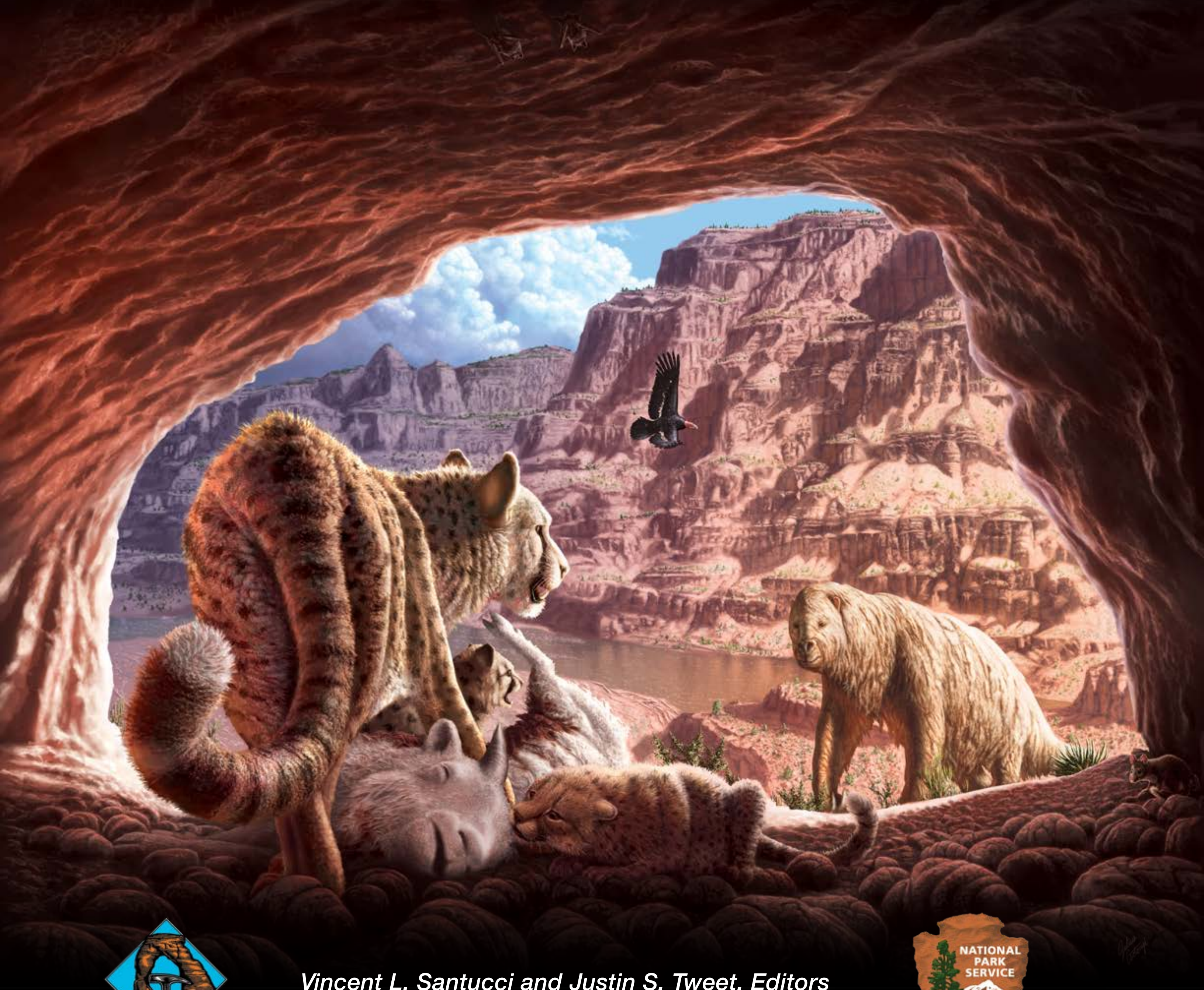
Utah Geological Association Special Publication 1

GRAND CANYON NATIONAL PARK CENTENNIAL PALEONTOLOGICAL RESOURCES INVENTORY

A CENTURY OF FOSSIL DISCOVERY AND RESEARCH



Vincent L. Santucci and Justin S. Tweet, Editors

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Spectacular double rainbow as viewed from Yavapai Point on the South Rim of Grand Canyon National Park.

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Cover illustration: A Pleistocene open woodland scene from Rampart Cave in the western portion of the Grand Canyon. The painting by artist Julius Csotonyi features American cheetahs (*Miracinonyx trumani*), Harrington’s mountain goat (*Oreamnos harringtoni*), Shasta ground sloth (*Nothrotheriops shastensis*), Stock’s vampire bats (*Desmodus stocki*), California condor (*Gymnogyps californianus*), and a woodrat (*Neotoma*). Fossils of all of these prehistoric animals have been found in Rampart Cave. See chapter 11 by Mead and others in this volume, “Pleistocene/Holocene Cave Fossils from Grand Canyon National Park—Ice Age (Pleistocene) Flora, Fauna, Environments, and Climate of the Grand Canyon, Arizona,” for more details.

Design and layout by Stevie Emerson

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The Utah Geological Association (UGA) is a non-profit organization of geologists and other geoscientists that share a common interest in Utah's geology. The purpose of the UGA is to increase and disperse geological information to the scientific community, and promote public awareness of the usefulness of geology in general. The UGA does this through the voluntary efforts of its members.

Become a member of the UGA to help support the work of the Association and receive notices for monthly meetings, annual field conferences, and new publications. Annual membership is $20 and annual student membership is only $5. Visit the UGA website at www.utahgeology.org for information and membership application.

The UGA board is elected annually by a voting process through UGA members. However, the UGA is a volunteer-driven organization, and we welcome your voluntary service. If you would like to participate please contact the current president or committee member corresponding with the area in which you would like to volunteer.

FORWARD
Paleontology of Grand Canyon National Park

On an otherwise unremarkable fall day in 2017, National Park Service Senior Paleontologist Vincent Santucci made an astonishing proposal: he offered to lead a comprehensive paleontological inventory of Grand Canyon National Park. Astonishing, in that such a survey had not yet been accomplished at what is arguably the world's most geologically iconic national park and that the timing could not have been better. We were preparing to celebrate the 2019 Centennial of Grand Canyon National Park; the first complete paleontological park inventory would be a highlight of the celebration.

This proposal kicked off a whirlwind of activity and collaboration that resulted in a year-long effort by a world-class team of multi-disciplinary geologists and paleontologists to research, investigate, and ground-truth the astonishing array of fossils up to 1.25 billion years old that are exposed in the canyon. This adventure included the first-ever PaleoBlitz at a national park in October 2019, development of a popular set of paleontology trading cards, presentations during the Grand Canyon National Park Paleontology Symposium, and hosting of the tenth anniversary of National Fossil Day. The culmination of this extensive work was the publication of a volume presenting the remarkable history of life and its evolution as uniquely exposed in GRCA. Out of this effort would come an improved understanding of ancient environments, extinction events, the discovery of new life forms, and a catalogue of ancient life.

Lead Paleontologist Vince Santucci sets the context for this study, the impetus for the largest effort of its kind by the NPS, and the critical work behind the scenes. Dr. Earl Spammer provides an evocative and fascinating account of the 160-year history of fossil exploration at the canyon. The following paleontology inventory chapters are organized chronologically, by stratigraphic strata, and taxonomically, characterizing trace fossils, invertebrates, vertebrates, and plants found in the predominantly Precambrian to Paleozoic rocks of the Grand Canyon. Several of the life forms presented by these authors were newly discovered during the week-long PaleoBlitz held at the canyon.

A series of experts presents the inventory of life in the canyon's fossil record, from the very earliest life forms starting around 1.25 billion years ago in the Precambrian era (stromatolites and microfossils), through explosions of ancient life, punctuated by extinction events, in the Paleozoic era from the Cambrian (~541–485 million years ago) up into the Permian (~270 million years ago), as seen by the diversity of fossils (trilobites, brachiopods, mollusks, corals, fish, sharks, horsetails, seed ferns, clubmosses, conifers) preserved in these rocks. This variety of ancient life was abruptly cut off in the late Permian by earth's most catastrophic extinction event, which was followed by the slow recovery of life between approximately 252 and 215 million years ago in the early Mesozoic era, barely represented in the youngest GRCA rocks by fossil logs and reptilian trackways. A separate chapter presents the much more recent lifeforms of the Ice Age (Pleistocene and Holocene), represented by fossils (extinct mountain goats, ground sloths, tortoises, packrats, camels) found in GRCA's caves. Finally, the inventory is capped by a section outlining appropriate paleontological resource inventory, monitoring, and protection efforts, with recommendations for outreach, education, and stewardship of these unique treasures.

During these hectic times, it is important to contemplate the long history of life, punctuated by massive extinction events, to imagine ancient worlds with exotic climates, and to ponder what lifeforms are yet to be discovered in these rich environments exposed so uniquely at Grand Canyon. This volume will reward you with the opportunity to celebrate the wonderous diversity of plants, animals, and environments that have inhabited this now iconic setting, and invite you to explore the complete inventory more deeply, and perhaps even add to it.

Jeanne A. Calhoun
Division Chief, Science & Resource Management, Grand Canyon National Park

DEDICATION

On behalf of the Grand Canyon National Park Centennial Paleontological Resource Inventory team we would like to dedicate this report to Colleen Hyde and Kim Besom (GRCA Museum) and to all National Park Service curators, museum specialists, museum technicians, collections managers and archivists.

Kim Besom (left) and Colleen Hyde (right) standing at an overlook on the Grand Canyon rim.

First, we recognize that the work we are involved with in the NPS Paleontology Program and at GRCA has consistently benefited by the dedicated professionalism of park museum staff. For paleontology, maintaining fossil collections in museums is a fundamental and core value of the science. The meticulous detail and care provided for fossil collections in the NPS, not only contributes to the science of paleontology, but it is fundamentally important to our preservation/conservation mission and goals in the NPS. This is especially true for our non-renewable remains of ancient organisms preserved in our national parks.

