expanded somewhat over the ulna. This expansion in *Ceratotherium* is not as extensive as in *Hyracodon* and seems to be an adaptation for weight bearing. The proximal articular surfaces of the radius of *Ceratotherium* are shallow, while *Hyracodon* has more deeply notched surfaces. These would seat the humerus more firmly into place and help restrict movement to a single plane. The distal end has simpler articular surfaces than *Ceratotherium*. The facet that articulates with the lunar of the carpus is concave. The facet for the scaphoid has both concave and convex components but they are not as pronounced as in *Ceratotherium*.

The ulna of *Ceratotherium* is much better developed than the ulna of *Hyracodon*. Both genera have a well developed, posteriorly deflected olecranon process. This is the insertion point for the triceps, and the origin for the flexor digitorum profundus. The olecranon of *Hyracodon* has a concave area to increase surface area for the origin of these muscles. The posterior deflection of the olecranon allows for a more complete extension of the elbow for weight bearing by the radius. In *Ceratotherium* the distal ulna is tightly associated with the radius, in *Hyracodon* the ulna/radius association is over the entire length of the radius. This and the reduction of the distal articular surfaces of the *Hyracodon* ulna inhibit rotations of the forearm. This reduction in rotational abilities would reduce weight distally by reducing the muscles associated with this action.

The manus of *Ceratotherium* has large carpals and metacarpals while *Hyracodon* has a lightly built manus. The manus of *Ceratotherium* is large and fleshy to distribute its weight. *Hyracodon* had a relatively lighter manus due to its smaller size and weight. This smaller manus size, along with the muscle reductions mentioned above, results in a lighter distal portion of the front limb for *Hyracodon*.

The femora of *Ceratotherium* and *Hyracodon* have well developed rugosities for origin of the gastrocnemius. The tibia and fibula of *Hyracodon* have a long close association with the fibula being reduced and slender. The tibia and fibula of *Ceratotherium* are well developed. The distal articulations on *Hyracodon* tibia are more deeply grooved than in *Ceratotherium*. This difference indicates *Hyracodon* was more tightly limited to movement in a single plane than *Ceratotherium*. Both genera have well developed calcanea for insertion of the gastrocnemius. The tarsals and metatarsals of *Ceratotherium* are large and well developed, much like the carpals and metacarpals of the forelimb. *Hyracodon* has a lightly built pes similar to its manus. These arrangements result in a higher angular momentum possible for the hind feet of *Hyracodon* as was described for the forefeet.

LIMB INDICES

Measurements of limb bones were used to generate various indices useful in determining the actual locomotor capabilities of *Hyracodon*. Table 1 presents a comparison of these figures for *Hyracodon* and various modern ungulates. The indices range from the cursorial, *Antilocapra*, to the graviportal *Elephas*, accurately reflecting the different lifestyles of these two animals. The radius/humerus and tibia/femur indices for *Antilocapra* were 123.17 and 123.81 respectively. The MCIII/radius index was 105.45 and the MTIII/tibia index was 83.85. The olecranon/radius index was 21.34 and the calcaneum/MTIII index was 37.42. The same indices for *Elephas* are as follows: radius/humerus=84.57; tibia/femur=60.59; MCIII/radius=26.72; MTIII/tibia=22.33; olecranon/radius=23.81 (no calcaneum measurements were available for *Elephas*). *Hyracodon* grouped closer to *Ceratotherium* and *Sus* for all indices than to any of the truly cursorial ungulates.

MUSCLE GEAR RATIOS

Muscle vectors for selected limb muscles of *Hyracodon* and *Ceratotherium* were used to determine lever arms, l_i and l_o , for the in and out forces (Figures 1 and 2). Computed ratios for these lever arms are compared to *Lama* in Table 2. The ratios for the flexor group of *Hyracodon* and *Ceratotherium* are similar, 29.97 and 27.32 respectively. The flexor group ratio for *Lama* was 32.89. The triceps ratio was also similar for the two rhinos (*Hyracodon* 19.35 and *Ceratotherium* 22.80). The triceps ratio for *Lama* was 12.36. The only ratio showing a marked difference between *Hyracodon* and *Ceratotherium* was the gastrocnemius ratios of 30.07 and 40.85 respectively. *Hyracodon* was, however, still far from the value for the cursorial *Lama* which had a gastrocnemius ratio of 11.28.

DISCUSSION

The osteological characteristics of *Ceratotherium* and *Hyracodon* limb elements show a spectrum of similarities and differences. Similarities between the two are the product of their

common ancestry and to comparable locomotor adaptations. Differences between the two appear to be due primarily to size.

Most of the front-limb ratios of *Hyracodon* and *Ceratotherium* do not reflect any significant cursorial adaptations. The olecranon/epipodium ratio of 28.46 for *Hyracodon* does compare favorably with *Dama* at 25.08. This indicates a higher gear muscle system than the figure of 33.31 for *Ceratotherium*. The radius/humerus indices for *Ceratotherium* (98.13) and *Hyracodon* (99.52) show no lengthening of epipodium relative to propodium. The cursorial *Antilocapra* has a radius/humerus index of 123.17, and the graviportal *Elephas* has a radius/humerus index of 84.57. The index for MCIII/radius for *Ceratotherium* (48.71) and *Hyracodon* (54.56) compare well to the mediportal *Hippopotamus* (56.30, Osborn, 1929) but falls far below that of *Antilocapra* (105.45).

The hind limb of each genus is similarly lacking in cursorial adaptations. The tibia/femur index indicates a longer propodium than epipodium for both genera (68.13 for *Ceratotherium* and 83.72 for *Hyracodon*). These compare well to *Hippopotamus* (66.67, Osborn, 1929), *Elephas* (60.59), and *Sus* (86.69), but not at all with *Antilocapra* (123.81). The MTIII/femur index for *Hyracodon* (43.80) is somewhat higher than that of *Ceratotherium* (31.96) but far below that of *Antilocapra* (103.81).

The calcaneum/MTIII index for *Ceratotherium* (76.81) is almost two times that of *Dama* (38.86). The same index for *Hyracodon* is 65.49, somewhat lower than *Ceratotherium* but high compared to the cursorial animals. This figure and the olecranon/epipodium figure given above indicate relative importance of different gear ratio muscles for the different genera. The lower numbers indicate higher gear ratios for these two muscle systems which would be advantageous in cursors.

The triceps in force, out force and muscle vectors for *Hyracodon* and *Ceratotherium* (Figure 1, 2 and Table 2) produce l_i/l_o ratios of 19.35 and 22.80 respectively. This indicates a slightly higher gear ratio for *Hyracodon* relative to *Ceratotherium* for the triceps, but is not comparable with the figure for *Lama* of 12.36. This represents a class I lever system and a short in force lever arm is needed to produce a high velocity at the out force contact point. The gastrocnemius represents a class II lever system. The gastrocnemius index for *Hyracodon* of 30.07 is much higher than that for the cursor *Lama* (11.28), but is well below that of *Ceratotherium* at 40.85.

The flexor group of the forearm represents a class III lever system. In class III levers l_o is always longer than l_i therefore the best mechanical advantage comes from having l_i long relative to l_o (i.e. a higher l_i/l_o index). This is the situation cursors would benefit most from. *Lama* has a flexor index of 32.89 while *Hyracodon* has an index of 29.97 and *Ceratotherium* has an index of 27.32.

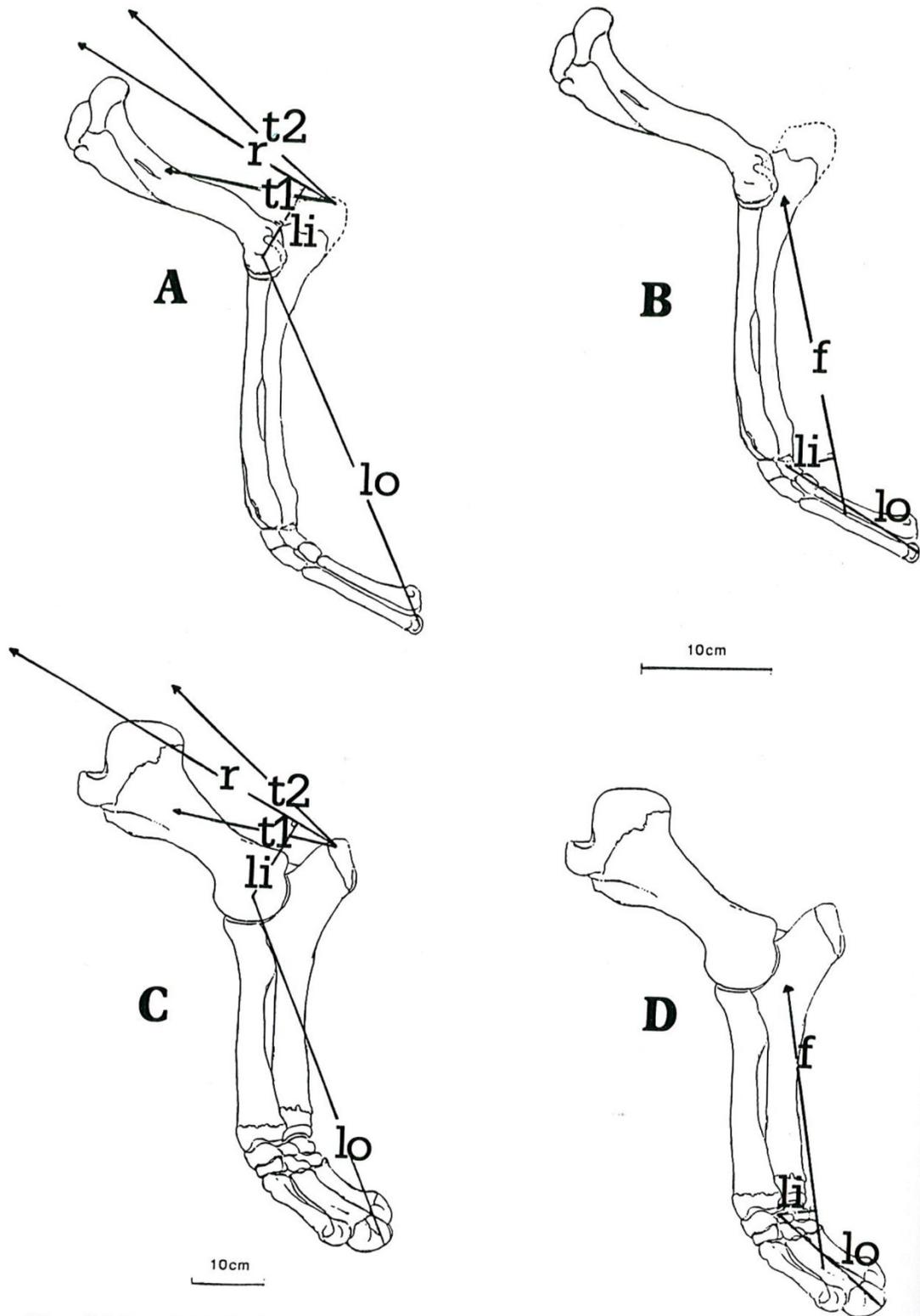


Figure 1. A and B, medial views of right forelimb of Hyracodon. C and D, medial views of right forelimb of Ceratotherium. In A and C the in force (*li*) and out force (*lo*) lever arms of the resultant force (*R*) of the lateral and medial heads of the triceps (*T₁*) and the long head of the triceps (*T₂*) are shown. In B and D the muscle vector for the flexor group (*F*) is illustrated, its in force (*li*), and out force (*lo*) lever arms.

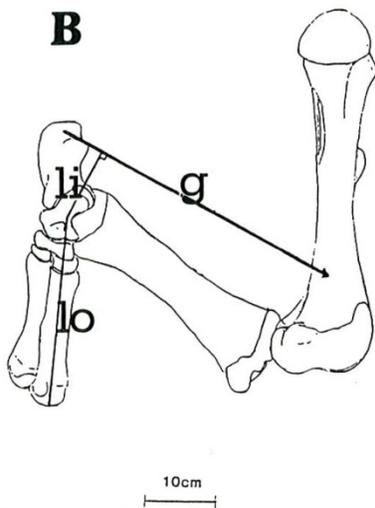
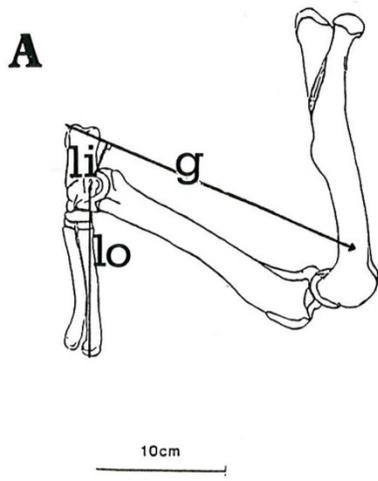


Figure 2. A, medial view of left hindlimb of *Hyracodon*; B, medial view of left hindlimb of *Ceratotherium*; showing the muscle vector for the gastrocnemius (G), its in force (li), and out force (lo) lever arms.

CONCLUSION

The muscle/bone systems, limb bone indices, and locomotor muscle in force/out force ratios all indicate that *Hyracodon* was not a cursorial animal. It would seem that *Hyracodon* was only slightly better at running than *Ceratotherium*. Although *Ceratotherium* can run fast for short distances, it has to use muscle power alone to attain such speeds, and cannot sustain them for long periods of time. *Hyracodon* does not have any significant adaptations to increase stride length necessary for a cursorial way of life. Its smaller size alone would make it easier for *Hyracodon* to run than *Ceratotherium*, but it was not a truly cursorial animal. Wild pigs or peccaries would be better locomotor analogs for *Hyracodon* than any of the modern cursorial ungulates. It would seem that *Hyracodon* was not subjected to the same selection pressures as the horses of its time. If *Hyracodon* had been a truly cursorial animal it should have flourished in the emerging savannas of the Miocene (Savage and Russell, 1983), instead of dying out.

Table 2. Muscle lever arms and gear ratios (li/lo). Measurements in mm.

Genus	Triceps	Li/lo	Flexor	Li/lo	Gastrocnemius	Li/lo	
<i>Hyracodon</i>	li	26.68	19.35	16.65	29.97	17.21	30.07
	lo	137.89		55.56		57.23	
<i>Ceratotherium</i>	li	28.89	22.80	13.35	27.32	24.97	40.85
	lo	126.70		48.87		61.12	
<i>Lama</i>	li	64.00	12.36	7.40	32.89	65.00	11.28
	lo	518.00		22.50		576.00	

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COMPARISON OF FEEDING MECHANICS IN OLIGOCENE AGRIOCHOERIDAE AND MERYCOIDODONTIDAE FROM BADLANDS NATIONAL PARK

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ABSTRACT

A comparison of feeding mechanics in Oligocene agriocherids (*Agriocheris*) and oreodonts (*Merycodon* and *Promesodon*) is presented. Measurements and observations obtained in this study resulted in the recognition of different dietary habits for agriocherids and oreodonts. The most significant measurements were of tooth rows. Ratios of premolar to molar row length show a greater grinding area for food in the oreodonts. Examination of occlusal surfaces of dentition showed that oreodonts made tooth/tooth contact (characteristic of grazers), while agriocherids made only tooth/food contact (more typical of browsers). Cranial morphology, jaw muscle reconstructions, and vector analyses showed significant differences between agriocherids and oreodonts. The large sagittal crest and shallow angle of the jaw indicate agriocherids were well adapted for shearing modes of plant mastication by means of a well developed temporalis. Oreodont skulls show adaptation for a grinding type of mastication emphasizing the masseter. Additionally, the oreodonts possess a complete orbit, which acted as a buttress to allow for increased jaw adductor musculature. Agriocherids probably occupied a woodland habitat while oreodonts show specialization for a savanna grassland.

INTRODUCTION

Agriocherids are a little known group of mid-Tertiary artiodactyls. Prior research on agriocherids was primarily taxonomic or faunal in scope, leaving much speculation as to what niche and habitat this group occupied. Little is known about the feeding mechanics of agriocherids, or their ecologic relationship to their more successful relatives, the oreodonts.

During the middle Eocene, primitive selenodonts gave rise to the superfamily Merycodontoidea, which is subdivided into the families Agriocheridae and Merycodontidae (Carroll, 1988). Agriocherids range from the middle Eocene to the late Eocene. The more abundant oreodonts first appeared in the late Eocene and survived to the middle Pliocene.

The genus *Agriocheris*, Scott (1929), a rare member of the White River Fauna of Badlands National Park, is the focus of this study. Like oreodonts, agriocherids were endemic to North

America, and are thought to have lived in open woodland or riverside areas (Osborn, 1910). Agriocherids and oreodonts share various morphological characteristics in the skull and jaw region primarily due to common ancestry. These similarities imply that agriocherids and oreodonts occupied similar niches. Like the oreodonts, agriocherids have tusks formed from the upper canines and lower first premolars, also, in both, the lower canines are incisiform (Scott and Jepsen, 1940). Selenodont dentition is shared by both, however, there are subtle differences between occlusal patterns and general tooth structure. Both groups possess a small braincase, large temporal fossa, and prominent sagittal crest (Wortman, 1895). We undertook a comparative study of the jaw mechanics of agriocherids and oreodonts to shed light on what niche the agriocherids filled, and how this niche, if at all, overlapped with that of the oreodonts. The fact that agriocherid fossils are rare and oreodont fossils are numerous could be important in determining habitat as well as indicating the relative success of these two families of artiodactyls.

SYSTEMATIC REVIEW

The family, Agriocheridae, contains three genera: *Protoreodon*, *Diplobunops*, and *Agriocherus*. According to Golz (1976), this family is nothing more than a primitive form of oreodonts. *Protoreodon* represents the basal stock from which agriocherids, as well as oreodonts arose (Carroll, 1988). This genus first appeared in the Uintan, and survived into the Chadronian (Savage & Russell, 1983). *Protoreodon* was the most abundant of all Uintan mammals, and inhabited areas now represented by California and the western interior of North America (Scott, 1889). The skull of *Protoreodon* is more primitive than *Diplobunops* and *Agriocherus* in two significant ways. The skull is longer and narrower (more dolichocephalic), and its zygomatic arch is less robust than that of the other two agriocherid genera (Golz, 1976). *Diplobunops* exhibits a mosaic of characters intermediate between *Protoreodon* and *Agriocherus* (Coombs, 1983). Like *Protoreodon*, *Diplobunops* retains the paraconule, a cusp between the paracone and protocone of the superior molars, lost in *Agriocherus* (Golz, 1976). The molars tend to be relatively narrow, and their labial crescents are less extended across the crown than those of *Agriocherus*. The dentary bone of *Diplobunops* shows a trend towards the condition in *Agriocherus*, in that it becomes a little more robust and broadened than that of *Protoreodon* (Scott, 1945). *Agriocherus*, the most advanced of the agriocherids, appears to be a chimera of discordant body parts. *Agriocherus* resembles oreodonts in the skull region, calicothers in the foot region, and cats in the posterior limb region (Scott, 1929). *Agriocherus* is reported from the upper Duchesnean, but the poor quality of these specimens makes this designation uncertain. The first positive identification of this genus is from the Chadronian beds of the White River Formation. According to Osborn (1910) agriocherids inhabited forested woodland areas and were arboreal. Coombs (1983) concluded from an analysis of the manus and pes that agriocherids show little adaptation for grasping and therefore were probably not arboreal.

Agriochoerus has an incomplete posterior ocular orbit, and is lacking a lachrymal pit (Wortman, 1895). The auditory bullae are inflated, but not filled with calcareous tissue distinguishing them from oreodont bullae (Wortman, 1895). The zygomatic arch is long and expanded, as in oreodonts, but its palate and jaws extend further laterally (Greaves, 1978). The nasals narrow proximally (Gregory, 1920), providing an easy visual distinction from oreodonts. The mandible of *Agriochoerus* is little different from *Diplobunops*.

The teeth of *Agriochoerus* are brachyodont and selenodont, with the same primitive dental pattern as that of all agriochoerids, 3/3, 1/1, 4/4, 3/3. Although there are some differences between the teeth of *Agriochoerus* and oreodonts, most researchers stressed the similarities between the two groups when interpreting possible dietary habits. *Agriochoerus* has a diastema between the superior canines and the first premolar in the maxilla, and between the caniniform first premolar, and second premolar of the mandible (Wortman, 1895). All fourth premolars are molariform in appearance, and there is a reduction in the hypocone of the fourth superior premolar (Greaves, 1972). The molars of *Agriochoerus* are tetraselenodont, lacking a protoconule, which was present in *Protoreodon* and *Diplobunops* (Carroll, 1988). The inferior molars are of the typical selenodont pattern, however, the superior molars differ, resembling those of the anthracothere possessing high cusps, and an anterior cingulum (Zittel, 1925), with deeply concave external crescents which are rounded (Wortman, 1895). The third inferior molar possesses a hypoconulid.

MATERIALS AND METHODS

This study is divided into two sections: First, the teeth of *Agriochoerus* were compared to Oligocene anthracotheres and oreodonts. Observations of the teeth included a visual inspection of tooth cusp patterns, wear facets, relative size of tooth rows, and presence or absence of diastemas. Measurements of the teeth included length, width, surface area (length multiplied times width), and height (tooth/jaw interface to highest cusp). Various aspects of tooth rows were also measured, such as: size of diastema, if present, length of entire tooth row, and length of molar row. Wear facets on teeth were interpreted in accordance with Butler (1972) and Greaves (1973). If enamel is present over the majority of the occlusal surface, the teeth are considered to exhibit abrasion facets. However, if enamel dentine interfaces are present, the teeth are considered to exhibit attrition facets (Peyer, 1968). Specific aspects of the facets were also examined, such as the leading and trailing edge of the facets, to help determine where chewing cycles were initiated and terminated. Attrition facets can also define the manner in which food is broken down during mastication, i.e., puncturing, shearing, or grinding. These three methods of mastication greatly contribute to unique wear facets and may be used to define masticatory relationships between taxa (Butler, 1972).

The second major section of this study involves description, measurements, and biomechanical analysis of cranial structures. *Agriochoerus* cranial proportions were compared to oreodonts and

anthracotheres using distortion grids (Hildebrand, 1988). Cranial measurements were chosen based on their significance in showing similarities or differences among the taxa. A vector analysis of the jaw regions of these artiodactyls was performed. The vectors drawn in this section represent the lines of action of the major adductor muscles in these herbivorous mammals, the masseter, temporalis, and pterygoideous (for comparison with modern ungulates see Herring, 1976; and Janis, 1983). The muscular anatomy of the head/jaw region of the selected artiodactyls was reconstructed using a method similar to Greaves (1972). After the origins and insertions for the adductor muscles were determined, individual muscle masses were estimated by the size of grooves and ridges located in the areas of tendon attachment. The exact size or mass of a muscle is impossible to determine from these attachments, however, relative sizes can be estimated, which are sufficient for comparative purposes. Once the relative size of each muscle was determined, vector diagrams were drawn; a separate vector was drawn for each muscle analyzed. The direction of each vector was determined by locating the center of mass for each muscle, and magnitude was estimated based on the relative size of the muscle. The total of all adductor muscles was set at one hundred percent. The contribution of each muscle towards the total was then determined, through observation of the muscle reconstructions. A scale of ten percent equals one centimeter of vector length was used to obtain the magnitude of each vector in the original drawings. After all the muscle vectors were properly placed, their lever arms were determined. To simplify the study we selected the jaw joint as the fulcrum for our analysis (see Gans, 1974; Alexander, 1983; Greaves, 1991; and Hildebrand, 1988, for the relevance of lever arm studies in biomechanics).

All measurements were taken with a Helios calipers accurate to 0.01mm. All of the specimens used in this study were collected in Badlands National Park, South Dakota and are housed in the Georgia College Vertebrate Paleontology Collection (GCVP), Milledgeville, Georgia.

RESULTS

There was a gradual increase in the upper premolar to molar ratio from the anthracothere *Aepinacodon*, the most primitive genus, to *Merycoidodon* and *Promesoreodon* (oreodonts), the most advanced organisms in this study. The upper premolars of *Aepinacodon* are approximately forty-four percent of the length of the upper molars, in *Agriochœrus* this ratio was approximately fifty-one percent, and in the two oreodont genera the upper premolars were fifty-seven percent of the length of the molars. The ratio of lower premolars to molars in *Agriochœrus* was seventy-four percent, and the average ratio for the oreodonts was sixty-five percent.

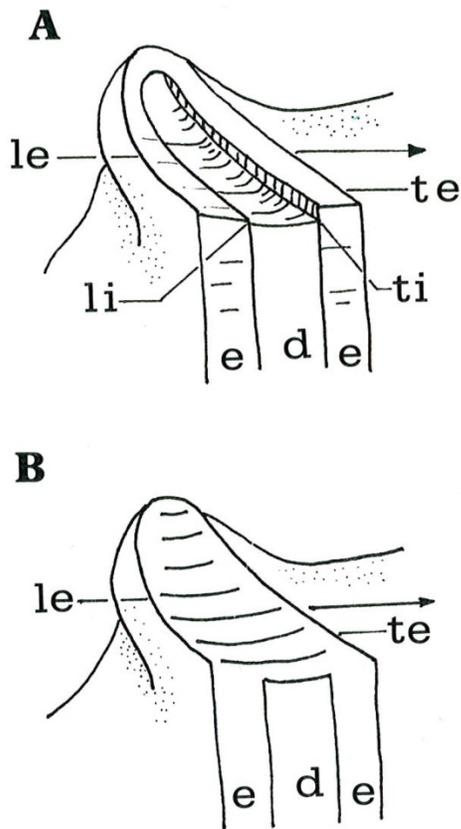


Figure 1. A. Cross section of an oreodont tooth (modified from Greaves, 1973). B. Cross section of an agriochoere tooth. Arrows indicate direction of occluding tooth. Figure abbreviations: le-leading edge, li-leading interface, te-trailing edge, ti-trailing interface, d-dentine, and e-enamel.

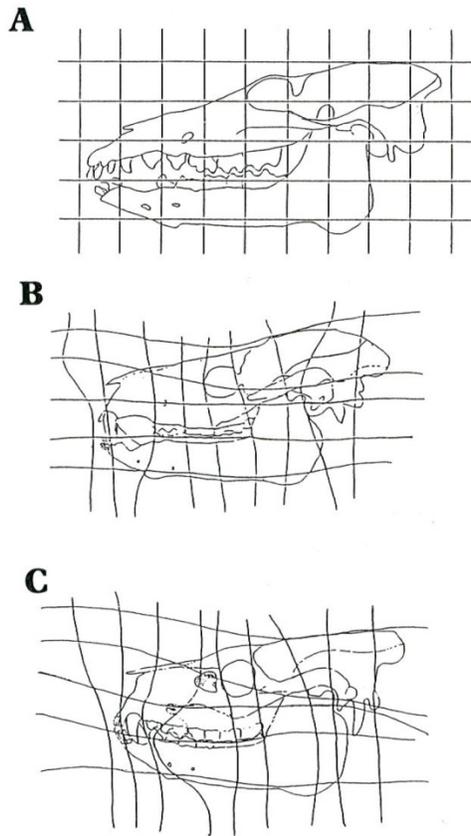


Figure 2. Distortion grid comparison using an Aepinacodon skull (A) a standard for Agriochoerus (B) and Merycoidodon (C) skulls.

Facet patterns on the cheek teeth showed a clear transition from primitive to advanced forms. The occlusal surfaces on the upper and lower dentition of *Agriochoerus* and *Aepinacodon* primarily exhibited abrasion facets. Even though abrasion marks, indicative of jaw motion during mastication, were observed, enamel covered the entire occlusal surface (Figure 1B). In addition, leading and trailing edges of the wear facets could be identified but were not greatly pronounced. Contrasting this, the oreodonts had attrition facets on their occlusal surfaces which show a well developed dentine/enamel interface. The leading edges of this interface were sharp and highly developed, in comparison to the developed, but rounded trailing edges (Figure 1A).

Significant cranial differences between the three families are revealed by the distortion grids (Figure 2). The anthracothere skull shows a greater resemblance to the agriochoere skull than it does to the oreodont. A lachrymal pit, just anterior to the orbit, is present in the oreodont, but absent in the anthracothere and agriochoere. The orbit is open posteriorly in the anthracothere and agriochoere, while the more advanced oreodont orbit is complete. Several changes in the oreodont jaw are also evident. First, there is no diastema in oreodont dentition, but a pronounced diastema exists in agriochoeres and anthracotheres. Second, the angle of the jaw, as well as the

entire posterior jaw of the oreodonts is expanded compared to that of agriochoeres and anthracotheres. A final difference in skull structure is the sagittal crest, which is less prominent and less convex in the oreodont than in the more primitive forms.

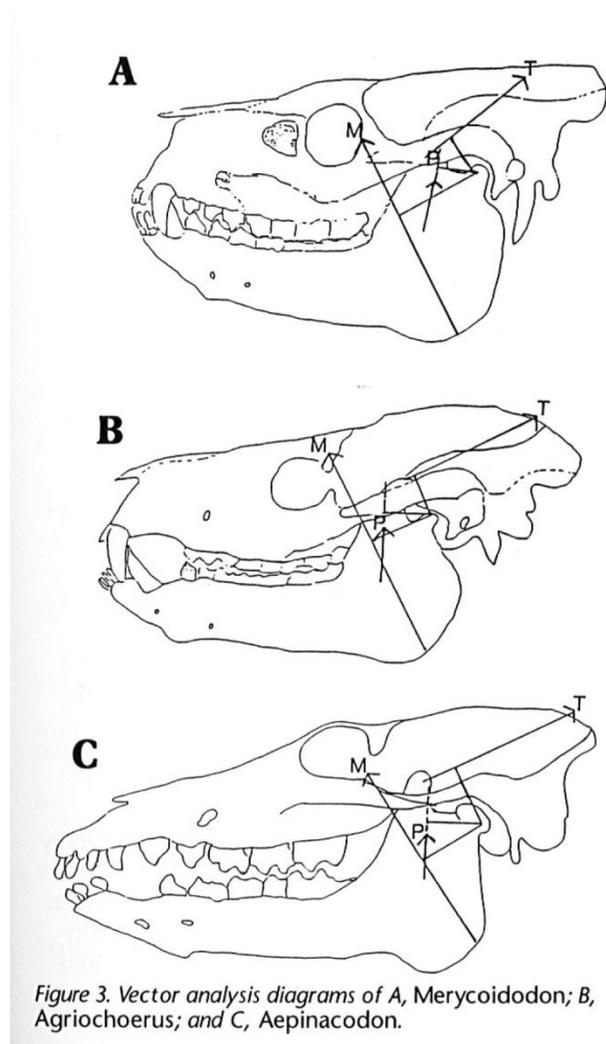


Figure 3. Vector analysis diagrams of A, Merycoiodon; B, Agriochoerus; and C, Aepinacodon.

Muscle reconstructions involving the three major adductors of the jaw indicate muscle mass increased from anthracotheres to oreodonts. The relative importance of each muscle also differs in these taxa. The anthracothere adductor mass was 50% masseter, 40% temporalis, 10% pterygoideus, for the agriochoere 55% masseter, 35% temporalis, 10% pterygoideus, and for oreodonts 60% masseter, 30% temporalis, 10% pterygoideus. These results show there is a gradual increase in the size of the masseter and a gradual decrease in size of the temporalis from anthracotheres to oreodonts. Vector analyses drawn from these reconstructions are shown in Figure 3. The lever arm of the temporalis exhibited a gradual decrease in size from anthracotheres to oreodonts. Contrasting this, the lever arm of the masseter shows an increase in the more advanced forms. Changes in the lever arm are due to changes in muscle mass and from variation of skull morphologies centered around the craniomandibular joint.

DISCUSSION

Results obtained from the tooth measurements indicated a higher premolar to molar ratio in the upper dentition, and a lower ratio in the lower dentition, for Oligocene oreodonts compared to *Agriochoerus*. Even though the upper premolars of oreodonts occupied a greater portion of the total tooth row, the ratio of M^3 to M^2 was significantly higher in oreodonts indicating an increase in the total length of their molars. The large value for the molar region shows that oreodonts were better adapted for grinding foodstuffs than agriochoeres.

The occlusal surfaces of the dentition in both oreodonts and agriochoeres exhibited facet wear patterns that are typical of ungulate mastication. Subtle differences in these facet patterns, however, indicate emphasis on different parts of this cycle. The abrasion facets of agriochoere

teeth indicate there was no actual contact between teeth during occlusion. Mastication was achieved through tooth/food contact, which is typical of organisms whose chewing cycles are dominated by shear chewing methods. Shearing mastication would allow agriochoeres to break down larger, tougher plant sources, including shrubs and roots. Striations found on the occlusal surfaces of agriochoere teeth are oriented labial/lingual, showing that most of the work done by the teeth was performed in a transverse motion. Therefore, it may be assumed that tooth/food contact was made during the late oral retraction phase through the early buccal phase of the chewing cycle, when transverse motion of the jaw is initiated. The attrition facet patterns found on the occlusal surfaces of oreodont dentition show that tooth/tooth contact was made during mastication. The dentine/enamel interface on occlusal surfaces causes a rasping action during chewing cycles and allows a greater processing of foods which require much grinding, such as grasses. The attrition interfaces of the oreodont are arranged in a transverse orientation, like the agriochoere's, however, the dentine/enamel interface indicates a more powerful grinding action during mastication. This means tooth/tooth contact occurred primarily during the buccal phase, which is the most powerful stroke of the chewing cycle. Differences in occlusal facet patterns between oreodonts and agriochoeres are evident in the relative development of adductor jaw musculature in the two groups.

Skull and jaw morphologies of agriochoeres and oreodonts exhibit differences which can best be attributed to selection for optimal mastication in these organisms. The complete orbit found in oreodonts, but absent in agriochoeres, gave oreodonts a structural advantage by allowing for a greater power stroke and larger range of lateral motion of the jaw than in agriochoeres. The posterior portion of the orbit in oreodonts serves as a buttress which adds support to the orbit area. According to Scapino (1972) and Greaves (1984) this extra support permits increased muscle mass along with increased lateral motion of the entire jaw, which are both characteristic of oreodont mastication.

The lack of a diastema in the lower jaw of oreodonts, provides more room for teeth, however, other factors are of greater significance. The purpose of a diastema in herbivorous mammals is to allow manipulation of food, with the tongue, during mastication. The space provided by the diastema allows food to be moved from the cropping mechanism to the molars, via the tongue. Modern grazers, such as horses, show good examples of diastema function, however, the surface area ratio of premolars to molars, as well as the entire palate area, is much greater in these modern grazers than in oreodonts and agriochoeres. Organisms with such a limited palate area, like the oreodonts, would not have much trouble moving material, such as grass, from the cropping mechanism to the grinding mechanism during mastication, without the aid of a diastema. Also, lack of a diastema would shorten the length of the jaw, thereby decreasing the magnitude of the resistance arm of the adductors. This would give the oreodonts a greater capacity for powerful grinding motions of the teeth near the proximal end of the jaw. The presence of a diastema in agriochoeres is substantial evidence that food was manipulated by the tongue during the chewing cycle. Tongue manipulation would allow tougher and larger

vegetation, such as shrubs and roots, to be consumed in an organism with a palate the size of an agriochoere's.

These two groups also differ in the relative development of the angle of the jaw and sagittal crest. The expanded angle of the jaw of oreodonts permits greater insertion of the masseter. Action of the masseter is greatest during the buccal phase of the chewing cycle, when grinding is taking place. Thus, a larger region for insertion of the masseter would reinforce the hypothesis that grinding predominated in oreodont mastication. Conversely the sagittal crest in agriochoeres provides a large area for the temporalis to originate. A large temporalis would have been used in three ways. First, a large temporalis, whose action causes upward and rearward adduction of the jaw, would allow agriochoeres to more easily acquire large vegetation and/or roots from the ground. Second, resistance from the root or shrub would generate a force at the craniomandibular joint as the animal pulled on the plant. This stress on the jaw joint can best be countered by a force in the opposite direction. The temporalis is the only adductor muscle in proper alignment to resist this force and thereby stabilize the jaw joint. And third, action of the temporalis is maximized during the orthal retraction and early buccal phases of mastication, when shearing predominates. Larger plant material must be sheared into manageable particles before it can be ground into a small bolus suitable for swallowing. Muscle reconstructions and vector analyses presented in the results also support the hypothesis that agriochoeres were browsers. The large lever arm of the masseter in oreodonts reinforces the idea that grinding predominated in oreodont mastication. Contrasting this, the large lever arm of the temporalis in agriochoeres would be advantageous in shearing modes of mastication. Even though the pterygoideus represents 10% of the jaw adductor muscle mass in agriochoeres and oreodonts, there is an increase in the overall mass in oreodonts. Increase in total muscle mass would represent increased development of the pterygoideus, which along with the masseter acts to pull the jaw transversely. Thus, oreodonts would exhibit greater efficiency at grinding food.