Moreover, much of this important and often behind the scenes work undertaken by museum professionals, is the foundation for our scientific research and resource management related to non-renewable fossil resources. We have clearly benefited by the support from many museum professionals in the NPS, who through their work contribute to the scientific integrity of the important legacy data associated with park museum fossil collections. We are reminded continuously during our work in the NPS Paleontology Program of how we have benefited from the meticulous work of museum professionals at all levels (WASO, regions and parks).

Both Colleen and Kim exemplify the best of the best in professional museum curators. Not only do they maintain the huge database of knowledge related to what is now more than 100 years of GRCA history and museum objects that preserve the rich stories of the park, but they do so with passion and dedication. Colleen and Kim have been so very helpful to each one of our GRCA Paleontology Team with our many requests for assistance. As long as we have worked together with Colleen and Kim, they have always been so helpful and friendly in support of our research. They have accommodated a long list of researchers that were sent their way to view collections and obtain curatorial records to support their research. A number of current and past paleontology interns praise Colleen and Kim on a regular basis.

This GRCA Paleontological Resource Inventory project is an important one for us all—and it is equally important that we are able to extend our thanks and tribute to the museum professionals who have supported our work and we have all come to call our friends and colleagues.

UTAH GEOLOGICAL ASSOCIATION PRESIDENT'S MESSAGE

The Utah Geological Association (UGA) is proud to present UGA Special Publication 1, Grand Canyon Centennial Paleontological Inventory—A Century of Fossil Discovery and Research. The Grand Canyon is rightly world famous as a geologic laboratory, with well-exposed outcrops that span the ages, from the Proterozoic through the early Mesozoic Eras, and showcases nearly two billion years of Earth's history. Because of is scientific, scenic, and social significance, the Grand Canyon has been the subject of numerous paleontological and geological studies since Major John Wesley Powell traveled through it by boat in 1869. It is timely that the most current collection paleontologic studies have been compiled into a single volume for the 100th anniversary of Grand Canyon National Park.

My first exposure to this marvelous terrain and geology of the Grand Canyon was as a young teen when my family left St. George, Utah, early on a beautiful fall morning, drove over the Hurricane fault, up and around the volcanic Mt. Trumbull, and arrived at my grandfather's old ranch near Toroweap, on the Canyon's North Rim. Brachiopods and horn corals seemed to pop out of the rocks everywhere, and the lava flows contained rounded xenoliths, filled with bright green olivine crystals. Driving to the Toroweap Overlook, the narrowest portion of the Canyon, the layering that records the geologic architecture of the region was plain even to me. The Colorado River roared as it parted around an ancient volcanic neck that rises in the center of the stream. The whole area screams to be explored and studied. That was the trip when I decided to be a geologist.

It may seem strange to have the UGA publish a paleontological volume on the Grand Canyon, which is in Arizona. The mission of the UGA is "…the increase and diffusion of geological knowledge and the encouragement of public appreciation and knowledge of the utility and application of geologic science." The largest portion of the Colorado Plateau is in Utah, containing the formations and fossils that are so brilliantly displayed in the Canyon. The reason that the UGA is delighted to publish this work is because it is directly related to Utah's geology and that it will help all geoscientists and geoenthusiasts to better understand ancient ecosystems across the region. Even a basic understanding of the paleontology of the Grand Canyon will enhance your visit to the canyon and the many parks and monuments across the Colorado Plateau.

We'd like to thank the U.S. National Park Service for the opportunity to publish this volume and the support they've provided to the authors and editors. Many thanks to the authors who donated countless hours preparing their articles. The editors are to be commended for their labor of love in bringing this all to pass. Geologists and paleontologists, as a rule, love their profession, and that enthusiasm is obvious in this book.

Riley Brinkerhoff
President, UGA 2020–2021

ABOUT THE EDITORS

Vince Santucci

Vincent L. Santucci is the Senior Paleontologist and Paleontology Program Coordinator for the U.S. National Park Service (NPS). Beginning in 1985, Vince has held assignments at Badlands, Petrified Forest, Grand Canyon, Yellowstone, Fossil Butte, Tule Springs Fossil Beds and other national parks, as well as supported geology and paleontology projects in over 200 national park areas. Vince has been a leader for paleontological resource management, protection, education, stewardship and science in the U.S. and has published more than 200 articles and reports related to NPS paleontology. Vince was instrumental in establishing "National Fossil Day" in 2009 and is the recipient of various honors and awards including the Brunton Compass, George Wright Natural Resource and George Hartzog Stewardship awards. Recently Vince was recognized as a "Public Lands Hero" by Leave No Trace Center for Outdoor Ethics. Vince completed his B.S. and M.S. in geology and paleontology at the University of Pittsburgh and is currently enrolled as a doctoral candidate in the Department of Recreation, Parks and Tourism Management at Penn State University involved with research on human dimensions of paleontological resources.

Justin Tweet

Justin Tweet is an associate of the Paleontology Program of the National Park Service. His primary responsibilities are writing, editing, and conducting research for inventories, publications, and other documents concerning paleontology in the National Parks. Although his work has intersected a great diversity of fossil groups and geologic units, he is most familiar with the denizens of the Cambrian and Ordovician of Minnesota. Justin completed a B.A. in geology with a minor in biology at the University of St. Thomas in St. Paul, Minnesota, and completed a M.S. in geology at the University of Colorado–Boulder.

DRAGONFLY WING
Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Dragonfly Wing
Scientific Name: *Typus whitei*
Geologic Age: 285 million years ago (Permian)
Geologic Formation: Hermit Formation

Interactive 3D model

Abundant plants, like this seed fern, increased oxygen in the atmosphere.

This fossil is the type specimen of *Typus whitei*. This nearly complete fore-wing is from an early, but much larger, insect similar to a dragonfly. Insects were able to grow much larger during this time, because there were more plants releasing oxygen into Earth's atmosphere.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

3 of 9

Grand Canyon National Park Fossil Trading Card featuring a wing of the fossil dragonfly-like insect Tupus whitei *(originally named* Typus*).*

THE PALEONTOLOGICAL HERITAGE OF GRAND CANYON NATIONAL PARK

Vincent L. Santucci[1]

ABSTRACT

The fossil record of Grand Canyon National Park is expansive from geospatial, geologic, temporal paleotaxonomic and paleoenvironmental perspectives. The fossiliferous sedimentary strata are heavily dissected throughout the park's 4,950 square kilometers (1,904 square miles), with a 446 km (277 mile)-long canyon cut by the Colorado River reaching an average depth of approximately 1.6 km (1 mile). The earliest fossils of the Grand Canyon date to around 1.2 billion years ago during the Mesoproterozoic. The thick sequence of overlying Paleozoic sedimentary strata preserve abundant fossil remains and traces of marine and terrestrial invertebrates, vertebrates and plants. An extensive cave system developed into the marine limestones of the canyon preserve the remains of a diverse Pleistocene fauna. The human dimension of the paleontological resources are shorter-lived and span back to the 1857 Ives Expedition and the first documented collection of fossils in the Grand Canyon. The Grand Canyon National Park Centennial Paleontological Resource Inventory attempts to compile the many dimensions of the park's paleontological heritage to support current and future scientific research and public education.

INTRODUCTION

Throughout my life I have been bestowed the privilege of experiencing the world-renowned landscape and resources of the Grand Canyon from many perspectives and viewsheds (figure 1). My first views were standing and taking photos from the many vantage points and overlooks along the North and South rims. I have enjoyed many hikes into the canyon with colleagues from the National Park Service (NPS) or with academic geologists and paleontologists. On a few occasions I ventured down and then back up the trails of the canyon with my children Sarah, Bethany, Luke, Jacob, Brianna and Abigail, often carrying one or more in my arms on the climb against gravity. I traversed by foot to the base of the canyon at Phantom Ranch and gained a greater appreciation for the geologic story preserved in the park strata. I have gazed intensely out the window of many commercial aircraft from above this geologic wonder of Earth, contemplating the geomorphic "grandeur" created over "Deep Time" and the artistry of processes perfected by "Mother Nature." I pinch myself when I recall the opportunity when my friend Justin Tweet and I were granted permission to fly into the western portion of the Grand Canyon on a small NPS plane operated by a pilot from Lake Mead National Recreation Area. As we meandered above the Colorado River and below the canyon rim, we celebrated when we located one of the paleontological crown jewels of the NPS: the entrance to Rampart Cave. I have studied the Grand Canyon through many scientific articles and geologic/topographic maps, and in my contemplation and dreams, I always ask myself, "What is still out there? What fossilized remains from our past are yet to be discovered?" I love this Grand Canyon!

The stars were aligned in 2019 to assemble a team, with the support of the Grand Canyon National Park leadership, to undertake a comprehensive paleontological resource inventory for the park. One of the primary catalysts to this ambitious task was tied to the centennial celebration for Grand Canyon National Park, in recognition of the 100th anniversary of the park's establishment on February 26, 1919. The discussions for the paleontological resource inventory began between the NPS Paleontology Program and Grand Canyon Nation-

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[1] *National Park Service*
Geologic Resources Division
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Washington, D.C. 20240

Santucci, V.L., 2021, The Paleontological Heritage of Grand Canyon National Park, *in* Santucci, V.L., and Tweet, J.S., editors, Grand Canyon National Park Centennial Paleontological Resources Inventory—A Century of Fossil Discovery and Research: Utah Geological Association Special Publication 1, p. 1-10.

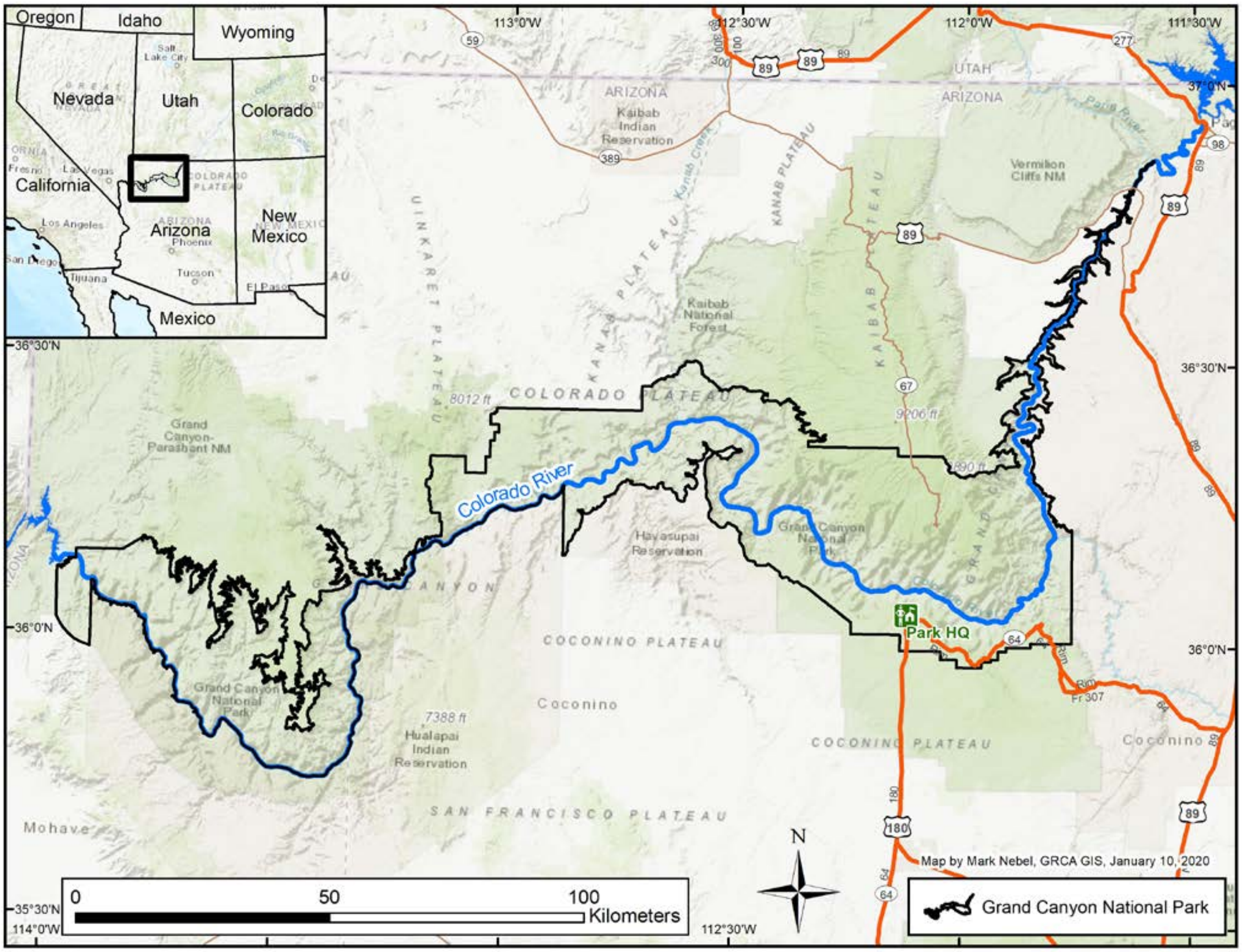

Figure 1. *Map of Grand Canyon National Park (NPS/MARK NEBEL).*

al Park staff in 2018, which led to tremendous support to move forward with a park-specific paleontological resource inventory in conjunction with the centennial. A multidisciplinary team of subject matter experts were assembled to assist in the development of the thematic manuscripts which make up this publication and to assist with a number of paleontology-focused tasks and activities related to the paleontological resources of Grand Canyon National Park. In addition to this publication focused on the paleontology of Grand Canyon National Park, two other major tasks were undertaken during the park's centennial. One consisted of hosting the Grand Canyon National Park PaleoBlitz, only the second such undertaking sponsored by the NPS Paleontology Program (the first was hosted at Chickasaw National Recreation Area in 2016). The other was the hosting of the 2019 National Fossil Day Celebration at Grand Canyon National Park (figure 2). As part of the Grand Canyon National Park Centennial events, in September 2019 we gathered together at Mather Point and celebrated National Fossil Day with our friends, partners and the public. Diana Boudreau (2020) summarizes the various components and accomplishments in an after-action report available through IRMA at **https://irma.nps.gov/DataStore/Reference/Profile/2268299.**

A PALEONTOLOGICAL RESOURCE INVENTORY FOR GRAND CANYON NATIONAL PARK

The principal goals and objectives for the Grand Canyon National Park Centennial Paleontological Resource Inventory were to identify the scope, significance, distribution and management issues associated with the fossils of the park. Through this effort we compiled baseline paleontological resource information for park managers and staff to better understand the non-renewable resources under their stewardship, and in turn help to inform park planning and decision-making which may relate to park fossils. This publication is written for park managers, in the language and content most useful for considering the many aspects of management, protection, interpretation and scientific study of National Park Service fossils.

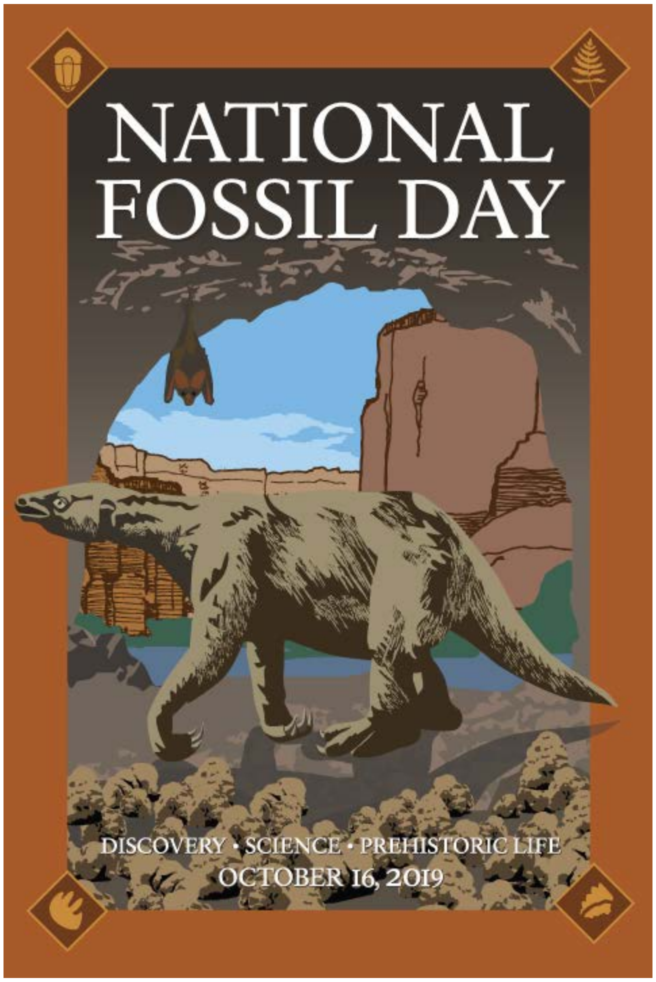

Figure 2. *2019 National Fossil Day logo featuring Pleistocene fauna from Rampart Cave in Grand Canyon National Park (NPS).*

It is also important to recognize the role of the Paleontological Resource Preservation Act of 2009 (PRPA) in defining the need for undertaking this paleontological resource inventory for Grand Canyon National Park. Specifically, Section 6302 of PRPA (16 USC 470aaa-1) mandates for the NPS and other Department of Interior bureaus that "The Secretary shall manage and protect paleontological resources using scientific principles and expertise. The Secretary shall develop appropriate plans for inventory, monitoring, and the scientific and educational use of paleontological resources." The work undertaken in conjunction with the 2019 Grand Canyon National Park Centennial Paleontological Resource Inventory exemplifies this legal standard and scientific principle.

The Grand Canyon National Park Centennial Paleontological Resource Inventory represents the largest such inventory in National Park Service history. The work required the collaboration of a team of paleontologists, NPS staff, and a number of partners. Subject matter experts with previous research and experience involving Grand Canyon fossils were involved in various aspects of this inventory including drafting or peer review of the manuscripts presented in this undertaking. The collective work is represented by this publication, by new fossil specimens cataloged in the park's museum collection, and through new interpretive media focused on Grand Canyon paleontology. This work represents the compilation of historical and current research and fossil collections associated with paleontology of Grand Canyon National Park. In addition, fossils documented from outside the administrative boundaries of the park, from the greater Grand Canyon region, have also been considered as part of this inventory.

The first technical article in the Grand Canyon National Park Centennial Paleontological Resource Inventory is *History of Paleontological Work at Grand Canyon National Park—Up and Down the Long Federal and NGO Trails of Paleontology in Grand Canyon National Park, 1858–2019* by Earle E. Spamer. This article presents a historic overview of the park's paleontology, including fieldwork and research. This rich history begins with the first discovery of a fossil in the Grand Canyon in April 1858 in the Diamond Creek area by members of the Ives Expedition and published in 1861 by John Strong Newberry (Newberry, 1861). A long list of notable paleontologists have worked in Grand Canyon and are summarized in Spamer's article (figure 3).

An article devoted to a basic overview on the *Stratig-*

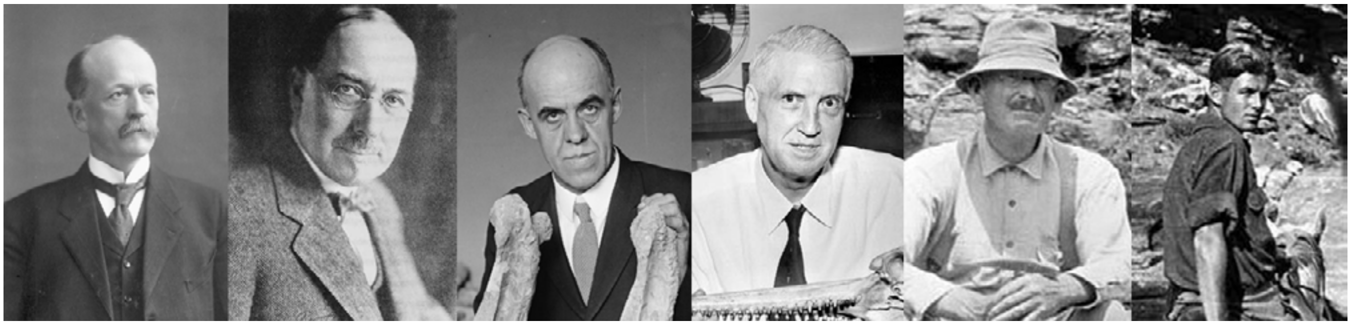

Figure 3. *Notable paleontologists who worked in areas now administered as Grand Canyon National Park including (from left to right): Charles Doolittle Walcott (USNM photo); John C. Merriam (NPS); Charles Gilmore (USNM); Remington Kellogg (USNM); David White (NPS); and Edwin McKee (USGS).*

raphy of Grand Canyon National Park was prepared by Tim Connors and others. Given the paleontological focus of this inventory, there was a need to provide a consistent stratigraphic context for the individual article. This article was not intended to present a comprehensive guide to the geology of Grand Canyon National Park, nor to address unresolved or controversial interpretations or perspectives on the park's geology. The focus on the stratigraphy was viewed as important given the close relationship to the park's paleontology and paleoenvironments represented by the various stratigraphic units.