Post cranial characters corroborate our analysis of feeding in agriochoeres and oreodonts. Oreodonts have a reduced number of digits and digitigrade stance, locomotor traits suitable for the cursorial lifestyle typical of many grazers. The manus and pes of agriochoeres indicate a different lifestyle. Their plantigrade stance is suited for a subcursorial mode of locomotion. Additionally, the prominent claws on agriochoere digits, whose presence is still not adequately explained, could have been used for digging and probing for roots. Coombs (1983) disagrees with this idea, pointing out that the hind limb of agriochoeres is not as developed as most diggers. This, however, does not rule out the possibility that agriochoeres were occasional diggers, and dug for roots as a secondary food source.

CONCLUSIONS

Our study suggests that agriochoeres and oreodonts maintained low levels of competition during the Oligocene since they did not compete directly for food resources. Agriochoeres favored a diet of large vegetation and tubers. This choice of food and the fact that agriochoeres retained a

primitive digit formula supports the notion of Osborn (1910) that agriochoeres were woodland specialists. Oreodonts, on the other hand, probably fed on grass, and had a reduced number of digits, making them more agile runners. These two characteristics made them better adapted for survival in a savanna habitat.

The early extinction of agriochoeres probably resulted from changes in the ecology of Nearctica. During the late Oligocene to early Miocene, woodland areas, which predominated up to this point (Wolfe, 1971) were giving way to savannas (Savage & Russell, 1983). This left abundant resources for oreodonts, but restricted the habitat for agriochoeres. The early demise of agriochoeres was probably due to their inability to successfully compete with their specialized relatives in a purely savanna environment.

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MIDDLE TURONIAN (CRETACEOUS) MOSASAUROIDS FROM BIG BEND NATIONAL PARK, TEXAS

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ABSTRACT

Fragmentary remains of mosasauroids have recently been recovered in Big Bend National Park from lower portions of the Ernst Member of the Boquillas Formation. Some of these are equivalent in age to the previously oldest known mosasaurs from North America but others are possibly older. The youngest of these remains are associated with *Collignonicerias woolgari* which indicates an early Middle Turonian age. Foraminiferal correlations suggest that the oldest material may be Early Turonian age but inoceramid correlations suggest a slightly younger age. Preserved material presents two characters which suggest the represented taxon is more closely related to a Tylosaurinae + Plioplatecarpini clade than to a Mosasaurinae clade. This also indicates that a divergence between these two major clades occurred during or before the early Middle Turonian. Presence of very small vertebrae in this interval suggests that some conservative mosasauroid or possibly a dolichosaur was also present. This is the only report of vertebrate fossils from the Ernst Member other than indeterminate chondrichthyans.

INTRODUCTION

The purpose of this paper is to describe and discuss some new finds of early mosasaurs and closely related specimens of a less derived nature. The latter show some morphological similarity with taxa and specimens previously referred to the family Aigialosauridae [a group that includes *Aigialosaurus dalmaticus* Kornhuber, *Opetiosaurus buccichi* Kramburger, *Carsosaurus marchesetti* Kramburger, and the "Trieste aigialosaur" (Carroll and DeBraga, 1992)], and perhaps to the Dolichosauridae (Romer, 1956:562). The new finds are very fragmentary but provide information concerning a minimum age for diversification and radiation of the two most successful clades of mosasaurs. They also indicate that lizards with features similar to the above specifically named taxa were more widespread than their previously known distribution in Croatia, Slovenia, and England.

Camp (1923:321) included Aigialosauridae within the superfamily Varanoidea and mosasaurs as the superfamily Mosasauroidae, even though several authors including Camp (1923), Dollo (1904), Knopcsa (1903), and Williston (1904) believed aigialosaurs to be the ancestors of mosasaurs. A recent phylogenetic analysis (Bell, 1993:243) provides evidence that Aigialosauridae is only an artificial grouping, the members of which are associated by possessing

numerous plesiomorphic characters, especially in the limbs. Because some of these more conservative taxa are imbedded within phylogenetic lineages which include acknowledged typical mosasaurian taxa, this author chooses to include those basic taxa previously referred to Aigialosauridae (Romer, 1956:560) within Mosasauroida.

In the following discussion, use of informal names will follow these criteria: mosasauroid refers to members of the most generalized taxon, Mosasauroida, which includes the less derived forms (previous members of paraphyletic Aigialosauridae) and Mosasauridae; mosasaurid or mosasaur refers to members of Mosasauridae, which includes all of the more derived, fully marine forms (including *Halisaurus*); and mosasaurine refers to members of a diverse lineage which includes *Mosasaurus* (as opposed to a lineage which includes *Tylosaurus* and *Platecarpus*). (See Russell, 1967:202).

Mosasauroid fossils have a worldwide distribution and are known from marine Cretaceous rocks ranging from Late Cenomanian to terminal Maestrichtian age (Russell, 1967). However, very little is known of the representatives of this group before Coniacian time. Basal members with relatively underived terrestrial limbs have been found in Slovenian and Croatian rocks of Late Cenomanian to Turonian age (Langer, 1961; Carroll and DeBraga, 1992). The oldest record of derived mosasaurids consist of small vertebral fragments from the latest Cenomanian (*Holaster subglobosus* Zone) of England (Woodward, 1905:187). The latter have never been figured or described; therefore verification of this record has not been established. Cenomanian mosasaurids are also recorded from Texas (Stenzel, 1944:443; Thurmond, 1969), but examination of the two jaw portions has resulted in their reinterpretation as *Pachyrhizodus leptopsis*, a teleost (Stewart and Bell, 1989; Stewart and Bell, 1994).

The next oldest mosasaurids are known from a few fragments from the Fairport Chalk Member and the Blue Hill Shale Member of the Carlile Shale in Kansas (Martin and Stewart, 1977). A single maxillary fragment was recovered from 6 meters below the top of the Fairport Chalk. The entire Fairport Chalk is included within the *Collignonicerus woolgari* Zone, which is assigned by Cobban (1984:76) to the earliest part of the Middle Turonian. The jaw fragment is unidentifiable. Martin and Stewart (1977) reported also two posterior caudal vertebrae from the lower Carlile Shale. Stewart (pers. com., 1994) indicated this specimen is actually from the Blue Hill Shale Member. Martin and Stewart remarked that these caudals resemble those of *Clidastes*, but stop short of referring them to that taxon. In that same paper, a specimen consisting of four vertebrae and fragments, also collected from the Blue Hill Shale Member, was referred to *Clidastes*. The Blue Hill Shale Member is considered to be late Middle Turonian age (Hattin, 1962:79).

Within the past three years, the author has discovered fragmentary remains of mosasauroids in the eastern end of Big Bend National Park, Texas. These occurrences are near the bottom of a shaley sequence about 30-40 meters above the base of the Ernst Member of the Boquillas

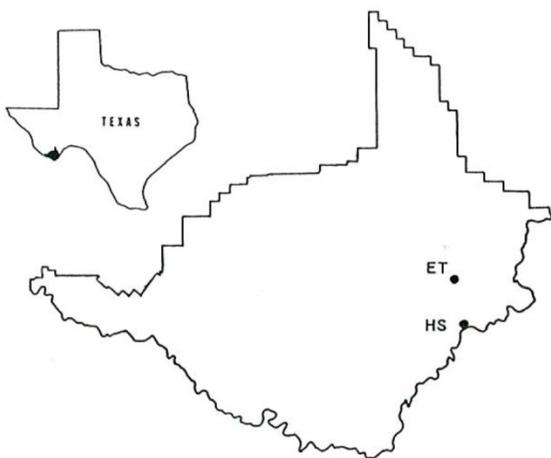
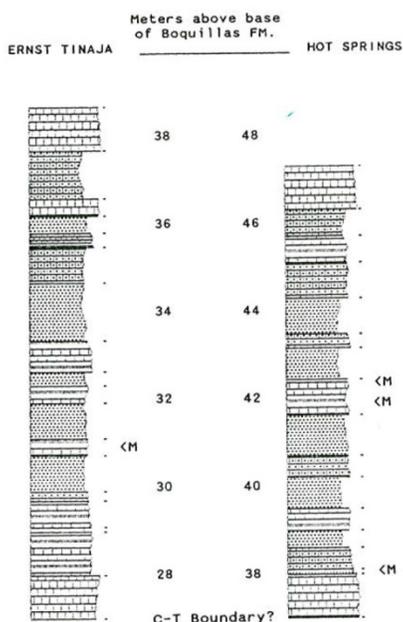


Figure 1. Map of state of Texas with enlargement of Big Bend National Park showing localities and measured sections mentioned in text: ET = Ernst Tinaja, HS = Hot Springs.

Formation. These are also the first vertebrate fossils other than unidentified chondrichthyans reported from the Ernst Member (Langston et al., 1989:19). Ammonites directly associated with the stratigraphically highest fragments are identified as *Collignoniceras woolgari*. Therefore, the minimum age for these remains is equivalent to the oldest mosasaurids from Kansas.

All Big Bend National Park specimens reported herein are repositated at the Vertebrate Paleontology Laboratory of the Texas Memorial Museum at Balcones Research Center, University of Texas at Austin. Abbreviation for that facility is TMM.

STRATIGRAPHIC POSITION AND CORRELATION

Mosasauroid remains were recovered from two localities in Big Bend National Park. The first locality is on bluffs along the Rio Grande River from a point 50 meters downstream of the Hot Springs to a point about 150 meters upstream. Here, a fragment of a mosasaur prootic (TMM 43352-1) was found within a vertebrate hash bed situated 38 meters above the formational contact with the Buda Limestone.

At the same locality, 42 meters above the base of the Boquillas Formation, two caudal vertebrae (TMM 43352-2, 43352-3) were recovered from thin calcarenite beds. These were also associated with fragments of other vertebrates, including mostly elasmobranchs and osteichthyans. Only 0.4 meters above this level, a single tooth (TMM 43352-4) was found near the top of a bed of fine grained, finely laminated, argillaceous limestone. This same horizon also provided two specimens of *Collignoniceras woolgari* (Mantell).

Frush and Eicher (1975) sampled the foraminiferans from this locality and found (fig. 3) that the Cenomanian-Turonian boundary occurred 37 meters above the base of the Boquillas Formation, based on the last occurrence of *Rotalipora*. These results are also supported by Sanders (1988) in an unpublished masters thesis. Sanders found essentially the same ^{18}O and ^{13}C excursions noted near the Cenomanian-Turonian boundary in the mid-continent Greenhorn Limestone (Pratt, 1985) between 33 and 42 meters above the base of the Boquillas section at the Hot Springs locality.

The Cenomanian-Turonian boundary as established by foraminiferans occurs only about 1 meter below the lowest mosasaurid fragment found. Only 5.4 meters above the boundary, *C. woolgari* indicates an early Middle Turonian age: thus, the entire Lower Turonian could be represented within about 5 meters or less of limestone and marlstone.

However, at Pico Etereo just east of Big Bend N. P., Powell (1965:521) picked the base of the Turonian no higher than 22.5 meters (75 ft.) above the lower contact with the Buda Limestone, based on the molluscan fauna, especially *Tragodesmoceroides* and *Inoceramus labiatus*. By these criteria, the Lower Turonian may be as much as 15 meters (4X) thicker than indicated by foraminiferans.

The second mosasauroid-bearing locality is along the north wall of the canyon about 200 meters below (west of) Ernst Tinaja, which is about 11.5 km (7.5 mi) north of the Hot Springs locality. Two very small mosasauroid vertebrae were found in a thick (0.4m) bed of calcarenite, the base of which lies 32.4 meters above the Buda-Boquillas contact. This is approximately equivalent to the mosasaur-bearing interval at the Hot Springs, based on position within the shaly interval and several associated bentonite layers as well as a rusty weathering, siliceous limestone marker bed that occurs uniformly about 12 meters above this horizon in both outcrops. Sanders (1988, fig. 2.1) also measured this section but did not report isotope data. These two vertebrae, a posterior trunk (TMM 43056-3) and an anteriormost caudal (TMM 43056-4), were found only centimeters apart and could possibly belong to the same individual. Their age is assumed to be essentially equivalent to that of the specimens from the Hot Springs section.

DESCRIPTION AND TAXONOMIC ASSOCIATIONS

The prootic fragment (TMM 43352-1) is from the right side but the paroccipital process as well as the anteroventral and anterodorsal rami are broken. The lateral side is fairly well preserved and shows several structures of the inner ear, including the fenestra ovale, the anterior vertical and horizontal semicircular canals, and entrances for the seventh and eighth cranial nerves. Numerous small nutrient canals and foramina are preserved within these structures, indicating that the individual was not fully grown. Its size is approximately equivalent to that of a medium sized *Clidastes propython*, but the morphology clearly is unlike that taxon or any other mosasaur for which this morphology is known. The material cannot be assigned to any taxon less general

than Mosasauridae.

One of the two caudal vertebrae (TMM 43352-2) found at the Hot Springs locality is relatively well preserved (Fig. 2A) and measures 36 mm. in length. It has the bases of broadly ovate transverse processes and part of the neural spine. There is no indication of a postzygopophysis on the preserved part of the neural spine. In posterior aspect, the centrum has a hexagonal outline that is higher than wide, although some lateral compression is evident. Ventrally, two facets are present for articulation of the hemal arches. This vertebra is from immediately posterior to the pygal series.

Lack of fusion of the hemal arches to the caudal centra (until late in life) is a plesiomorphic character present in all the basal Slovenian and Croatian mosasauroids and retained throughout a clade of relatively derived mosasaurs including all the known basic taxa within *Tylosaurus*, *Ectenosaurus*, *Platecarpus*, and *Plioplatecarpus* (Bell, 1993:125). Fusion of the arch to the centrum is a diagnostic character of Mosasaurinae and is convergent in *Halisaurus*; therefore, TMM 43352-2 cannot represent a member of either of these latter two clades.

TMM 43352-4 is a marginal tooth (Fig. 2B) that measures 14 mm. high and about 6.5 mm. near the base of the enamel. The portions of the tooth below the crown are not preserved. A distinct, non-serrate carina is exposed on the posterior side but the anterior side is imbedded within marlstone matrix and the fragile nature of the specimen prevents removal. A cross section of the crown would seem to be essentially round, but with the lingual side slightly more convex. Several striations are apparent on the lingual surface of the crown near the base and extend upward more than half the distance to the tip.

Lingual (medial) tooth striations are a synapomorphy contributing to the diagnosis of a major mosasaur clade that includes all the known basic taxa within *Tylosaurus*, *Ectenosaurus*, *Platecarpus*, and *Plioplatecarpus* (Bell, 1993:105). This specimen then indicates that the divergence of this clade from mosasaurine mosasaurs had already occurred by early Middle Turonian time.

The two vertebrae found near Ernst Tinaja (Fig. 2C) are quite small. TMM 43056-3 is 8.5 mm long and TMM 43056-4 is approximately 5 mm long. The former is still partially imbedded within fine calcarenite matrix with the ventral surface exposed. This surface is essentially flat with two small nutrient foramina near the midline. The lateral surfaces of the centrum are also relatively flattened, which results in a relatively sharp ventrolateral ridge that trends posteriorly from the synapophysis to the posterior condylar surface. Pre- and postzygopophyses are present, and a zygosphene seems to be exposed on a broken surface of the matrix. The posterior and anterior outlines cannot be seen without further preparation. Size of the vertebra and presence of zygosphenes implies relationships with the most conservative mosasauroids, dolichosaurs, or

Coniasaurus. However, this vertebra is unlike *Opetiosaurus buccichi*, the Trieste specimen, and *Coniasaurus crassidens* in that those taxa have a pair of rounded ventral ridges immediately adjacent to the ventral midline of the posterior trunk vertebrae. The condition is unknown in *Aigialosaurus dalmaticus* and, in the dolichosaurs where the ventral posterior trunk vertebrae are visible, those seem to be more convex. Another possibility is that this vertebra belongs to a ontogenetically young mosasaur individual; however, the sharp ventrolateral ridge has not been observed on any mosasaur specimen regardless of age.

The small caudal vertebra is exposed in dorsal aspect with the ventral side and parts of transverse processes imbedded within matrix. Posterior edges of the transverse processes are exposed on the broken rock surface and identify this as a pygal vertebra. These transverse processes are quite elongate laterally and very thin dorsoventrally. The thinness is similar to the condition seen in *Coniasaurus crassidens*, but the processes of this vertebra are not as long relative to the centrum diameter. The neural arch and spinous process are broken away. The posterior profile is subrounded and slightly dorsoventrally depressed. The posterior condyle is 3.9 mm. wide and 3.1 mm. high. A single large nutrient foramen penetrates the dorsal surface of the centrum within the neural canal. The overall proportions and general structure of the neural canal are quite unlike that of *Coniasaurus crassidens*, but similarity to any of the Yugoslavian taxa, including dolichosaurs, cannot be ruled out.

These two small vertebrae are distinctly unlike *Coniasaurus crassidens* Owen, which is the only New World taxon referred to Dolichosauridae (Bell et al., 1982) and otherwise found only in England. They are also distinctly unlike the basal mosasauroid from Dallas, Texas, reported by Bell (1993:239) in which a cross section of the posterior vertebral centra is essentially round, not trapezoidal as would be the Big Bend vertebra. Thus, of the two most similar taxa known from Texas (and North America), these specimens cannot be referred to either. The dolichosaurs from Yugoslavia or *Dolichosaurus* from England and *Aigialosaurus dalmaticus* from Yugoslavia cannot be definitely eliminated from a list of taxa to which these vertebrae might be referred. It is also quite possible that they represent an unknown new taxon.



A



B



C

Figure 2. Mosasauroid specimens recovered from Ernst Member of Boquillas Formation: A - TMM 43352-2, anterior caudal vertebra from Hot Springs locality (arrow designates facet for hemal arch articulation); B - TMM 43352-4, marginal tooth from Hot Springs locality; C - TMM 43056-4, pygal vertebra on left and TMM 43056-3, posterior trunk vertebra on right.

CONCLUSIONS

New specimens of mosasaurs from Big Bend National Park are at least as old as the oldest previously reported from North America and some are potentially older, but not as old as the English specimens. These demonstrate that small amounts of material can have important consequences. The parts that were recovered do not provide extensive information but are sufficient to indicate that a major divergence between the mosasaurine lineage and the lineage including Tylosaurinae + Plioplatecarpini took place during or before the Early Turonian.

Additional tiny vertebrae from Ernst Tinaja suggest that smaller semi-aquatic forms similar to those from the Cenomanian-Turonian of Slovenia, Croatia, and England were also present during the Early or early Middle Turonian in west Texas. Whether these remains represent basal mosasauroids or dolichosaurs is unknown, but they cannot with certainty be referred to any of the previously described forms. It is hoped that discovery of more complete specimens will help resolve these problems.

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THE PALEOCENE/EOCENE TRANSITION ON TORNILLO FLAT IN BIG BEND NATIONAL PARK, TEXAS

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ABSTRACT

Reexamination of the Paleocene/Eocene transition in the most complete applicable section in Big Bend, in light of several recent revisions of taxonomy and of early mammalian biostratigraphy, still leaves some taxa apparently out of synchronization with the picture developed further north, suggesting that ecologic and/or geographic factors are playing a role. Some of the global changes at the Paleocene/Eocene boundary being studied elsewhere, such as a warming trend, appear to be recognizable in the Big Bend region, which has yielded the southernmost large Paleocene mammalian faunas on the North American continent.

INTRODUCTION

Deposition of the Chilicotol Group (Aguja and Tornillo Formations) in Big Bend National Park spans both the Cretaceous/Tertiary and Paleocene/Eocene boundaries. It begins with the first significant influxes of terrestrial sediments as the Cretaceous sea retreated, continues through increasing uplift in the region, and ends with the onset of local volcanism in the Chisos Mountains, which lie today at the heart of the park (Schiebout et al., 1988). The contact of the fluvial Black Peaks and Hannold Hill Members of the Tornillo Formation (Figure 1) is the focus of interest for consideration of the Paleocene/Eocene transition. The longest Tornillo Formation section, the one containing the southernmost major late Paleocene mammal-bearing sites of this continent (Ray's Bonebed and Joe's Bonebed), and the type sections of the Black Peaks and Hannold Hill Members, occurs on western Tornillo Flat in the northern part of Big Bend National Park.

Upper case letters are used to distinguish upper teeth from lower throughout. Abbreviations for North American Land Mammal Ages are shown on Figure 1.

THE PALEOCENE/EOCENE BOUNDARY

Current strong interest in the Paleocene/Eocene boundary is evinced by the formation of the IGCP 308 Paleocene/Eocene Stratotype Working Group, working under the auspices of UNESCO. Although the details of boundary stratotypes will be worked out in marine sections, the new plethora of data on events at this time plus developments in understanding of mammal paleogeography, make a close reexamination of data on a good section including the boundary,

potentially rewarding. The Paleocene/Eocene boundary is currently considered to lie within magnetochron C24R (Rea et al., 1990, p. 118; Berggren, 1993). Tornillo Flat paleomagnetic data (Rapp et al., 1983) place one vertebrate fossil site, the South Wall Site, in C24R. Among the events possibly associated with the boundary according to Rea et al. (1990) are: global warming produced by an increase in atmospheric CO² related to tectonism, a drier climate in continental interiors (Wolfe, 1978, 1979); a rapid turnover in mammalian faunas (Gingerich, 1989; Rea et al., 1990); and a lessening of latitudinality with warmer climates in higher latitudes, but a sea level change is not seen.

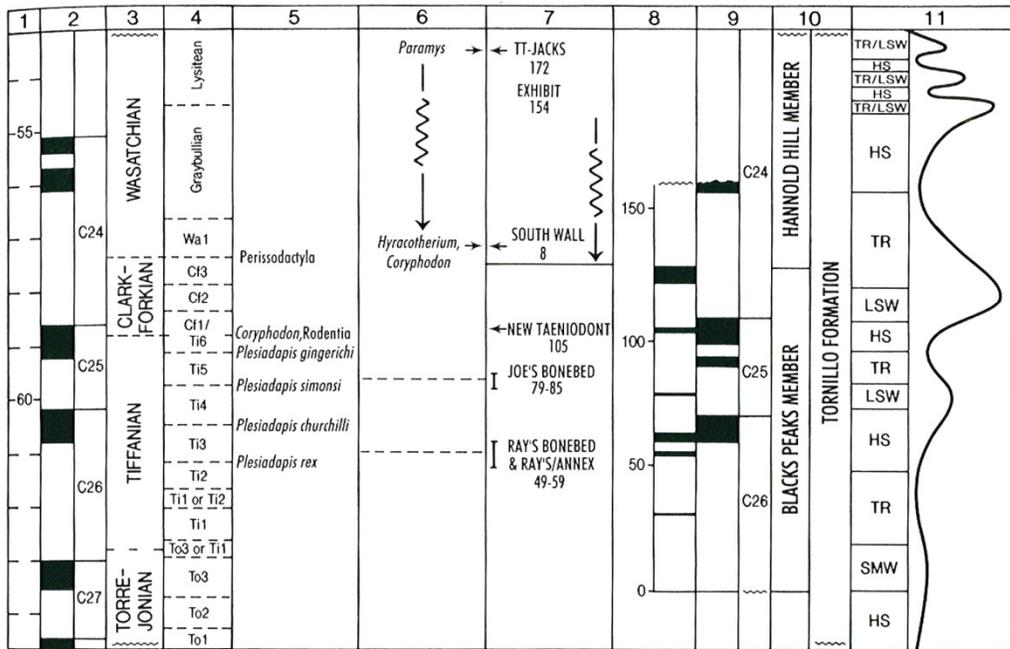


Figure 1. Big Bend biostratigraphy in global context. Where vertical zigzags are shown, a column has been condensed vertically, and where horizontal zigzags are shown, the column has been terminated (although further data is available).

Columns 1-6 are modified from Woodburne (1987) and relate to all of North America:

- Column 1—geochronology in millions of years;
- Column 2—magnetic anomalies;
- Column 3—North American Land Mammal Ages;
- Column 4—zones or subzones;
- Column 5—selected first appearances for North America;

Columns 6-8 refer to Tornillo Flat, Big Bend, Texas and are modified from Schiebout et al. (1988). Column 9 was derived from Rapp et al. (1983). The bases of anomalies 26 and 24 have been used to select a scale for the Tornillo Flat data and to align it with that from Woodburne (1987). All of the Tornillo Flat columns are aligned with column 9.

- Column 6—selected first appearances for Big Bend;
- Column 7—fossil sites with height of Member in meters;
- Column 8—partial stratigraphic section of Tornillo Flat in Big Bend, showing distinctive black mudstone layers;
- Column 9—magnetic anomalies measured on Tornillo Flat;
- Column 10—stratigraphic nomenclature in Big Bend;

Column 11 is extracted from Haq et al. (1987), which is global in scale. It was aligned with column 1 through a "time in millions of years" scale on the original. The short-term eustatic curve on the right side of column 11 was labeled for associated systems tracts as follows: high stand (HS), low stand wedge (LSW), shelf-margin wedge (SMW), transgressive deposits (TR).

Until the work of the Stratotype Working Group is complete and, as Berggren (1993) comments, the boundary selected and anchored by a "golden spike", for terrestrial sites it suffices to consider the Paleocene/Eocene boundary to lie at or near the Clarkforkian-Wasatchian Land

Mammal Age boundary (Butler et al., 1987; Rea et al., 1990; Gunnell et al., 1993). The North American Land Mammal Ages of Wood have recently been redefined in Woodburne et al. (1987) which defined the base of the Wasatchian at the first appearance of *Hyracotherium* (West, 1987, p. 85). In 1989, Gingerich defined a new zone at the very base of the Wasatchian (Wa0) based on twenty sites in the Bighorn and Clark's Fork basins of northwest Wyoming, in which he considered the environment to be well drained high floodplains with mature soil development, an environment much less frequently sampled than low floodplains. Gingerich named thirteen new species from Wa0 faunas, for the most part animals smaller than others of their genera, producing a picture of a distinctive zone, nonetheless not tremendously different taxonomically at the generic level from Wa1 (Gingerich, 1989, p. 90). A small *Hyracotherium*, *H. sandrae*, characterizes Wa0 (Gingerich, 1989, p. 58-63).

Gingerich (1989, p. 89-90) summarized a climate-driven hypothesis for the development and dispersal of the animals whose appearance marks the Wasatchian. He postulated a late Paleocene development of centers of endemism in equatorial areas (northern South America and central America, northern Africa or south Asia) followed by dispersal of a cosmopolitan fauna including modern orders such as the perissodactyls and artiodactyls northward within continents and between continents, across northern routes with the Paleocene/Eocene boundary warming (Gingerich, 1989, p. 89). Sloan (1969) had postulated a Central American source for animals such as rodents and perissodactyls, and Gingerich (1989, p. 90) postulated an African source. Krause and Maas (1990) summarized biogeographic data on the new mammals that mark the late Paleocene and early Eocene in western North America and also suggested a possible origin in Africa or in the Indian subcontinent. New work in China has uncovered the earliest rodents and a possible stem perissodactyl, *Radinskya* (McKenna et al., 1989). It is possible that China was a stop on the way from an African source (Gingerich, 1989). The pattern of *Hyracotherium* first occurrences does not unequivocally support this idea. Ting (1993) has named a new very primitive Chinese ceratomorph from an early Wasatchian site, *Orientalophus*, and suggested that the Mongolian early Eocene *Hyracotherium gabunai* may be referable to it. Flynn and Novacek (1984) consider the Punta Prieta vertebrate fauna of Baja California, which contains *Hyracotherium seekinsi*, to be Wasatchian and consider the fauna as a whole to argue against heterochrony for the Wasatchian of the western United States.

BIG BEND BIOSTRATIGRAPHY

Figure 1 summarizes the North American and Big Bend biostratigraphic issues. Columns one to five are extracted from Archibald (1987), 6 through 10 are Tornillo Flat data, and 11 is extracted from Haq et al. and tied to the time scale in column 1. The bases of anomaly 25 and 24 have been used to select a scale for the Tornillo Flat data, and all the rest of its columns hang from 10.

On Tornillo Flat, the stratigraphically lowest occurring *Hyracotherium* (a maxilla fragment with left upper M1-M3 from the South Wall Site) occurs only eight meters above the base of the

Hannold Hill Member as redefined by Schiebout et al. (1987). The Paleocene/Eocene transition falls in a rather small stratigraphic interval. Only 52 and 78 meters, respectively, lower in the well-exposed section lie Joe's Bonebed and Ray's Bonebed and the South Wall Site, fossils have remained very rare. Unfortunately it is in this interval that questions regarding the nature of the transition, particularly those raised by much new data on global changes at the boundary, will have to be answered. Also, no further *Hyracotherium* material has been forthcoming from the South Wall in over 20 years.

The differences between the Black Peaks and the Hannold Hill Members reflect environmental changes closely coincident with the Paleocene/Eocene transition in Big Bend. The Black Peaks Member is characterized by lenticular sandstones laid down by highly meandering rivers and prominent color banding of overbank mudstones, including readily recognized black layers representing wet floodplain conditions, which have been used as stratigraphic markers on Tornillo Flat (Schiebout, 1974; Schiebout et al., 1988). The Hannold Hill Member is characterized by (Schiebout et al., 1988): a higher proportion of lenticular sandstone bodies, a lower sandstone to mudstone ratio, lack of the distinctive black beds, and an increase of red coloration in overbank mudstones in comparison to gray mudstones. Given that the thickest of the black beds lies at the top of the Black Peaks Member, the lower Hannold Hill may well represent a considerable change in circumstances, probably combining the warming and drying seen worldwide with changes in base level related to minor sea level changes and/or tectonic uplift. Warming and drying would have resulted in vegetational changes as well as changes in soil regimes and additional erosion in source areas. There is no sea level change exactly related to the black mudstone in question, although earlier ones appear approximately correlated with high stands (Figure 1). The black layer in question appears to be forming early in a transgression (Figure 1) or, if the figure of 55.3 Ma is used for the Paleocene/Eocene (Cf3/Wa0) boundary after Kochet et al. (1992), in a high-stand. It must be remembered that the correlation to the sea level curve through the paleomagnetic and age scales also leaves room for some leeway due to shifts in rates of deposition. Aubry (1993) mentions the widespread formation of lignites and carbon rich sediments at the boundary, and the carbon rich black layer certainly fits this pattern. Geochemical work, including a look at the abundant, soil-formed carbonate nodules, is planned to see if some of the geochemical markers of the boundary recognized elsewhere are confirmable here. These abundant nodules greatly affect fossil preservation, hunting, and preparation, in that they cover and fragment bone.

Three sites in the Black Peaks Member and three in the Hannold Hill Member exposed on Tornillo Flat are of particular interest regarding the Paleocene/Eocene transition: Ray's Bonebed and Annex, Joe's Bonebed, the New Taeniodont Site, the South Wall, the Exhibit, and TT-Jacks (Figure 1). Screen washing at Ray's and Joe's has yielded small mammals including plesiadapoids which place Ray's in Ti3 and Joe's in Ti5 (Gingerich, 1976). The next stratigraphically higher site, New Taeniodont Site, has yielded the only significant vertebrate

find to come from the black mudstone layers, a taeniodont, *Psittacotherium* (Schoch, 1986). It can be considered a very late occurring member of the genus, if not the latest. Schoch (1986) considered extension of *Psittacotherium* into Ti5 to be questionable, and the stratigraphic situation suggests a Ti5 or a Clarkforkian age for the specimen, as later recommended in Archibald (1987, p. 28). Schoch (1986) speculated that the rarity of *Psittacotherium* in well known sites suggested that it was an upland animal. The environment of New Taeniodont Site is where one animal died, and cannot be helpful regarding where the bulk of the population lived. The wet lowland environment it represents, however, would have been widespread on the Gulf coastal plain, so if the animal was an upland dweller, it was far afield.

The South Wall Site has yielded two mammals, a mandible fragment of *Hyracotherium* and an incisor of *Coryphodon* (Schiebout et al., 1988), both from float on a sandstone overlying the thickest black mudstone layer in the Black Peaks Member. The Exhibit Site and TT-Jacks have both yielded fragmentary *Hyracotherium* material referred to *H. vasacciense* and *Coryphodon* (Wilson, 1967; Hartnell, 1980). The Exhibit Site received its name from an "in place" display of Wasatchian mammals, especially *Coryphodon*, and was the first "in place" display of fossil mammals in a U.S. national park (J.A. Wilson, personal comm., 1977). Screening at TT-Jacks has yielded isolated teeth of the rodent *Paramys*. Korth's (1984) revision of early Tertiary rodents included raising a small *Paramys*, *P. taurus*, to species rank. A recent study of late Paleocene and early Eocene rodents in the Clark's Fork Basin in Wyoming has involved considerable study of *Paramys* taxonomy (Ivy, 1990) and description of a new small species of the genus, *P. pycnus*, from the Wyoming earliest Wasatchian (Sandcouleean and Graybullian). She also discusses and gives measurements for *P. taurus*, approximately 15% larger, and ranging from the Clarkforkian to the middle Graybullian (Ivy, 1990, p. 34-37). The TT-Jacks *Paramys* is small (Figure 2), but there is little correspondence of comparable teeth with the small sample of *P. pycnus*, so the TT-Jacks material, also a very small sample, will not be reassigned at this time.

The South Wall is best considered to lie in zone Wa1, not in recently defined Wa0 bearing *H. sandrae*, as the Big Bend oldest *Hyracotherium*. The upper molars are on the upper boundary of size for *H. sandrae* and have more complete cingula. The specimen was originally referred to *H. angustidens* (Schiebout, 1974), which now has been synonymized with *H. index* (Gingerich, 1989, p. 58). *H. sandrae* may have ranged neither so far south nor so low on the coastal plain.

In addition to the missing Tiffanian and Wasatchian zones (Figure 1), the Clarkforkian Land Mammal Age and its three included zones cannot be recognized in Big Bend. *Paramys* and *Coryphodon* should mark the beginning of the Clarkforkian (Archibald, 1987, p. 64). However, each does not appear until the Wasatchian, with the first *Paramys*, 64 meters higher in the section than the first *Coryphodon*. Although the New Taeniodont site could be Clarkforkian, it need not be younger than Tiffanian.

Tornillo Flat lay much further from the uplands and nearer the sea than many classic localities such as those in the Bighorn Basin, and thus experienced a considerably lower rate of deposition, producing a condensed section. Sloan (1987, p. 187) has summarized rates of deposition for major Paleocene mammal collecting areas, finding a range from 15 bubnofs (meters per million years) for Big Bend to 568 bubnofs for the Hoback Basin in Wyoming. The Bighorn Basin ranged from 200 to 90 bubnofs from west to east (Sloan, 1987). Sloan's calculation for Big Bend used the interval Ti1 to Cf1. A recalculation that avoids an estimate for Cf1, calculating from Ti3 to Wa1, yields a figure of 21 bubnofs, still very low. Rapp et al. (1983) found rates of sedimentation in the Black Peaks Member exposed on Tornillo Flat to be relatively constant, averaging 2 centimeters per thousand years (20 bubnofs).

Table 1.

Size comparisons of Big Bend *Hyracotherium* from the South Wall Site and *Paramys* from TT-Jacks with comparable animals from the northern intermontane basins. Figures on Big Bend *Hyracotherium* from Schiebout (1974), on *H. sandrae* from Gingerich (1989), on Big Bend *Paramys* from Hartnell (1980) and on *P. taurus* from Ivy (1990).