Grand Canyon National Park preserves important fossiliferous exposures of Precambrian strata. Prior to the area being initially proclaimed a national monument in 1908, paleontologist Charles Doolittle Walcott ventured into the Grand Canyon on his quest for early fossils (figure 4). In the article titled *Precambrian Paleontology of Grand Canyon National Park* by Justin Tweet, he reports on the oldest known fossils preserved at the park and in some cases the earliest reported occurrences of unusual fossil forms such as *Chuaria circularis* and vase-shaped microfossils.

The invertebrate fossil record from the Paleozoic strata of Grand Canyon National Park represents by far the most abundant and diverse category of park fossils. This includes both invertebrate body fossils and trace fossils largely preserved in marine sedimentary rocks, and specific articles are dedicated to each. Linda Lassiter and others have prepared a detailed summary of the invertebrate body fossils titled *Paleozoic Invertebrate Paleontology of Grand Canyon National Park.* Anne Miller and others prepared a comparable work reporting on the invertebrate trace fossils which is titled *Paleozoic Invertebrate Ichnology of Grand Canyon National Park*.

Fossil vertebrates were first reported from the Devonian Temple Butte Limestone in Grand Canyon by Charles Walcott (1880) during the initial surveys undertaken by the U.S. Geological Survey. The Mississippian Surprise Canyon Formation has yielded a rich fossil chondrich-

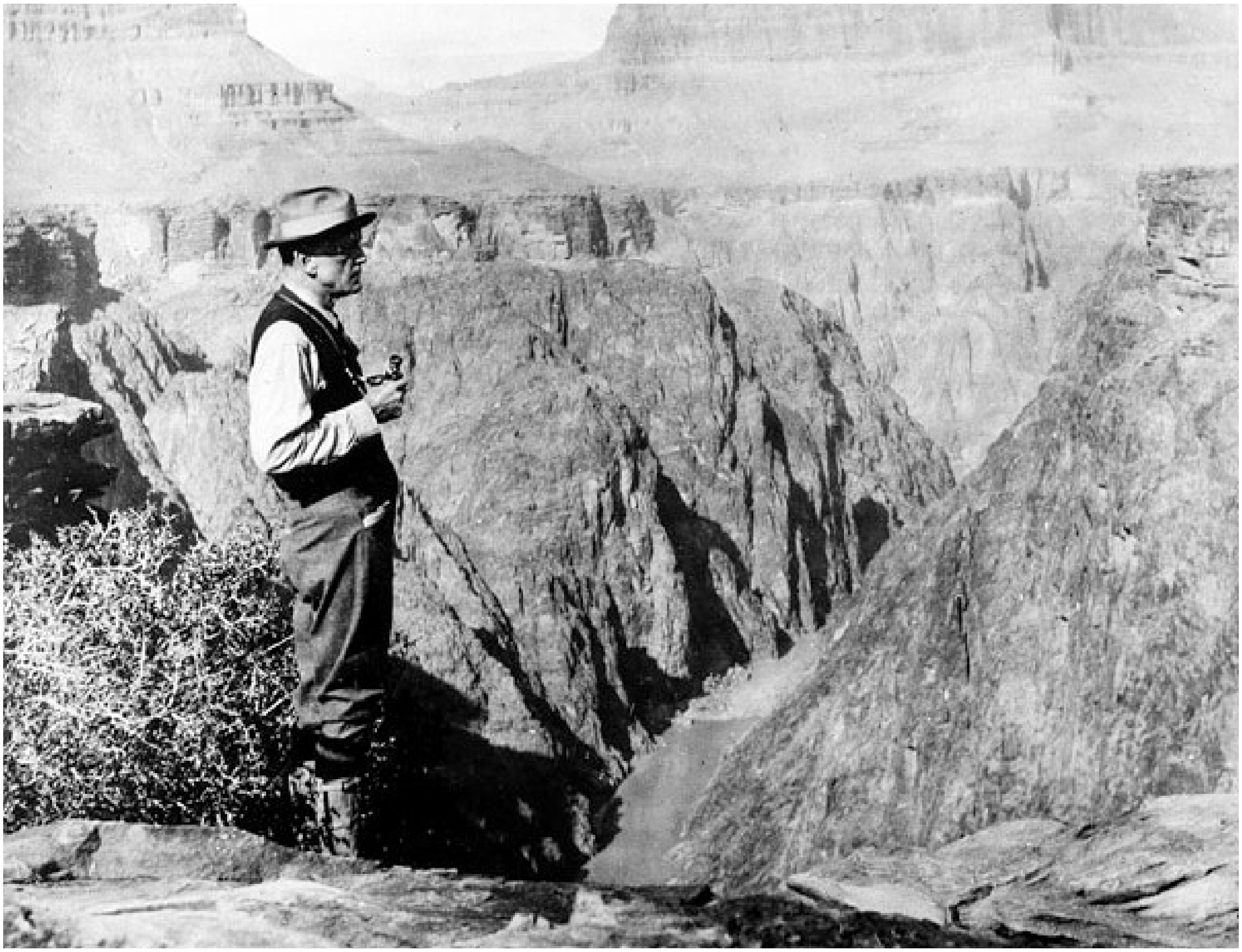

Figure 4. *Paleontologist Charles Doolittle Walcott explored the Grand Canyon's Precambrian and early Paleozoic strata for traces of early life (NPS).*

thyan fauna which has recently been described, with a number of new fossil shark taxa being named (Hodnett and Elliott, 2018) (figure 5). The authors who published on the Surprise Canyon Formation sharks, JP Hodnett and David Elliott, are also the authors for the article titled *Paleozoic Vertebrate Paleontology of Grand Canyon National Park: Research History, Resources, and Potential.*

Fossil plants are summarized by Cassi Knight in her article *Paleozoic Paleobotany of Grand Canyon National Park.* This article reviews the known Paleozoic plant macrofossil resources in Grand Canyon National Park, detailing previously published plant fossil occurrences from the Surprise Canyon Formation, the Supai Group formations, and the Hermit Formation (figure 6). Many of the taxonomic names used by David White in his 1929 monograph on the plant fossils of the Hermit Formation needed to be reviewed in light of more recent publications and taxonomic considerations.

An important Late Paleozoic vertebrate ichnofossil record has been documented from the Hermit Formation and Coconino Sandstone from within Grand Canyon National Park (figure 7). Smithsonian paleontologist Charles Gilmore made large collections of fossil vertebrate tracks from the park during the 1920s. The fossil tracks from the park include some of the oldest occurrences of tetrapod tracks preserved in eolian strata. Lorenzo Marchetti and co-authors review these and other finds in their article titled *Paleozoic Vertebrate Ichnology of Grand Canyon National Park*.

The limited exposure of Mesozoic strata in Grand Canyon National Park is represented by the Triassic Moenkopi Formation and the Shinarump Member of the Chinle Formation. Petrified Forest National Park paleontologists Adam Marsh and Bill Parker coordinated field inventories of the Triassic units in the park during 2019. Marsh and others prepared an article titled *Mesozoic Paleontology of Grand Canyon National Park: Trace Fossils, Stratigraphy, and Regional Correlations*. Marsh and his team documented both invertebrate and vertebrate trace fossils from the Moenkopi Formation in the park, which are the first examples of either reported from the Mesozoic rocks of Grand Canyon National Park.


SHARK TOOTH

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Shark Tooth
Scientific Name: *Amaradontella santuccii*
Geologic Age: 325 million years (Mississippian)
Geologic Formation: Surprise Canyon Formation

Illustration by Benji Paysnoe, AzMNH

Interactive 3D model

This very small shark is ancestral to all modern sharks, including Megalodon.

Amaradontella santuccii was a 17 centimeter (6.5 inch) long shark with microscopic teeth up to 1 millimeter (0.04 inches) in size. This tiny shark thrived in the shallow estuaries and reefs of an ancient bay, feasting on small crustaceans, worms, and fish.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.
Expansion Set 1 of 3

Figure 5. *Grand Canyon National Park Fossil Trading Card featuring the fossil shark* Amaradontella santuccii *from the Mississippian Surprise Canyon Formation (NPS).*

Figure 6. *Civilian Conservation Corps (CCC) constructing the in situ Fossil Fern Exhibit along the South Kaibab Trail during 1937 (NPS).*

Figure 7. *In situ block of Coconino Sandstone with* Ichniotherium sphaerodactylum *trackways in Grand Canyon National Park (NPS/CASSI KNIGHT). This find was documented in Francischini and others (2019).*

The area in and around Grand Canyon National Park contains more than 650 documented caves. Some of these dry caves preserve Pleistocene/Holocene paleontological resources including Ice Age mammals and birds (figure 8). Among these fossils, rare mummified remains of Pleistocene bats and other mammals are preserved with soft tissues and hair in a few of these caves within the canyon. One of the more notable caves in Grand Canyon is Rampart Cave, which preserved stratified sequences of ground sloth dung, but much of the material was lost to an accidental anthropogenic fire in the 1970s. Jim Mead and his team have contributed an article titled *Pleistocene/Holocene Cave Fossils from Grand Canyon National Park* to summarize these discoveries.

The final article of this inventory is specifically dedicated to the management of Grand Canyon National Park's rich and diverse paleontological resources. Diana Boudreau and others developed an article titled *Grand Canyon National Park Paleontological Resources Management and Protection* to help park managers and staff understand the range of activities and issues associated with the management of non-renewable resources. This article focuses not only on the management of fossils found within the rock strata of the park, but also presents information related to fossils in the park's museum collection and other outside repositories which maintain park fossil collections. This article also presents information related to a Geospatial Database developed and piloted by park staff to manage fossil locality data for Grand Canyon National Park.

In addition to article-specific appendices, four supplemental items are included at the end: fossil taxa named from specimens found within GRCA **(part A)**; fossil taxa named from specimens possibly found within GRCA **(part B)**; summary tables of Paleozoic taxa reported from GRCA **(part C)**; and paleontological resource law and policy information **(part D)**.

The study of the paleontological resources at Grand Canyon spans slightly more than 160 years since the first fossils were collected from Diamond Creek during the Ives Expedition in 1858. The team contributing to this publication is dedicated to the paleontology of Grand Canyon National Park and all recognize that we have just scratched the surface in terms of the potential for future fossil discovery. This report is intended to provide a baseline of paleontological resource information as of the 100th anniversary of Grand Canyon National Park in 2019. We collectively admire and benefit from the work of those paleontologists who have come before us and hope that our work will inspire and support the

Figure 8. *Fossil condor skull from Stevens Cave, Grand Canyon National Park (STEVE EMSLIE).*

work by those paleontologists and park managers who will come in the future.

ACKNOWLEDGMENTS

The Grand Canyon National Park Centennial Paleontological Resource Inventory was made possible through the collaboration, contributions and support of an extensive multidisciplinary team. Although the 100th anniversary of GRCA was an exceptionally busy year at the park, we received exceptional support from the park's leadership and staff throughout this project. Central to the decision-making in undertaking the various paleontology-focused projects and events during 2019 at GRCA was Jeanne Calhoun, Chief of Science & Resource Management. Planning for the GRCA Paleontological Resource Inventory and associated activities was initiated between Jeanne Calhoun and Vincent L. Santucci, NPS Senior Paleontologist during the summer of 2018. We are grateful for the enthusiastic support for this project from Jeanne, Deputy Chief of Science & Resource Management Sarah Haas, Acting Superintendent Woody Smeck, Deputy Superintendent Lisa Carrico, and Jan Balsom, Senior Adviser for Stewardship and Tribal Programs.

A long list of GRCA staff played a variety of roles during the planning and implementation of the paleontology-focused work at the park, especially the National Fossil Day Celebration. We extend our appreciation to members of the GRCA Interpretation Staff, Education and Creative Media, including: Laurel Brierly, Sharon Cawley, Vanessa Ceja-Cervantes, Jeremy Childs, Lillian Daniels, Celia Dubin, Jennifer Eberlein, Kevin Garcia, Joel Kane, Grace Lilly, Bryan Maul, Michael Quinn, Warren Rudkin, Todd Stoeberl, Chris Symons, and John Wishart. A number of GRCA staff provided assistance, technical support and information to the paleontological resource inventory, including: Joelle Baird, Santiago Garcia, Jered Hansen, Edward "Ted" McClure, and Eugenia Sullivan.

This project benefited through the work of the previous GRCA Physical Science Program Manager Deanna Greco and previous GRCA Deputy Chief of Science and Resource Management Jane Rodgers, who helped secure funding for a number of paleontology interns, including: Jeff Dobbins, Taylor Hartman, Cassi Knight, and James Super. Each of the interns assisted with compiling baseline paleontological resource data for GRCA during their assignments at the park and shared information that is presented in this report.

Important behind-the-scenes work for this project was put forth by staff from the NPS Geologic Resources Division (GRD), and we extend our thanks to Hal Pranger, Lima Soto, Paige Lambert, Jim Wood, Jack Wood, Jason Kenworthy and John Graham. Additional thanks is extended to staff from the NPS Office of Public Affairs, including Jeff Olson, Kathy Kupper, and Victoria Stauffenberg for helping to share information about this project with the public and media.

The ability to publish the Grand Canyon National Park Centennial Paleontological Resource Inventory in a peer reviewed formal publication was an important component of this research. We greatly appreciate the opportunity provided by the Utah Geological Association to publish this work as Utah Geological Association Special Publication 1. We are indebted and share our thanks to Doug Sprinkel and Stevie Emerson for the support and work in publishing this volume on the rich paleontological heritage of Grand Canyon National Park. We also extend our appreciation to the the American Geosciences Institute, especially Ed Robeck, for their support with this publication.

One of the components of the GRCA Paleontological Resource Inventory was the GRCA PaleoBlitz. The GRCA PaleoBlitz was a field-based inventory for paleontological resources by teams of specialist and subject matter experts in various disciplines of paleontology (e.g. fossil invertebrates, vertebrates, plants and trace fossils). We extend our appreciation to staff from the NPS Biological Resources Division (BRD) for awarding financial support to host the GRCA PaleoBlitz, including Elaine Leslie (Chief of BRD, now retired), and BRD staff Kiersten Jarvis and Kriston Barnes. We would like to extend our thanks to James "Max" Bovis and Tom Olson for the volunteer assistance and participation with the GRCA PaleoBlitz.

A National Fossil Day (NFD) Celebration was organized as a two-day event hosted on the South Rim of GRCA on Friday, September 27 and Saturday, September 28, 2019, as part of the paleontology-focused activities in conjunction with the park's centennial. On Friday evening, a Grand Canyon National Park Paleontology Symposium was organized at the Shrine of Ages and consisted of four fossil-themed presentations open to the public. The speakers included paleontologists Jim Mead (The Mammoth Site), John-Paul Hodnett (Maryland-National Capital Park and Planning Commission), Linda Sue Lassiter (Northern Arizona University) and Spencer Lucas (New Mexico Museum of Natural History and Science). On Saturday, the National Fossil Day Celebration was hosted outside of the GRCA South Rim Visitor Center for the public, and an evening program for the public was presented by NPS Senior Paleontologist Vincent L. Santucci. We wish to thank the many partners that participated in this event, meeting with the public and promoting the scientific and educational values of fossils. Thank you to Bruce MacFadden (Paleontological Society, Florida Museum of Natural

History); Jim Mead (The Mammoth Site); Ed Robeck, Geoff Camphire, Adam Blankenbicker, and Sequoyah McGee (American Geosciences Institute); David and Janet Gillette, Jennifer Glennon, and Richard McMichael (Museum of Northern Arizona); Doug and Hazel Wolfe (Zuni Dinosaur Institute for Geosciences); Andy Grass and Sherman Mohler (Arizona Museum of Natural History, Southwest Paleontological Society); John-Paul Hodnett (Maryland-National Capital Park and Planning Commission); Joel Despain (National Cave and Karst Research Institute); Sandy Croteau (Protectors of Tule Springs); Tom Olson (Geology for Kids); and Anne Scott and Eleanour Snow (US Geological Survey). We are also grateful to our colleagues from the NPS for their participation in the Grand Canyon Centennial National Fossil Day Celebration, including: Jason Kenworthy and Justin Tweet (NPS Geologic Resources Division); Mary Carpenter (Badlands National Park); Maria Rodriguez (Glen Canyon National Recreation Area); Erin Eichenberg and Mary Ontiveros (Tule Springs Fossil Beds National Monument); and Robyn Henderek (Zion National Park).

One of the main components of the 2019 GRCA Centennial Paleontological Resource Inventory was the compilation of the extensive paleontological resource information for the park. The park preserves an extraordinary record of Paleozoic flora and fauna which have been the focus of scientific collection and study for approximately 150 years. A team of notable paleontologists were selected to develop original manuscripts documenting the scope, significance and distribution of fossils throughout GRCA. The final report contains thematic articles presenting a comprehensive overview of the paleontological resource of GRCA. A sincere thank you to each of the lead authors and co-authors who prepared original peer-reviewed manuscripts which are included in this publication, including: P. J. Bergman (Northern Arizona University); Kim Besom (Grand Canyon National Park); Diana Boudreau (Geoscientists-in-the-Parks, American Conservation Experience); Mary Carpenter (Badlands National Park); Carol Chambers (Northern Arizona University); Ronnie Colvin (Grand Canyon National Park); Tim Connors (NPS Geologic Resources Division); Dave Elliott (Northern Arizona University); John Foster (Utah Field House of Natural History State Park Museum); Heitor Francischini (Federal University of Rio Grande do Sul); John-Paul Hodnett (Maryland-National Capital Park and Planning Commission); Adrian Hunt (Flying Heritage and Combat Armor Museum); Colleen Hyde (Grand Canyon National Park); Cassi Knight (Paleoworks Consulting); Linda Lassiter (Northern Arizona University); Spencer Lucas (New Mexico Museum of Natural History and Science); Lorenzo Marchetti (Prehistoric Museum Geoskop); Adam Marsh (Petrified Forest National Park); Jim Mead (The Mammoth Site); Anne Miller (Northern Arizona University); Mark Nebel (Grand Canyon National Park); William Parker (Petrified Forest National Park); Vincent Santucci (NPS Geologic Resources Division); Earle Spamer (retired—American Philosophical Society); Fred Sundberg (retired—Show Low High School); Shawn Thomas (Bat Conservation International); Benjamin Tobin (University of Kentucky); Justin Tweet (NPS Geological Resources Division); Sebastian Voigt (Prehistoric Museum Geoskop); and Klara Widrig (Geoscientists-in-the-Parks).