Animal and Basin	Tooth	N	Range	Mean	Std. Dev.
<i>Hyracotherium</i> (Big Bend)	M1L	1	6.4		
	M1W	1	7.6		
	M2L	1	7.1		
	M2W	1	8.4		
	M3L	1	7.1		
<i>H. sandrae</i> (Bighorn)	M3W	1	8.2		
	M1L	5	5.9-6.4	6.15	.22
	M1W	5	6.9-7.4	7.10	.23
	M2L	5	6.3-7.0	6.53	.29
	M2W	5	7.7-8.0	7.85	.13
<i>Paramys</i> (Big Bend)	M3L	6	5.8-6.5	6.13	.29
	M3W	6	6.7-7.6	7.26	.34
	M1or2L	2	1.8-2.6		
	M1or2W2		2.3-2.5		
	M3L	1	3.1		
	M3W	1	3.1		
	P4L	2	1.9-2.6		
<i>Paramys taurus</i> (Clark's Fork)	P4W	2	1.8-2.5		
	M1L	10	2.4-2.9	2.61	.19
	M1W	10	2.5-3.6	2.97	.29
	M2L	2	2.6-2.7	2.60	
	M2W	2	2.7-3.0	2.85	
	M3L	5	2.7-3.2	2.98	.17
	M3W	5	2.7-2.9	2.85	.09
P4L	10	2.2-2.7	2.41	.19	
P4W	10	1.4-1.9	1.76	.15	

The thickest black mudstone of the Black Peaks section represents a long period of conditions which could well have been inimical to some of the animals of major biostratigraphic significance, followed by a significant environmental change in the switch to characteristic Hannold Hill lithology. The eight meters above the base of the Hannold Hill at which the *Hyracotherium* was found in float may represent very little time, as the most likely scenario is that the maxilla fragment eroded from the channel sandstone on which it was found and that the sandstone was much more rapidly deposited than the mudstone. More rapid deposition and more upland floodplain conditions rapidly replacing a wet lowland floodplain could very well have been a situation not congenial for types from all zones of the northern intermontane basins where the Clarkforkian and early Wasatchian were defined.

Another possibility is that some types reached Big Bend, but many have done so at considerably different times. It has been estimated that animals with an Asian source dispersing southwards in North America could have arrived in Big Bend later than they do in Wyoming. Rodents, represented by *Paramys*, have been suggested as an example of this phenomenon (Schiebout et al., 1988) and *Coryphodon* may also have been affected. The preservation and recovery of fossils in Big Bend is particularly rare, so stratigraphically important types seen in the north may have been here, but will never be found or will be found with future diligent long term search and increasing numbers of washing sites. Twenty years ago, no Big Bend Puercan mammals had been found, although rocks were exposed that seemed likely candidates to yield them. Puercan faunas have now been recovered from several Big Bend sites (Standhardt, 1986). The late first occurrence of *Paramys* may reflect only that isolated rodent teeth are tiny, and that no screen washing has been done in the stratigraphic interval between Joe's Bonebed and TT-Jacks.

CONCLUSIONS

If the Big Bend Eocene is considered to begin with the arrival of a member of the early Wasatchian (Wa1) cosmopolitan fauna, at the first appearance of *Hyracotherium*, the Eocene appears to be "on time" paleoclimatically and paleomagnetically with the current global picture. It appears that rodents and *Coryphodon* arrive later in Big Bend than in the very well known faunas of Wyoming, and a lot of zones are "missing". Continued hunting and screening is in order, but it must be remembered that the Big Bend section is condensed and the odds of preservation and recovery are diminished in comparison to the northern intermontane sites. Significant faunal differences between very local upland and lowland areas of fluvial deposition have been documented by Gingerich (1989) in Wyoming, so it is no surprise that the pattern observed in Big Bend is different. Big Bend was an usually wet floodplain environment in comparison to northern intermontane sites immediately pre-Wasatchian, and the Black Peaks-Hannold Hill lithologic transition represents a significant local environmental change coincident to the global Paleocene/Eocene changes.

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EARLY PALEOCENE (PUERCAN) VERTEBRATES OF THE DOGIE LOCALITY, BIG BEND NATIONAL PARK, TEXAS

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ABSTRACT

A diverse fauna of fossil vertebrates is reported from the Dogie Locality, an early Tertiary (Paleocene) site in the lower Tornillo Formation in Big Bend National Park, Texas. Remains of fish, amphibians, turtles, lizards, snakes, crocodiles, and mammals were recovered by screen washing of sediments. The occurrence of mammal species previously known from classic early Paleocene localities indicates a Puercan age (Pu2 or Pu3) for this locality. To date Dogie has yielded the largest mammalian fauna of early Paleocene age in the Big Bend area.

INTRODUCTION

Early Tertiary continental sediments containing vertebrate fossils are preserved within a graben in the Big Bend area of southwest Texas. The sequence of Late Cretaceous/early Tertiary sediments exposed in the area has been interpreted as the southernmost Laramide-age intermontane basin (the Tornillo Basin) of the North American cordillera (Lehman, 1991). It lies approximately 850 kilometers southeast of the San Juan Basin of New Mexico. Terrestrial deposits of the Tornillo Formation extend from the lower, intergradational boundary with the Aguja Formation upward to the base of the Chisos Formation, which consists predominantly of volcanic deposits. The Javelina Member of the Tornillo Formation spans the Cretaceous/Tertiary boundary (Standhardt, 1986; Schiebout et al., 1988). Maastrichtian dinosaurs (Lawson, 1976) and the giant pterosaur *Quetzalcoatlus northropi* (Lawson, 1975) occur in the lower Javelina Member of the Tornillo Formation. Lawson (1972) also first reported mammalian fossils from the upper Javelina Member of the Tornillo Formation, from a locality known as Tom's Top, which has since been recognized as early Paleocene in age, probably from the same time period as Dogie (Standhardt, 1986).

This report is preliminary. More detailed descriptions of fossil finds and formal descriptions of new taxa are in preparation.

THE LOCALITY AND ITS SETTING

The Dogie locality, in the northwestern part of Big Bend National Park (Figure 1), was discovered by Robert Rainey (Davies, personal comm. 1983). Fossils

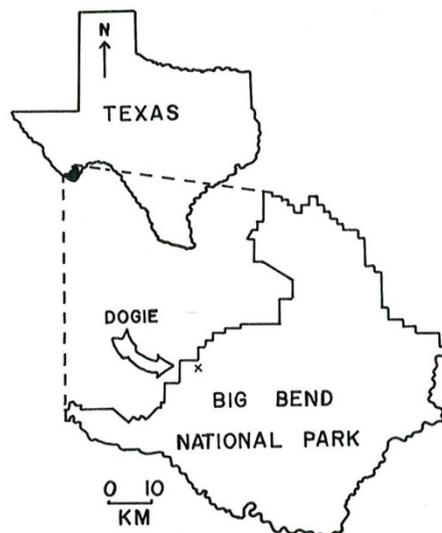


Figure 1. General location of the Dogie fossil site.

occur in light gray and pink bentonitic mudstones with interbedded sandy siltstones lenses that contain limonitic and gypsiferous concretions. Some chalcedony is present in the sediments, and gypsum and authigenic clays are common. From 1983 to 1988, numerous fossils were recovered from surface prospecting and from screen washing 3.3 metric tons of sediment. The degree of preservation of individual fossils is extremely varied. Many very fragile, small bones are silicified and opalized; other fossils are less well-preserved, and some appear to have partially digested. Coprolites are common. Some creep of the soft sediments is evident on the low hills, which are undermined by pseudokarst that has formed deep holes. The locality is stratigraphically 73 meters above the highest occurrence of dinosaurian remains in the local section (Figure 2), and 88 meters above a locality which has yielded teeth of Cretaceous mammals.

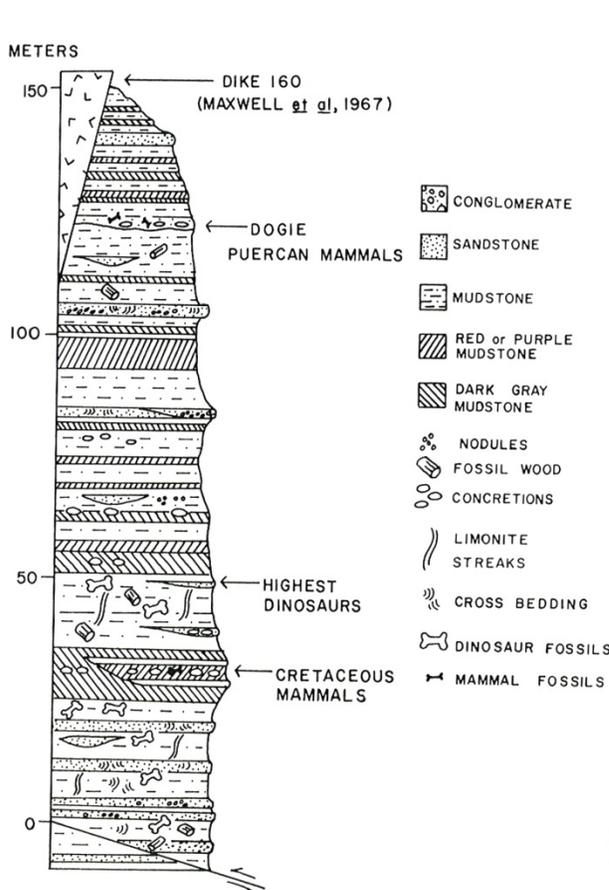


Figure 2. Local stratigraphic section at Dogie from fault to dike #160 (Maxwell et al. 1967); Tornillo Formation, upper Javelina Member.

the San Juan Basin, New Mexico. Dogie mammals already known from other areas include the multituberculate *Mesodma thompsoni*, the periptychid condylarths *Carsiptychus coarctatus* and *Haploconus inopinatus*, and the mioclaenid condylarth *Bomburia prisca*.

VERTEBRATE FAUNA

Fish remains recovered from Dogie include teeth of a new species of freshwater ray (*Dasyatis*), bones and teeth of bowfins (*Amia*), gars (*Atractosteus*) and indeterminate teleosts. Amphibians are represented by frog limb bones. Abundant turtle remains have been found, which indicate the presence of several types of turtles. Glyptosaurine lizards are represented by teeth and scutes. Snakes were also present, as shown by vertebrae of the boid *Dunnophis* and of a new blind snake (*Scolecophidia*, new genus and species). This is the earliest known occurrence of blind snakes in the fossil record. Both piercing and crushing crocodylian teeth are very common.

Mammalian fossils from Dogie include teeth of new forms as well as of species known from other deposits yielding fossils of early Paleocene age, particularly from

Dogie new mammalian taxa representing genera known from other areas include new species of the multituberculates *Ptilodus*, *Cimolodon*, and *Viridomys*, and possibly new species of the marsupial *Peratherium*, the palaeoryctid *Gelastops*, the carnivore *Protictis*, and the condylarth *Baioconodon*. In addition, several teeth of a new genus and species of mioclaenid condylarth have been recovered.

CONCLUSIONS

The Dogie fauna at Big Bend most closely resembles Puercan faunas of the San Juan Basin of New Mexico, as might be expected from their relative proximity. On the basis of the presence of *Bomburia prisca* and *Carsiptychus coarctatus* the Dogie locality is assigned a late Puercan age. As no remains have yet been recovered of *Taeniolabis taoensis*, exact placement in either the Pu2 or Pu3 interval-zone (Archibald et al., 1987) cannot be made.

The occurrence of a new species of *Viridomys*, which was previously known only from the early Campanian of Canada (Fox, 1971), represents a significant range extension for this genus. Range extensions are also indicated for *Haploconus inopinatus*, previously reported from the Torrejonian Dragon Canyon local fauna (Gazin, 1941), *Gelastops*, and *Protictis*. The appearance of *Peratherium* at Dogie is markedly earlier than previously known. The southerly position of the Big Bend region may have contributed to the establishment of a biotic refugium for forms such as *Viridomys*. The region could also have been a source area for peripatric speciation. The discoveries at Dogie show that a significant southern area can be added to the list of North American sites containing faunas spanning the Cretaceous-Tertiary boundary.

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THE TRIASSIC SINBAD FORMATION AND CORRELATION OF THE MOENKOPI GROUP, CANYONLANDS NATIONAL PARK, UTAH

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ABSTRACT

The eastern limit of the Lower Triassic Sinbad Formation is a 0.2-0.3-m-thick fossiliferous limestone bed in the Holeman Spring Basin (T28S, R18E) of Canyonlands National Park, Utah. The Sinbad Formation here intertongues with uppermost strata of the Ali Baba Formation of the Moenkopi Group.

INTRODUCTION

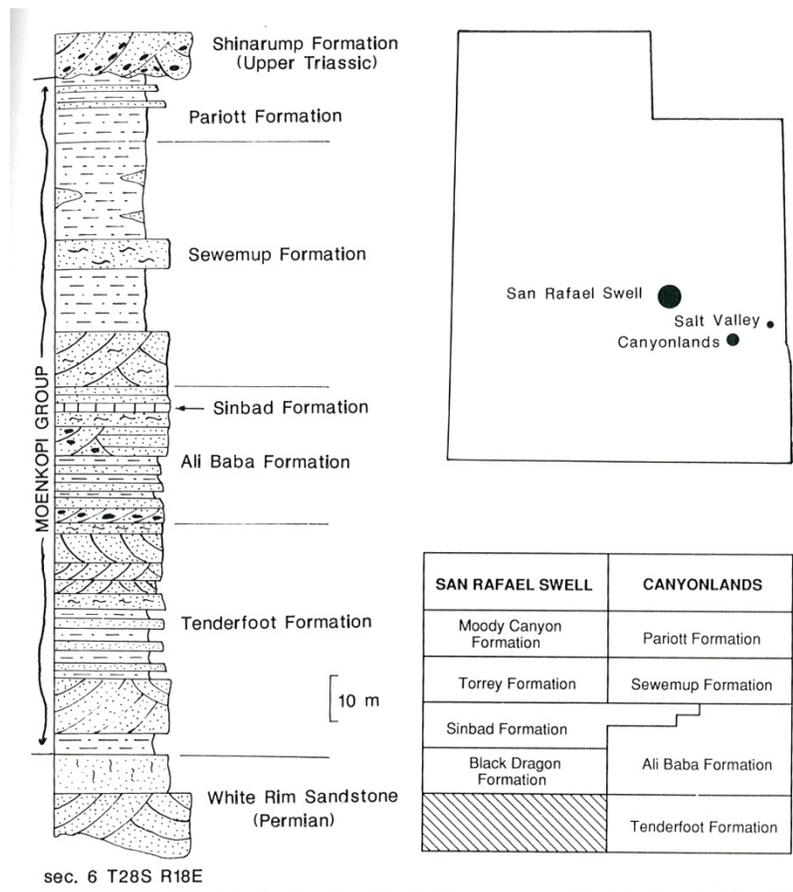
Early-Middle Triassic strata exposed in Canyonlands National Park belong to the Moenkopi Group (sensu Poborski, 1954) and are a sequence of mostly marine red beds as much as 160 m thick. McKnight (1941) identified a very distinctive, thin bed of limestone in the Stillwater Canyon region of the Canyonlands as part of the Sinbad Formation. My purpose here is to (1) document the stratigraphic position of the Sinbad Formation in Canyonlands; (2) describe the eastward extent of the Sinbad Formation in eastern Utah; and (3) correlate Moenkopi strata in the Canyonlands and Moenkopi strata to the west in the San Rafael Swell.

SINBAD FORMATION

McKnight (1941, p. 57-58) accurately described the Sinbad Formation in the Canyonlands as an "Impure limestone, 15 inches in thickness, that lies near the base of the greenish-gray shale series on the Green River, 220 feet above the base of the [Moenkopi] formation." He noted that it is "muddy and also carbonaceous" and "gray in color, though it weathers to a buffy yellow." McKnight reported that Girty identified the following taxa from fossil collections made from the Sinbad Formation in the Canyonlands: *Lingula* sp., *Monotis* ? aff. *M. thaynesiana*, viviparoid gastropods and *Meekoceras* ? sp. Gastropods (Figure 2D) dominate the fossil assemblage and are poorly preserved steinkerns and impressions that resemble the gastropods Batten and Stokes (1986) described from the Sinbad Formation in the San Rafael Swell.

Moenkopi Group strata exposed in the Canyonlands along the flank of Steer Mesa (sec. 6, T28S, R18E) include the Sinbad Formation and are presented here as a characteristic section (Figs. 1-2). These strata can be assigned to the Moenkopi Group formations named by Shoemaker and Newman (1959). The lower 46 m of red-bed, fine-grained sandstones and siltstones belong to the Tenderfoot Formation of Permian? or Early Triassic? age. About 25 m of reddish-brown to

brown, coarser-grained sandstones, conglomerates and siltstones overlies these strata and are assigned to the Ali Baba Formation. The Sinbad Formation is 0.2-0.3 m of limestone near the top of the Ali Baba Formation. A definite change in color, grain size and lithology to yellow-gray and pale green, gypsiferous siltstones and fine sandstones marks the base of the 52-m-thick Sewemup Formation. Overlying reddish-brown sandstones and siltstones are 12 m thick and are assigned to the Pariott Formation. Siliceous conglomerate of the Shinarump Formation of the Chinle Group (Upper Triassic) disconformably overlies the Pariott Formation. Previous claims that the Sinbad Formation is laterally equivalent to the Sewemup Formation (Shoemaker and Newman, 1959; Stewart et al., 1972) thus are incorrect. The Sinbad intertongues with uppermost Ali Baba Formation.



EASTERN LIMIT OF THE SINBAD

The eastern limit of the Sinbad Formation has long been placed in the Salt Valley northeast of Moab in T22S, R20E, Grand County, Utah (e.g., Blakey et al., 1993, Fig. 8). Shoemaker and Newman (1959, p. 1849) identified a thin limestone in supposed Sewemup strata here as Sinbad based on the putative presence of silicified juvenile specimens of the Smithian ammonoid *Meekoceras*. Recent examination of this limestone (especially in the SE1/4 NE1/4 SE1/4 sec. 31, T22S, R20E) reveals it

contains a diverse silicified fossil assemblage of Early Cretaceous gastropods, unionid bivalves, charophytes and ostracods; the supposed juvenile *Meekoceras* are specimens of the planorbid gastropod *Gyraulus veternus* (Goodspeed et al., 1992). Doelling (1985) correctly mapped this limestone and the adjacent "Sewemup" strata as Lower Cretaceous Cedar Mountain Formation. The eastern limit of the Sinbad Formation thus is in the Canyonlands in the Holeman Spring Basin (T28S, R18E), as originally documented by McKnight (1941).

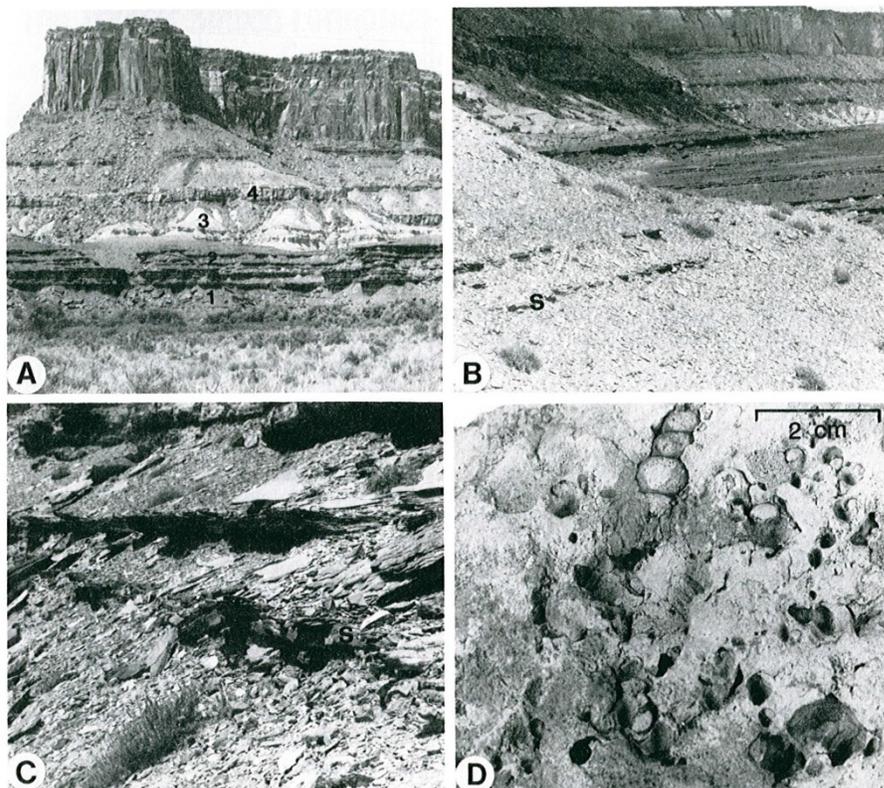


Figure 2. Moenkopi Group strata at the measured section (fig. 1) along the flank of Steer Mesa in the Canyonlands (sec. 6, T28S, R18E). A, Overview of section; units are: 1 = Tenderfoot Formation, 2 = Ali Baba Formation, 3 = Sewemup Formation, 4 = Pariott Formation, 5 = Shinarump Formation. B-C, Close-ups of Sinbad Formation limestone bed(s). D, Gastropod steinkerns in Sinbad Formation limestone at this section.

CORRELATION

Correlation of Moenkopi strata between the San Rafael Swell and the Canyonlands-Arches area (Fig. 1) can be achieved through lithostratigraphy, very limited biostratigraphy and sequence stratigraphy. The Sinbad Formation provides an early Smithian datum upon which to hang this correlation.

Like most previous workers (e.g.,

Shoemaker and Newman, 1959; Stewart et al., 1972), I consider the Tenderfoot Formation to be older than Moenkopi Group strata exposed in the San Rafael Swell. Black Dragon Formation strata in the San Rafael Swell represent a transgressive systems tract equivalent to the lower-middle Ali Baba Formation. The highstand systems tract represented by the Sinbad Formation overlies the Black Dragon in the San Rafael Swell and is at the approximate top of the Ali Baba in the Canyonlands. Overlying Sewemup Formation strata are generally correlative with the Torrey Formation. Correlation of the Moody Canyon and Pariott Formations is tentative.

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CRAYFISH FOSSILS AND BURROWS FROM THE UPPER TRIASSIC CHINLE FORMATION, CANYONLANDS NATIONAL PARK, UTAH

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ABSTRACT

A large number of fossil freshwater crayfish in the Petrified Forest and Owl Rock Members of the Upper Triassic Chinle Formation, adjacent to Canyonlands National Park in southeastern, Utah are described as three morphotypes of body plan. The specimens are the earliest known true Cambaridae and record the earliest known occurrence of fossil crayfish with their burrow. Five individuals were found within burrows, whereas thousands of others occur within a multi-layer mass-mortality bed in the Owl Rock Member. Twenty specimens form the basis for description of two new genera, and three new species of freshwater crayfish. The taxonomy of the new crayfish is also based on their burrowing ability categorized as Type I, II, and III and correlated with Hobbs' classification of primary, secondary, and tertiary, burrowers, respectively.

INTRODUCTION

The earliest known fossils of freshwater crayfish are found in association with their burrows in the Upper Triassic Chinle Formation, on the boundary of Canyonlands National Park, southeastern Utah. The only other known freshwater crayfish fossils from Triassic continental rocks are the taxonomically undescribed crayfish from the Durham Basin of North Carolina (Olsen, 1977), and a small, single specimen in a mudstone from the Petrified Forest Member of the upper part of the Chinle Formation in Arizona (Miller and Ash, 1988), neither of which are associated with burrows. Previously described fossil crayfish occur in strata of the Early Cretaceous/Late Jurassic of Eurasia (Glaessner, 1969), the Early Eocene of North America (Feldmann et al., 1981), and an astacid (United States west coast crayfish family) crayfish from the Miocene and Pliocene of Oregon (Rathbun, 1929). None of these crayfish fossils have been reported in or associated with burrows.

This paper presents a discussion of two new genera of Triassic freshwater burrowing crayfish from the Canyonlands area of southeastern Utah, as well as a discussion of their evolutionary and paleoecologic significance. The Chinle crayfish document new taxa and represent lineages to the origins of North American crayfish families, the Astacidae and Cambaridae. The evolution of freshwater crayfish is reconsidered, as well as their zoogeographical distribution and paleomigrational patterns.

GEOLOGIC SETTING

The Upper Triassic Chinle Formation occurs throughout the Colorado Plateau, ranging in thickness from 0 to 400 meters. It was deposited as layers of continental clastic and carbonate sediments (Stewart et al., 1972). In the Canyonlands study area, the upper part of the Chinle Formation is approximately 100 meters thick comprising the Moss Back, Petrified Forest, Owl Rock, and Church Rock Members in ascending order (Stewart et al., 1972; Blakey and Gubitosa, 1983; Hasiotis and Mitchell, 1993). The Chinle Formation comprises multiple phases of stream, lake, and swamp deposition in the study area (e.g., Blakey and Gubitosa, 1983). The paleolatitude of southeastern Utah is considered to have been sub-tropical to tropical from paleotectonic reconstructions of continents that formed the supercontinent Pangea during the Permian and Triassic (Van der voo et al., 1976; Dubiel et al., 1991).

DESCRIPTION OF CRAYFISH FOSSILS AND BURROWS

The Chinle Formation in the Canyonlands area yielded three morphologically distinct types of crayfish fossils from fluvial and overbank deposits. Some of these fossils were discovered in the bottoms of burrows, which were attributed to the crayfish activity based on the burrow morphology. The burrow morphologies are briefly described first because the morphology of the burrows is related to the morphology of the crayfish and its inferred behavior. The Chinle Formation also contains numerous burrows whose architectural and surficial morphologies indicate these are burrows constructed by crayfish (Hasiotis, 1990; Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). Architectural burrow morphologies and their classification as Types I, II, III (Fig. 1A) (in decreasing order of complexity) suggests the possibility that at least three different burrowing species occurred in this area (Hasiotis, 1990; Hasiotis and Mitchell, 1993). This, in turn, is born-out in the diversity of crayfish fossils recovered from Steven's Canyon and Hart's Point near Canyonlands National Park.

The crayfish fossils were collected from the Petrified Forest and Owl Rock Members of the Upper Triassic Chinle Formation in Stevens Canyon and Harts Point, adjacent to Canyonlands National Park, San Juan County, southeastern, Utah (Fig. 1C-F). Fossils that occurred within burrows were collected Stevens Canyon near the intersection with Indian Creek Canyon, in the Owl Rock Member. The mass-mortality bed, where the majority of the specimens were collected, occurs in the Owl Rock Member of Stevens Canyon near the Canyonlands National Park boundary. Three disarticulated specimens were collected from the Petrified Forest Member at Harts Point. Modern and ancient crayfish taxonomy is based on the morphology of the chelae, rostrum, antennal scale, antennae, groove patterns and shape of areola, telson and uropods, and relative length and ornamentation of the cephalothorax and abdomen (Fig. 1B).

Morphotype 1

Five crayfish fossils were recovered from thousands of burrows occurring in the Canyonlands area of southeastern, Utah, and are the first known fossil freshwater crayfish to be associated

with burrows. The crayfish exhibit a triangular rostrum with lateral spines and delicate tuberculated architecture of the cephalothorax. The carapace contains cervical and branchiocardiac grooves with a dorsomedian longitudinal suture. These crayfish may or may not be strongly heterochelous.

This type of crayfish morphology is associated with **Type I** burrows. **Type I** burrows exhibit complex architecture with multiple branches and multiple chambers. Because of the morphology exhibited by this morphotype (strong shovel-shaped chelae, rounded terga, small triangular rostrum, lack of spines and coarse ornamentation) this crayfish can be identified as a **Type I** burrower, equivalent to Hobbs' (1981) primary burrower. Hobbs' (1981) classification of burrowers is based on the amount of time the crayfish spends in the burrow and its connection to open water. Primary burrowers are crayfish that spend the greatest amount of time in the burrows, which have no connections to open water. With only a few exceptions, primary burrowers create relatively complex burrows.

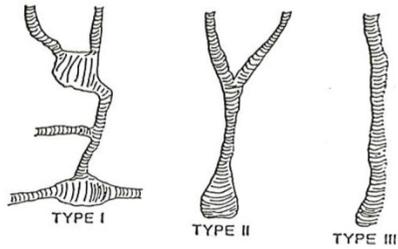
Morphologically, this species is consistent with modern primary burrowers. Compared to individuals of *Cambarus diogenes diogenes* (Girard) (Hasiotis and Mitchell, 1993), both burrowers exhibit relatively short triangular rostra, weakly tuberculated cephalothorax, lack of many spines on the cephalothorax and pereopods, small scale of antennae, shovel-shaped broad chelae, and a reduced abdomen that exhibit smooth, rounded pleura and terga.

Morphotype 2

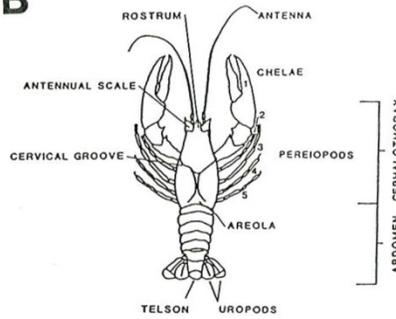
Two morphotypes (morphotypes 2 and 3) of crayfish fossils make up the majority of body fossils from the mass-mortality beds in the lower part of the Owl Rock Member. One of these morphotypes exhibits a long triangular rostrum, and has a well impressed cervical groove with a well developed areola. The body contains a moderately tuberculated cephalothorax, possesses elongate slender chelae, and have a telson with a transverse suture, and uropods with diaeresis.

The features of this type of crayfish are similar to those characters exhibited by modern secondary and tertiary burrowing crayfish (Hobbs, 1981). These Triassic crayfish possess relatively long rostra, chelae longer than those of primary burrowers and tend to be heavy to slender, exhibit more ornamentation and spines, and have more rounded versus sharply rounded shapes (H. H. Hobbs Jr. personal comm., 1989). The **Type II** and **Type III** burrows (Hasiotis and Mitchell, 1993) that occur in the upper Chinle Formation that are similar to modern secondary and tertiary burrows, respectively. Because of the similarity between the anatomy these Triassic crayfish to modern secondary burrowers and the presence of **Type II** burrows in locales in which these fossils occur, they are equivalent to modern secondary burrowers.

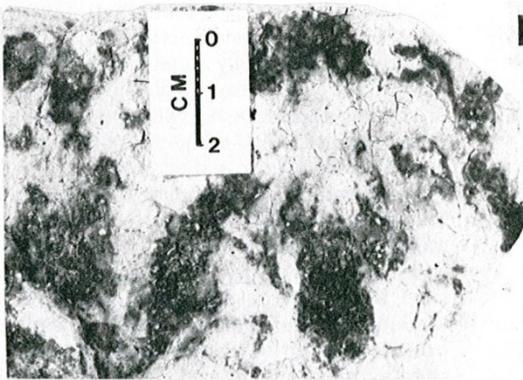
A CLASSIFICATION OF ARCHITECTURAL MORPHOLOGY EXHIBITED BY TRIASSIC BURROWING CRAYFISH



B



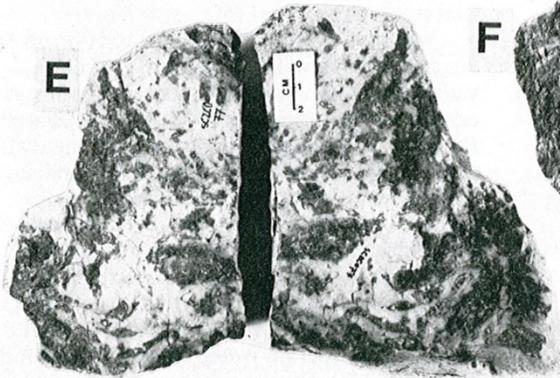
C



D



E



F

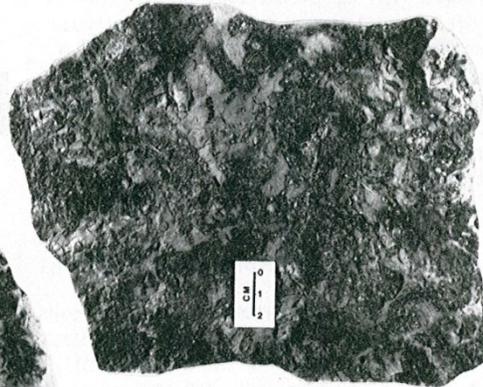


Figure 1A-F. A. Triassic crayfish burrow architecture based on burrow complexity and overall depth. B. Anatomical parts used in taxonomic descriptions of modern and ancient crayfish. C-F. Examples of crayfish fossils recovered from mass-mortality beds in the Owl Rock Member, upper Chinle Formation.

Morphotype 3

The second crayfish morphotype (3) collected from the mass-mortality beds exhibit a small triangular rostrum with large antennae scales of approximately equal length. The chelae are small and slender, and moderately tuberculated. The abdominal somites bear weak transverse grooves, pleura exhibit a rounded angle with the terga that terminates in a sharp spine directed posteroventrally.

The highly ornate and spiny characteristics exhibited by morphotype 3 crayfish are those shared by most modern crayfish that are classified as tertiary burrowers (Hobbs, 1981). The morphology of tertiary burrows is simple, and are only constructed for mating or during periods of water deprivation. **Type IIIA** and **Type IIIB** burrows of the upper part of the Chinle Formation are those that exhibit the most simple burrow architecture (Hasiotis and Mitchell, 1993). Even though no crayfish were discovered within any **Type III** burrows, the crayfish anatomy suggests these crayfish were **Type IIIA** burrowers and most likely spent most of their life outside the burrow, mainly in streams, rivers, and lakes. **Type IIIB** burrows are greater than 1 m in length are most similar to modern primary burrowers and would have a body plan similar to morphotype 1 Triassic crayfish. These Triassic crayfish lived away from open bodies of water in areas such as proximal and distal floodplains and burrowed to the water table to depths up to 4 m (Hobbs, 1981; Hasiotis and Mitchell, 1993).

EVOLUTIONARY AND PALEOECOLOGICAL IMPLICATIONS

The discovery of burrowing crayfish fossils in late Triassic strata of the Colorado Plateau has significant implications to the evolution of freshwater crayfish, as well as the paleohydrologic structure and dynamics of depositional systems of Triassic paleoecosystems. Paleohydrologic and paleoecologic information obtained from this study can be applied to crayfish burrow-bearing rocks elsewhere in the geologic record to reconstruct ancient water table levels and estimates of seasonal and annual precipitation.

Previous to the Chinle discovery, crayfish were thought to have evolved early in the Cretaceous (130 million years ago) from minor invasions into brackish water by marine lobsters from the late Triassic (230 million years) to the late Jurassic (145 million years) (Glaessner, 1969; Feldmann et al., 1981; Hobbs personal comm., 1989). Burrowing crayfish were thought to have evolved during the early to mid Tertiary (55 to 35 million years ago) after they had become established in freshwater aquatic ecosystems (Hobbs, 1976).

The diversity and distribution of North American Triassic terrestrial burrowing and aquatic freshwater crayfish fossils demonstrates that their evolution began earlier and may reciprocate our views of the lobster-crayfish relationship. Crayfish fossils and the burrows attributed to their activity in the Upper Triassic Chinle Formation date to about 225 million years in age during the presence of the Pangean supercontinent. Trace and body fossil evidence confirms that crayfish were established across ecological settings ranging from fully terrestrial to fully aquatic. The distribution of Triassic aquatic crayfish also included areas in Arizona (Miller and Ash, 1988) and in North Carolina (Olsen, 1977). The diversity, paleogeographic distribution, and ecological specialization of the Triassic crayfish implies that the group evolved possibly as early as or earlier than the Permian (286 million years ago). The crayfish body and trace fossil evidence may suggest that lobsters, thought to have evolved early in the Triassic (245 million years ago), evolved from aquatic freshwater crayfish that inhabited coastal streams, rivers, and lakes. The

majority of lobster body fossils occur in the Jurassic and Cretaceous with only a hand full from the Triassic (e.g., Glaessner, 1969).

Paleoecologically, Triassic crayfish exhibited nearly identical behavior with respect to burrow architecture, depth, and the seasonal and annual distribution and fluctuation of the water table (Hasiotis and Mitchell, 1993). Triassic crayfish burrows that exhibit short lengths and complex architectures reflect a shallow water table with dampened fluctuations (usually due to a nearby body of water). Crayfish burrows that exhibit long lengths and simple architectures reflect a deep and fluctuating water table (Hasiotis and Mitchell, 1993). The architecture, depth, and distribution of Triassic crayfish burrows can be used to reconstruct local and regional water table depths and fluctuations that could be related to seasonal and annual precipitation during the Triassic monsoonal climate.