We want to extend our appreciation and thank you to Don Weeks (DOI Regions 6–8 [formerly NPS Intermountain Region]), who served as the peer review coordinator for the GRCA Paleontological Resource Inventory Report. The peer review process for so many individual articles was an involved process, and Don did a great job in completing the peer review for the many sections of this large report. Additional thanks are extended to the many peer reviewers who help us to improve the content, quality and scientific integrity of information contained in this publication. Thanks are extended to: Harry Butowsky (retired—NPS); Don Corrick (Big Bend National Park); Carol Dehler (Utah State University); Bill DiMichele (Smithsonian Institute); Erin Eichenberg (Tule Springs Fossil Beds National Monument); David Elliott (Northern Arizona University); Matt Friedman (Museum of Paleontology, University of Michigan); Hendrik Klein (Saurierwelt Paläontologisches Museum Neumarkt); Cindy Looy (Smithsonian Institute); Spencer Lucas (New Mexico Museum of Natural History and Science); Jeff Martz (University of Houston); Andrew Milner (St. George Dinosaur Discovery Site); Nicholas Minter (University of Portsmouth); Gary Morgan (New Mexico Museum of Natural History); Sterling Nesbitt (Virginia Polytechnic Institute and State University); Susannah Porter (University of California: Santa Barbara); Wayne Ranney (Grand Canyon river guide, writer, and educator); and Rick Toomey (Mammoth Cave National Park).

Finally, we want to acknowledge the Grand Canyon National Park Paleontology Project Core Team. The individuals below contributed to all aspects of planning, implementation, research, field work, museum collections review, specimen photography, and development of interpretive media. They also reviewed draft manuscripts, issued research and collecting permits, and coordinated communication with park staff, cooperating paleontologists, partners and other individuals involved with the GRCA Centennial Paleontological Resource Inventory. An After Action Report for this project was prepared by paleontology intern Diana Boudreau and is available to download at the following website: **https://irma.nps.gov/DataStore/Reference/Profile/2268299.**

Two paleontology interns, Diana Boudreau and Klara Widrig, were hired for this project and served six months

helping to coordinate the many components of the paleontology-focused activities at GRCA. Colleen Hyde and Kim Besom of the GRCA Museum have been long-term advocates for GRCA paleontology and were extremely helpful with the many museum-related requests during this project. We dedicate this report to Colleen and Kim in appreciation for their years of service supporting GRCA paleontology. GRCA Interpretive Ranger Ronnie Colvin inspired our team with her creative energy, wonderful ideas, and the experiences she has gained by hosting National Fossil Day events at GRCA in the past. Our National Fossil Day Coordinator John-Paul Hodnett (Maryland-National Capital Park and Planning Commission) first suggested hosting a NFD event at GRCA and was instrumental in the success of this special event during the park's centennial. We were fortunate to share in the successful completion of a Master's Thesis from Northern Arizona University by paleontologist Anne Miller. Anne's contributions to this project were many, and her previous work at GRCA prepared her well to help plan field logistics to ensure that all our team remained safe during their ventures for fossils in the canyon. Our scientific advisor for the project, Ronda Newton, helped our team to navigate important discussions and requirements, including our research and collecting permit, to support our planning and project activities. GRCA GIS Program Manager Mark Nebel served many key roles during the 16 months of work involved with the early planning, developing of funding requests, and providing cutting-edge technical geospatial support that we can benefit from in our paleontology work in other NPS areas. Vincent Santucci and Justin Tweet from the NPS Paleontology Program provided coordination of project planning, weekly assignments and meeting, communication, and development of the GRCA Paleontological Resource Inventory Report.

The GRCA Centennial Paleontological Resource Inventory represents the largest and most comprehensive park-specific paleontological resource project ever undertaken by the NPS. Our hope is that this effort will not only contribute to the understanding of the extensive fossil record at GRCA, but to also comprehensively assemble important baseline paleontological resource data to support and inform park management. This report has benefited from the work of those who have come before us, and during this 100th Anniversary we offer the GRCA Paleontological Resource Inventory Report to serve and inspire rangers, visitors and those others who will be the stewards of the GRCA fossil record in the future.

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HISTORY OF PALEONTOLOGICAL WORK AT GRAND CANYON NATIONAL PARK— UP AND DOWN THE LONG FEDERAL AND NGO TRAILS OF PALEONTOLOGY IN GRAND CANYON NATIONAL PARK, 1858–2019

Earle E. Spamer[1]

ABSTRACT

The Grand Canyon! Anywhere in the world the name rouses recognition. Monumentally impossible to describe (or so have said thousands of writers who then effused their own descriptions), it has been a lure to geologists since 1858. From the start, the rocks were read for the clues of their relative ages. It has been the draw of government agencies and non-government organizations (NGO) alike. The national park is a century old now; the canyon six to 70-some million years (depending upon with whom you argue, and about which parts of the canyon you consider); and fossils in the canyon have awaited the hammer and scanning electron microscope for even more than a billion years. So, to avoid the traps of superlatives and the gulping periods of time, this is a fast trot through "the best of" Grand Canyon paleontology, refreshed with bits of human history, with a few pauses on peculiar details—a 100th birthday present to the national park. Here, beginning with the first Grand Canyon field trip in 1858, is an accounting of how the first explorers, and scientists and educators over the years, have fashioned our understanding and encouraged our participation in the story of ancient life presented in Grand Canyon's strata and secluded deposits. With this long look backward, we also may gain an appreciation for how paleontologists, federal administrators, and NGO champions built up the scientific and educational programs that modern resource managers receive as a legacy.

INTRODUCTION

There is a lot of "business" behind this paper, in the form of stratigraphic and taxonomic summaries, which I provided in a lengthy overview of Grand Canyon paleontology (Spamer, 1984). It still stands as a fairly reliable history of research, with an extensive list of references, and some handy species lists. For those so interested, there is also a corresponding general-audience overview from the perspective of the geologists in Grand Canyon (Spamer, 1995; see also Ranney, 2013, 2014). The present paper, in celebration of the national park's centennial anniversary and saluting National Fossil Day 2019, looks at the history from the perspective of the people and the agencies responsible for fossil studies in the canyon, and some of the educational projects that came about due to these studies. To this is added a brief rundown of research handed in since 1984.

So much is available in Grand Canyon publications that deal with paleontology that to supplement this paper I have prepared a *Bibliography of Paleontology in the Grand Canyon Region and in the Stratigraphic Continuity of Grand Canyon Formations.* This PDF with more than a thousand citations also complements the commemorative events of 2019. Occasionally updated, it can be downloaded from the web at **https://ravensperch.org/bibliography-of-paleontology-of-the-grand-canyon-region/.**

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In this day and age it has become so easy to search online for reliable additional basic information—such as photos of the many people who are mentioned here, as well as maps and beautifully detailed representations of Grand Canyon's stratigraphic column (which even this year has been revised)—that it seems needless to fill out this paper with numerous asides and portraits. Instead, the illustrations here show a few places, things, and events of interest that are mentioned.

And a note of thanks to Park Service managers: *These* are the very kinds of work that rely on the lands and resources you oversee, even if much of it never comes to your attention.

UPHILL

"Not really on the way to anywhere" pretty much describes the Grand Canyon; even the earliest trail-blazing expeditions in the neighborhood did not go there. In those days the canyon was known only vaguely and unimaginatively as "Big Cañon"; big and impassable (so it was heard). Although the name "Grand Canyon" was first used by physical scientist and statistician Lorin Blodget [1823–1901] (1857:90, 97), it was overlooked until John Wesley Powell [1834–1902] popularized it a decade later. The first field trip that *did* go to Big Cañon was quite out of the ordinary.

John Strong Newberry [1822–1892] was the first geologist to arrive, on mule, back in 1858. He had come to the region aboard a 50-foot sternwheel steamboat, made of iron and wood, commissioned by the U.S. Army in Philadelphia. It was little more than a bucket and a boiler. The mission was to explore the Colorado River from the sea upstream in order to determine the river's navigable reach and thus the possibilities of communicating with the interior West from the sea. (There also was a bit of secret political intrigue, too, only more recently understood, that indicates that this was a reconnaissance in the face of a potential civil war with Utah's Mormons; but that's a whole separate story having nothing to do with science.)

Three steamers already on the lower Colorado River were deemed too expensive to hire. *Explorer* (figure 1), built in a hurry during the summer of 1857 and tested by a spin on the Delaware River between Pennsylvania and New Jersey, was seen as more economical even with shipping costs. It was sent in eight pieces first to New York, then by ship to the two-year-old railroad across the Isthmus of Panama, and, after two more voyages by steamer and schooner in the Pacific, unloaded and wrestled together at Robinson's Landing, an improvised shipyard on the mudflats of the Colorado River delta in Mexico. There, during December, it was decided that the three-ton boiler could make groundings on sandbars a dangerous affair for the low-sided, deckless boat, so two heavy timbers were bolted lengthwise beneath the hull. Unfortunately, that increased the vessel's draft, a serious concern on such a shallow river. The slot in the transom, through which the engine's drive rod passed to the paddlewheel, was too deep and would have allowed water into the boat underway on the Colorado, a river not as placid as the tidewater Delaware. The engine was raised and an iron patch was fitted over the lower part of the slot.

The expedition commander, veteran western explorer Lt. Joseph C. Ives [1829–1868], engaged there at Robinson's Landing steamer captain David C. Robinson [1833–1874] to pilot the craft on the river. With Robinson at the tiller perched atop *Explorer's* small aft cabin (the boat did not even have a wheel), Andrew Carroll [ca. 1830–?], the engineer who had accompanied the boat from Philadelphia, and a skeleton crew, *Explorer* beat its way 150 miles to Fort Yuma, constantly challenged by the deceptive, wiggly channels of the delta and shifting river bottoms. At Fort Yuma on the California side of the Colorado and Gila River confluence, the rest of the small crew, who had traveled through the desert from San Diego, came aboard. Ives' (1861) formal report provides a detailed record of all of these happenings, as well as a fascinating travelogue of the remainder of the expedition.