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DINOSAUR FOOTPRINT FROM THE UPPER TRIASSIC ROCK POINT FORMATION OF THE CHINLE GROUP, CANYONLANDS NATIONAL PARK

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ABSTRACT

The first dinosaur footprint discovered in Triassic strata of the Canyonlands is a single *Grallator* footprint from the Upper Triassic Rock Point Formation near Upheaval Dome. This discovery further confirms the restriction of virtually all Late Triassic tetrapod footprints in the western United States to uppermost strata (Rock Point Formation and correlatives) of the Chinle Group.

INTRODUCTION

Dinosaur footprints from the Upper Triassic Chinle Group have been reported from central Wyoming, northwestern Colorado, northeastern Utah and east-central New Mexico (Conrad et al., 1987; Hunt et al., 1989; Lockley et al., 1992, 1993; Lockley and Hunt, 1994 a, b). Dinosaur footprints have also been reported from the Chinle Group of eastern Utah, but they have not been described in as much detail as those from other areas (Lockley, 1986; Lockley et al., 1992). Here, we add to this record a dinosaur footprint discovered by the senior author near Upheaval Dome in Canyonlands National Park, Utah.

STRATIGRAPHIC CONTEXT

Upper Triassic strata exposed in Canyonlands National Park, Utah, belong to the Chinle Group of Lucas (1993). Here, Chinle Group strata disconformably overlie rocks of the Lower-Middle Triassic Moenkopi Group and are overlain disconformably by the Lower Jurassic Wingate Formation of the Glen Canyon Group. Southwest of Upheaval Dome in the Canyonlands, the Chinle Group section dips 20 degrees to N60 degrees E and is as follows (in ascending order): (1) Shinarump Formation, 16 m thick, trough-crossbedded extraformational conglomerate (clasts of chert, quartzite and Paleozoic limestone) and sandstone; (2) Cameron Formation, 9 m thick, thin, intercalated beds of ripple laminated sandstone and mudstone; (3) Blue Mesa Member of Petrified Forest Formation, 18.2 m thick, bentonitic mudstone and nodular calcrete, variegated green, red and purple; (4) Moss Back Formation, 7.6 m thick, trough-crossbedded and laminated intraformational conglomerate (sandstone and calcrete clasts) and sandstone; (5) Painted Desert

Member of Petrified Forest Formation, 14.2 m thick, reddish brown bentonitic mudstone and siltstone; (6) Owl Rock Formation, 8.3 m thick, mottled pink and green, bioturbated siltstone; (7) Rock Point Formation, 64.9 m thick, reddish brown siltstone intercalated with laminated/ripple laminated sandstone except for the upper 9.2 m, which are the Hite Member, trough-crossbedded sandstone and siltstone-clast conglomerate.

The dinosaur track illustrated here was collected from the top of the bed just beneath the base of the Hite Member of the Rock Point Formation, a 0.6 m thick laminated sandstone. The locality is northeast of the loop trail from Upheaval Dome through Syncline Valley at UTM 4254500N, 591740E, zone 12, San Juan County, Utah.

IDENTIFICATION

The dinosaur footprint illustrated here (Fig. 1) was not collected. It is preserved as a concave mold in epirelief. The footprint has three toe impressions, the middle of which (impression of digit III) is much longer than the side toes (mesaxonic). All toe impressions have acute tips, and the posterior heel impression is pointed as well. Footprint length is 142 mm, and the angle of divarication of the digits is about 33 degrees. The track is an underprint, and no pad impressions are preserved. The tridactyl morphology, narrow, elongate digit impressions and impressions of clawed unguals of this footprint indicate that it is a theropod dinosaur footprint. Like most poorly preserved Triassic theropod footprints, this specimen is best assigned conservatively to the ichnogenus *Grallator*.

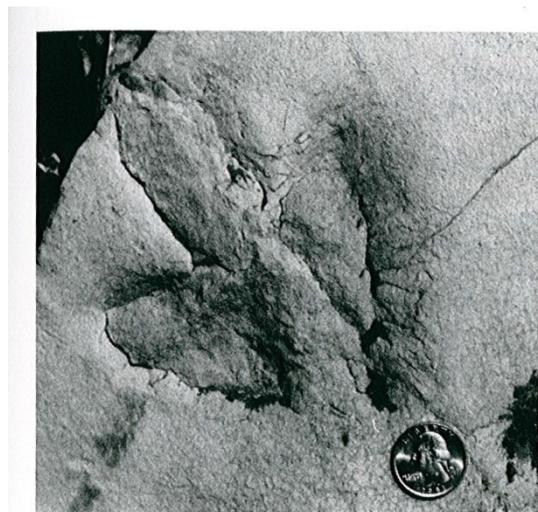


Figure 1. Footprint of theropod dinosaur, ichnogenus *Grallator*, from the Rock Point Formation of the Chinle Group near Upheaval Dome, Canyonlands National Park.

DISCUSSION

Hunt and Lucas (1992) first noted that virtually all Chinle Group tetrapod footprints are confined to the upper Rock Point Formation and its correlatives (also see Hunt et al., 1993). The *Grallator* footprint from the Rock Point Formation in Canyonlands further strengthens this conclusion. Where extensive footprint assemblages are known from the upper Chinle Group, theropod dinosaur footprints are the dominant track type (Lockley et al., 1992).

Therefore, it is not surprising that a theropod footprint is the first tetrapod footprint found in the Rock Point Formation in the Canyonlands area. Lockley (1993a, b) and Lockley and Hunt (1994a) noted a marked increase in small grallatorid tracks

in the upper part of the Chinle Group relative to other vertebrate track types. Therefore, they informally recognized a small grallatorid zone in the uppermost Chinle Group.

The footprint illustrated here remains in the field, and its conservation should be undertaken. Furthermore, this is the first dinosaur footprint found in Triassic strata in the Canyonlands. Its discovery should be an impetus to explore Rock Point Formation strata in the Canyonlands for additional tetrapod footprints.

ACKNOWLEDGMENTS

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NEW TRACKSITES FROM THE MOENKOPI FORMATION (LOWER-MIDDLE TRIASSIC), GLEN CANYON NATIONAL RECREATION AREA

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ABSTRACT

Vertebrate and invertebrate subaerial traces are abundant in the Triassic Moenkopi Formation and have been documented in numerous publications. Subaqueous traces are equally common and widely distributed within the Moenkopi Formation, yet they are not nearly as well documented.

Subaqueous traces, observed on lands administered by the National Park Service from Dinosaur National Monument in the north to Glen Canyon National Recreation Area in the south, are perhaps the most common trace fossils in the Moenkopi Formation. Two new tracksites described herein from the Glen Canyon National Recreation Area are representative of subaqueous traces in the Moenkopi Formation.

Three types of subaqueous traces are found at two tracksites in the Moenkopi Formation in Glen Canyon National Recreation Area: (1) Vertebrate swim traces; (2) invertebrate swim traces; and (3) other enigmatic traces. They represent a trace fossil assemblage, or ichnofauna, unique to the Moenkopi Formation and its equivalents.

INTRODUCTION

The Moenkopi Formation has a wide geographic distribution in the Western Interior of the United States and crops out in numerous localities on lands administered by the National Park Service in the western United States. Terrestrial or subaerial tracks and traces (ichnotaxa) in the Moenkopi include the vertebrate traces *Chirotherium*, *Rhynchosauroides* (Fig. 1d), *Therapsipus*, and *Rotodactylus*. Five taxa of invertebrate (subaerial and subaqueous) trace fossils are found in the Moenkopi and include subaqueous arthropod trails made by limulids (Peabody, 1956; Morales, 1987; Hunt et al., 1993). Often, vertebrate and invertebrate swim traces are found on the same surface (Peabody, 1956).

The purpose of this paper is to briefly describe vertebrate and invertebrate subaqueous traces found at two new localities in Glen Canyon National Recreation Area (GLCA). One locality is in the Trachyte Point area and was found by the authors. The second is in the Farley Canyon area and was reported to us by Martha Hayden.

VERTEBRATE TRACES OF SUBAQUEOUS ORIGIN

Although the vertebrate ichnofossil record is reported to be dominated by *Chirotherium*, *Isochirotherium*, and *Synaptichnium*, vertebrate swim traces are also very common in the Moenkopi (Peabody, 1956; Morales, 1987; Hunt et al., 1993). This conclusion is consistent with the observation of Frank Peabody, who stated that swim or scrape marks are the "most common impressions occurring in Moenkopi strata" (1956, p. 373). Such traces are also observed in an area covering most of the geographic distribution of the Moenkopi, and so can be found in many of the preserves administered by the National Park Service.

Typical large traces have been described as "straight grooves" up to 10 cm in length and 1.5 cm in width (Hunt and Lucas, 1993, p. 20). The numbers of parallel grooves may vary from 1 to 5 (Hunt and Lucas, 1993; Fig. 1e herein). Peabody (1956) observed that the swim traces are nearly always preserved as casts on the under side of a lens of thin limestone, but we have also observed them on the underside of sandstone. Hunt and Lucas (1993) report traces in association with mudcracks, but Peabody (1956, p. 737) stated "no shrinkage cracks indicative of subaerial desiccation occur anywhere on surfaces bearing 'swim' tracks". He also stated that no salt crystal pseudomorphs or ripple marks are found on surfaces bearing swim tracks (Peabody, 1956). The lenses containing trackbearing layers may exceed a thousand square feet (92.9 square meters), and are roughly circular (Peabody, 1956).

New tracksites at GLCA exhibit three types of subaqueous traces. The same trace fossil assemblages, or ichnocoenoses, recur in the same sedimentary facies throughout the Moenkopi Formation and its equivalents (Boyd & Loope, 1984; Lockley and Hunt, in press a, b).

Vertebrate traces (Fig. 1e) are parallel scrape marks thought to be formed when a buoyant animal touched the substrate (probably with a manus) during a swimming "stroke". Vertebrate swim traces at the GCNRA sites vary in size from approximately 5 to 15 cm in length, and 3 to 6 cm in width. Individual digit impressions, probably representing the width of the trackmakers' digits, range from 1 to 3 cm in width. The digit impressions have rounded ends, with no indication of claws, and therefore probably represent amphibians. Note that *Rhyncosauroides* was not found on the same surfaces as the swim traces.

Invertebrate traces (Fig. 1a, 1b, and 1c) at the GLCA tracksites are small swim traces attributed to limulids. These traces often occur in large numbers indicating considerable activity by these animals. Crescent shaped traces (Fig. 1a) are very similar to limulid traces described by Wang (1993). The so called "comb-like" traces (Fig. 1b) and *Kouphichnium*-like traces (Fig. 1c) are also characteristic of other limulid traces known from the Mesozoic of North America and Europe.

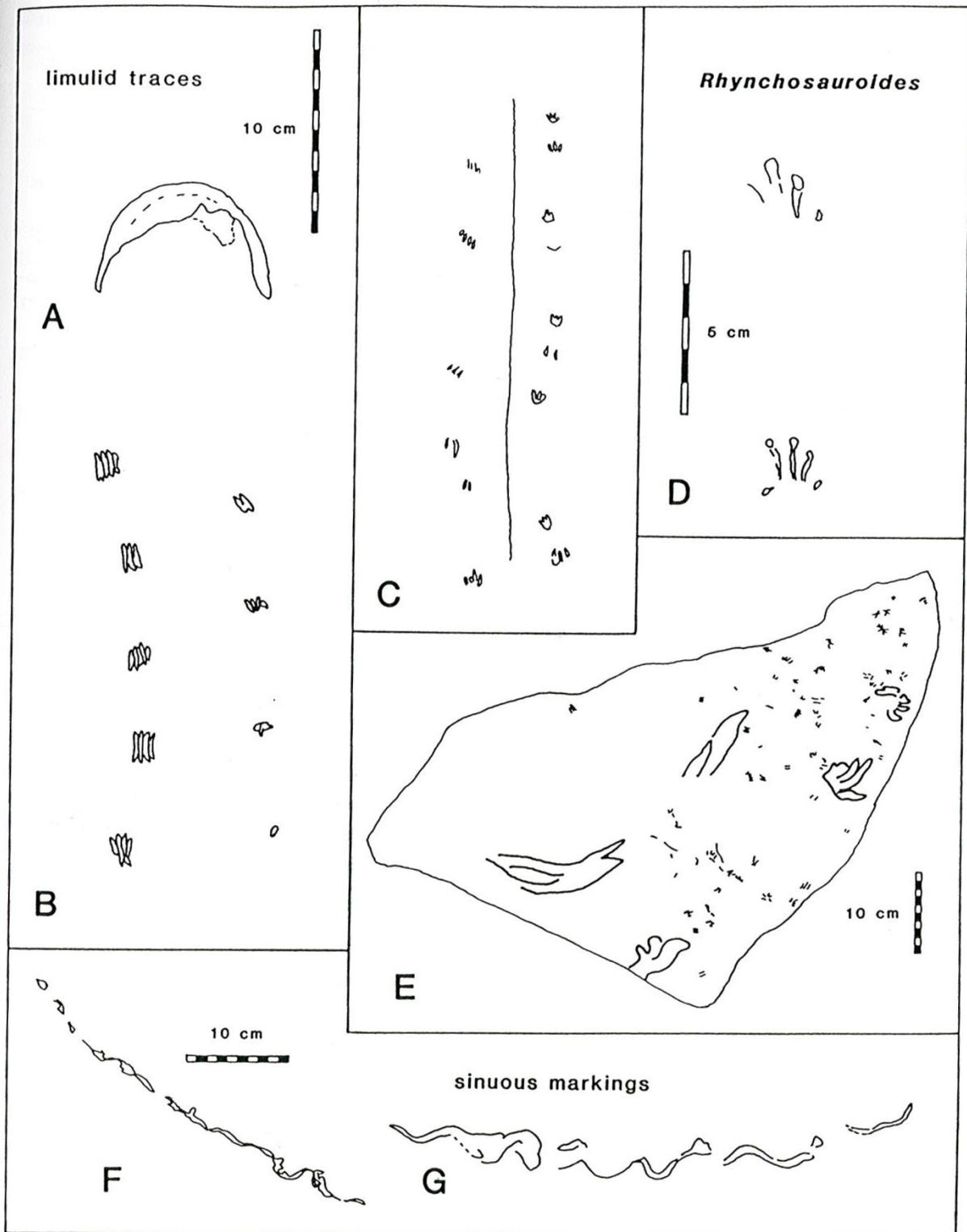


Figure 1. Tracks from the Moenkopi Formation. A, trace of head shield and B, comblike traces, both attributed to limulids from the Trachyte Point locality. C-G, traces and markings from the Farley Canyon locality. C, limulid trace (cf. Kouphichnium). D, Rhynchosauroides. E, Elongate swim traces and limulid footprints. F and G, Enigmatic sinuous markings.

Two enigmatic traces (Fig. 1f and 1g) were found at the tracksite in GLCA. These traces are narrow sinuous traces from less than 1 to 3 cm in width. The origin of these traces is unknown.

Observations at GLCA reveal that traces are preserved on the underside of a thin lens of sandstone in alternating sandstone-shale sequences. No evidence of subaerial desiccation is present at the two tracksites at GLCA. No ripple marks were found on the trackbearing surface.

DISCUSSION

Although the Moenkopi Formation has yielded over 22 named vertebrate ichnotaxa, it is perhaps best known for traces such as *Chirotherium*, *Isochirotherium*, and *Synaptichnium*. However, swimming or "scrape" marks probably formed by subaqueous locomotion of amphibians, are common and widely distributed geographically. These traces, observed from Dinosaur National Monument in the north to GLCA in the south, are perhaps the most common trace fossils in the Moenkopi Formation (Peabody, 1956; Boyd and Loope, 1984; Lockley and Hunt, in press a, b).

Documentation of vertebrate subaqueous traces in previous literature contains little stratigraphic information. Sites from at least 16 geographic localities in the Moenkopi Formation are documented, but little is known of their stratigraphic location. It appears that these traces are found on at least 17 stratigraphic levels in the Moenkopi. Trace fossil sites found on lands administered by the National Park Service are located in the Upper Red Member in Capitol Reef National Park, Utah (possibly two stratigraphic levels); the lower Moenkopi near Vernal, Utah (near Dinosaur National Monument); the Wupatki Member in Wupatki National Monument, Arizona; and the upper Moenkopi at Glen Canyon National Recreation Area, Utah (Peabody, 1956; Morales, 1987; Hunt and Lucas, 1993; Lockley and Hunt, in press b; and this paper).

In general, subaqueous traces have a long history of being misunderstood (see Lockley and Rice, 1990 for review). They have been reported as terrestrial tracks of hopping dinosaurs (Bernier et al., 1984.), and later re-identified as swim traces (Thulborn, 1989). They have been misidentified as driftwood prod marks and bird tracks (McAllister, 1989; Lockley et al., 1992). Crescent-shaped traces in the Moenkopi were reported as tracks, but were later identified as current crescents by Frank Peabody (1947).

Because subaqueous tracks are incompletely preserved and seldom studied in detail, little is known about the tracks and the affinity of the trackmakers (Lockley and Rice, 1990). Several authors (Peabody, 1956; Lockley and Hunt, in press a; Morales, 1987) suggest that these traces could be attributed to amphibians, citing subaqueous origin, abundant body fossils of amphibians in the Moenkopi, and clawless toe impressions as evidence that the trackmakers were amphibians. We agree with this interpretation, but believe that a complete understanding of these traces and the ecology of the Moenkopi Formation requires further systematic study of these and other subaqueous traces. For example we have already pointed out that multiple swim tracksites (ichnocoenoses) indicate a characteristic swim track ichnofacies in parts of the Moenkopi Formation (Lockley et al., 1994; Lockley and Hunt, 1994b). Further analysis may yield a better

understanding of the affinity and behavior of vertebrate subaqueous trackmakers and paleoecology of the Moenkopi Formation.

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CLIMBING UP SAND DUNES IN THE PERMIAN: NEW TRACKSITES FROM GRAND CANYON NATIONAL PARK, ARIZONA

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ABSTRACT

Grand Canyon National Park, Arizona, is famous for Late Paleozoic ichnofossils. However, little work on the vertebrate trace fossils has been done in the park for nearly 70 years. A preliminary reconnaissance of the Coconino Sandstone within the park, during 1993, indicates that tracks are very common. Further work should be conducted on the Paleozoic tracks in the Grand Canyon for both scientific research and to assist park management.

INTRODUCTION

Grand Canyon National Park (GRCA) has been well known for Late Paleozoic tracks since 1918 when Richard Swann Lull of Yale University described some specimens collected by Charles Schuchert in the Hermit basin. Charles Gilmore, of the Smithsonian Institution, later visited GRCA and collected many specimens. Gilmore described these trace fossils in a series of papers (Gilmore, 1926, 1927, and 1928). Over the next 40 years other specimens were described from the same strata outside the park, but virtually no further work has been performed within GRCA. We have recently conducted a preliminary survey for tracks in the area around the Hermit Trail in the Permian Coconino Sandstone. The purposes of this paper are to briefly review the ichnology of the Coconino and to present some initial observations on the new finds.

PREVIOUS ICHNOLOGICAL WORK IN THE COCONINO SANDSTONE

Gilmore (1926, 1927, 1928) and Lull (1918) described all of the known ichnotaxa from the Coconino at GRCA (Tables 1, 2). Gilmore collected most of his Coconino specimens along the then Hermit Trail which has subsequently been abandoned (Spamer, 1984). Additional work has been carried out south of GRCA by Brady and Alf. Baird (in Spamer, 1984) provided a partial revision of the ichnotaxonomy although further work needs to be done. Most of the described ichnogenera are probably monospecific, notably *Laoporus*. Middleton (1990) illustrated additional specimens from the Coconino Sandstone but it is not clear if they came from GRCA.

NEW TRACKSITES

We conducted a preliminary reconnaissance of the Coconino sandstone in the area of the present Hermit Trail. The ichnofauna in this area is abundant and merits further study. The majority of specimens appear to be in the lower two-thirds of the formation. Most trackways represent *Laoporus* although another four ichnogenera are also present. Virtually all specimens occur on inclined bedding planes in crossbedded strata with dips averaging about 40-60°, representing individuals walking up dune faces. Analysis of in situ trackways could help resolve the recent debate as to whether any of the Coconino footprints could have been formed underwater (Brand and Tang, 1991) which we consider doubtful on sedimentological characters.

Table 1. Invertebrate Ichnofauna of the Coconino Sandstone at Grand Canyon National Park (Spamer, 1984).

Diplopodichnus sinuosus
Mesichnium benjami
Octopodichnus didactylus
Paleohelcura tridactyla
Triavestigia niningeri

Table 2. Vertebrate Ichnofauna of the Coconino Sandstone at Grand Canyon National Park (Spamer, 1984).

Agostopus matheri
A. medius
Amblopus pachypodus
Anomalopus sturdevanti
Baropezia arizonae
B. eakini
Barypodus palmatus
B. metszeri
B. tridactylus
Laoporus schucherti
L. coloradoensis
L. merriami
L. noblei
L. tetradactylus
Palaeopus regularis

FURTHER WORK

It is abundantly clear that there are numerous undescribed vertebrate trackways in the Coconino Sandstone at GRCA. There is a need for an inventory of sites, as inscriptions in the rocks indicate that many tourists are aware of their presence. The park management needs to be provided data regarding the distribution and abundance of this valuable resource. Selected excavation could greatly enhance visitor interpretation at the Visitor Center and in situ displays could be of great interest to hikers. Scientifically, much work needs to be accomplished in order to understand the ichnotaxonomy of the Coconino Sandstone and its potential for interpreting ancient environments.

ACKNOWLEDGMENTS

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GEOLOGY OF THE LATE EOCENE CLARNO UNIT, JOHN DAY FOSSIL BEDS NATIONAL MONUMENT, CENTRAL OREGON

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ABSTRACT

Through detailed stratigraphic section description and lithostratigraphic mapping in the type area of the Eocene Clarno Formation we have generated a geologic framework for the numerous fossil sites in the Clarno Unit of the John Day Fossil Beds National Monument. Two widespread conglomeratic units of andesitic composition are recognized in the area and are separated by red claystones (paleosols). The lower conglomerates of the Palisades consist of channel and floodplain debris flow conglomerates and hyperconcentrated flood flow or lahar runout deposits. The overlying conglomerates of Hancock Canyon also contains channel and floodplain debris flow conglomerates, but has in addition fluviually reworked conglomerates and pebbly sandstones, reworked tuff beds, a distinctive amygdaloidal basalt flow and the "Nut Beds" fossil site. The Palisades unit is interpreted as a debris flow apron on which there was little lateral fluvial reworking. The Hancock Canyon unit is interpreted as a debris flow apron to a braidplain in an area of complex topography, with multiple sources of volcanic sediments. Above these two debris flow dominated units is the thick, but discontinuous, claystones of "Red Hill." These very clayey red beds record a long period of volcanic quiescence, slow floodplain aggradation and long periods of tropical and subtropical soil formation. A climatic change is inferred during the accumulation of the red beds from the presence of very strongly developed Ultisol-like paleosols in the lower half of the unit and well developed, Alfisol-like paleosols in the upper half. The changes between these two packages of paleosols may reflect climatic cooling and drying during late Eocene times. The overlying siltstones of the "Mammal Quarry" and associated andesite of Horse Mountain accumulated in response to renewed andesitic volcanism. The "Mammal Quarry" unit consists of tan and gray clayey sandy siltstones, gravel conglomerates and a basal andesitic breccia. The late Eocene mammal assemblage of the "Mammal Quarry" was preserved in a channel and floodplain sequence that accumulated rapidly in response to the eruption of the large and widespread flows of the andesite of Horse Mountain.

INTRODUCTION

The scenic high desert of north-central Oregon contains a colorful volcanic and alluvial sequence of Tertiary age. The combination of low precipitation (320 mm annually in Antelope) and seasonal temperature extremes (January mean of -1 °C and August mean of 19 °C; Ruffner,

1978) favors xerophytic, sparse vegetation and good exposures. In contrast, fossil flora of Eocene age from sites in the Clarno Unit indicates paratropical conditions analogous to that of modern southeast Asia (Manchester, 1981, in press). The transition from steamy jungles of the past to the open ranges of today is recorded in a copious fossil record of a diverse flora, invertebrates, freshwater fish, reptiles, and mammals in this region (Stearns, 1900; Stearns, 1906; Merriam and Sinclair, 1907; Dallas, 1920; Merriam and others, 1925; Chaney, 1925; Stirton, 1944; Scott, 1954; Downs, 1956; Cavender, 1968; Mellet, 1969; Naylor, 1979; Manchester, 1981; Wolfe, 1981a and 1981b; Ashwill, 1983; Martin, 1983; Rensberger, 1983; Manchester and Meyer, 1987; Hanson, 1989). These profound paleoenvironmental changes are also reflected in a sequence of paleosols ranging in age from middle Eocene to the present (Fisher, 1964; Retallack, 1981, 1991a, 1991b; Pratt, 1988; G.S. Smith, 1988). Three units of the John Day Fossil Beds National Monument (Sheep Rock, Clarno, and Painted Hills) were established for the protection and appreciation of these significant geologic and paleontologic resources.

This paper outlines geologic and paleoenvironmental findings of a three year study of the Clarno Unit. We describe new informal lithostratigraphic subdivisions of the Clarno Formation, with stratigraphic and paleoenvironmental data and preliminary interpretations. Data presented in this report were largely gathered from measuring and describing stratigraphic sections of outcrops, with extensive trenching to exposed fresh rock beneath badlands mantled with soil.

Basement rocks in north central Oregon consist of highly deformed metasediments of Permian age. In some areas, these are overlain by a thick sequence of Cretaceous marine rocks. In the Clarno area, phyllites and argillites of uncertain affinity (either Permian or weakly metamorphosed Cretaceous shales) are exposed in the Muddy Ranch dome. These basement rocks are intruded and overlain by andesitic volcanic and alluvial rocks of the Clarno Formation, which ranges in age from middle to late Eocene, some 54 to 37 my old (McKee, 1970; Enlows and Parker, 1972; Rogers and Novitsky-Evan, 1977; Manchester, 1981; Vance, 1988; Walker and Robinson, 1990). Volcanic plugs, lava flows, and lahars with convergent-margin andesitic compositions and textures indicate accumulation in and around andesitic volcanic cones of the Eocene Clarno volcanic arc (Noblett, 1981; Suayah and Rogers, 1991; White and Robinson, 1992).

Rhyolitic ash-flow tuff and dacitic to rhyodacitic tuffs are conspicuous in the latest Eocene, Oligocene, and early Miocene (22-to 39-my) John Day Formation (Peck, 1964; Woodburne and Robinson, 1977; Robinson and others, 1990; Bestland and others, 1993). These primary pyroclastic, alluvial and lacustrine deposits were supplied with volcanic ash from vents to the west in the present area of the Western Cascades (Robinson and others, 1984). Thus the Clarno and John Day formations of central Oregon record a late Eocene westward jump of the subduction zone in the Pacific Northwest and a corresponding change from Clarno andesitic volcanism to Cascade volcanism and John Day back-arc basin deposition.

The Clarno Unit-Hancock Field Station area can be divided into two areas based on structure: 1) relatively flat-lying strata of Horse Mountain, and 2) these same strata folded along a NE-SW fold limb. Other smaller folds are present in the area, however, the NE-SW fold dominates the local structure. This fold has the same orientation as the Muddy Ranch dome (Robinson, 1975), to the southwest of the project area. The fold dies out in the northeastern part of the project area (Fig. 1). In the Clarno Unit area, the geologic sequence is complicated by this NE-SW fold limb, intrusion of a dacitic dome, another small structural dome, and laterally variable volcanic facies.

STRATIGRAPHIC SUBDIVISIONS

Lower Clarno conglomerates- A sequence of boulder-sized, matrix-supported conglomerates exposed just to the west of Hancock Canyon is the oldest and most deformed unit in the mapped area. Its clasts are boulders and cobbles of altered plagioclase porphyritic andesite. The unit lacks tuff beds or paleosols and was recognized first by Hanson (1973). This unit forms the southwestern half of a structural dome. Another but less likely possibility is that this unit is part of the Palisades conglomerate unit that has been locally faulted and folded.

Hancock Dacite Dome-

A plagioclase-hornblende porphyritic dacite body is exposed in the hills and gullies to the northeast of Hancock Field Station (Fig. 1). Excellent exposures of this unit in tributary gullies of Hancock Canyon indicate that it is a homogenous igneous body and not boulders of dacite weathering out of a debris flow. However, intrusive features such as baking, veining, alteration and mineralization of the surrounding country rock were not observed. Boulder deposits containing clasts exclusively of this dacite are

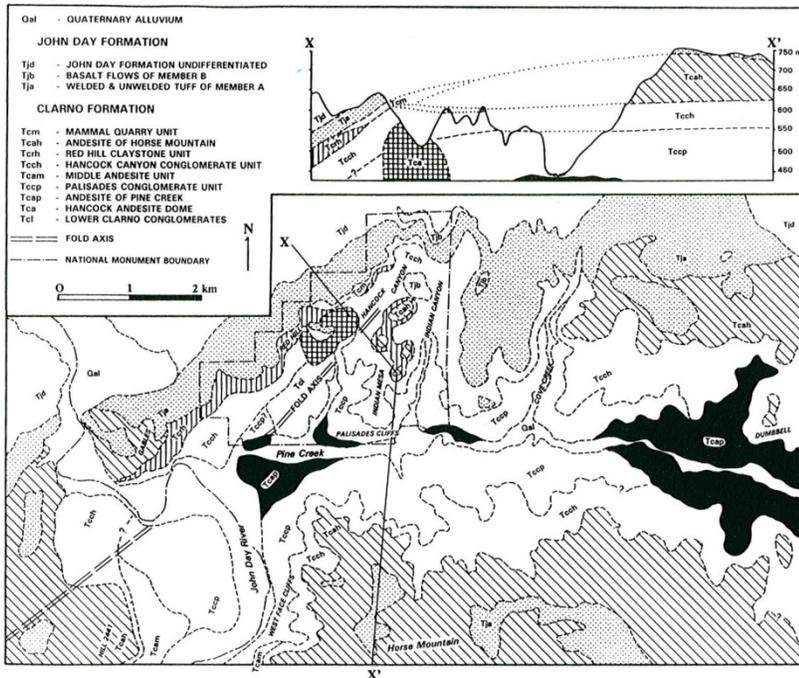


Figure 1. Geologic sketch map of the Clarno Formation from the John Day River near Clarno bridge and along Pine Creek. Quaternary landslide deposits have been omitted for clarity.

present in well developed paleosols overlying the dacite. Thus the dacite body was an erosional feature that was mantled by colluvium and soils. The Hancock dacite dome is also pervasively altered, probably by deep weathering during the Eocene.

Main sequence- In the study area, the Clarno Formation contains laterally extensive and mappable lithostratigraphic units (Fig. 1). The units are of two types: 1) andesitic debris flows and 2) andesite lava flows. Smaller-scale lithostratigraphic units, such as clayey red beds, basalt flows, and tuff beds are also present in this area (Fig. 2). These large debris flow and andesite flow units constitute the majority of the cliffs along the John Day River in the area south of Clarno bridge and along the western part of Pine Creek.

Andesite of Pine Creek- The base of the coherent section mentioned above consists of a thick andesite unit referred to as the andesite of Pine Creek. The unit consists of thick lava flows of dark-colored pyroxene-plagioclase andesite that are commonly altered by varying degrees. The unit has a very irregular upper surface which is mantled by a well developed reddish saprolite breccia. Pockets of red and white claystones are preserved between the andesite and overlying debris flows. The clayey saprolite and claystones erode to form an erosional bench which is occupied in part by the modern Pine Creek floodplain. Basal sapping of the overlying debris flows due to the erodability of these claystones is partly responsible for the Palisades cliffs. To the east of Cove Creek, the basal andesite unit is again extensively exposed. Thick, autobrecciated andesite flows are present beneath hill 2932 ("Dumbbell Hill") and include several basaltic andesite flows that onlap the highly porphyritic andesite and andesite breccia from the Dumbbell Section (Fig. 2).

Conglomerates of the Palisades- Onlapping the irregular surface of the andesite of Pine Creek is a thick sequence of matrix-supported andesitic debris flows. This unit has weathered into the spectacular hoodoos along Pine Creek and in the "West Face cliffs" along the John Day River (Fig. 1). Most of the debris flows are of the matrix-supported, moderately clast-rich floodplain debris-flow type (Scott, 1988). In the "Palisade cliffs," numerous clast-rich, channelized debris flows are present, some being clast supported at their base. Hyperconcentrated flood flow deposits (in the sense of G.A. Smith 1987; and Nemec and Muszynski, 1982) are also common. These grade into debris-flow deposits and occur as interbeds between debris flows. Well exposed at approximately the middle of the member are several thin, green, clayey paleosols with wood fragments and leaf impressions. These thin, green paleosols are present in the Palisades section and are well exposed in the lower part of the cliffs along the John Day River. Above the green clayey horizons is a tuffaceous breccia layer which grades up into a massive debris flow. This debris flow weathers brownish-orange and crops out prominently along the "West Face cliffs." To the east of Cove Creek, the Palisades unit debris flows onlap, thin and pinch-out against the andesite of Pine Creek (Figures 1 & 2).

Middle Clarno andesite- This thick andesite is locally present in the southern part of the project area along the John Day River south of Clarno bridge. The unit makes-up the lower half of the monolithic buttes on the west side of the John Day River (hills 2441 and 2373, Clarno 7.5 min. series) where the unit fills a paleovalley cut into the conglomerates of the Palisades on the west side of the river. The unit is onlapped by conglomerates of Hancock Canyon. It is a blocky, dark-colored, pyroxene-plagioclase andesite. Saprolite mantles the andesite and in places red

claystones (paleosols) are present above this andesite. Where the andesite is absent, reddish claystones overlie the conglomerates of the Palisades. These claystones erode to form a bench on the mesa between Hancock Canyon and Indian Canyon (Indian Mesa on Fig. 1). This bench is also present on the north and west sides of Horse Mountain.

Conglomerates of Hancock Canyon- Overlying the red claystones at the top of the conglomerates of the Palisades is the conglomerates of Hancock Canyon. This unit includes tuffaceous beds and a distinctive basalt flow, but is dominated by matrix-supported boulder debris flows. The amygdaloidal, high silica basalt flow is laterally extensive, mappable, and stratigraphically in the upper

half of the unit. The basalt is a holocrystalline, plagioclase and pyroxene basalt with common pahoehoe flow structures and local columnar jointing. The basalt can be mapped from the Hancock Field Station area to the Gables, is thickest in the "West Face cliffs," but is not present east of Indian Canyon.

The conglomerates of Hancock Canyon contain the "Nut Beds" fossil site and the Muddy Ranch Tuff, both dated at 44 Ma; C. Swisher obtained a date of 44 Ma from a plagioclase separate from a reworked crystal tuff in the "Nut Beds" using the $^{40}\text{Ar}/^{39}\text{Ar}$ method (pers. comm., 1992) and Vance (1988) obtained a date of 44

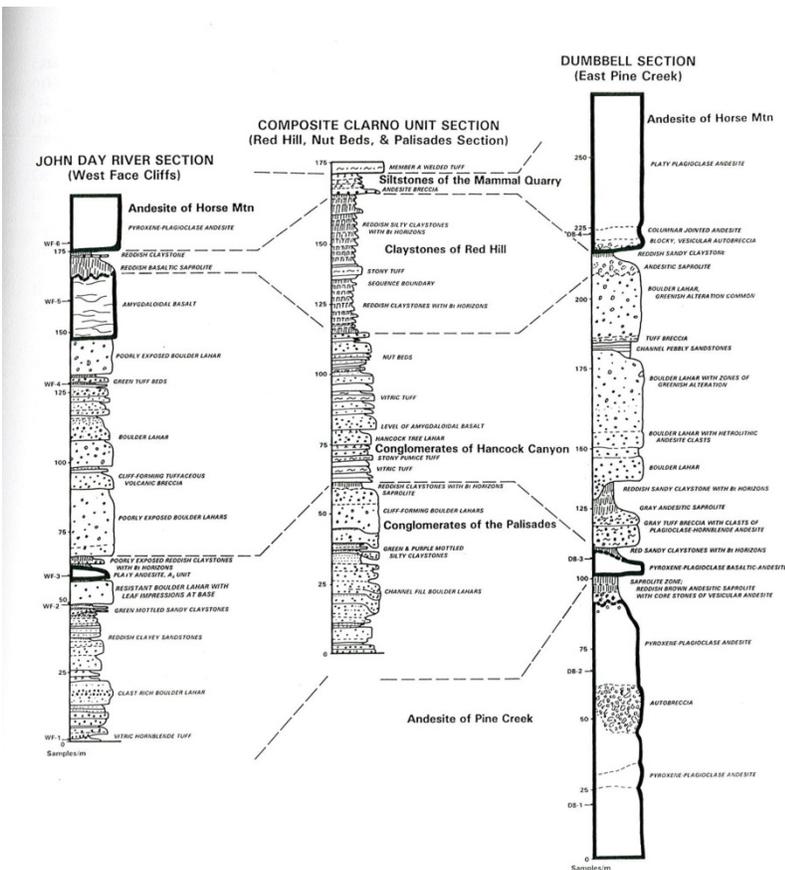


Figure 2. Stratigraphic fence diagram of the Clarno Formation.

Ma from fission track of zircon crystals in the Muddy Ranch Tuff (also known as the Rajneesh Tuff) near the Gables. The Muddy Ranch tuff is stratigraphically below the "Nut Beds," also dated by Vance (1988) at 44 Ma. Many large, well-preserved *Cercidiphyllum* (katsura) and *Macginitea* (sycamore) permineralized tree trunks and limbs are in this unit, similar to the "fossil forests" found in comparably-aged Lamar River Formation on the Yellowstone plateau (Dorf, 1964).

Claystones of "Red Hill"- In the Clarno Unit area, a thick sequence of reddish and grayish-purple claystones is present above the Hancock Canyon conglomerate unit. The unit is 59 meters thick in the "Red Hill" area (Fig. 2) but thins dramatically to the east (Fig. 1). In the

cliffs on the west and north side of Horse Mountain, only a reddish saprolite with thin clay layer is present at this stratigraphic level. The unit at "Red Hill" contains a lower reddish paleosol sequence of very deeply weathered Ultisol-like paleosols and an upper less well developed, Alfisol-like paleosol sequence (G.S. Smith, 1988; Retallack, 1991a). A stony tuff bed divides the two paleosol sequences.

Andesite of Horse Mountain- This thick andesite unit is extensively exposed in the project area where it caps much of Horse Mountain. The unit consists of platy to blocky andesite which varies from pyroxene-plagioclase andesite to very porphyritic plagioclase dacite with traces of hornblende. Along the west and north side of Horse Mountain, the unit overlies a thick red saprolite developed on the amygdaloidal basalt flow in the Hancock Canyon unit. Ramp-like flow structures are common in lava flows exposed in the "West Face cliffs." The base of the unit dips gently to the west, probably following a paleoslope.

Siltstones of the "Mammal Quarry"- The tan, clayey siltstones and cobble conglomerates of the Mammal Quarry beds are only locally present in the "Red Hill"- "Indian Canyon" area. A diverse vertebrate fauna has been excavated from the "Mammal Quarry," in the uppermost Clarno Formation below member A of the John Day Formation (Hanson, 1973 and pers. comm., 1993). Several taxa in this assemblage have close affinities with Asiatic faunas of the early Duchesnean North American Land Mammal Age. Pratt (1988) described Inceptisol-like paleosols from the "Mammal Quarry." By her interpretation, the fossil remains accumulated as carcasses and were disarticulated in a fluvial point bar. Stratigraphic work during this project has shown that the Mammal Quarry unit was deposited in response to the eruption of the andesite of Horse Mountain. At several exposures east of the "Mammal Quarry," red claystones of the Red Hill claystone unit are overlain by andesite breccia which can be traced to outcrops of andesite of Horse Mountain. This breccia grades into the tan clayey siltstones of the Mammal Quarry unit.

Welded tuff of member A- Rhyolitic pyroclastic volcanism of the John Day Formation is first recorded in north central Oregon by an ash-flow tuff re-dated at 39 Ma (Bestland et al., 1993). The John Day Formation in its western facies has been divided into informal members A-I based largely on the stratigraphy of ash flow tuff sheets (Peck, 1964; Swanson and Robinson, 1968; Robinson, 1975). The distinctive and widespread ash flow tuff of member A is very useful in delineating the Clarno surface at the onset of John Day volcanism.

Distinctive basalt flows and associated intrusions immediately overlie member A. They consist of aphanitic to sub-glassy basalt that weathers into cobble-sized blocks. These basalts correlate with the member B trachyandesites (Peck, 1964) well developed in the Ashwood area (Swanson, 1969), but also mapped in this area (Robinson, 1975).

DISCUSSION

The stratigraphic framework of these Clarno Formation lithostratigraphic units and corresponding fossil sites is complicated by rapid lateral stratigraphic changes. These changes

are largely caused by erosional disconformities between units, original topography of many volcanic units, and local accumulation of some types of volcanic units (i.e. lava flows). Folding and faulting in the Clarno area and onlapping of the Hancock andesite dome have added to the local stratigraphic complexity. On a regional basis, the Clarno Formation remains largely undivided due to these factors as well as the lack of widespread Clarno marker beds.

The conglomerates of the Palisades are interpreted as a debris flow apron because they consist of debris flow deposits and largely lack reworked or fluvial interbeds. This Palisades debris flow apron was probably part of the constructional edifice of an active volcano. A volcanic apron to braidplain depositional setting is interpreted for the conglomerates of Hancock Canyon because they contain a variety of deposits including fluvial conglomerates, thin, reworked tuff beds, and matrix-supported debris flows. The variety of deposit types indicate a floodplain setting which received material from a variety of sources. Floodplain aggradation was largely controlled by volcanic eruptions and their corresponding debris flows. During volcanic hiatus there was fluvial reworking. On the earlier Palisades volcanic apron, in contrast, incision of the deposits predominated during volcanic hiatus thus giving rise to deeply nested channelized debris flows.

Within the Clarno area are numerous fossil plant localities (including several new sites, revealed during excavation for this study) that indicate apparently dissimilar climates. The classic "Nut Beds" site yields plant fossils strongly indicative of a tropical to paratropical climate (Manchester, 1981, in press). In contrast, at the same stratigraphic level and in a similar debris-flow depositional environment, the fossil plants found in Hancock Canyon suggest temperate conditions. These contrasting floral types are probably not different stages in ecological succession, because early successional fossil soils and plants are also found in this unit, and are dominated by horsetails and ferns. It is more likely that the "Nut Beds" flora represents a lowland rainforest, like the selva of tropical Mexico, whereas the Hancock Tree flora represents a higher altitude forest of cooler climatic affinities like the liquidambar oak forests of Mexico (Gomez-Pompa, 1973). Thus, according to this interpretation, the conglomerates of Hancock Canyon contain the ecotone between these two distinct forest types: an upland paratropical forest and a lowland tropical forest.

Deciduous forests of volcanic and other Eocene uplands were an important source of new plant communities as paleoclimate became cooler and drier from middle to late Eocene and then again in the early Oligocene (Wolfe, 1987). The vertebrate faunas also reflect these climatic shifts. Fossil mammals of the Clarno "Nut Beds" are comparable to the middle Eocene forest-dwelling faunas of much of North America. The "Mammal Quarry" fauna however, represents an immigration of new mammals from Asia, adapted to cooler and drier conditions. The Clarno volcanic arc provides some of the earliest evidence of these later faunas and may represent a staging area for the widespread North American faunas of the Chadronian NALMA (Retallack, 1991a).

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RESOLVING BLURRED FAUNAS: BIOSTRATIGRAPHY IN JOHN DAY FOSSIL BEDS NATIONAL MONUMENT

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INTRODUCTION

The value and role of many National Park System units in paleontological studies is becoming increasingly evident. In addition to fostering research efforts and interpretation within "outdoor laboratories", these areas contain key depositional sequences for the calibration of biotas throughout North America. This GSA symposium volume offers an opportunity to address an important aspect involved in our renditions of ancient ecosystems, biostratigraphic correlation.

Generally speaking, certain attributes characterize outstanding depositional sequences that are important for biostratigraphic analyses.

1. There are large numbers of very well to excellently preserved specimens available, both in the field and in repositories.
2. The taxonomic diversity of the assemblages is high, sampling a broad spectrum of the ecosystem. Ideally, there are associations of flora and fauna.
3. The fossiliferous strata span a long time interval with few depositional unconformities.
4. The sequence was deposited during momentous processes and events in earth history, such as major climatic changes, adaptive radiations, or mass extinctions.
5. A variety of dateable volcanoclastic marker beds permit ready correlation of the strata both within the depositional reservoir and with those documented from elsewhere.

Outstanding portions of such a record exist in central and eastern Oregon, and include over three hundred and fifty localities within the Clarno Group and the John Day, Mascall, and Rattlesnake Formations. Among early workers, Merriam (1901, 1907) and Chaney (1924) recognized the area as one of a few in the world with such a complete record written on the canyon walls. This is a benefit of proximity to volcanic sources of clastics, from a variety of vents, over a long time. In fact, few Tertiary fossiliferous areas in North America compare to those of the John Day Basin in terms of their importance in documenting long term change.

The accuracy of this "big picture" of biotic change is largely governed by the precision with which the detailed data are collected. At least two critical aspects of the biological assemblages must be addressed. Firstly, the taphonomic biases must be detected and analyzed. Secondly, good stratotypic data must exist for the type specimens; if not, the faunal ranges must be ascertained and a detailed biostratigraphic analysis conducted (see, for example, Rensberger, 1984). This latter problem continues to plague many historically important North American sites in general and the John Day Basin in particular (see Woodburne, 1977).

The John Day Formation itself has had a long and complicated history of investigation, adequately reviewed elsewhere (e.g., Robison, 1990; Rensberger, 1984). Regrettably, the major collections of vertebrate fossils (UCB, UW, UO, YPM, USNM, and AMNH) from the area lack useful stratigraphic and site data, or the locality information is inaccessible. As a result, confusion has arisen concerning the "John Day fauna", which cannot be viewed as a single fauna, but consists of at least eight different lithosympatric assemblages (*sensu* Stucky, 1990). The eastern component of the strata has been subdivided into 4 members (Fisher and Rensberger, 1972), recognized largely by color and/or zeolitization features. These subdivisions, while useful for diagenetic analyses, are not as useful for either chronostratigraphic or lithostratigraphic understanding of the strata.

In this short paper, we shall narrow the focus and describe work performed on one taxonomic group, occurring in a restricted interval, in a small geographic area known as "Turtle Cove", of the John Day Formation (*sensu* Robison, 1984, 1990). These data are culled from a larger taxonomic work on the John Day canids (Wang and Fremd, in prep).

MATERIALS AND METHODS

Beginning in 1982, field investigators began to retrieve specimens under more systematic conditions (Wagner and Ruben, 1983) than had generally been the case. A system of "cyclic prospecting" begun in 1984 at John Day Fossil Beds National Monument (JODA) has resulted in the salvaging of thousands of specimens that would have been lost to weathering or inadequate data recording (Fremd, 1992a). Work outside the national monument was begun with cooperative agreement with the BLM (Hanson and Allen, 1988, Fremd, 1989, 1992b); this has since grown to include work in the other occurrences of the strata in the state.

Instead of simply duplicating existing and inadequate collections, an effort was made to avoid collecting biases as much as possible. For each specimen encountered, the taxon, element, coordinates (on detailed aerial photography), *in situ* or float, stratigraphic height, and numerous other features were recorded into the field notes. All collections have been made relative to a number of prominent ash-flow tuffs (see Figure 1.), which permit a much more refined reconstruction of narrow biostratigraphic intervals.

Each item collected was accessioned and catalogued, using the standard DBASEIII+ Automated National Catalog System in use in all national park system units. Additionally analysis was

facilitated by interlinking these data supplemented by specimen and locality databases, including information compiled at other major repositories, linked together in IDEALIST, APPROACH, and ECCO in Windows.

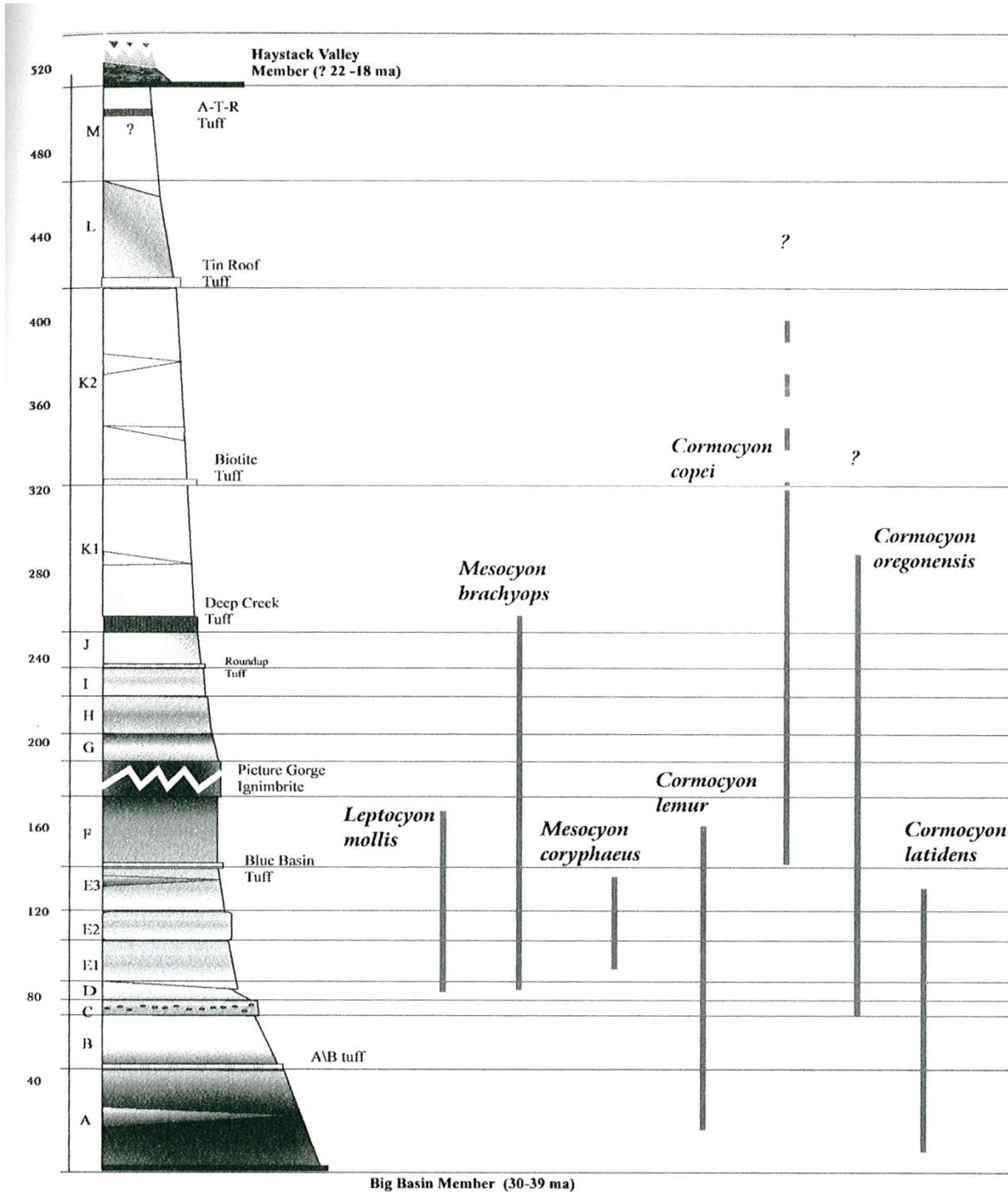


Figure 1. Stratigraphic column of the Turtle Cove member of the John Day Formation, with ranges of selected canid taxa from the Turtle Cove area, John Day Fossil Beds National Monument. Scale in meters. Ar^{40/39} dates for tuffs permit precise calibration of events.

As a result of these efforts over 7,000 specimens have been salvaged from strata in the park environs, including a variety of canids, with most specimens pinpointed to within a few meters. One of us (XW) examined specimens of the Canidae (Carnivora, Mammalia) with their preliminary identifications and field numbers, but no stratigraphic information. Tend species, belonging to three subfamilies, can be recognized on morphological grounds. Only *after* precise taxonomic assignments were made did we plot these into our stratigraphic column, avoiding in such fashion *a priori* biases and circular reasoning.

Within the newly defined Turtle Cove Member of the John Day Formation, the biostratigraphic distribution of the canids can now be resolved with high precision. Confidence is highest in small canids (the 4 species of Borophaginae) in the lower 2/3 of the Turtle Cove Member, because of the relatively larger samples. Within this new stratigraphic framework, most canid species have more restricted occurrences than have been assumed in the traditional practice of lumping all taxa into a broad "Turtle Cove" unit (Figure 1).

The earliest canids in the John Day Formation are represented by the simultaneous occurrence of the sister-species "*Cormocyon*" *lemur* and "*C.*" *latidens* in strata equivalent to the upper Brule Formation (Whitneyan) of the northern Great Plains. Both of these small borophagine taxa disappeared just below the Picture Gorge Ignimbrite (PGI, 28.7 m.y. from single-crystal Ar/Ar date), which serves as a prominent marker bed in the regional stratigraphy. Approximately 70

Family Canidae
Subfamily Borophaginae
<i>Cormocyon lemur</i>
<i>Cormocyon latidens</i>
<i>Cormocyon oregonensis</i>
<i>Cormocyon copei</i>
Subfamily Hesperocyoninae
<i>Mesocyon brachyops</i>
<i>Mesocyon coryphaeus</i>
<i>Philotrox condoni</i>
<i>Enhydrocyon</i> sp.
<i>Paraenhydrocyon josephi</i>
Subfamily Caninae
<i>Leptocyon molli</i>

Figure 2. Systematics of canids from the Turtle Cove member, John Day Fossil Beds National Monument

meters above the lowest occurrence of the *lemur-latidens* pair begins the first appearance of *Cormocyon oregonensis*, a small, primitive borophagine canid whose ancestry may be traced to the Orellan strata of the Plains (e.g., *Hesperocyon pavidus*, see Wang, in press; Wang and Tedford, in press). The stratigraphic range of *C. oregonensis* extends considerably above the PGI, whereas a larger, more derived species, *C. copei*, is almost entirely confined above the PGI.

Stratigraphic distribution of the median, coyote-sized hesperocyonines can also be tied with their Plains' relatives. The two John Day species of *Mesocyon* (*M. coryphaeus* and *M. brachyops*) can be traced to rocks well below

the PGI, close to the earliest occurrence of *Cynodesmus* in the upper Brule strata of the Plains. Such a contemporary appearance of two genera in the same stage of evolution on either side of the Continental Divide is potentially useful for biostratigraphic correlations, and indicates a pre-Whitneyan divergence time of the *Mesocyon-Cynodesmus* sister-clades.

CONCLUSION

This work is being linked with several other concurrent taxonomic and stratigraphic investigations, including a contracted project involving highly detailed mapping of the ash-flow sheets, paleosols, and other sediments from the Painted Hills and Clarno Units of JODA (see Bestland et al., this volume). The John Day Basin is assuming an increasingly important role in refining Tertiary biostratigraphy in North America. The results of these efforts are increased resolution of evolutionary processes and events that have long been blurred.

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A NEW PRINCIPAL REFERENCE SECTION FOR THE MANCOS SHALE (LATE CRETACEOUS) AT MESA VERDE NATIONAL PARK

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ABSTRACT

The Mancos Shale crops out extensively across nearly the entire Colorado Plateau, where it ranges from 200 to 1500 m in thickness and spans up to 20 myr of the Late Cretaceous. The formation is of interest because it records dynamic changes in relative sealevel that resulted in complex intertonguing relationships with terrestrial strata and, consequently, the development of important organic fuel resources. Although the Mancos Shale has received much study, no detailed investigation previously had been undertaken at its type area in the Mancos Valley of southwestern Colorado, where the formation was named for poorly exposed slopes of marine strata that lie between benches formed by the Dakota Sandstone and Mesaverde Formation.

Because of poor exposure in the Mancos Valley, we selected a principal reference section just to its west, below Point Lookout at the north end of Mesa Verde National Park and extending out of the park to the north. This site was chosen because it presented a steep but accessible exposure of the entire Mancos Shale, and the National Park status of much of the section insured its protection and accessibility to researchers in perpetuity.

High-resolution event stratigraphic principles (HIRES) were employed in measuring and sampling the section. This method entails trenching the entire sequence to fresh rock and sampling extensively for sediments, geochemistry, microfossils, and macrofossils. Although some short-term disturbance of the land resulted from this work, an extraordinary data base was generated for the Mancos Shale that can benefit both science and Mesa Verde National Park.

INTRODUCTION

The Mancos Shale was named by Cross (in Cross and Purington, 1899) for "typical exposures" in the Mancos River Valley between the La Plata Mountains and the Mesa Verde near Mancos,

Colorado (Fig. 1A). Cross estimated a thickness of 1200 feet (366 m) for the Mancos in its type area and provided a brief description of the formation, but no specific type section was designated. While acknowledging that fossils of the Mancos Shale were characteristic of several distinct formations east of the Front Range, Cross concluded that subdivision west of the Front Range in the Mancos was not practical. Cross and others (1899) first noted that "the whole formation was well exposed along the north face of Mesa Verde near Mancos". Subsequent workers have investigated these nearly continuous exposures below Point Lookout on the north side of Mesa Verde National Park. In this area, Pike (1947) measured 2191 feet (668 m) of section in the Mancos and recognized five faunal zones, and Wanek (1959) measured a total thickness of 1997.5 feet (609 m), not including the transition interval with the overlying Point Lookout Sandstone.

This previous work on the Mancos Shale in its type area was superficial in comparison to recent detailed research conducted on contemporaneous marine strata of the Western Interior in other areas (e.g., Pratt, et al., 1985, Nations and Eaton, 1991). As such, we initiated a study utilizing modern high-resolution event stratigraphic methods (HIRES; Kauffman, 1988) in order to establish a principal reference section for Mancos Shale in the type area. In the Cretaceous of the Western Interior, this study represents one of the greatest stratigraphic thicknesses and time intervals to ever be explored utilizing HIRES techniques. The copious data gleaned will be under analysis for years to come.

HIGH-RESOLUTION EVENT STRATIGRAPHIC METHODS AND PRINCIPLES

Kauffman (1988) introduced the term HIRES to describe high-resolution correlation methods that employ the detailed collection of all types of physical, geochemical, and bioevent data in order to maximize chronostratigraphic correlation. This technique was first pioneered in the Western Interior by Hattin (1962), in a study of the Carlile Shale of Kansas, and was subsequently employed by him in numerous other detailed studies of the Cretaceous in Kansas. Kauffman and others (1991) noted many studies that have used this methodology and provided examples of useful types of event stratigraphic information that can be collected. In brief, this method requires a freshly exposed outcrop section on which lithological features to cm-scale can be observed (i.e., ash beds, limestone or concretion beds, shell beds, storm beds, sediment bypass or disconformity surfaces). After the physical data are recorded, the section is excavated for microfossil collection, and closely-spaced bulk samples are taken for microfossil and geochemical analyses. This collecting methodology results in the definition of diverse event data that are integrated into a composite event stratigraphy for that section and compared to event stratigraphies of other sections to yield highly refined correlations. In addition, these diverse data provide detailed information that can be used to interpret depositional history.

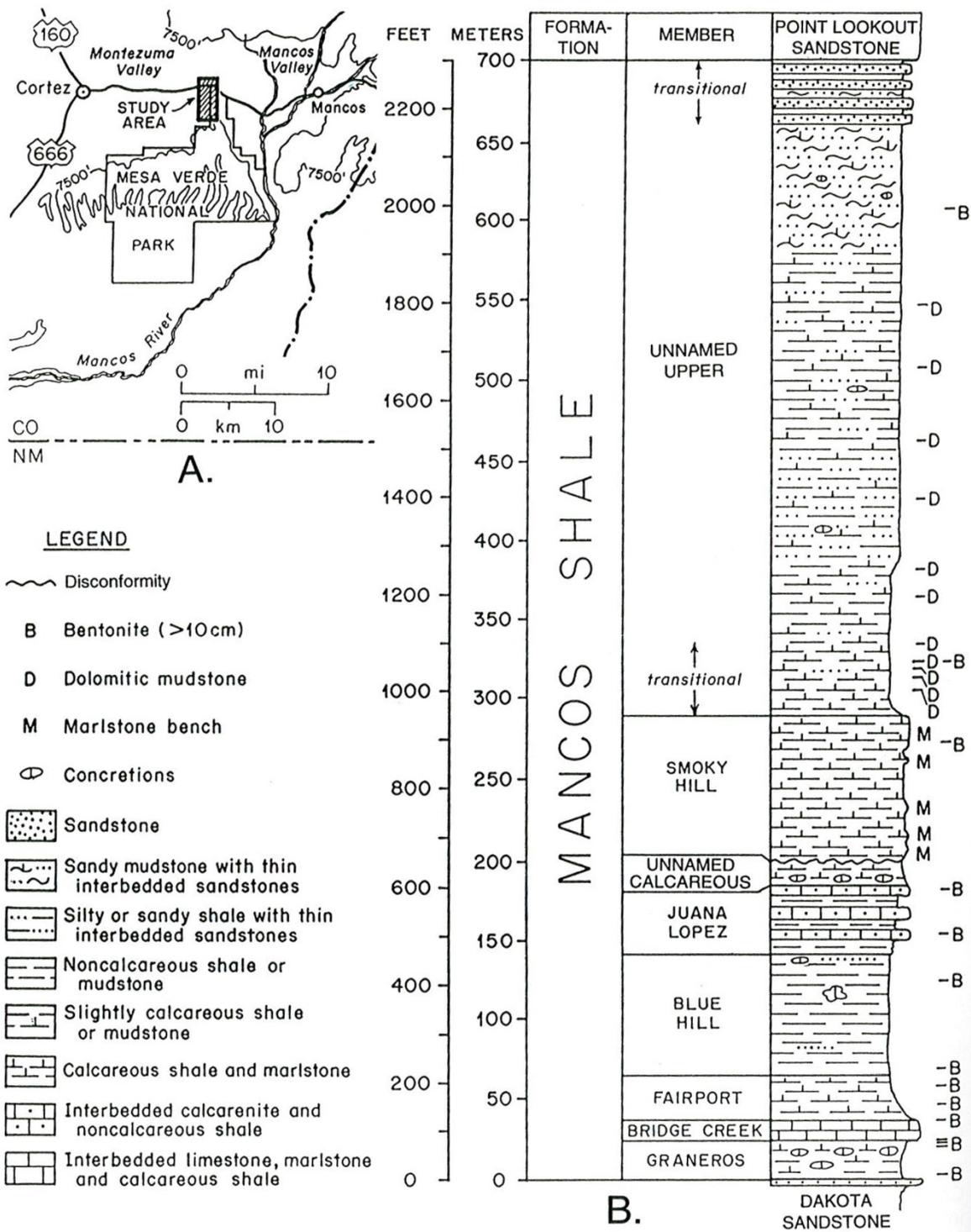


Figure 1. (A) Generalized location map of the study area. (B) Lithostratigraphy of the new principal reference section of the Mancos Shale at Mesa Verde National Park, Colorado.

THE MESA VERDE STUDY

The principal reference section at Mesa Verde was measured, described, and collected during the summers of 1988 and 1989 (48 days on the outcrop). The entire Mancos Shale thickness (700 m) was exposed in 95 trenches dug in 23 different areas from sections 19 and 20, T36N, R14W, north of Mesa Verde National Park, to section 5, T35N, R14W, at the base of Point Lookout within the park (Fig. 1A). Numerous event stratigraphic units (particularly ash beds) present throughout the Mancos allowed precise correlation between trenches and the establishment of a composite section for the formation (Fig. 1B). The section was measured using a refined Jacob's staff (Elder, 1989), and lithologic units and meter levels were marked by flagged nails prior to detailed description and collection. In order to allow correlation to the subsurface data, gamma-ray measurements were taken through the entire section using a portable gamma-ray scintillometer.

After section description, two-kilogram bulk sediment samples were taken at one-meter intervals or less through the lower 494 m of section and at two-meter intervals or less above, resulting in a total of 664 bulk samples. These samples are being analyzed for micropaleontology, clay mineralogy, and geochemistry (e.g., Leckie and others, 1991). Finally, the trenches were extensively sampled for macrofossils, which were locally abundant. Many macrofossils are not recoverable unless fresh unweathered rock is examined. After all sampling and analyses, the trenches were backfilled. No evidence of the trenches was apparent after a few rains.

Although the methods used in this study required some land disturbance, long-term impact is minimal and is greatly out-weighed by benefits to both science and the Park Service. These benefits include the documentation of the paleontologic resources at Mesa Verde National Park and their preservation for future scientific study. The Park Service plays a role in this preservation not only by protecting the land on which the fossils are found, but also by the housing of the many molluscan specimens collected in this study at the Mesa Verde Research Center, where they will be available to scientists for further study.

RESULTS

Among the initial results of the project are the recognition of 686 lithological units and numerous bioevent levels in the 700 m thick Mancos Shale (Fig. 1B). Fossiliferous strata in the lower 647 m of section provided age control through that interval, and fossils in the overlying Point Lookout Sandstone allowed a lowermost Campanian age to be placed on the top of the section. Several thousand macrofossil specimens representing over 110 species, several of which are new (Fig. 2), were recovered through the 20 late Cenomanian to early Campanian molluscan biozones recognized. Refined placement of molluscan biozone boundaries was facilitated by both compacted specimens from the shale and uncrushed fossils from concretions and calcarenite beds (Fig. 2). The recovery of a specimen of *Uintacrinus* in the upper Santonian *Desmoscaphites erdmanni* Zone indicates a significant range extension for this rare taxon. Study of the

foraminifers also is under way (Fig. 2), and an integrated molluscan-microfossil biostratigraphy is being developed.

In addition, we have greatly refined the lithostratigraphy in the Mancos Shale type area. We now recognize most of the Colorado Front Range lithofacies units in the thick shale and mudrock sequence at Mesa Verde reference section, where we can differentiate eight members in the Mancos; these members include the Fairport, Blue Hill, and Smoky Hill lithofacies equivalents, and two new members with regional extent, an unnamed calcareous member and an unnamed upper member (Fig. 1B). Also, several stratigraphic breaks were noted in the sequence. The most significant break occurs at the basal contact of the Smoky Hill member, where the entire lower Coniacian and much of the middle Coniacian are omitted, reflecting the "Carlile-Niobrara" disconformity. Finally, the outcrop gamma-ray profile has permitted correlation into the subsurface of the northern San Juan Basin, including the recognition of prominent bentonites.

CONCLUSIONS

This study demonstrates that paleontologic research in national parks can be beneficial to both science and the Park Service. Science benefits by having research sites that are protected and accessible to researchers in perpetuity and the Park Service benefits by having increased knowledge of their paleontological resources and by being able to distribute this knowledge to the public through resultant papers and public brochures. Our results are being prepared for an illustrated scientific publication that also will be suitable for sale to the public at Mesa Verde National Park. Although short-term land disturbance is necessary to bring sedimentological and paleontological research up to modern standards, this can be done without undo impact or long-lasting effects. These types of detailed research studies are compatible with the mission of our national parks.

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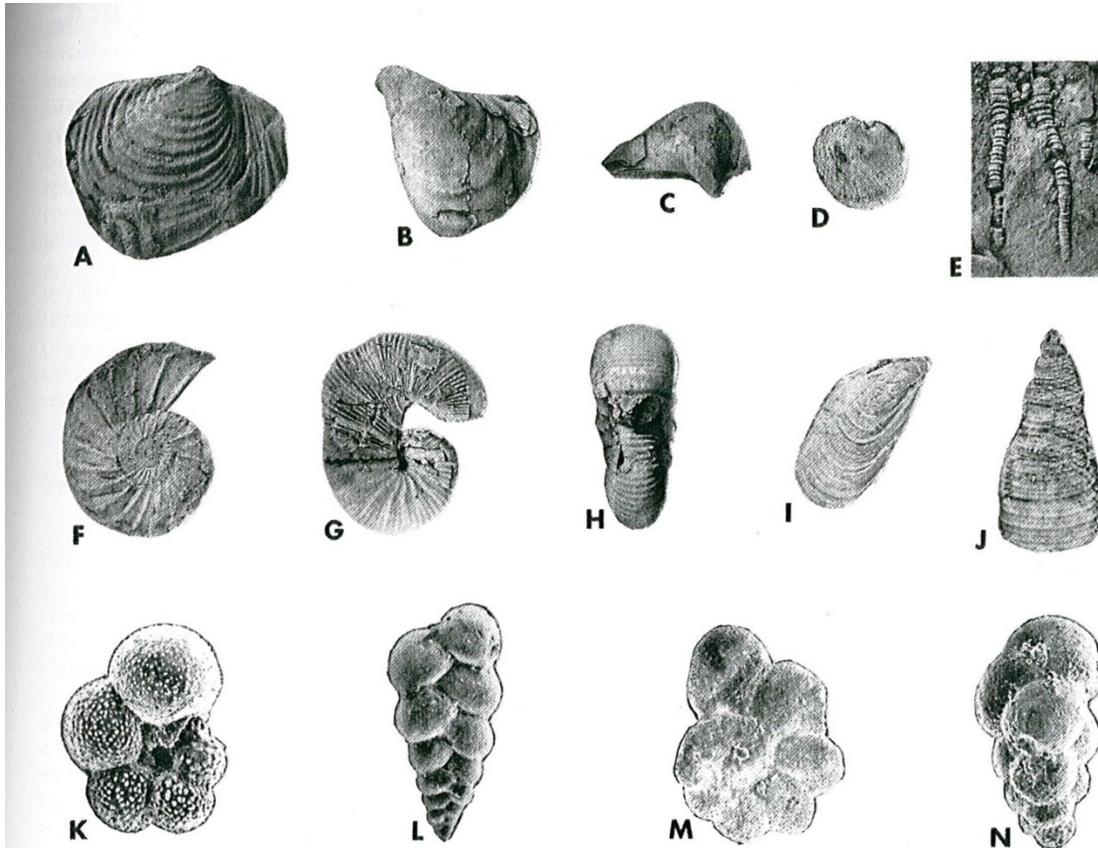


Figure 2. Selected fossils from the Mancos Shale. All specimens from the Mesa Verde section unless otherwise indicated. (A) *Inoceramus* (*Magadiceramus*) *subquadratus* Schlüter, x1, MEVE 65842, compacted juvenile from shale, Smoky Hill calcareous member. (B-C) *Inoceramus* n. sp., x1, MEVE 65843, (B) side and (C) dorsal views, uncrushed juvenile from calcarenite, Juana Lopez Member. (D) *Plicatula* n. sp., x2, MEVE 65844, latex peel of specimen from limestone, Bridge Creek Limestone Member. (E) *Uintacrinus* sp., x1, MEVE 65845, partial specimen from shale, unnamed upper member. (F) *Collignoniceramus* *woollgari* (Mantell), x1, MEVE 65846, latex peel of crushed juvenile from shale, Fairport calcareous member. (G-H) *Scaphites* *whitfieldi* Cobban, x1, MEVE 65847, (G) side and (H) apertural views, uncrushed specimen from limestone concretion, Juana Lopez Member. (I) *Modiolus* n. sp., x1, MEVE 65848, compacted specimen from shale, Smoky Hill calcareous member. (J) *Turritella* n. sp., x2, MEVE 65849, compacted specimen from shale, Graneros Member. (K) *Hedbergella* *delrioensis* (Carsey), x110, umbilical view, planktonic foraminifer from Lohali Point, Arizona. (L) *Heterohelix* *globosa* (Ehrenberg), x180, side view, planktonic foraminifer from Lohali Point, Arizona. (M) *Gavelinella* *dakotensis* (Fox), x70, spiral view, benthic foraminifer, Graneros Member. (N) *Neobulimina* *albertensis* (Stek and Wall), x120, side view, benthic foraminifer, Graneros Member.

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CONTINENTAL TRACE FOSSILS, PETRIFIED FOREST NATIONAL PARK: TOOLS FOR PALEOHYDROLOGIC AND PALEOECOSYSTEM RECONSTRUCTIONS

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ABSTRACT

Continental trace fossils from the Petrified Forest Member of the Upper Triassic Chinle Formation in Petrified Forest National Park (PEFO), Arizona, were made by beetles, termites, soil arthropods, horseshoe crabs, and crayfish. These and other organisms lived in fluvial, marginal fluvial, lacustrine, and floodplain environments that had distinct paleoecosystem and paleohydrologic characteristics. Each trace fossil and its depositional environment represents individual behaviors that reflect specific organism-substrate relationships not preserved by body fossils. Trace fossils are important for paleohydrologic and paleoecologic reconstructions because they preserve: 1) the physiological characters of the organisms that are regulated by their environments, 2) the biodiversity of invertebrates and vertebrates not typically represented in the fossil record, and 3) the distribution of paleo-water table and soil moisture levels, and the seasonal and annual amounts of precipitation and temperature.