Explorer's crew was an unlikely bunch: Captain Robinson and engineer Carroll; Lt. Ives and soldiers; Newberry as the mission's physician, geologist, and general naturalist; Friedrich von Egloffstein [1824–1885], a German baron who served as cartographer and illustrator and who was a veteran of western explorations elsewhere; and Balduin Möllhausen [1825–1905], a burly German draftsman, illustrator, and naturalist's field assistant, another western exploration veteran who had already visited the lower Colorado River. The expedition was cheerfully waved on its way by the fort's soldiers and smirking townspeople. *Explorer* promptly ran aground within sight of the fort. One might be forgiven if it brings to mind the campy 1960 Jack Lemmon film, *The Wackiest Ship in the Army.*

Still they did make their way upstream to find the head of navigation. They reached a suitable point in Black Canyon, not far downstream from where Hoover Dam was built eight decades later—by violently crashing into a rock, casting Ives, Newberry and Möllhausen from the cabin top, not to overlook "the fireman, who was pitching a log into the fire [and] went half-way in with it" (Ives, 1861, Pt. 1: 82). Three days later, after a brief survey farther upstream in a skiff and *Explorer* patched, they glided back down to meet up with a long army packtrain of mules. Ives divided his command, sent the boat back to Yuma and set out overland to the east en

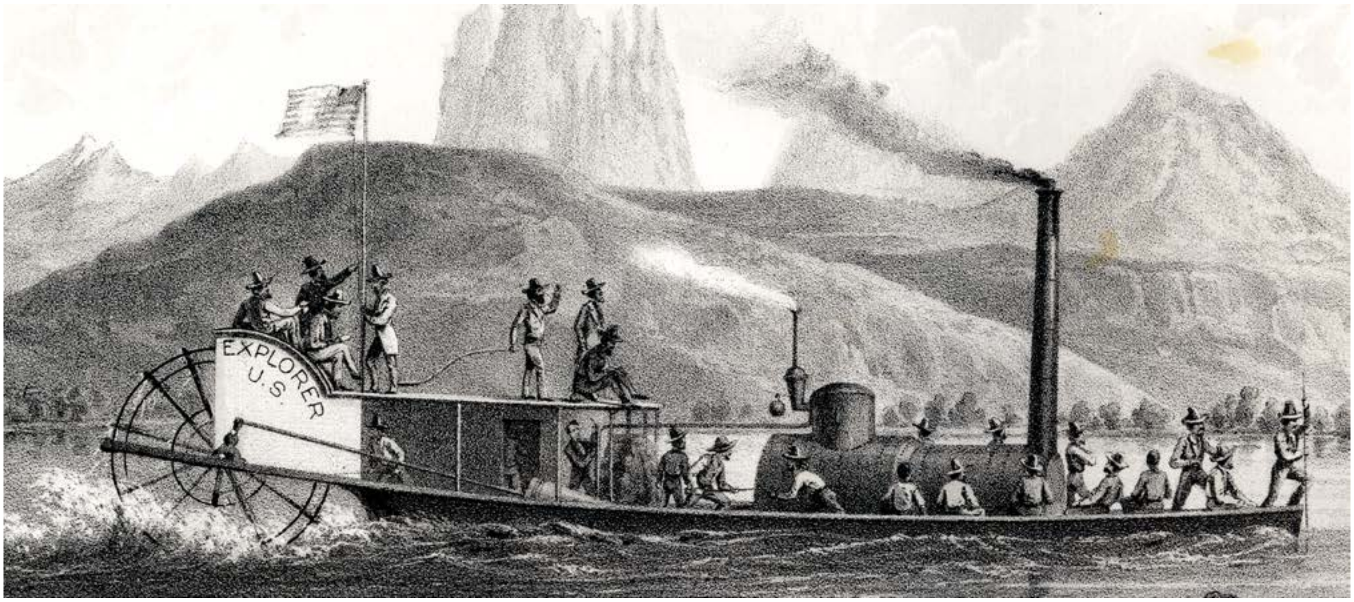

Figure 1. *The steamboat* Explorer *on the lower Colorado River; the first field trip en route to Grand Canyon (Ives, 1861: frontispiece).*

route to Fort Defiance with soldiers, Native Americans, a hundred-odd mules, Mexican packers, the Germans, our faithful Newberry, and a dog, "Grizzly."

The direction of travel was different, amidst this age of explorers who blazed wagon roads and railroad routes westward. However, the region they entered was not wholly unknown to Ives and Möllhausen. They had already traveled the general route near the 35th parallel a few years earlier when they were attached to a westbound expedition led by Lt. Amiel Whipple [1817–1863]. Laboring up from the Basin and Range to the Colorado Plateau, the now landward expedition approached the Grand Canyon—and thus, finally, the first geologist arrived. Somewhere in the vicinity, Newberry (or perhaps Möllhausen, Newberry's field assistant) gathered fossils that established a "Carboniferous" age (Permian today) for the rim rocks (figure 2). The Hualapai people they had met might have been amused by men who hammered on rocks. A small party rode down to Diamond Creek's confluence with the Colorado River, the first non-Indigenous people to reach the bottom of the canyon.

While Möllhausen sketched, Newberry made geological observations and drew up an accurate stratigraphic column from the rim to the Colorado River. In his measured section (Newberry, 1861: 55; and see his figure 12, page 42), he noted "*Euomphalus, Spirifer,* &c.", "imperfect corals," "corals (*Chaetetes?*)" (a genus now known as a sponge), and "green shales with mud furrows, resembling casts of worm holes." Even though the fossils of the rim rocks were helpful in establishing the relative age of those strata, Newberry bemoaned in his written report (page 55), "In the absence of [index] fossils it is impossible to determine the precise geological age of any of the strata composing the … section below the limestone which forms the summit of the cliffs." When all was said and done, though, Newberry drew up a detailed collection list for the whole expedition, itemizing nearly a thousand specimens of rocks, including fossils galore. Newberry also made his one most astute observation for the ages, that even the dry side canyons were created by running water rather than by cataclysm.

The Ives party pressed on to Cataract Creek, its lower end now known as Havasu Creek, where the mules could barely be turned around when the way became too sketchy for animals. The teams were sent back twenty miles to the last known water while some men went ahead on foot. The weighty Egloffstein managed to wreck a precarious Havasupai ladder, stranding himself. He wandered off to the Havasupai village of Supai, the first "foreigner" to go there since Spanish padre Francisco Garcés [1738–1781] arrived in July 1776. (Egloffstein was rescued when the soldiers lowered gun slings to hoist him up.)

Thus was the first brief, but productive, field trip to the Grand Canyon. Regrouped, Ives continued eastward, sending most of the party off toward Fort Defiance (Möllhausen had traveled the route with Whipple) while he, Egloffstein, and a few men made a side trip to visit the Hopi. After the expedition disbanded, Ives returned to Yuma, where he sold *Explorer* six months after its maiden (and only government) voyage. It served anonymous local companies for a while, broke loose in a flood, and drifted away toward the sea.

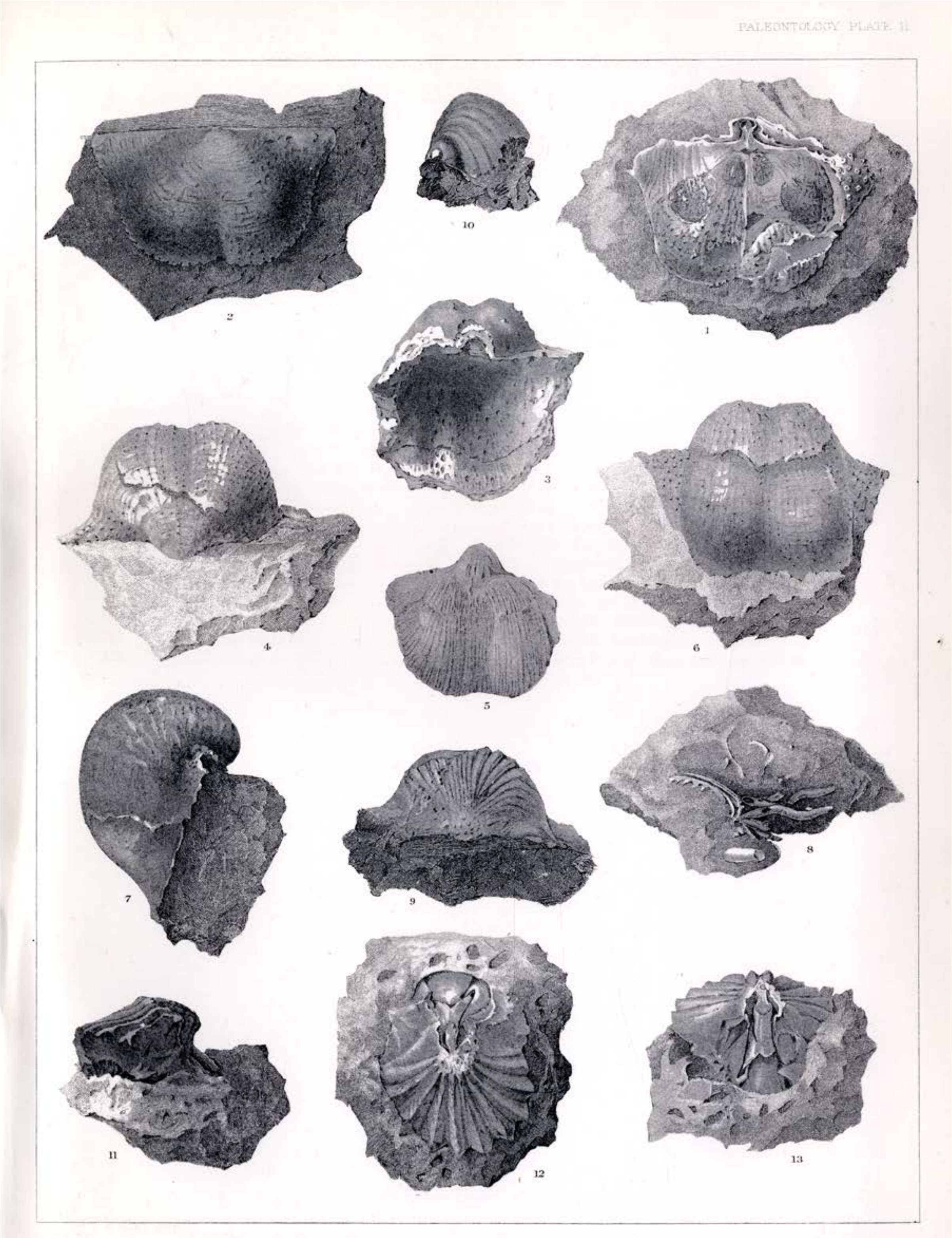

Figure 2. *Grand Canyon paleontology begins here, April 1858 (Newberry, 1861: Paleontology Plate 2). All are from the undifferentiated Permian Kaibab Limestone–Toroweap Formation.* ***Figures 1–8.*** Productus ivesi*, a new species;* ***Figures 9 and 10.*** P. occidentalis*, a new species; from "Middle Carboniferous limestone, banks of the Colorado, near mouth of Diamond river" [Peach Springs Canyon between Peach Springs and the confluence of Diamond Creek];* ***Figures 11–13.*** Streptorhynchus pyramidalis*, a new species, from "Carboniferous limestone over red cross-stratified sandstone at Camp 70, on high mesa west of Little Colorado" [western part of the Coconino Plateau not far east from Diamond Creek]. These localities today are a part of the Hualapai Indian Reservation.*

DOWNHILL

A decade later, another government-sponsored expedition arrived in the canyon—this time from the north, by river from Wyoming and Utah. In August 1869, Civil War veteran Maj. John Wesley Powell, now a civilian and with eight crew members aboard three boats, passed into Grand Canyon having charted the Green and Colorado Rivers to the mouth of the Little Colorado River. They had support from the Smithsonian Institution and some military favors in the form of supplies. Although they had passed sequentially down through all of the Colorado Plateau's strata, there hadn't been much time for collecting. From this point onward was Powell's "Great Unknown." They were effectively off the map now, with only Egloffstein's generalized physiographic map (in Ives, 1861) as an informer, a map good for the lower Colorado River region but quite inaccurately portraying the Grand Canyon region.