INTRODUCTION

Diverse and abundant trace fossils occur in the continental deposits of the Petrified Forest Member of the Upper Triassic Chinle Formation in the Petrified Forest National Park (PEFO), Arizona. The traces represent different behavioral patterns of numerous insects and crustaceans, as well as the interactions of different plant rhizoliths and substrates. Because of the lack of preservation of organic material in many substrates, trace fossils play an important role in the documentation of paleoecology, including the behavior, biodiversity, paleohydrology, and paleoclimate in the paleoecosystems of the Chinle Formation. Paleoecologic information and methodology gathered at PEFO can be applied to other continental deposits in the geologic record.

Various types of Chinle continental trace fossils occur within the boundaries of the Petrified Forest National Park (PEFO), and they record a biodiversity of organisms not preserved in the fossil record of the Park. This diversity is presented below as category types and as preassigned ichnotaxonomic designations. Our objective is to familiarize others with the diversity and

distribution of trace fossils in PEFO and present their unequivocal utility as paleohydrologic, paleoecologic, and paleoclimatic indicators.

Invertebrate organisms (primarily insects and crustaceans) that inhabit both terrestrial and freshwater aquatic environments represent nearly 80 % of the world's biodiversity and biomass. They are typically under-represented in the fossil record of many geologic deposits because of the common lack of preservation as body fossils (Hasiotis and Bown, 1992). Invertebrates today make up a large part of food webs and ecosystems, but paleoecosystem reconstructions commonly ignore or consider invertebrate fossil components insignificant due to this lack of body fossil preservation. Recognition of invertebrate trace fossils in the geologic record will increase our awareness of ancient biodiversity and inter-relationships between organisms and their environments. Understanding these relationships will allow for better and more concise paleoecosystem reconstructions in the future.

GEOLOGIC SETTING

The Upper Triassic Chinle Formation was deposited in an intracontinental basin of the Pangaeon supercontinent, which marks an exceptional time in the earth's paleogeographic and paleoclimatic history. The Chinle Formation was deposited between 5° and 15° north paleolatitude in the western equatorial region of Pangaea. Throughout most of the Colorado Plateau, the Chinle unconformably overlies the Lower and Middle Triassic Moenkopi Formation and equivalent rocks. In the Defiance uplift region of western Colorado and northeastern Arizona, the Chinle overlies Permian or older strata. The Chinle reaches thicknesses of 500 m and is unconformably overlain by the Lower Jurassic Wingate Sandstone or Moenave Formation and locally by the Middle Jurassic Entrada Sandstone in central Colorado and northwestern New Mexico.

Depositional systems of the Shinarump Member, and Monitor Butte Member in northern Arizona and in the vicinity of Petrified Forest National Park comprise valley-fill sequences at the base of the Chinle that are overlain by fluvial, floodplain, marsh, delta, and lacustrine strata (Stewart et al., 1972; Dubiel et al., 1991). In Petrified Forest National Park, the Petrified Forest Member consists of siliciclastic and intrabasinal conglomerates and laterally extensive, variegated sandstones and mudstones. These units have been interpreted as a complex succession of evolving fluvial channel systems and associated floodplain mudstones, many of which have endured extensive pedogenic modification (Dubiel et al., 1991).

ICHOLOGY

Trace fossils documented in this preliminary report are presented as types (designated 1, 2, 3 etc.) that are based on their architectural and surficial morphology. Each type is followed by either: 1) a preassigned ichnotaxonomic designation minus the ichnospecies assignment; 2) a general designation already in use; or 3) by a descriptive designation reflecting the burrow architecture. Each trace fossil type contains a simple diagnosis and a discussion of its origin

related to its morphologic features, as well as its paleohydrologic significance within the paleoecosystem.

TYPE 1: *Scoyenia* White 1929 (Fig. 1)

Diagnosis: Slender burrows with rope-like surficial morphology. Burrow diameters range from 0.2 cm to 10 cm, and lengths from a few cm to 10 cm. Burrows are unbranched, quasi-horizontal to vertical in orientation, and sometimes exhibits peristalsic thickening. Burrow interior is meniscate, backfilled.

Discussion: This ichnofossil is composed of a small diameter, is sinuous, exhibits a radially scratched surface, and is back-filled. Its orientation in outcrop is quasi-horizontal, and sometimes exhibits quasi-vertical variations. The burrow surficial morphology suggests that the trace was produced by deposit feeding insect larvae probably of beetle or true bug origin. The scratch mark marks appear to be paired with an extension of a third, smaller scratch periodically preserved in the burrow wall. These scratches suggest a limb morphology and the organism was adapted to burrowing in moist, compact substrates such as the silty clay in which *Scoyenia* is found. *S. gracilis* is common in the floodplain mudstones and paleosols of various immature stages of development in the Petrified Forest Member. It is absent from more mature paleosols and coarser-grained deposits. In other Triassic rocks, *Scoyenia* occurs in marginal-lacustrine and lacustrine deposits (i.e., Olsen, 1977). The mode of occurrence would suggest that this ichnofossil is indicative of very high soil and sediment moistures approaching 100% saturation of freshwater. In general, *Scoyenia* occurs only in continental and marginal marine deposits with thin continental interbeds (Hantzschel, 1975).

Scoyenia is an indicator of moist to saturated substrates (100% saturation of the pore space), which include immature paleosols and marginal fluvial and lacustrine strata. The *Scoyenia* ichnofacies currently embodies all continental deposits regardless of the presence of *Scoyenia*, its abundance, or the diversity and abundance of other ichnofossils in continentally deposited strata. We suggest that the *Scoyenia* ichnofacies should be limited to perennially moist to wet depositional environments where *Scoyenia* is the dominant ichnofossil, and the ichnofacies can be subsequently subdivided based upon the depositional setting and co-occurring faunal, floral, and ichnobiotal elements (Hasiotis, in press). Strata in which *Scoyenia* occurs as a minor ichnofaunal element should not be included in the *Scoyenia* ichnofacies because the trace represents either an ecological moisture tier in a sediment profile or a remnant population from wetter syn- or post-depositional periods.

TYPE 2: *Koupichnium* Nopcsa 1923 (Fig. 2)

Diagnosis: Heteropodous tracks of great variability. Two kinds of track imprints are common: 1) Two chevron-like series of tracks each of 4 oval to round holes or bifid V-shaped impressions or scratches, and 2) one pair of digitate or flabellar, toe-shaped imprints with or without a medial drag mark.

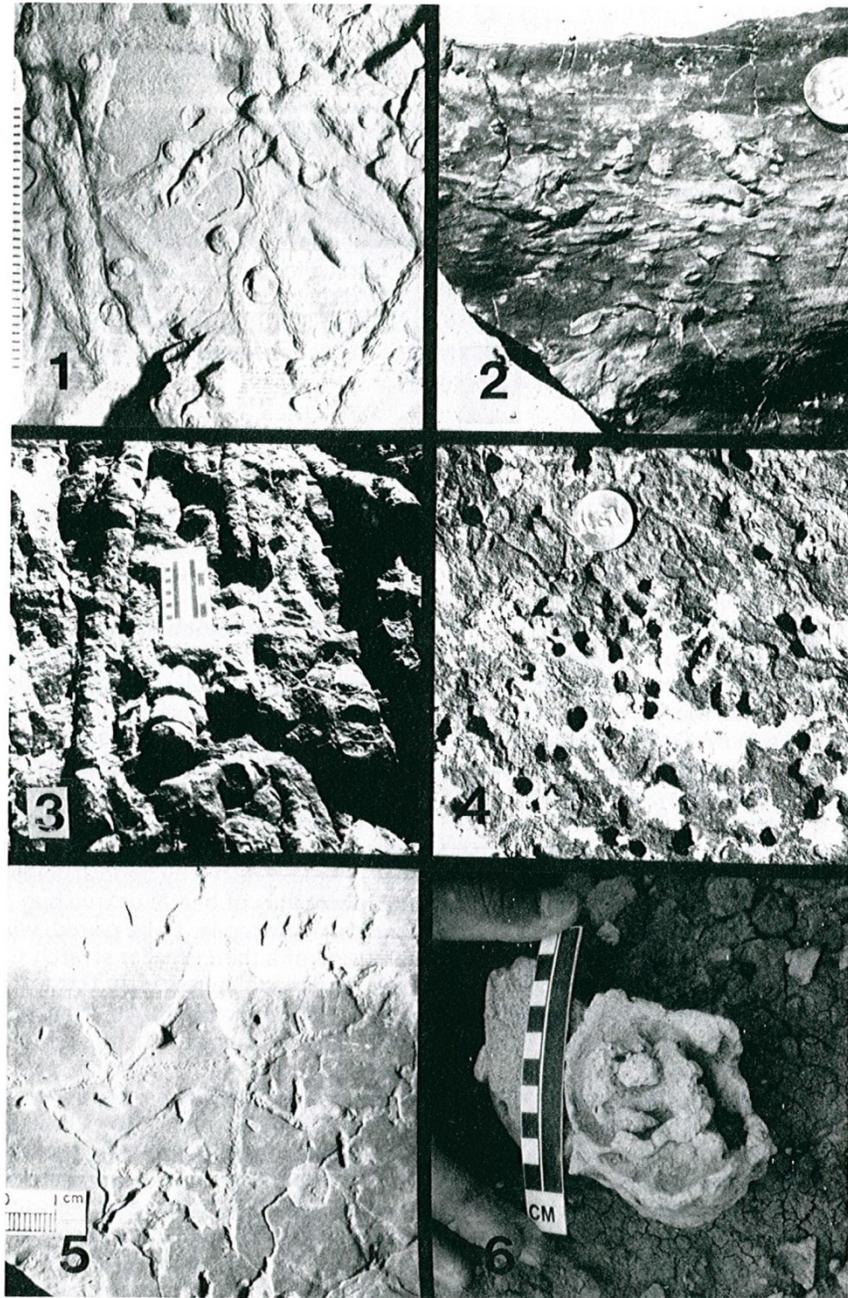


Figure 1.—1) Type specimen of the burrow *Scoyenia Gracilis* typically found in the Triassic overbank deposits of Petrified Forest National Park. The Chinle specimens are not as photogenic as the type specimen. 2) Trail made by a horseshoe crab designated as *Koupichnium*. Note the body impressions of the organism below and to the left of the dime. 3) Crayfish burrows designated as *Camborygma* from rocks outside the PEFO boundary. Burrows in PEFO are not as well preserved. The best-preserved burrows are typically found weathered out of the outcrop as loose tubes. Scale marked in centimeters and inches. 4) Shallow, test-tube shaped, smooth-walled brood cells designated as *Cylindricum*. 5) Alternating back-filled burrows designated as Type 5 burrows. 6) Nests of Triassic termites designated as Type 6 and currently named as the ichnogenus *Archeoentomoichnus*.

Discussion: At least two ichnogenera are recognized for horseshoe crab (limulid) traces in the ichnofossil volume from the invertebrate treatise. These and a host of other ichnogenera were named for various limulid traces some of which were originally thought to be tracks of amphibians, birds, and mammals. *Koupichnium* and *Merostromichnites* are just two of the many overlapping limulid ichnogenera that create many problems in ichnology.

Freshwater limulid crawling and resting ichnofossils occur in marginal fluvial (point bar) and lacustrine deposits in the Petrified Forest Member. Freshwater limulid ichnofossils in continentally deposited strata have been recorded in Paleozoic and Mesozoic rocks throughout the world (Seilacher and Goldring, 1971) and are not unique to continental depositional systems. From the similarity to modern and well documented ancient marine limulid tracks, we assume that the continental limulids were nearly identical in morphology.

Continental freshwater limulids are indicative of environments that contained ample amounts of water in continental depositional systems. Their traces are often found in strata that represent shorelines of lentic and lotic paleoenvironments, and are best preserved when the sediments were moist but not submerged. Experiments with tracks of other arthropods have shown that they are best preserved in moist and saturated conditions (i.e., Caster, 1938; Brady, 1939; McKee, 1947; Seilacher and Goldring, 1971). The limulid ichnofossils represent foraging out of the water onto the shoreline. Since they were morphologically similar, a separate ichnospecies should be created to encompass freshwater continental limulid ichnofossils because they had different biological requirements and lived in different environments than did their marine counterparts.

TYPE 3: *Camborygma* Hasiotis and Mitchell 1993 (Fig. 3)

Diagnosis: Architectural morphology varies from complex structures with multiple openings, shafts, corridors, and chambers, to simple, quasi-vertical shafts with simple chambers. Burrows sometimes preserve chimney structures at their tops. Burrows diameters in centimeters and lengths from 30 cm to 200+ cm. Surficial burrow morphology includes scrape marks, scratch marks, mud-and lag-liners, knobby and hummocky surfaces, pleopod striae, and body impressions.

Discussion: Large-diameter continental ichnofossils exist in the Petrified Forest Member of PFNP. They also in the members of the Upper Triassic Chinle and Dolores Formations on the Colorado Plateau as well as the Upper Triassic Dockum Formation of northwest Texas and eastern New Mexico. The burrows in PEFO occur in floodplain and paleosols and in marginal fluvial facies. These burrows were originally thought to be the product of spring water action (Gableman, 1955), rhizoliths (Lucas et al., 1985), and aestivating lungfish (Dubiel et al., 1987, 1988, 1989). Recent study has demonstrated that the majority of these large-diameter ichnofossils were created by crayfish (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993).

Comparison of Triassic burrows to modern crayfish burrows concluded that the Triassic burrows were produced by crayfish using identical burrowing methods and exhibiting similar behavior

patterns despite 220 million years in time (Hasiotis, 1990b, 1991; Hasiotis and Mitchell, 1993). The ichnogenus *Camborygma* is defined on the crayfish surficial burrow morphology that includes scratch marks, scrape marks, pleopod striae, knobby-hummocky surfaces, mud- and lag-liners, and body impressions.

Four ichnospecies of crayfish burrows (*Camborygma eumekenomos*, *C. symplokonomos*, *C. araioklados*, and *C. litonomos*), similar to modern crayfish burrow architecture, reflect the depth and fluctuations of the water table, thus indicating the hydrology of the Chinle in PFNP on the west coast of Late Triassic Pangea (Hasiotis, 1990a, 1991; Hasiotis and Dubiel, 1993). Burrow length and complexity of the architecture reflects the depth and stability of the water table in that area. Extensive, three dimensional outcrops allow for the reconstruction of the paleohydrology in the many areas where burrows occur.

In general, crayfish burrows are useful for paleohydrologic, paleoclimatic, and paleoenvironmental reconstructions of the strata in which they occur. Crayfish burrows and their stratigraphic succession reflect the depths and fluctuations of the water table, as well as the amount of water in a system (overall precipitation), seasonality, and climate.

TYPE 4: *Cylindricum* Link 1949 (Fig. 4)

Diagnosis: tube fillings or tubes shaped like test tubes with rounded terminations; walls smooth; diameter up to 5 cm and lengths up to several centimeters; preserved in groups oriented perpendicular to bedding.

Discussion: The architecture of these burrows are most similar *Cylindricum* and also resemble the marine trace fossil *Skolithos*, but differs in many ways. *Skolithos* is commonly long, slender, and less than 1 cm in diameter and occurs in marine nearshore environments in cohesive sands. *Cylindricum* occurs in groupings of 10 to 100 individuals in fine- to medium-grained crevasse splay sandstones and levee deposits. Many workers often confuse the usage of these two ichnotaxa due to their lack of familiarity with trace fossil literature and a working knowledge of continental and marine ecosystems.

Cylindricum faintly resembles the workings of solitary bees that are designated to the ichnotaxa *Celliforma*. Because of nomenclature problems and need for further study, the specimens in PFNP are grouped into TYPE 4 traces. Based on comparisons to modern burrowing and nesting organisms, these structures were probably used as brood nests by an unknown flying insect where eggs were deposited.

Paleoenvironmentally, these burrows represent time intervals of lower water table in crevasse splays and in levees deposits. Lowered water tables would allow many types of flying insects to occupy these types of deposits for weeks or even months; the time necessary for development and growth of larvae and pupae to adulthood.

TYPE 5: Alternating-fill, back-filled burrows (Fig. 5)

Diagnosis: Back-filled burrows that range in diameter from 2 mm to 20 mm; showing alternating fills of fine and coarse material; occur individually or as cross-cutting masses; never branched nor with chambers; entrances and terminations rare.

Discussion: These are the backfilled burrows with alternating fine and coarse material, with mainly the coarse furrows preserved. These PFNP burrows are similar to the marine back-filled trace fossils *Taenidium* and *Muensteria*, but differ from the marine traces which are often branched in multiple directions and places along their paths.

These continental back-filled burrows were most likely produced by soil-dwelling organisms that preferred moist, but not saturated environments. The Triassic burrows are very similar to modern soil-dwelling organisms that forage in substrates with moistures between 7 and 37 % (Hasiotis and Bown, 1992).

TYPE 6: *Archeontomoichnos* Hasiotis and Dubiel 1994 (Fig. 6)

Diagnosis: Multistory ramps, floors, and walls constructed in a cylindrical structure approximately 7 cm in diameter; associated with mm to cm diameter-sized corridors greater than 5 cm in length; walls, ramps, and floors, range in thickness from 2 mm to 5 mm. Combined nests and galleries represent polycalic edifices.

Discussion: These nests represent the earliest known examples of social behavior in insects as well as the oldest evidence of termite activity. The ichnofossil evidence predates the body fossil evidence of termites by 135 million years (early Cretaceous). The nests are composed of calies (nest proper), galleries (runways between nests), and peripheral calies (storage chambers). Nests like these termite edifices are important because they preserve the behavior of a group of organisms that reflect the division of labor amount individuals that allow such colonies of insects to perpetuate themselves.

SIGNIFICANCE IN PALEOECOSYSTEM RECONSTRUCTIONS

Some of the more interesting and informative trace fossils were briefly described here to demonstrate that a diverse group of organisms exists with little or no fossil record within the Park. These traces, through comparisons to modern burrowing analogs, permit reconstruction of organism behavior with respect to various environments, the mechanisms that operated within environments that physiologically regulated organisms, and the internal and external components that shaped the paleoecosystem.

Triassic invertebrates identified through trace fossils such as larval and adult beetles, solitary bees, termites, horseshoe crabs, and crayfish, lived in environments with distinct depositional energies and hydrologic characteristics. These and other invertebrates were physiologically sensitive to intra- and extra-channel depositional events, as well as substrate moisture regimes,

which regulated their occurrence within the paleoecosystem. The lateral and vertical stratification or tiering of the traces (organisms) reflected the zonation of the ancient soil moisture levels and ground water table during and after the deposition of the various beds within Petrified Forest Member during the late Triassic. Modern climate studies indicate that water table and soil moisture levels across the continents are controlled by seasonal and annual amounts of precipitation and temperature, which are in turn controlled by regional and global climatic patterns (e.g., Dubiel et al., 1991; Hasiotis and Bown, 1992). Therefore, recognition of trace fossils within Triassic strata yields better reconstructions for invertebrate biodiversity, and paleohydrologic and paleoclimatic characters that shaped Chinle paleoecosystems.

Future field work will continue to document the occurrence and distribution of trace fossils with respect to their association with bed stratification, sedimentary facies and lateral variations, and vertical distribution within the Park. Information gathered from ongoing studies in PFNP and in other national parks and monuments can greatly enhance our understanding of paleoecosystems and their changes as a result of climate changes during the Late Triassic.

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TWO LATE TRIASSIC VERTEBRATE FAUNAS AT PETRIFIED FOREST NATIONAL PARK

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ABSTRACT

Two different vertebrate faunas are present in the Petrified Forest Formation (Upper Triassic) at Petrified Forest National Park, Arizona. The older fauna is Adamanian (late Tuvalian) in age, occurs in the Blue Mesa Member and is characterized by the presence of *Rutiodon*, *Desmatosuchus* and *Stagonolepis*. The younger fauna is Revueltian (Norian) in age, occurs in the Painted Desert Member and is characterized by the presence of *Pseudopalatus* and *Typothorax*. These faunas indicate that there was no major extinction at the Carnian\Norian boundary.

INTRODUCTION

Petrified Forest National Park (PEFO) has yielded a very large number of Late Triassic vertebrate fossils dating back to the excavations of Charles Camp in 1921 (Long et al., 1989). Since then, large collections have been amassed which are housed principally at the University of California Museum of Paleontology, Berkeley. Friedrich von Huene recognized in the 1920's the presence of two different faunas in the Upper Triassic of northeastern Arizona (note that Huene considered one fauna to be Middle Triassic in age), but Camp's (1930) influential revision of the phytosaurs only recognized one. Colbert and Gregory, (1957) similarly only recognized one fauna within the Triassic strata which are exposed at PEFO. However, Gregory (1957) resurrected Huene's concept of two faunas within the Chinle of the Colorado Plateau region (Table 1), which has been followed by all later workers. The aforementioned studies were hindered by the poor taxonomic state of the majority of the common families of Late Triassic vertebrates. Notably, the Carnian aetosaur *Longosuchus* and phytosaur *Rutiodon* were not distinguished from the Norian taxa *Typothorax* and *Pseudopalatus* respectively. However, in the last decade there have been complete or partial revisions of these groups, notably the metoposaurs (Hunt, 1993a, 1994; Hunt and Lucas, 1993b), phytosaurs (Ballew, 1989; Hunt, 1993b, 1994) and aetosaurs (Long and Ballew, 1985; Hunt and Lucas, 1991, 1992b). Utilizing these advances in taxonomy various authors have discussed the twofold division of PEFO vertebrate faunas but none have provided updated faunal lists at the species level (e.g., Long and Ballew, 1985; Long and Padian, 1986, Murry and Long, 1989; Parrish, 1989, 1993; Murry 1990; Hunt and Lucas, 1993b; Lucas, 1993). Lucas (1993) has recently published a revised stratigraphy

of PEFO which allows the stratigraphic distribution of these faunas to be reevaluated. The purposes of this paper are threefold: (1) to provide updated faunal lists for both Late Triassic faunas at PEFO; (2) to evaluate their stratigraphic distribution and age; and (3) to comment briefly on the differences between the faunas. UCMP is the University of California Museum of Paleontology, Berkeley.

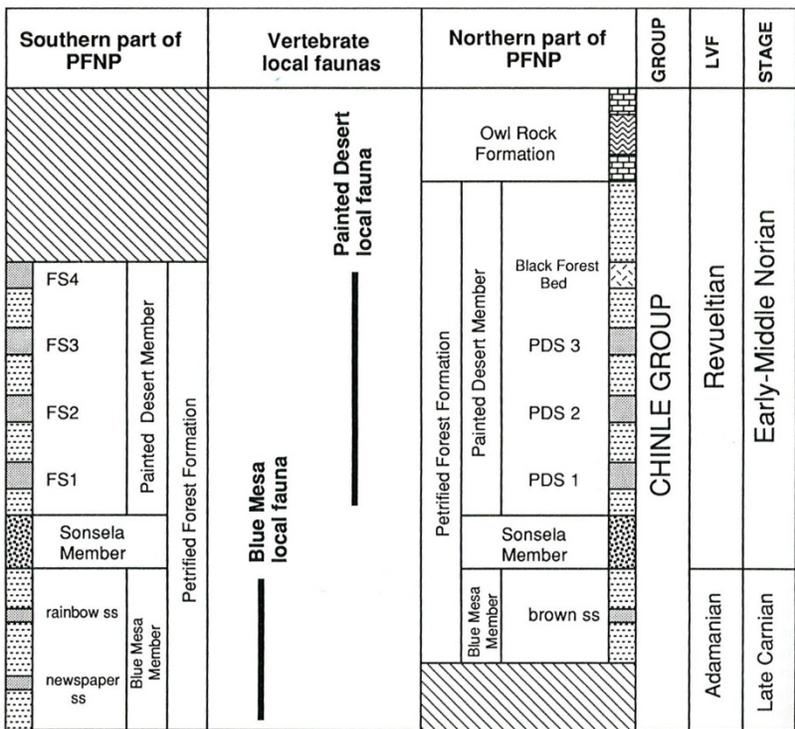


Figure 1. Stratigraphic distribution of the Blue Mesa and Painted Desert local faunas at Petrified Forest National Park, Arizona. FS is Flattops sandstone and PDS is Painted Desert sandstone.

BLUE MESA LOCAL FAUNA

The older of the two vertebrate faunas from PEFO comes from the Blue Mesa Member of the Petrified Forest Formation, Chinle Group (Table 3). Most fossils from this unit come from the southern end of PEFO (south of Interstate 25) where the Blue Mesa Member has its main exposures within the park. This is the type fauna for the Adamanian land-vertebrate faunachron and is late Tuvalian (late Carnian) in age (Lucas and Hunt, 1993b). This fauna, like most late

Carnian vertebrate faunas of Laurasia and northern Gondwanaland, is dominated by parasuchid reptiles (phytosaur). Second most common in abundance are metoposaurid amphibians followed by aetosaurs. Other taxa together form a small minority of the fauna. The vast majority of specimens of this fauna come from a thin stratigraphic interval in the upper portion of the Blue Mesa Member (Lucas, 1993; Fig. 1).

PAINTED DESERT LOCAL FAUNA

The upper of the two vertebrate faunas at PEFO is from the Painted Desert Member of the Petrified Forest Formation. This unit is mainly exposed in the northern half of the park (north of Interstate 25), and this area has produced the majority of the Painted Desert local fauna. Some specimens come from the southern portion of the park in the Flattops area.

The Painted Desert fauna is Revueltian (Norian) in age on the basis of the presence of the phytosaur *Pseudopalatus* and the aetosaur *Typtothorax* (Lucas and Hunt, 1993b). This fauna is also dominated by parasuchid specimens, but metoposaurs are rare and mainly restricted to

localities dominated by terrestrial reptiles (Hunt and Lucas, 1993b; Hunt et al., 1993). Specimens of the aetosaur *Typhorax* are the second most abundant vertebrate fossils. Note that previous reports of a traversodontid from the Painted Desert Member (e.g., Murry and Long, 1989) are in error (Hunt and Lucas, 1993c). We identify the partial skeleton of a sphenosuchian (UCMP 129740), previously assigned to cf. *Sphenosuchus* sp. (Parrish, 1991), as cf. *Hesperosuchus* sp. and consider Padian's (1986) specimen of *Coelophysis* (UCMP 129618) to represent a new genus (Hunt and Santucci, 1993). Like the Adamanian fauna, the Revueltian fauna at PEFO is stratigraphically restricted and the majority of specimens occur in the lower part of the Painted Desert Member (Lucas, 1993; Fig. 1).

FAUNAL EVOLUTION ACROSS THE CARNIAN/NORIAN BOUNDARY

The Adamanian and Revueltian faunas at PEFO straddle the Carnian/Norian boundary, which has been postulated as a time of a major tetrapod extinction (e.g., Benton, 1994), but this has been disputed recently (Hunt and Lucas, 1992a; Lucas, 1994). Comparison between the two

Table 1. Gregory's (1957) twofold division of the Chinle vertebrate faunas in the Petrified Forest Formation (sensu Lucas, 1993) in the region of what is now Petrified Forest National Park. Note that *Hesperosuchus* was found outside the park.

Lower portion of formation	Upper portion of formation
Fish: <i>Ceratodus</i> <i>Semionotus-Lepidotes</i>	
Amphibians: <i>Eupelor</i>	Rarer <i>Eupelor</i>
Phytosaurs: Primitive species of <i>Phytosaurus</i>	Primitive species of <i>Phytosaurus</i> Advanced species of <i>Phytosaurus</i>
Aetosaurs: <i>Typhorax</i> <i>Desmotosuchus</i>	Rarer <i>Typhorax</i>
Sphenosuchians: <i>Hesperosuchus</i>	
Mammallike reptiles: <i>Placerias</i>	

faunas at PEFO should provide a test of extinction theories. Even a cursory examination of Table 3 reveals that there is no major extinction at the Carnian/Norian boundary in the America Southwest, which is typified by the faunas at PEFO. The major groups of tetrapods (phytosaurs, aetosaurs, metoposaurs) exhibit generic level turnover at most. Terrestrial tetrapods appear more common in the Painted Desert fauna (Parrish, 1993), but this is biased by the fact that the older portion of the Revueltian is an acme zone for terrestrial tetrapods across the

southwestern United States (Hunt and Lucas, 1993a). Aquatic/semiaquatic elements of the fauna (fish, metoposaurs), with the notable exception of phytosaurs, are less numerous in the Revueltian fauna (Hunt and Lucas, 1993a; Parrish, 1993). The only extinction at the Carnian/Norian boundary which has any global significance is the demise of the last dicynodont *Placerias* which disappears globally at this time though its disappearance precedes the end of the Carnian (Lucas and Hunt, 1993a). The replacement of xenacanth sharks by hybodonts at the Carnian/Norian boundary is consistent with a pattern throughout the Chinle Group (Huber et al.,

1993). Some other rarer taxa may have become extinct at this time for example the enigmatic reptile *Trilophosaurus*. The apparent extinction of the prosauropods between the two faunas is an example of the Lazarus effect because these dinosaurs are known from Norian and Rhaetian (by footprints) portions of the Chinle Group elsewhere.

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Table 2. Vertebrate faunas of Petrified Forest National Park (Long and Ballew, 1985; Murry, 1989, 1990; Murry and Long, 1989; Huber et al. 1993; Hunt, 1993a, b, 1994; Hunt and Lucas, 1993b; Lucas and Hunt, 1993b; Parrish, 1993; Santucci and Hunt, 1993; PEFO archives; original identifications). * indicates nomina nuda in Murry and Long (1989).

Blue Mesa Member local fauna	Painted Desert Member local fauna
Sharks:	
<i>Xenacanthus moorei</i>	
<i>Lissodus humblei</i>	
undescribed shark	hybodont
Lungfish:	
<i>Arganodus dorotheae</i>	<i>Arganodus dorotheae</i>
Coelacanths:	
indeterminate coelacanthid	indeterminate coelacanthid
Other fish:	
cf. <i>Turseodus</i> sp.	cf. <i>Turseodus</i> sp.
indeterminate redfieldiid	indeterminate redfieldiid
indeterminate colobodontid	indeterminate colobodontid
Metoposaurid amphibians:	
<i>Buettneria perfecta</i>	<i>Buettneria</i> sp.
<i>Apachesaurus</i> sp.	<i>Apachesaurus gregorii</i>
Primitive reptiles:	
<i>Trilophosaurus buettneria</i>	
undescribed ? proterochampsid	indeterminate sphenodontid
Phytosaurian reptiles:	
<i>Rutiodon carolinensis</i>	
<i>Rutiodon crosbiensis</i>	
"Rutiodon" <i>gregorii</i>	<i>Pseudopalatus pristinus</i>
	<i>Pseudopalatus andersoni</i>
Aetosaurian reptiles:	
"Acaenasuchus geoffreyi"*	
<i>Stagonolepis wellesi</i>	
<i>Desmatosuchus haplocerus</i>	
<i>Paratypothorax andressi</i>	<i>Typothorax coccinarum</i>
"Rauisuchian" reptiles:	
<i>Postosuchus kirkpatricki</i>	<i>Postosuchus kirkpatricki</i>
	"Chatterjeea elegans"*
Sphenosuchian reptiles:	
	cf. <i>Hesperosuchus</i> sp.
Theropod dinosaurs:	
indeterminate theropod	"Chindesaurus bryansmalli"*
	undescribed ceratosaurian
Prosauropod dinosaurs:	
indeterminate prosauropod?	
Ornithischian dinosaurs:	
	<i>Revueltosaurus callenderi</i>
Mammallike reptiles:	
<i>Placerias</i> sp.	
Vertebrate trace fossils:	
coprolites	coprolites
<i>Rhynchosauroides</i> sp.	

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A SIMPLIFIED KEY TO IDENTIFYING ISOLATED FOSSIL TEETH FROM LATE TRIASSIC ROCKS IN PETRIFIED FOREST NATIONAL PARK

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ABSTRACT

Isolated teeth and jaw fragments are some of the most common fossils found in Upper Triassic rocks at Petrified Forest National Park. All these specimens can be identified to at least the family level using an identification key.

INTRODUCTION

Isolated teeth or jaw fragments are among the most common remains of fossil vertebrates found at Petrified Forest National Park. These fossils occur in the Petrified Forest and Owl Rock Formations of the Chinle Group that are Late Triassic (about 210-230 million years old) in age. All well-preserved teeth can be identified to at least the generic level, and the purpose of this key is to provide a nontechnical means by which National Park Service personnel can identify them. We hope that this key will also be of use to students and amateur paleontologist working with Late Triassic vertebrates in other areas.

A FEW BASICS

Why so many teeth? Isolated teeth (teeth not associated with jaws) are common in Late Triassic rocks for several reasons:

1. Most Late Triassic teeth are from reptiles that replace their teeth continuously. Reptiles do not have a limited number of teeth (two sets) like mammals. Therefore, one reptile will produce hundreds of teeth in its lifetime.
2. Most reptiles have teeth that are simple, cone-shaped elements that fit in cylindrical sockets in the jaw. Reptile teeth do not have complicated roots as do most mammal teeth,

so when a reptile dies after a relatively brief interval of decay its teeth often fall out of the sockets.

3. Because reptile teeth are not well rooted these teeth are often lost when the animal feeds.

Most lower vertebrate (reptile, amphibian, fish) teeth consist of an upper part, the crown and a lower part, root. The crown is covered by enameloid, similar to the enamel of human teeth, and the enameloid shiny if it is well preserved. The crown is often cone-shaped and has serrations on its edges. The crown is the "working part" of the tooth that is exposed in the mouth.

The root is the part of the tooth that fits in the jaw and it is usually cylindrical and not shiny, because it lacks an enameloid covering. When a reptile is about to replace a tooth it resorbs (dissolves and absorbs) the root of the tooth. Therefore, if you find a tooth with a large root you know that it came from a dead animal and was not a tooth that was replaced during life.

The teeth of carnivorous reptiles have small square serrations that are at right angles to the edge of the tooth (Fig. 1A). In contrast, the teeth of herbivorous reptiles have larger serrations that are blunt and point towards the top of the tooth (Fig. 1B).

THE CAST OF CHARACTERS

More than 90% of isolated teeth at Petrified Forest National Park represent 7 types of reptiles and amphibians. We have included here one type of tooth (prosauropod) which is not known from the park but which may be found in the future.

The most common Late Triassic vertebrates are phytosaurs, which are superficially crocodile-like reptiles with elongate snouts. Metoposaurs are one of the last of the groups of giant primitive amphibians that had large, flat heads shaped like shovels. The most common herbivores were aetosaurs which were large (up to 5 meters long) armadillo-like reptiles with heavy armor on their backs. The largest predators were rauisuchians which were quadrupedal animals with large heads. Rarer carnivores were the small and slightly built sphenosuchians, which were the ancestors of modern crocodiles.

Three groups of dinosaurs are found in the Late Triassic. All carnivorous dinosaurs were bipedal saurischians which were usually much shorter than a human in height. Similarly sized plant-eating dinosaurs are ornithischians, which were also bipedal. The largest Late Triassic dinosaurs were prosauropod which look like emaciated versions of their descendants, the sauropods (e.g., *Diplodocus*, *Camarasaurus*, *Apatosaurus* [*Brontosaurus*]).

Note that phytosaurs have several different kinds of teeth in the same jaw and so these appear at different places in the key. This condition is referred to as heterodonty.

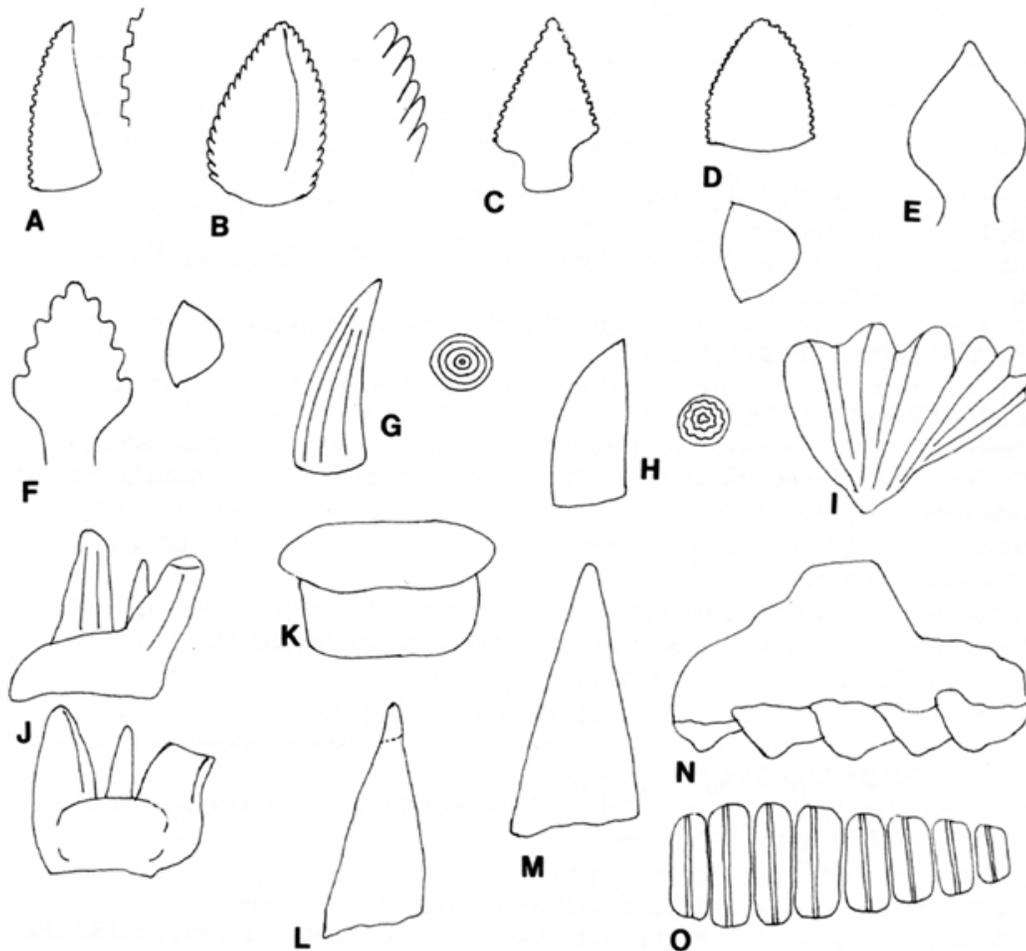


Figure 1. The main kinds of isolated teeth and jaw fragments found in Upper Triassic rocks at Petrified Forest National Park. A, Saurischian tooth in side view with a close-up of the "carnivorous serrations"; B, Prosauropod tooth in side view with close-up of "herbivorous serrations"; C, Sphenosuchian tooth (stylized) in side view; D, Phytosaur tooth in side and top views; E, Aetosaur tooth in side view; F, Ornithischian tooth (stylized) in side and top views; G, Phytosaur tooth in side and bottom views; H, Metoposaur tooth in side and top views; I, Lungfish toothplate in top view; J, Three-pronged shark teeth; K, Button-like shark tooth; L-M, Conical fish teeth; N, Sphenodont upper jaw in side view with five triangular teeth; O, Trilphosaur teeth in top view.

MISCELLANEOUS TEETH

Lungfish- Lungfish have fan-shaped teeth with sharp ridges radiating out from the center (Fig. 1I).

Sharks- Triassic sharks have very small teeth of several different shapes. Common shapes are a three-pronged form (Fig. 1J) and a flat button-shaped form (Fig. 1K).

Other fish- Other fish teeth are usually very small, conical, smooth and shiny, sometimes with an opaque base and a translucent top (1L-M).

Sphenodonts- Sphenodonts were lizard-sized animals with laterally compressed (flattened side to side), triangular teeth that are fused to the jaw (Fig. 1N).

Trilophosaurs- Trilophosaurs were bizarre animals with very large feet which had small rectangular teeth with three crests arranged in a row (Fig. 1O).

Key

1. If you have the root go to 3. If you do not have a root go to 2.
2. If the tooth has "herbivorous serrations," go to 6.
 - a. If the tooth has "carnivorous serrations" and is laterally compressed (flattened side to side) all the way down, go to 8.
 - b. If the tooth has "carnivorous serrations" and is laterally compressed but has a bulbous base it is a **SPHENOSUCHIAN** (fig. 1C).
 - c. If the tooth has "carnivorous serrations" and is D-shaped when you look down from the top it is a **PHYTOSAUR** (fig. 1D).
 - d. If the tooth has no serrations, is round in cross section and is parallel-sided, go to 9.
 - e. If the tooth has no serrations, has a very wide base and narrows towards the top it is an **AETOSAUR** (fig. 1E).
3. If the crown has a bulbous base (bottom of crown is much wider than root), go to 4; if it does not have a bulbous base, go to 7.
4. If the tooth has serrations, go to 5; if it does not, go to 6.
5. If the tooth has "carnivorous serrations" it is a **SPHENOSUCHIAN** (fig. 1C).
 - a. If the tooth has "herbivorous serrations," go to 6.
6. If the tooth has no serrations it is an **AETOSAUR** (fig. 1E).
 - a. If the tooth has "herbivorous serrations" and is symmetrical when you look down from the top, it is a **PROSAUROPOD** (fig. 1B).
 - b. If the tooth has "herbivorous serrations" and is asymmetrical when you look down from the top, it is an **ORNITHISCHIAN** (fig. 1F).
7. If the tooth is round in cross section, go to 9.
 - a. If the tooth is laterally compressed (flattened from side to side), go to 8.
 - b. If the tooth is D-shaped when you look down from the top it is a **PHYTOSAUR** (fig. 1D).
8. If one side (actually the back side) is concave it is a **SAURISCHIAN** (fig. 1A).
 - a. If both sides are straight it is a **RAUISUCHIAN**.
9. If the height of the tooth is more than 5 times its maximum width and/or the inside of the tooth is composed of simple rings, it is a **PHYTOSAUR** (fig. 1G).
 - a. If the inside of the tooth is composed of crinkly rings it is a **METOPOSAUR** (fig. 1H).

ACKNOWLEDGMENTS

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LATE TRIASSIC VERTEBRATE TAPHONOMY AT PETRIFIED FOREST NATIONAL PARK

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ABSTRACT

Three vertebrate taphofacies can be recognized within the Petrified Forest Formation (Upper Triassic) at Petrified Forest National Park (PEFO), Arizona. Channel-hosted assemblages are characterized by fragmentary, abraded specimens, floodplain-hosted assemblages by abundant fossils, complete phytosaur skulls and skeletons of large tetrapods and paleosol-hosted assemblages by common terrestrial tetrapods and skeletons of small tetrapods. Paleosol-hosted assemblages are restricted to the Norian at PEFO.

INTRODUCTION

Petrified Forest National Park (PEFO) in northeastern Arizona preserves an abundant and diverse vertebrate fauna which has been widely studied (e.g., Murry and Long, 1989). However, there has been surprisingly little written about the taphonomy of the vertebrate occurrences (e.g., Murry and Long, 1989; Parrish, 1989). The objects of this paper are threefold: (1) to briefly review previous taphonomic work; (2) to describe the major vertebrate taphofacies that are present at PEFO; and (3) to refer major localities to these taphofacies. The paleontological collections of Petrified Forest National Park are assigned the acronym PEFO and UCMP to the University of California Museum of Paleontology, Berkeley, collections.

GEOLOGIC CONTEXT

Two formations of the Upper Triassic Chinle Group (sensu Lucas, 1993) are present at 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).

These faunas are respectively, Adamanian (late Carnian: late Tuvalian) and early Revueltian (early Norian), in age (Lucas and Hunt, 1993).

PREVIOUS TAPHONOMIC WORK

Murry and Long (1989) and Parrish (1989) have provided most of the previous observations on vertebrate taphonomy at PEFO. Murry and Long (1989) described the Dying Grounds and Crocodile Hill localities in the Blue Mesa as being within mudrock units associated with organic-rich mudstones and minor conglomerates. This package of facies obviously represent floodplain deposition. They noted that Dinosaur Hill and the Lungfish locality in the Painted Desert Member are associated with mottled mudrocks, reduction haloes and calcrete nodules indicative of paleosols. Parrish (1989) noted similar features at Dinosaur Hill (his Bolt quarry). Parrish (1989) also made general comments on the taphonomy of the "Blue Forest area" by which he meant the area which includes most of the Blue Mesa Member localities (Dying Grounds etc.). He concluded, like Camp (1930), that these localities were formed in ponds and marshes. We consider that these localities formed in a proximal floodplain environment.

THREE TAPHOFACIES AT PETRIFIED FOREST NATIONAL PARK

Hunt and Newell (Newell, 1992; Hunt, 1994; Newell and Hunt, in prep.) recognize three taphofacies in the Norian Bull Canyon Formation of east-central New Mexico. These are: (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 in the Bull Canyon Formation 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. During the past 5 years we have examined all major vertebrate localities at PEFO and can recognize these three taphofacies at the park.

Assemblages derived from channelform sandstones at PEFO have received little study because most specimens are poorly preserved. Specimens derived from channels principally represent phytosaurs, metoposaurs and aetosaurs in the Blue Mesa Member and phytosaurs and aetosaurs in the Painted Desert Member. No significant vertebrate fossils derive from this taphofacies.

The vast majority of vertebrate fossils from PEFO come from the floodplain taphofacies. Characteristic modes of preservation include the occurrence of isolated phytosaur skulls and of articulated/disarticulated, but associated, skeletons of large (dorsal centra > 6 cm in length) tetrapods (e.g., Camp, 1930; Hunt and Lucas, 1990; Figs. 1-2). Notable specimens include all the phytosaur skulls and skeletons described by Camp (1930) from the area that is now PEFO (e. g.,

UCMP 26699, holotype of *Machaeroprotoposus adamanensis*: Fig. 1) and the partial aetosaur skeleton (Fig. 2) described by Hunt and Lucas (1992).

Paleosol assemblages are characterized by the presence of specimens of small terrestrial reptiles and articulated skeletons/partial skeletons of small (dorsal centra < 6 cm in length) tetrapods. Significant specimens from this taphofacies include the partial skeletons of a new small

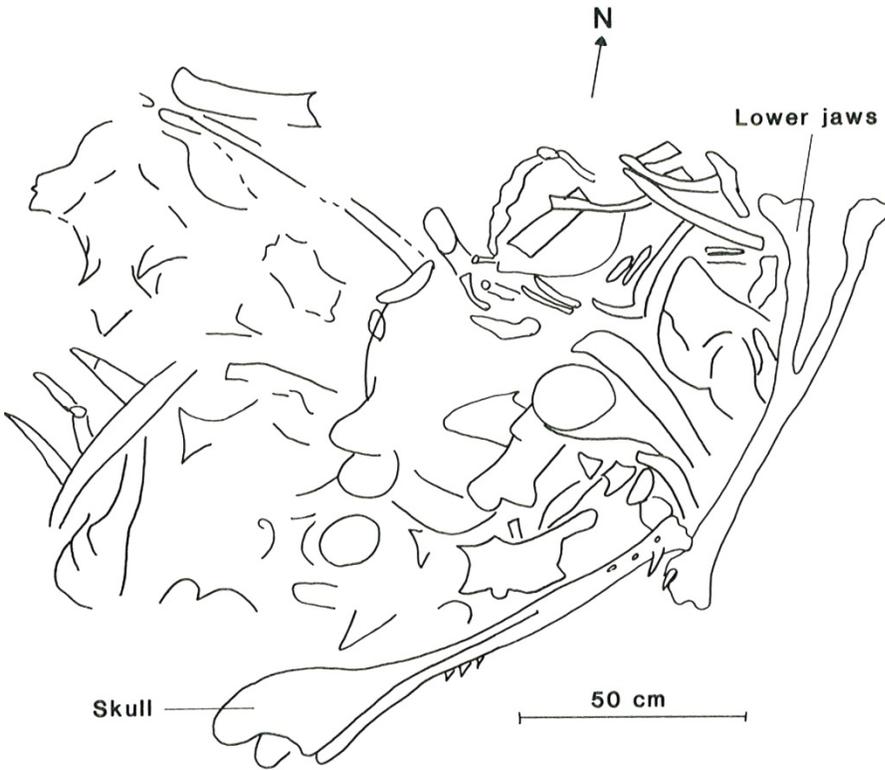


Figure 1. Quarry map of excavation of UCMP 26699, holotype of *Machaeroprotoposus adamanensis* (= *Rutiodon crosbiensis* of Hunt, 1993) from UCMP locality 7038 (scale is approximate). Adapted from two partial quarry maps (dated June 18th and 19th 1921) in the unpublished field notes of Charles L. Camp, in the archives of Petrified Forest National Park (courtesy of UCMP).

ceratosaur (cf. *Coelophysis* sp. of Padian, 1986), a small sphenosuchian skeleton (cf. *Sphenosuchus* sp. of Parrish, 1991) and the "holotype" of the nomen nudum *Chindesaurus bryansmalli* (Murry and Long, 1989). Incomplete specimens of terrestrial tetrapods from this taphofacies include isolated teeth of the ornithischian dinosaur *Revueltosaurus*

callenderi (Padian, 1990).

STRATIGRAPHIC DISTRIBUTION OF TAPHOFACIES

All major vertebrate localities at PEFO can be categorized as either floodplain- or paleosol-hosted (Table 1). It is clear that the stratigraphic distribution of the taphofacies is not random (Table 1). Vertebrate accumulations of the paleosol taphofacies are restricted to the Painted Desert Member. This, in part, explains taxonomic differences between the faunas of the two units Parrish, 1993; Hunt and Lucas, this volume). Both faunas are dominated by semiaquatic/aquatic taxa, but those of Blue Mesa contain very few terrestrial reptiles (e. g., dinosaurs, sphenosuchians) relative to those from the Painted Desert. Specimens of terrestrial reptiles are almost entirely restricted to the paleosol taphofacies which is most common in the Painted Desert Member. The paleosol taphofacies is prominent in all vertebrate faunas of the

American Southwest in the early Revueltian (early Norian) which explains the acme zone of terrestrial tetrapods at this time (Hunt and Lucas, 1993).

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We thank Petrified Forest Museum Association for supporting diverse projects on the Triassic vertebrates of Petrified Forest National Park.

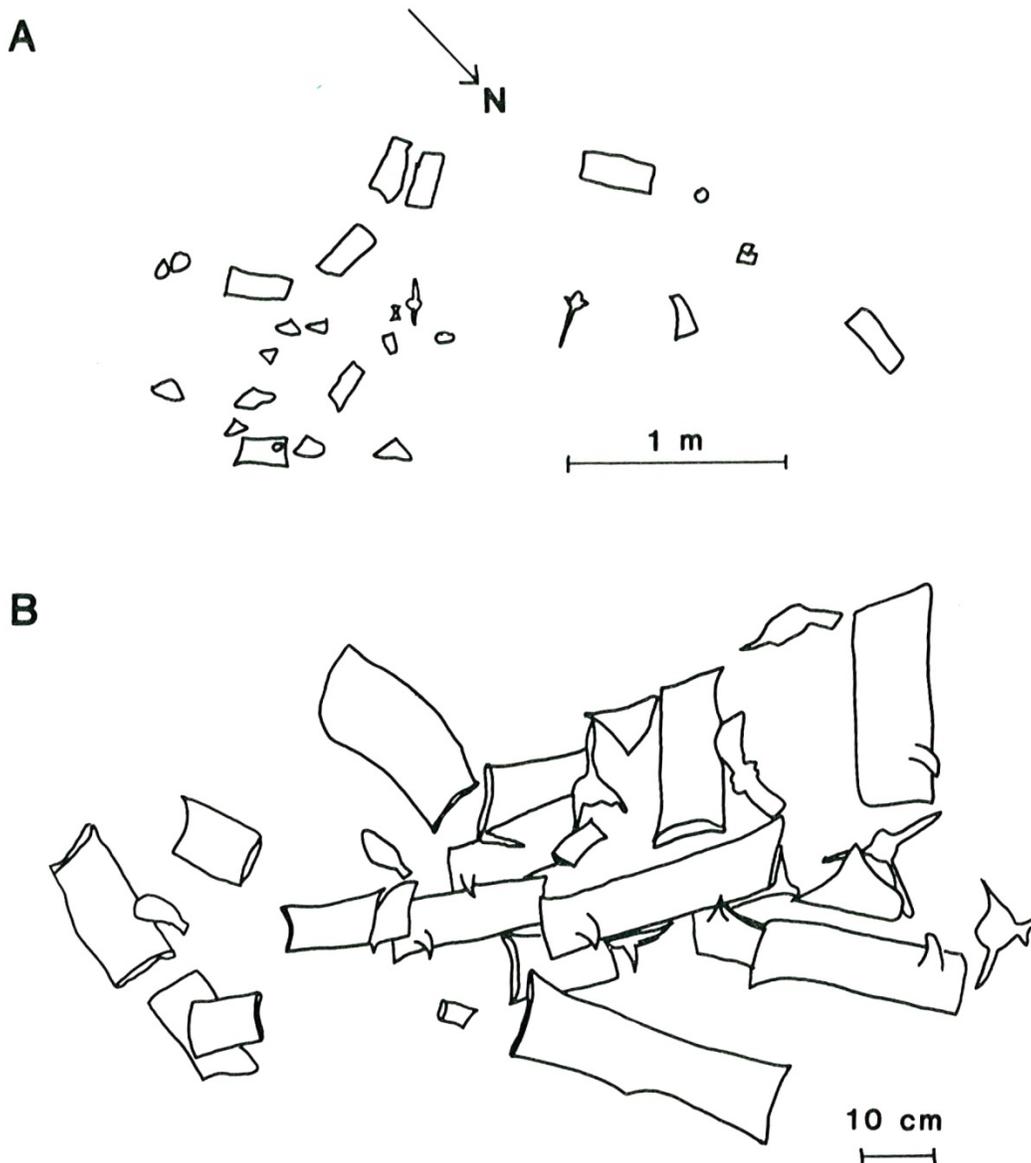


Figure 2. Quarry plans of partial skeleton of *Paratypothorax andressi* (PEFO 3004) from archives at Petrified Forest National Park. Most elements are dorsal osteoderms or vertebrae. (A) Overview of whole quarry (scale is approximate). (B) Map of underside of principal jacketed block.

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 (e.g., Murry and Long, 1989; Hunt and Lucas, 1993).

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
Flattops		Painted Desert
Black Forest		Painted Desert
Billings Gap		Painted Desert
Lungfish Locality	Painted Desert	
Dinosaur Hill	Painted Desert	
Dinosaur Hollow	Painted Desert	

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REVISED UPPER TRIASSIC STRATIGRAPHY PETRIFIED FOREST NATIONAL PARK

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ABSTRACT

Upper Triassic strata exposed in the Petrified Forest National Park belong to the Petrified Forest and Owl Rock Formations of the Chinle Group. In the park, the Petrified Forest Formation consists of the (ascending order) Blue Mesa, Sonsela, and Painted Desert Members. Fossil vertebrates and other biochronologically significant fossils indicate that Chinle Group strata in the park are of late Carnian-middle Norian age, about 222-212 million years old.

INTRODUCTION

The Petrified Forest National Park (PEFO) encompasses 93,492 acres located in Navajo and Apache Counties, northeastern Arizona (Figure 1). Most of this acreage is spectacular badlands developed in Upper Triassic nonmarine strata. These rocks have long been referred to as Chinle Formation with various informal and formal subdivisions (Cooley, 1957; Roadifer, 1966; Espegren, 1985; Billingsley, 1985). Recent revisions of Upper Triassic stratigraphic nomenclature throughout the western United States affect the nomenclature of Upper Triassic strata at PEFO (Lucas, 1993a, b). Here, I summarize these changes by reviewing the Upper Triassic stratigraphy and chronology of PEFO.

CHINLE GROUP

Lucas (1993a, b) assigned all Upper Triassic nonmarine strata in the western United States (Wyoming, Idaho, Utah, Colorado, Nevada, Arizona, New Mexico, Oklahoma and Texas) to the Chinle Group to emphasize the lithostratigraphic integrity of these strata, which were deposited in a single, vast depositional basin. Upper Triassic strata exposed at PEFO belong to two formations of the Chinle Group, the Petrified Forest and Owl Rock Formations (Figure 1).

PETRIFIED FOREST FORMATION

Most of the Chinle Group strata exposed at PEFO belong to the Petrified Forest Formation (Figure 1). Three members are present (ascending order): Blue Mesa, Sonsela and Painted Desert.

Blue Mesa Member

Lucas (1993b) coined the name Blue Mesa Member for strata previously termed "lower Petrified Forest Member". The type section is in the Tepees-Blue Mesa area of the southern part of PEFO.

Blue Mesa strata are the oldest rocks exposed at PEFO and are as much as 83 m thick here, but their base is not exposed in the park. Mudstone dominates the Blue Mesa Member and is bentonitic, mostly not calcareous and displays variegated hues of purple, blue, gray and red. Interbedded sandstones (about 20-30% of the Blue Mesa Member) are mostly trough-crossbedded micaceous (biotite-rich) litharenites. The Blue Mesa Member is best exposed in the southern portion of PEFO from the Tepees south. Exposures in the northern portion of the park are limited to the Alexander Wash-Wildhorse Wash area.

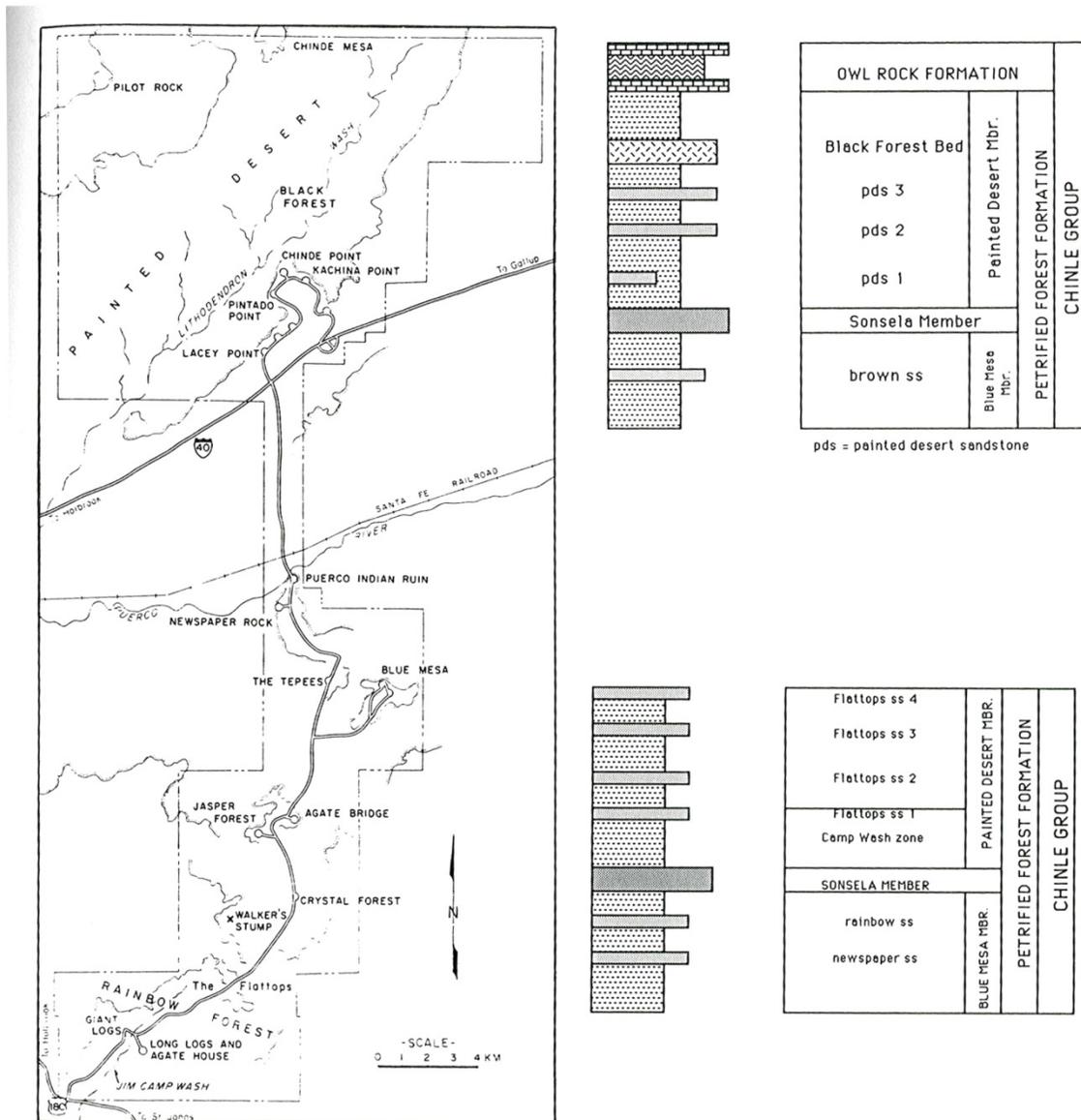


Figure 1. Index map (left) of Petrified Forest National Park and generalized stratigraphy of the northern portion of the park (upper right) and the southern portion of the park (lower right).

In Petrified Forest National Park, informal stratigraphic nomenclature exists for three locally persistent sandstone beds in the Blue Mesa Member (Figure 1):

1. Newspaper sandstone - Billingsley (1985) used the term Newspaper sandstone (it was the newspaper rock sandstone in Daugherty, 1941) to refer to the lowest ledge-forming sandstone in the Blue Mesa Member at PEFO. The Newspaper sandstone is very localized; it is only present along the mesa exposed primarily in secs. 9, 15 and 16, T19N, R24E in the southern part of PEFO. It is as much as 10.7 m thick and has 4.5 to 6.1 m of erosional relief at its base. This light brown, medium- to coarse-grained sandstone is ripple laminated and trough-crossbedded.
2. Rainbow sandstone - Cooley (1957) introduced the term rainbow forest sandstone for the stratigraphically lowest persistent sandstone bed in the southern part of PEFO; it is stratigraphically between the newspaper sandstone and the Sonsela Member. At Rainbow Forest, the stratigraphically lowest fossil-log field in the park occurs in the rainbow sandstone. All outcrops of the rainbow sandstone are in the Giant Logs-Agate House area at the southern end of PEFO. About 6 m thick, the rainbow sandstone is generally trough-crossbedded, locally conglomeratic and lithologically similar to the Sonsela Member.
3. Brown sandstone - Billingsley (1985) applied the name brown sandstone to the lowest mappable sandstone in the northern part of PEFO. It forms a persistent ledge along the banks of Lithodendron Wash between I-40 and the park boundary where it is a trough-crossbedded, pale orange to yellowish-brown, micaceous litharenite with a basal intraformational conglomerate of mudstone and calcrete pebbles.

Sonsela Member

The Sonsela Member is a cliff- and bench-forming sandstone and conglomerate throughout the southern part of PEFO that is only very locally exposed in the Alexander Wash-Wildhorse Wash area of the northern part of the park. It defends the mesa tops at Jasper Forest, Agate Bridge, Blue Mesa and Crystal Forest. The Sonsela Member is as much as 20 m thick and is mostly through-crossbedded litharenite and chert-pebble conglomerate (Deacon, 1990).

In the northern part of PEFO, there are local pinchouts of the Sonsela Member (Billingsley, 1985). This is particularly evident in the SE 1/4, NE 1/4 sec. 11, T19N, R23E along the eastern flank of Wildhorse Wash where a thin Sonsela sandstone ledge pinches out laterally into muddy sandstone and mudstone that lithologically resemble beds of the Blue Mesa Member.

The base of the Sonsela Member marks a major change in lithology from underlying Blue Mesa Member mudstones and siltstones to Sonsela conglomerates and sandstones. This contact shows clear evidence of channeling and erosion, marking it as an unconformity.

Painted Desert Member

The Painted Desert Member of Lucas (1993b) overlies the Sonsela Member conformably. The northern portion of PEFO, the "Painted Desert", is the type area of this unit and is badlands mostly developed in the Painted Desert Member. At PEFO, the Painted Desert Member is as much as 147 m thick, and 80-90% of its thickness is reddish-brown, calcareous, bentonitic mudstone. Several informally named sandstone beds are present in the lower part of the Painted Desert Member, as is a formally named bed of reworked tuff. The informally named sandstones are the Flattops and Painted Desert sandstones of Roadifer (1966) and Billingsley (1985).

The Flattops sandstones are exposed in the southern portion of PEFO, principally on the low buttes called the Flattops in secs. 29-32, T17N, R24E. These sandstones are four, locally persistent ledges separated by mudstone and siltstone slopes. They are trough-crossbedded, laminated and ripple laminated, micaceous litharenites and contain basal, intraformational conglomerates.

The Painted Desert sandstones are exposed only in the northern portion of the park, along and near Lithodendron Wash. Three sandstones have been identified and numbered (in ascending order) 1 through 3. Painted Desert Sandstone 1 is very localized, only cropping out along Lithodendron Wash near Zuni Well in sec. 7, T19N, R24E. Painted Desert sandstones 2 and 3 are more persistent, forming prominent benches throughout the Lithodendron Wash area. The Painted Desert sandstones are lithologically very similar to the Flattops sandstones, and the two sandstone complexes are broadly correlative (Roadifer, 1966).

The Black Forest Bed of Ash (1992) (formerly Black Forest tuff: Billingsley, 1985) is a prominent, white, ledge-forming bed of very tuffaceous sandstone and conglomerate as much as 10.6 m thick. Its base is typically brown-weathering limestone-pebble conglomerate overlain by white-weathering pink to purple reworked tuff. The "Black Forest" is a log and stump field - mostly of *Araucarioxylon arizonicum* - in the tuff. Ash (1992) reported a K-Ar age of 239 ± 9 Ma from biotite in the upper tuffaceous part of the Black Forest Bed. This is a Middle Triassic age by any timescale and underscores the fact obvious from outcrop examination that the volcanic detritus in the Black Forest Bed has been reworked from an older source. Painted Desert Member strata above the Black Forest Bed are dominantly reddish-brown mudstones and siltstones with some lenticular sandstones.

OWL ROCK FORMATION

The Owl Rock Formation conformably overlies the Painted Desert Member of the Petrified Forest Formation at Chinde Mesa and Pilot Rock along the northern edge of PEFO. Lucas (1993b) and Dubiel (1993) described Owl Rock strata here, which are at least 30 m thick and mostly consist of pale red litharenite and orange-pink silty mudstone and siltstone with color mottled ledge-forming beds of pisolitic limestone. Owl Rock strata are the youngest Triassic rocks exposed in the park, being overlain unconformably by upper Cenozoic rocks.

CHRONOLOGY

Fossil vertebrates of two land-vertebrate faunachrons are present at PEFO: Adamanian vertebrates from the upper part of the Blue Mesa Member and Revueltian vertebrates from the lower part of the Painted Desert Member (Lucas and Hunt, 1993). These vertebrates and other biostratigraphically significant fossils (especially palynomorphs) indicate a late Carnian age for the Blue Mesa Member and an early-middle Norian age for the lower part of the Painted Desert Member (Murry and Long, 1989; Murry, 1990). The Carnian-Norian boundary is thus at or near the base of the Sonsela Member. Evidence from outside of the park indicates the Owl Rock Formation is no younger than middle Norian. Thus, by the Harland et al. (1990) timescale, the Upper Triassic strata at PEFO were deposited about 212 to 222 million years ago.

ACKNOWLEDGEMENTS

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ANATOMICALLY PRESERVED PLANT REPRODUCTIVE STRUCTURES FROM THE UPPER TRIASSIC CHINLE FORMATION IN PETRIFIED FOREST NATIONAL PARK, ARIZONA

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ABSTRACT

Anatomically preserved plant reproductive structures including seeds, seed-bearing, and pollen-bearing organs occur in calcareous nodules embedded in a lens of cuticular shale in the

Upper Triassic Chinle Formation in Petrified Forest National Park, Arizona. The fossil plant material in the nodules is significant because it represents the first nonstem material with internal anatomical preservation from the Chinle Formation, and promises to provide new information about Triassic seed plants and their affinities. Currently under study are small, isolated radiospermic seeds, four-chambered sac-like seed-bearing structures and synangiate pollen organs with nonstriate bisaccate *Alisporites* pollen. Affinities of these reproductive organs appear to be with the Mesozoic pteridosperms; this is of particular interest because so few confirmed Mesozoic pteridosperms have been described from North America.

INTRODUCTION

The Upper Triassic Chinle Formation, which outcrops extensively in northeastern Arizona and adjacent areas of New Mexico, Colorado and Utah, contains one of the most floristically rich Upper Triassic fossil plant deposits in the world (Ash, 1980). Over 70 plant taxa are known from the Chinle Formation, including lycopods, ferns, cycads, conifers, bennettitaleans, and several forms that are currently unclassified. Most of these fossils occur as compression-impression remains which show the outer form of the plant and often provide well preserved cuticular remains of taxonomic utility (e.g., Ash, 1980). A considerably smaller proportion of the Chinle flora is known from petrified stems that can show internal anatomical structure. This latter type of material includes the famous logs of *Araucarioxylon arizonicum*, of the Petrified Forest National Park, Arizona (Daugherty, 1941), as well as the enigmatic stem *Schilderia adamanica* and several smaller plants such as the lycopod *Chinlea* (Miller, 1968) and the cycad *Charmorgia* (Ash, 1985). However, although currently known Chinle megafossils provide a good bit of

information on the diversity of the Late Triassic flora of North America, relatively little is known about the internal anatomical structure of these plants.

A small lens of cuticular shale which outcrops in the lower part of the Petrified Forest member of the Upper Triassic Chinle Formation (Ash, 1980; Pigg, Davis and Ash, 1993) in Petrified Forest National Park, Arizona contains plant remains with internal anatomical preservation. The lens represents an overbank deposit of transported mud, silt and plant fragments. This unusual material offers the first opportunity to study anatomically preserved seeds, leaves and reproductive material in the Chinle Formation. The nodules contain a variety of fragmentary plant remains including leaves with preserved cuticle of the conifers *Brachyphyllum* and *Pagiophyllum* and of *Dinophyton*, a plant of uncertain taxonomic affinity, small woody twigs, seeds and seed- and pollen-bearing reproductive structures (Pigg, Davis and Ash, 1993).

DESCRIPTION

Illustrated here are some of the most completely preserved gymnospermous reproductive structures found thus far in the Petrified Forest nodules. The radiospermic seeds are about 2.2 x 2 mm with a megaspore membrane, a typically prominent nucellus, and three-zoned integument (Fig. 1). The nucellus is free from the integument for most of its length. The innermost integumentary layer is composed of tangentially elongate, thin-walled cells, the middle layer of darker, radially elongate, barrel-shaped cells and the outermost layer which is typically poorly preserved, but appears to be composed of smaller, compact cells. Some of these seeds show a slightly elongate beak-like prolongation of the micropylar end. Four-chambered seed-bearing structures (not figured), also under study, may have borne these seeds.

The pollen organs are synangiate and contain bisaccate *Alisporites*-type pollen. These organs are up to 1.4 mm thick in transverse section and are attached to fragmentary laminar tissue (Fig. 2-6). Within the pollen organ, clusters of pollen are surrounded by a uniseriate sporangial wall composed of cuboidal cells and to the inside, a region of thin-walled tissue up to several cells thick (Fig. 3-5). Larger palisade-like cells with dark contents surround the pollen organ (Fig. 2-5), which is sometimes found adhering to laminar tissue (Fig. 5). Up to five pollen sacs have been counted in the incompletely preserved specimens that have been studied. Based on the six specimens presently under study, it is estimated that pollen organs were probably composed of about 10-12 pollen sacs, which are fairly completely fused to one another for at least part of their length. Dehiscence slits have not yet been observed in the pollen sacs. The pollen is of the *Alisporites* type, bisaccate, nonstriate, and up to 80 μm (Fig. 6).

DISCUSSION

Based on the structural features of this material, we suggest that seeds, seed-bearing and pollen-bearing organs are most similar to those of the Mesozoic pteridosperms (seed ferns), and may represent a previously unknown plant in the Triassic Chinle Formation. The proposed seed fern affinities of this material are based on the following criteria: size, shape and morphology of

seeds, organization of the integument of the seeds, fused, cupulate nature of four-armed, presumed seed-bearing structures, the pollen organ nature of pollen-bearing structure, and in situ occurrence of *Alisporites* pollen which is known to belong to the Corystospermales, a group of primarily Southern Hemisphere pteridosperms (Taylor and Taylor, 1993). Interestingly, however, the present material appears to include synangiate pollen organs, while typical corystosperm pollen organs are nonsynangiate (Taylor and Taylor, 1993). Earlier, Stone (1978) noted the presence of a corystosperm-like fructification containing the pollen *Pityosporites* in the Chinle.

Until recently, Triassic seed ferns have been known primarily from the southern continents, with related groups not becoming common in the northern hemisphere until the Jurassic. The presence of possible Mesozoic seed ferns in the Chinle Formation therefore is of considerable importance, in extending their paleogeographic range.

ACKNOWLEDGEMENTS

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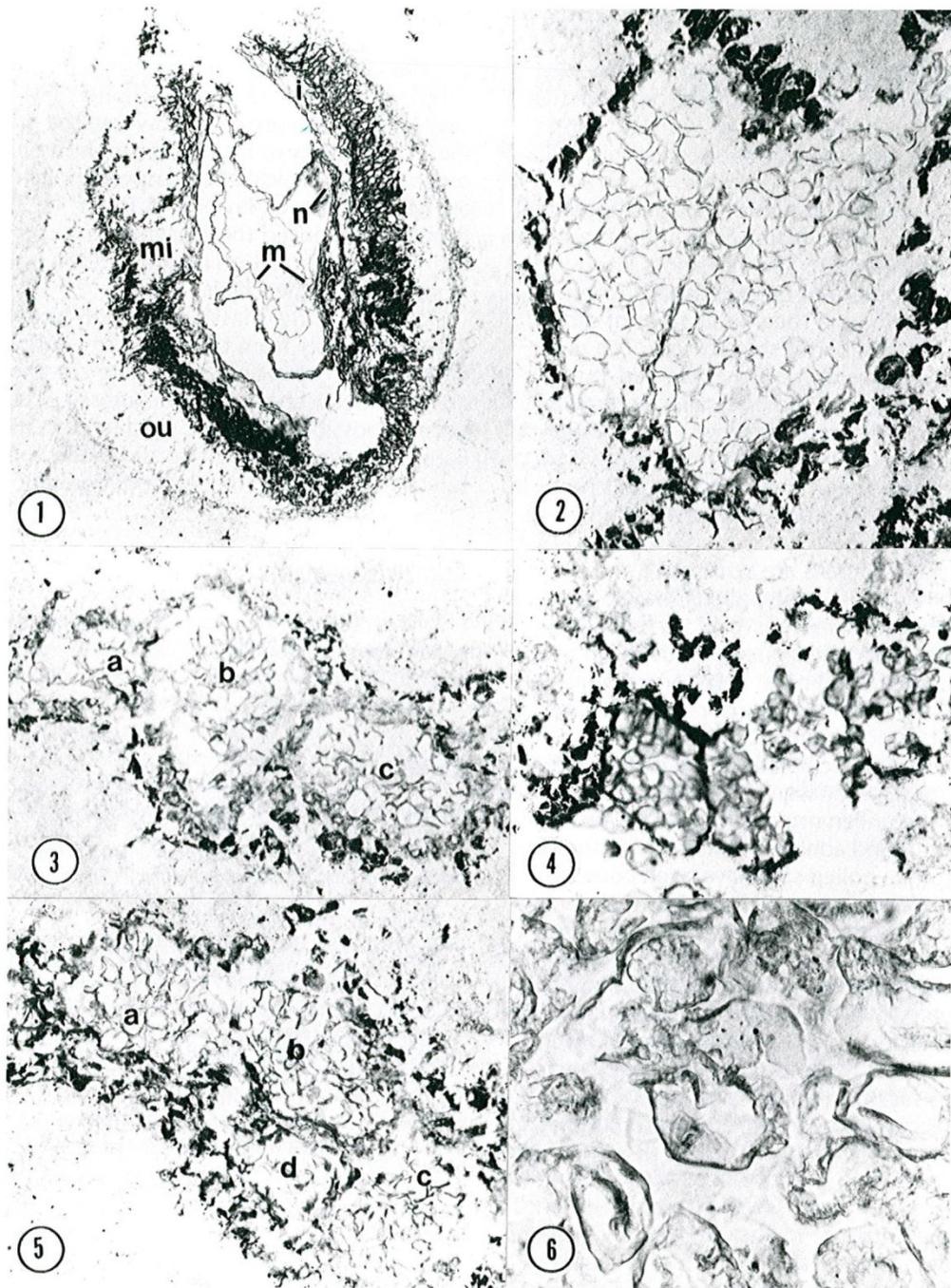


Figure 1. (1). Longitudinal section of radiospermic seed showing megaspore membrane (m), nucellus (n), and three-parted integument. Inner zone of integument (i) is composed of tangentially elongate, thin-walled cells, middle cone (mi) of radially elongate, barrel-shaped cells with dark walls, and outer zone (ou) is incompletely preserved but apparently of small, compact cells. 2F Top #40 x 36. (2). Oblique longitudinal section of pollen organ showing two pollen sacs and thick outer sporangial wall (at top left). 2E Bot #24 x 90. (3). Oblique transverse section through pollen organ showing three pollen sacs (a-c), sporangial wall (at lower right), thin-walled tissue surrounding pollen within sacs, and outermost dark-celled tissue delimiting pollen organ (more proximal view of specimen in 5). 12E Top # 21 x 90. (4). Oblique section of pollen-bearing structure with in situ pollen. 2E Top a #3 x 90. 5: More distal view of specimen in 3, showing four pollen sacs (a-d). 12E Top #36 x 90. 6: Detail of in situ bisaccate pollen in 4. 12E Top #21 x 300.

LATE TRIASSIC VERTEBRATE TRACKS FROM PETRIFIED FOREST NATIONAL PARK

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ABSTRACT

The first documented vertebrate tracks from Upper Triassic rocks of the Petrified Forest National Park represent three morphotypes. Elongate parallel grooves are "swim tracks" and two morphologies of small pentadactyl tracks represent *Rhynchosauroides* sp. These are some of the few vertebrate tracks from the Carnian of the Chinle Group. *Rhynchosauroides* sp. are known from several Rhaetian units in the Chinle.

INTRODUCTION

Petrified Forest National Park (PEFO) in northeastern Arizona is one of the most fossiliferous areas for Late Triassic fossils in North America. The range of fossils is also very large and includes petrified wood, plant compressions, bivalves, gastropods, crustaceans, invertebrate trace fossils, fish, amphibians and reptiles. However, until recently virtually nothing was published about vertebrate trace fossils other than coprolites. Caster (1944, p. 82) noted that tracks "apparently of vertebrate origin" were found in the Newspaper sandstone (sensu Billingsley, 1985). These will not be discussed further. Unpublished notes of a National Park Service Naturalist on file at PEFO also mention the discovery of vertebrate tracks (Appendix). None of these specimens are apparently extant, but this occurrence is discussed further below. The first published documentation of tracks from PEFO was by Santucci and Hunt (1993). The purpose of this paper is to evaluate the previous records of vertebrate tracks, to provide descriptions of recently collected specimens and to briefly comment on their importance of vertebrate tracks from PEFO.

WALKER'S VERTEBRATE TRACKS

Myrl V. Walker, former Naturalist at PEFO made detailed notes on tracks from the park which were never published (Appendix). Copies of these notes were sent to several geologists including E. D. McKee. These notes describe the tracks in great technical detail (Appendix) and appear to have been intended to be the draft of a formal description which was never published. Unfortunately, no photographs or drawings accompany this description.

Several points of Walker's description suggest that some or all of these supposed vertebrate tracks actually pertain to limuloids. In the early part of the century this misidentification was relatively common until the seminal paper of Caster (1938). These points are: (1) many trackways are present at one locality; (2) tail drags (caudal traces) are straight not sinuous; (3) first digit of pedal impression is directed posteriorly; (4) tracks occur on sloping beds in Sec. 22, T. 18N., R. 24E) from the Blue Mesa Member of the Petrified Forest Formation; and (5) manual impressions are placed markedly medial to the pedal impressions. These facts all suggest that the tracks, at least in part, do not represent vertebrates because: (1) Carnian vertebrate tracks are rare in western North America (see below) and it would be unusual to find them in abundance, whereas limuloid tracks are commonly found in abundance (Caster, 1938; Hunt et al., 1993a) and have been reported as locally common at PEFO (Caster, 1944); (2) Vertebrate tail drags are almost always sinuous whereas limuloid tail drags are usually straight (Caster, 1938); (3) not many vertebrate tracks have a posteriorly directed digit, an exception being the Early-Middle Triassic *Rotodactylus* (Peabody, 1948), whereas the ectognathic feet of limuloids have a prominent "toe" directed posteriorly (Caster, 1938, fig. 1c); (4) Caster's (1944) limuloid tracks and Walker's specimens both come from sloping beds of the Blue Mesa Member in the same Section (Caster 1944: Appendix); and (5) it would be rare for a vertebrate trackway to have the manual impressions markedly medial to the pedal impressions. In addition, Carnian limuloid trackways have been reported from PEFO (Caster, 1944; Hunt et al., 1993a), limuloid tracks were preserved in the PEFO collection in the middle part of the century (Caster, 1944) and limuloid tracks have frequently been misidentified as pertaining to vertebrates (Caster, 1938, 1944). Thus, it appears that some, if not all, of Walker's specimens pertain to limuloids. Caster (1944) notes that vertebrate tracks occur in the same stratigraphic unit in the same area as the limuloid trackways (see also below) and thus it is possible that some of Walker's specimens are vertebrate in origin. Finally, it is worth noting that if it were not for the detail of Walker's descriptions, we would not be able to reevaluate his specimens and also that it has been a common mistake for limuloid tracks to be misinterpreted as vertebrate in origin. Of Walker's and Caster's specimens, only the holotype of the limuloid *Kouphichnium arizonae* is extant at the National Museum of Natural History with a mold at the University of Cincinnati and a cast at the University of Colorado at Denver. Other specimens were misplaced or discarded.

DESCRIPTION OF NEW TRACKS

In 1993, vertebrate tracks were observed at two localities in sandstones of the Blue Mesa Member of the Petrified Forest Formation (sensu Lucas, 1993) in the southern portion of PEFO. These specimens are from Sec. 22, T. 18N., R. 24E (the same Section as Walker's and Caster's specimens) from the Newspaper sandstone or its equivalents (exact locality information on file at PEFO). One specimen was collected (Santucci and Hunt, 1993, unnumbered fig.). Three morphologies of tracks are present.

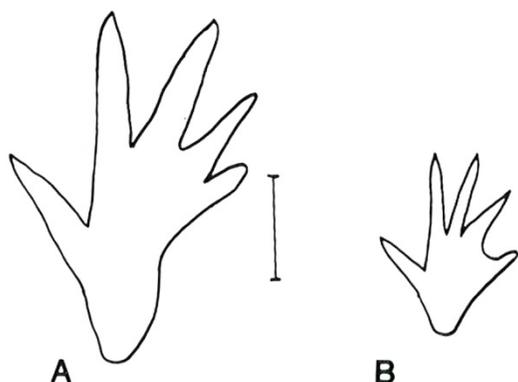


Figure 1. Two specimens of *Rhynchosauroides* sp. from the Blue Mesa Member of the Petrified Forest Formation (Late Carnian), Petrified Forest National Park. Scale bar is 1 cm.

1993, unnumbered fig.). This print represents the impression of a left pes. The impression of digit V diverges from the others. Digit impressions IV-I showing decreasing length. The heel impression is narrow and elongate. In overall morphology this track is similar to ichnospecies referred to *Rhynchosauroides* which probably represents the track of a sphenodontid (e. g., Haubold, 1971, fig. 28).

The third type of track is represented by isolated pentadactyl pedal impressions which are quite small (1.5 cm in length). The best print is a left (Fig. 1B). Digit impression V diverges from the others. Digit impressions IV and III are subequal in length with II being slightly shorter. The impression of digit I diverges from that of digit II. The heel impression is more indistinct than for the above morphotype but appears relatively shorter and wider. This specimen also falls within the range of *Rhynchosauroides* (Haubold, 1971, fig. 28).

DISTRIBUTION OF TRACKS IN THE CHINLE GROUP

Hunt and Lucas (1992) noted that vertebrate tracks are nonrandomly distributed stratigraphically within the Chinle Group. Most Chinle tracks are Rhaetian in age (e. g., Lockley, 1986; Conrad et al., 1987; Lockley et al., 1992). Few tracks are known from Norian units (e. g., Hunt et al., 1993b) and even less from late Carnian ones. In fact the only other Carnian tracks from the Chinle Group

At one locality there are elongate parallel depressions which are similar to others attributed to the toe-drag marks of swimming tetrapods. Such "swim traces" are common in the Early-Middle Triassic Moenkopi Formation in Arizona and Utah (Lockley et al., 1994) but are rare in the Chinle Group (Lockley, 1986).

The second type of track is known from an isolated pedal impression which is slightly weathered. This track is 3 cm long and pentadactyl (Fig. 1A: Santucci and Hunt,



Figure 2. Photograph of the left pes of *Rhynchosauroides* sp. from the Blue Mesa Member of the Petrified Forest Formation (Late Carnian), Petrified Forest National Park.

are undescribed tracks from the Bluewater Creek Formation in eastern New Mexico (Dubiel et al., in prep.)

Rhynchosauroides has been reported from several Rhaetian units of the Chinle Group including the Rock Point Formation in Utah, Bell Springs Formation in Utah and Colorado and the Sloan Canyon Formation in New Mexico (Lockley, 1986; Conrad et al., 1987; Lockley et al., 1992). It is also known from the Early and Middle Triassic portions of the Moenkopi Formation (Peabody, 1948; Hunt et al., 1993c, table 2). Thus, at the generic level *Rhynchosauroides* is of no biochronologic utility.

ACKNOWLEDGMENTS

We thank Bill and Jenny Cotton for assistance with fieldwork.

APPENDIX

The following document is preserved on file at PEFO and was retrieved by VLS and independently MGL obtained a copy from the papers of the late E. D. McKee. The document is undated and typed throughout (including signature) and is reproduced without corrections (e. g., typographical errors).

NOTES ON FOSSIL TRACES IN THE PETRIFIED FOREST NATIONAL MONUMENT, ARIZONA

Although a variety of animals and plant fossils have been reported from the Triassic beds (Chinle) of the Petrified Forest National Monument area, no report has as yet recorded the presence of tracks of animals. A few forms of tracks and trails have been known for some time, but they were so poorly preserved that no attempt was made to describe them. Recently, however, the writers attention was called to an area where a few tracks were discovered. Since that time quite a number of slabs of sandstone which carry trackways have been collected and placed in our study collections.

These recently discovered trackways are small and delicate, but very well preserved. They were apparently made by some small quadrupedal reptile or amphibian whose skeletal parts are as yet unknown from the Triassic of this region. The Triassic rocks of the Connecticut valley are of course noted for the wonderful series of trackways which have been described from that region, and it is very interesting to now record the existence of tracks and trackways in the upper Triassic (Chinle) of the western interior basin area. (See Lull's "Triassic Life of the Connecticut Valley").

At the present time no attempt is being made to refer these specimens to any known or described Triassic trackways. These tracks and trackways are found on the fine-grained sandstones (often ripple marked and mud cracked) which occur between a series of even bedded shales and clays in the lower Blue Forest area. The clays and shales produce impressions of Cycads, Ferns, and

the side branches of the Giant Neocalamites casts and the tracks and trackways of animals. Fossil vertebrate bones have not as yet been found in this series of alternating shales and sandstones, but they do occur in shales not more than a half mile from this area.

It is clearly evident that we have here discovered some of the old land surfaces of Triassic time. These land surfaces were apparently bordered by streams or lakes which frequently flooded the low-lying areas. Once more the Blue Forest region becomes a field laboratory of great interest, for it has told, through its tracks and trackways, of forms of animal life not previously known to have existed in this region in Triassic time, and has provided material for another scene in the picture of the old Triassic Forest.

DESCRIPTION OF FOSSIL TRACKWAY

Type -Catalogue number 190, Petrified Forest National Monument. This specimen consists of a slab of sandstone about 14" x 10" x 1" which carries a consecutive series of tracks and evidently made on a sloping "dune or ripple of sand". Collected by Mr. Clare Hepworth, B. P. R. Engineer.

Referred specimens -Numbers 192, 193, 195 and 196, Petrified Forest National Monument.

Type locality -Petrified Forest National Monument, Arizona. In the Blue Forest, 200 yards south of the road which runs west by northwest in the NW1/4 of Sec. 22, Twn. 18 N., R. 24 E.

Geological occurrence - Triassic (Chinle) about 150 to 200 feet above the Moenkopi contact.

Description -Small quadrupedal form of animal. Stride about 27 mm.; width of trackway--manus 30 mm., pes 55 mm. Three digits in manus. Five digits in pes. Manus digitigrade; pes slightly plantigrade. caudal trace straight, not undulating.

Manus -The impression of the manus is composed of three slender depressions. It appears that the three digits were made on a sloping surface and the manus was turned in or rotated, causing the digits to leave three impressions in a semi-circle. The claws were pointed in toward the body. Another specimen which has a trackway on a smooth surface shows the three digits making three parallel impressions paralleling the body, with the inner digit the longest.

Pes -The impression of the pes is composed of five depressions. The digits were long and slender and had sharp pointed claws. The first digit is directed backward, the other forward, but diverging from the center of the pes. The impression of the fourth digit is the longest. Where the trackway is made on a sloping surface, the pes is rotated and the four forward digits are pointed toward the body.

General -The position of the front feet, that is, close together and directed straight forward, would tend to indicate that the forward part of the body was carried well off the ground. The sharp pointed manus impressions indicate something of a digitigrade condition. It is impossible to determine which digits are present, but probably those represented are the 2nd, 3rd and 4th.

The slender, long, but diverging digits of the hind foot, and the well spread trackway, might indicate that the hind legs were considerably longer than the front legs. The peculiar rotation of the hindfoot when walking on a sloping surface, indicates a very flexible condition in these parts.

M. V. Walker.
Park Naturalist.

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SYSTEMATIC AND ECOLOGIC SIGNIFICANCE OF FOSSIL HARDWOODS

EXAMPLES FROM BIG BEND NATIONAL PARK, YELLOWSTONE NATIONAL PARK, AND FLORISSANT NATIONAL MONUMENT

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INTRODUCTION

Spectacular and abundant remains of petrified woods occur at Big Bend National Park, Texas, Yellowstone National Park, Wyoming, and Florissant Fossil Beds National Monument, Colorado, of Cretaceous and Paleocene, Middle Eocene, and late Eocene ages, respectively. These woods provide valuable data about the past distribution and diversity of flowering plants and changes in climate and vegetation through geologic time. Woody remains provide direct evidence of whether a fossil plant was a tree, shrub, or woody vine, and so are useful for interpreting vegetation type. Growth ring characteristics and the sizes and distributions of the water conducting element in fossil woods provide information valuable for interpreting past climates and climate change.

Usually the first questions asked about petrified wood are- What is it? What is its name? Visitors who see petrified wood ask these questions out of general curiosity, but these are questions that need answering before a wood can provide data useful for understanding the past distribution and diversity of woody plants. However, answering 'what is it?' often is not easy, particularly for hard wood from the Cretaceous and early Tertiary. Identifying a fossil wood generally requires preparation of thin sections of three different views of that wood and use of a microscope. Considerable comparative work is necessary to establish whether the wood is similar to or different from wood of present-day plants.

Today there are tens of thousand of tree species, and so determining the relationship of a fossil wood to recent plants often is quite time-consuming. Most present-day trees fall into two groups: softwoods (the conifers which produce their seeds in cones, for example, pine, spruce, redwood) and hardwoods (dicotyledonous angiosperms which produce seed in flowers, for example, oak, maple, and elm). These two groups have distinct wood structure. This paper only discusses only fossil hardwoods, in other words, woody dicotyledons, a group that is of more recent origin (Cretaceous) than the softwoods.

Generally, the older a wood is, the less likely it is that there is an extant wood with the same combination of characters as the fossil. In the eocene forests of North America, eastern Asia,

southeast Asia, Central and South America, or even Africa (e.g. the Clarno flora of eastern Oregon, in the John Day Fossil Beds National Monument, Manchester in press), this means that comparative work cannot be restricted to trees that grow in the geographic region at present. Databases with information on the anatomy of extant fossil woods help with this comparative work (Wheeler et al. 1986; LaPasha and Wheeler and Baas, 1991).

Following are brief summaries of some work done on fossil wood from Big Bend, Yellowstone, and Florissant. These summaries are intended to indicate the importance of the fossil woods from these localities for helping answer questions about the history of woody dicotyledons during a time interval (Cretaceous-Early Tertiary) that is famous for marking the extinction of the dinosaurs and the rise of mammals, but is also significant in the development of modern vegetation and the diversification of flowering plants.

BIG BEND NATIONAL PARK

Big Bend National Park provides a unique setting for studying changes in wood structure through time. In Big Bend there are localities with petrified trees ranging in age from Cretaceous through Miocene (Busbey and Lehman, 1989; Koeppe, Sanchez, Stephens, and Stephens, personal communications). A series of publications documenting the types of fossil woods and their ecologic and systematic significance has been initiated (Wheeler, 1991; Wheeler, Lehman, and Gasson, in press; Wheeler and Lehman, ms. in preparation). Most studies of fossil woods are based on fragments whose position within the plant is not known. Often fragments are small and it is not always possible to tell whether they represent root or stem wood. Most of our knowledge of wood structure (both systematic and ecologic) is of mature stem wood and so it can be difficult to determine affinities or make ecologic inferences for small samples that might represent root or branch wood. The fossil logs of Big Bend provide an opportunity to control sampling, in other words, a collector can be sure of where the sample came from, and a minimum diameter of the tree directly measures and with that information the height of the tree estimated.

What is particularly important about the localities within Big Bend is that there is considerable information on the geology and vertebrate paleontology in the Park (e.g. Lehman, 19985,1987,1990; Rowe,et al.1992). Thus, its possible to put the paleobotanical work into a stratigraphic framework, and interpretations of the woody plants' ecological anatomy can be integrated with the information derived from other studies.

How Big and How Common were Hardwoods During the Cretaceous? Woods from the Late Cretaceous (Campanian and Maastrichtian) of Big Bend National Park.

Although angiosperms were diverse and dominate late Cretaceous palynofloras and compression floras (Crane, 1990; Upchurch and Wolfe, 1987), it has been suggested that dicotyledonous trees were restricted to riverbanks and disturbed habitats and did not form forests (Wing et al., 1993). Moreover, it has been generalized that "Late Cretaceous angiosperm tree trunks were mainly less

than 10 cm in diameter and thus were of a size that they could have easily been knocked over by ceratopsids" (Dodson, 1993: p. 230). The preceding statement is based primarily on studies of fossils from the northern Rocky Mountains. There was latitudinal variation in the vertebrate faunas (Lehman, 1987), and so it should not be surprising that there is comparable variation in vegetation. The fossil woods from Big Bend National Park, Texas, suggest that some generalizations about Late Cretaceous angiosperms need revision because dicotyledons more than 10 cm in diameter were common in the Late Cretaceous of the Big Bend region.

Throughout the Aguja Formation (Campanian, Late Cretaceous) of Big Bend National Park, Texas, there occur petrified woods. At some localities dicotyledonous logs with a diameter of more than 50 cm are common, while at other localities, there are only relatively small wood fragments (2-3 cm diameter). Some localities and depositional settings have only dicotyledons, others have conifers and palms. To date, it appears that dicotyledons are the most common woods in the Aguja Formation, although only six types of dicotyledonous woods, all species different from present-day trees (Rich et al., 1986) suggest the fossil trees with a 50 cm diameter would have been more than 30 meters tall. These data indicate that Cretaceous angiosperms were as large as some of the common hardwoods of North America (e.g., sycamore, *Platanus occidentalis*).

In the younger Javelina Formation (Maastichtian, Late Cretaceous), there occurs *Javelinoxylon*, an ancient representative of the primarily tropical plant group Malvales. *Javelinoxylon* was a tree that had a diameter in excess of 70 cm, and so also was taller than 30 m (>100 feet) (Wheeler, Lehman, Gasson, in press). Additionally, there are stump fields in the lower portion of the Javelina with the stumps seemingly in growth position. Some of these stumps are over 1 m in diameter, and have exposed roots over 3 m long. Work on these woods is just beginning, but such occurrences can provide information about the spacing of dicotyledonous trees in the Cretaceous landscape, as well as the range in sizes within different types of Cretaceous trees. Some of these trees are of interest because they show evidence of heartrot; some stumps had hollow centers that were infilled with sediment during the Cretaceous. They can provide data about the interactions between trees and decay organisms of the past.

What Tree Types Survived the Terminal Cretaceous Event? North America's Best Known Paleocene Dicotyledonous Woods, Big Bend National Park

For the whole world fewer than 20 types of fossil dicotyledonous woods of unequivocal Paleocene age have been described. The only Paleocene dicotyledonous woods described from North America are from the Black Peaks Formation of Big Bend (Wheeler, 1991). In the Tornillo Flats region of the park, there are many logs, but the vast majority of these logs are of a single type, a wood assigned to the genus *Paraphyllanthoxylon*. *Paraphyllanthoxylon* type wood is seen in at least four different extant plant families, all of which are primarily tropical (Euphorbiaceae, Lauraceae, Anacardiaceae, Burseraceae). Moreover, all of these woods lack distinct growth rings as is characteristic of U.S. woods at present. The lack of distinct growth

rings and the size and number of vessels (water conducting elements) suggest that the woods grew in tropical climates, with year-round abundant water and warm temperatures, an environment that is in marked distinction to the Big Bend region of the present-day. In Big Bend, another Paleocene locality with abundant and large logs has been found, and superficial examination of these woods suggests that they too belong to the genus *Paraphyllanthoxylon*.

Woods with the structural patterns of *Paraphyllanthoxylon* are among the earliest known hardwoods, occurring in the Albian (mid-Cretaceous). Such woods were widespread in the Cretaceous and have been recovered from the Cretaceous of California, Alabama, Arizona, New Mexico, southern Illinois, Maryland, Utah, Baja California, Europe, and South Africa. This structural pattern is of interest as it was common in the Cretaceous as well as the Paleocene. Because it is rare to find attachment between reproductive structures (which are most important in defining plant families) and vegetative structures (woody stems or twigs) there is no way of being sure how many species of plants this one wood represents. It is likely that this successful wood pattern occurred in more than one species or genus. Additional work searching for woods of Paleocene age is important for shedding light on which tree types were successful in both the Cretaceous and Paleocene and were able to survive the Cretaceous-Tertiary terminal event, which was marked by massive extinctions.

YELLOWSTONE NATIONAL PARK

When Did Present-Day Genera Appear, and Tropical Forests? Yellowstone National Park - Eocene Forests - Mixtures of extinct and extant genera.

The Early Middle Eocene "Fossil Forests" of Yellowstone National Park are one of the most spectacular localities for early Tertiary fossil plants. At Specimen Ridge, Amethyst Mountain, and the Gallatin Forests there are "layer cakes" of fossil forests that were entombed in successive volcanic eruptions (Smedes and Prostka, 1972). Many of the fossil stumps are upright. There is debate about whether these stumps represent *in situ* remains of the fossil forests or whether some or all stumps were transported (Fritz, 1980; Yuretich, 1984; Wing, 1987). Resolution of this question is important for paleoecological inferences, but pending its resolution, the well-preserved woods at Yellowstone provide data that are useful in reconstructing the histories of different plant families and changes in dicotyledonous wood structure during the Tertiary.

The Middle Eocene was one of the warmest intervals of recent geologic history. The evolutionary radiations of many extant woody dicotyledonous families are recorded in the Eocene, e.g., in the Birch Family (Betulaceae; Crane, 1989), Beech/Oak Family (Fagaceae; Crepet and Nixon, 1989), Walnut Family (Juglandaceae; Manchester, 1989a), and Elm Family (Ulmaceae; Manchester, 1989b).

Although many of the stumps at Yellowstone are conifers, there are many dicotyledonous leaves. Conifer wood may be more likely to be preserved, as conifer lignins (the complex chemicals that make woody cell walls rigid) may be more resistant to decay organisms than hardwood lignins.

Also, conifers may be more permeable as there numerous interconnections between all the cells in conifer woods, so that petrification via infiltration of the cell wall with silica-carrying water is more likely in conifers than in angiosperms.

Among the hardwoods (dicotyledonous angiosperms) recognized at Yellowstone, some have wood structure identical to modern plants and at present occur in warm temperate to subtropical regions (e.g., cherry - *Prunus*, family Rosaceae; alder - *Alnus*, family Betulaceae; ironwood - *Carpinus*, family Betulaceae), others resemble trees that today occur primarily in the tropics (woods of the Sterculiaceae, Magnoliaceae, Lauraceae) (Wheeler et al., 1977, 1978). Some differ from extant plants. The sycamore-like woods of Yellowstone have a combination of features that indicates they are related to modern sycamores (*Platanus*), but differ in some features that wood anatomists have long considered to be "primitive" features. In these Eocene sycamore-like woods all the end walls of the water conducting cells (vessel elements) have bars across them (scalariform perforation plates), while modern sycamores, even those growing in Viet-Nam, have some water conducting with end walls without bars across them, and large open ends (simple perforation plates). The wood that resembles Chinese elm (*Zelkova*) differs from the modern genus in its distribution of vessel diameters.

FLORISSANT NATIONAL MONUMENT

Is the Late Eocene climatic change recorded in dicotyledonous woods?

There is a wide body of evidence from marine and terrestrial sediments that indicate that the end of the Eocene was marked by a dramatic change in climate (Wolfe, 1978). The characteristics of the three dicotyledonous wood types recovered from Florissant National Monument reflect this dramatic change.

One of the primary functions of wood is water conduction; the structure of wood reflects water availability. Carlquist (1977, 1988) and Baas (1986; Baas et al., 1983) have studied the geographic and ecologic distribution of different anatomies and have shown that there exists ecological trends in dicotyledonous wood anatomy. Their work indicates that with increasing drought or decreasing temperature there is an increase in vessel frequency, percentage of vessel groupings, incidence of spiral thickenings in the vessel elements, a shortening of vessel elements, and a decrease in vessel diameter. Ring porous dicotyledonous woods are characterized by the vessels of the first-formed portion of a growth ring being markedly larger than the vessels in the later-formed portion of a growth ring. In the present-day flora, ring porous woods are common in north temperate region, but very rare in the tropics and absent from very high latitudes.

Two of the three wood types from Florissant are ring porous with relatively short vessel elements, and one has spiral thickenings in the vessel elements. The diffuse porous wood (diffuse porous woods have vessels of near equal size throughout a growth ring) has many vessel groupings, and the average vessel diameter is less than 100 micrometers, a diameter usually

categorized as small. All three types have distinct growth rings. Thus, the anatomies of these woods indicate a markedly seasonal climate.

CONCLUSION

The localities briefly discussed above illustrate the uses that fossil dicotyledonous woods have for answering questions about the past distribution and diversity of ancient angiosperms. The differences between the Cretaceous and Paleocene woods from Big Bend, the Middle Eocene woods from Yellowstone, and the Late Eocene woods from Florissant illustrate the dramatic changes in climate and vegetation type that have been documented for the Cretaceous through early Tertiary (Wolfe, 1978; Wing, 1987; Upchurch and Wolfe, 1987). The Cretaceous and Paleocene woods of Big Bend lack distinct growth rings and are generalized in their structure, the Middle Eocene woods of Yellowstone have growth rings and most are referable to extant families and genera, the Late Eocene woods of Florissant have distinct growth rings and suggest pronounced seasonality and also have anatomy like that of extant woods. Continuing work on woods from these three areas will refine our knowledge of the history of woody plants, and wood itself, an important tissue deserving of study, as it functions in water conduction, support, and storage for trees and shrubs.

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Afterword

A review of currently published scientific articles associated with National Park Service units reveals an inconsistent use of park abbreviations and acronyms. Authors frequently utilize self-generated abbreviations 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 NPS acronyms have been incorporated during the preparation of this document. Listed below are the acronyms established for most of the national park units that have recognized paleontological resources.

AGFO	Agate Fossil Beds National Monument	FONE	Fort Necessity National Battlefield
AMIS	Amistad National Recreation Area	FOBU	Fossil Butte National Monument
ANIA	Aniakchak National Monument	GAAR	Gates of the Arctic National Park
APPA	Appalachian National Scenic Trail	GWMP	George Washington Memorial Parkway
ARCH	Arches National Park	GETT	Gettysburg National Military Park
ASIS	Assateague Island National Seashore	GLAC	Glacier National Park
BADL	Badlands National Park	GLBA	Glacier Bay National Preserve
BEOL	Bent's Old Fort National Historic Site	GLCA	Glen Canyon National Recreation Area
BELA	Bering Land Bridge National Preserve	GRCA	Grand Canyon National Park
BIBE	Big Bend National Park	GRTE	Grand Teton National Park
BICA	Bighorn Canyon National Recreation Area	GRBA	Great Basin National Park
BISO	Big South Fork National River	GRSA	Great Sand Dunes National Monument
BLCA	Black Canyon of the Gunnison National Monument	GUMO	Guadalupe Mountains National Park
BRCA	Bryce Canyon National Park	HAFO	Hagerman Fossil Beds National Monument
BUFF	Buffalo National River	HALE	Haleakala National Park
CABR	Cabrillo National Monument	HAVO	Hawaii Volcanoes National Park
CACH	Canyon de Chelly National Monument	HOSP	Hot Springs National Park
CANY	Canyonlands National Park	HUTR	Hubbell Trading Post National Historic Site
CARE	Capitol Reef National Park	ICAG	Ice Age National Scenic Preserve
CACA	Carlsbad Caverns National Park	INDU	Indiana Dunes National Lakeshore
CEBR	Cedar Breaks National Monument	JECA	Jewel Cave National Monument
CHCU	Chaco Culture National Historical Park	JODA	John Day Fossil Beds National Monument
CHIS	Channel Islands National Park	JOTR	Joshua Tree National Park
CHIC	Chickasaw National Recreation Area	KATM	Katmai National Park
COLO	Colonial National Historical Park	KEFJ	Kenai Fjords National Park
COLM	Colorado National Monument	KOVA	Kobuk Valley National Park
CRMO	Craters of the Moon National Monument	LACL	Lake Clark National Park
CUGA	Cumberland Gap National Historical Park	LAME	Lake Mead National Recreation Area
CURE	Curecanti National Recreation Area	LAMR	Lake Meredith National Recreation Area
DEVA	Death Valley National Monument	LABE	Lava Beds National Monument
DEWA	Delaware Water Gap National Recreation Area	MACA	Mammoth Cave National Park
DENA	Denali National Park	MEVE	Mesa Verde National Park
DETO	Devil's Tower National Monument	MOCA	Montezuma Castle National Monument
DINO	Dinosaur National Monument	MOCI	Mound City Group National Monument
DRTO	Dry Tortugas National Park	NATR	Natchez Trace Parkway
FIIS	Fire Island National Seashore	NABR	Natural Bridges National Monument
FLFO	Florissant Fossil Beds National Monument	NERI	New River Gorge National Scenic River
		NIOB	Niobrara/Missouri National Riverways

NOAT Noatak National Preserve
OLYM Olympic National Park
PAIS Padre Island National Seashore
PETE Petersburg National Battlefield
PEFO Petrified Forest National Park
PISP Pipe Spring National Monument
PORE Point Reyes National Seashore
REDW Redwood National Park
RICH Richmond National Battlefield Park
RIGR Rio Grande Wild and Scenic River
ROMO Rocky Mountain National Park
RUCA Russell Cave National Monument
SACN St. Croix National Scenic Riverway
SAMO Santa Monica Mountains National Recreation Area
SCBL Scotts Bluff National Monument
SEQU Sequoia National Park
THRO Theodore Roosevelt National Park
TICA Timpanogos Cave National Monument
VAFO Valley Forge National Historical Park
WACA Walnut Canyon National Monument
WICA Wind Cave National Park
WRST Wrangell-St. Elias National Park
WUPA Wupatki National Monument
YELL Yellowstone National Park
YUHO Yucca House National Monument
YUCH Yukon-Charley Rivers National Preserve
ZION Zion National Park



As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the 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 by encouraging stewardship and 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.