Powell, though geologically trained, reported little on fossils in his expositions on the strata; and anyway by this time he was more concerned with where the river was leading him, and getting his crew through on rapidly diminishing rations. He led a second trip in 1871–1872, pausing for a winter layover in Kanab, Utah, but he cut that journey short in the middle of Grand Canyon when he suddenly decided at Kanab Creek that they had achieved their objectives. Thereafter, the emphasis was on mapping the region on the plateaus. Powell's (1875, 1895) renditions of his river exploits remain classic tales of Grand Canyon and Colorado River running. The plateau surveys under his direction produced in 1882 what is probably the greatest (and most readable) scientific book on Grand Canyon physiography and geological history, *Tertiary History of the Grand Cañon District,* with its magnificent double-folio *Atlas*, by Clarence Edward Dutton [1841–1912].

LAYING A FOUNDATION

The first expeditions to and through the Grand Canyon were enough to establish that *this* was an interesting place, worthy of further study. By 1881, Powell had become the second director of the newly organized U.S. Geological Survey, and his ongoing surveys of the Colorado Plateau country at last brought a refined geologist's eye to the whole Grand Canyon. Powell, in the field, directed the construction of a trail into the northeastern corner of the canyon—today this is the tortuous, unmaintained Nankoweap Trail. He assigned the up-and-coming geologist, Charles Doolittle Walcott [1850–1927] (who would himself succeed Powell as USGS director), to spend the winter of 1882–1883 in the depths of the canyon, where with a collector, a cook, and a packer accompanying him, he studied for the first time the structural and stratigraphic relationships of the Proterozoic and lower Paleozoic rocks there—a remarkably instructive study to this day. Powell had recognized the basics of these relationships during his river expeditions, but now was the time to do some real field work.

Walcott saw quite a lot that piqued his interest in "Precambrian" fossils. He saw the stromatolites in these strata, which he called "an obscure Stromatopora-like group of forms" and "concretionary limestones." He also reported pteropods referred to *Hyolithes*, a trilobite fragment, a *Lingula*-like brachiopod, and a brachiopod related to *Acrothele*. This led Walcott to assume, with a Cambrian bias, that perhaps complex biological forms had evolved earlier than previously known. His research included ongoing observations, even if it was published in a paper on a wholly different geographic (and geologic) area. For example, see Walcott's (1884: 432) footnote in a paper on the Paleozoic of Texas: "Since the paper on the Pre-Carboniferous strata of the Grand Cañon was published [Walcott, 1883], a fragment of a trilobite, probably of the genus *Ptychoparia*, has been detected in a bit of shale from the Chuar group." Alas, all of these reports of body fossils have subsequently been reinterpreted as pseudofossils, the "fool's gold" of paleontology.

Yet in the process, Walcott also found a remarkable Neoproterozoic fossil, a megascopic alga he named in 1899 *Chuaria circularis*, which he believed to be a primitive brachiopod. Even though *Chuaria* has since been found around the world, so problematic this organism has been that it has been variously assigned to other phyla in the major kingdoms (it even once was considered to be a trilobite egg) and as a pseudofossil. Now *Chuaria*, definitely a fossil, is thought to be represented at different life stages also by *Tawuia* and *Longfengshania*. In a bizarre sort of way its form- and function-based taxonomies act like those of ichnofossils! Studies in China and India have been particularly robust; but the well-known, well-studied enigma persists. It all began in the Grand Canyon: Walcott's original, small shale chips are in the U.S. National Museum (the Smithsonian Museum of Natural History).

Walcott was hardly a Grand Canyon novice. A couple of years earlier, the young man had had his first hand at geologizing in the west when he worked along Kanab Creek, the large tributary to the Colorado coming down to Grand Canyon from Utah, getting his and our bearings on the canyon's entire Paleozoic sequence (Walcott, 1880, 1883). Fossils were not lacking. These collections and others contributed decades later to Walcott's very detailed series of publications on brachiopods and trilobites, produced during his 20-year position as the Secretary (director) of the Smithsonian Institution (see the paleontology bibliography online).

The usefulness of the canyon's fossil record was proven. Now geologists had a proper first analysis of the principal formations of the canyon.

ON THE MAP

Geologists need maps. By the late 1800s, rudimentary 1:250,000-scale maps were available for the Grand Canyon region, products of Powell's surveys. In summer 1902, the USGS's François Matthes [1874–1948] and crew began a heart-stopping mission—using plane tables and alidades to create 15-minute quadrangles of the eastern portion of Grand Canyon with contour intervals of 80 ft (24 m); a project completed the following summer. They traveled into the canyon as well, and blazed a trail for their horses up through Bright Angel Creek to the North Rim. The resulting quads still are masterful examples of scientific art, but at the time they provided geologists with important tools for detailing more of the Grand Canyon's lithology in the field.

While in the early 20th century some geologists were beginning to scrutinize the physiographic history of the canyon, others were heading into the chasm on foot and hoof.

Paleontology again took the back seat, serving only to assist in identifying relative ages, with no purposefully comprehensive collections being made. First on the ground now were Frederick Leslie Ransome [1868–1935], who in 1908 published a study of the Neoproterozoic sedimentary rocks and in 1916 produced correlations of Paleozoic strata in Arizona; Levi Fatzinger Noble [1882–1965], whose 1909 doctoral dissertation from Yale was based on his studies in the central Grand Canyon where Paleozoic and Neoproterozoic rocks are well exposed, with publications on this area in 1910, 1914, and 1922; Nelson Horatio Darton [1865–1948], who published in 1910 a reconnaissance of northern Arizona and in 1925 produced a very comprehensive résumé of Arizona geology; and Charles Schuchert [1858–1942], who published on the Grand Canyon Cambrian and "Carboniferous" (which included Permian strata) in 1918. This laid the groundwork for studies that, finally, began to look seriously at the fossil fauna and flora.

MAKING TRACKS

Paleontological studies in the Grand Canyon have in fact been vigorous. Valuable collections of acritarchs, invertebrates, vertebrates, plants, and cryptic remains have been taken from Neoproterozoic to Permian strata and Pleistocene–Holocene deposits. Some of these collections contributed to the development of new concepts in stratigraphy that since have become a part of basic geological principles. However, the findings of Grand Canyon paleontology began modestly, sometimes peculiarly.

A variety of trace fossils had been known for years. The first were Newberry's observations of green-shale "worm holes" that now are well recognized and beautifully exposed in much of the Cambrian Muav Limestone. (In 1892 Joseph Francis James [1857–1897] suggested that these casts should be named *Scolithus arizonicus,* but without a description they fall into the taxonomic wastebasket of *nomina nuda*, unfounded names.) Walcott, too, widely recognized these abundant "fucoids," which he attributed to annelid worm trails and trilobite burrows. It is the ichnofauna of the canyon that first brought Grand Canyon paleontology to the fore, both professionally and popularly. While we can dismiss an anonymous 1884 report from two miners who found footprints 5.5 m (18 ft) apart made by a human some 4.0 m (13 ft) tall, who thus was shown to have been "fairly bounding along," it nonetheless demonstrates the things that can capture the public's interest. This report was interesting enough to have been picked up in France, too, so public attention was there. It's a shame that the miners never fulfilled their promise to return to remove the footprints to "exhibit them to public gaze."

Richard Swann Lull [1867–1957] had first written about "Nature's hieroglyphics" in 1904, including passing mention of a trackway in the Grand Canyon. In 1918 he produced the first dedicated study of vertebrate tracks from the canyon, describing two new ichnospecies from the Pennsylvanian–Permian Supai Group and four new ichnospecies and the now well-known ichnogenus *Laoporus* from the Permian Coconino Sandstone. What made the Coconino fossils all the more remarkable, Lull noted, as had Schuchert who collected them, was that they all were preserved on the foresets of fossil sand dunes, always advancing upslope. This apparently peculiar trait would in later years become the subject of much study.

By this time, although the Grand Canyon was widely known and was a popular tourist destination, for a variety of political reasons it still had not been designated a national park. (Since 1893 portions of the canyon had been a national forest preserve [1893], national game preserve [1906], and national monument [1908].) Finally, with Congress making Grand Canyon a national park in February 1919, even more public attention was drawn to it. In response, the National Park Service, itself only three years old, was faced with the increasing pressures of "what to do with it." This entailed promoting the scenic, historic, and educational values the landscape holds, in addition to managing and entertaining visitors from around the world.

As might be expected, these programs came with the concerns of cost, promotion, and maintenance. Fortunately, the Santa Fe Railway had for more than two decades already been self-servingly advertising the Grand Canyon. Before government oversight of authorized concessionaires fully took root, the railroad independently completed a line to the rim in 1901, and by 1905 had built El Tovar Hotel and the adjacent Hopi House that drew visitors to buy American Indian crafts by the basketful. (In 1899 the rail line had been built from Williams, Arizona, to a site named Anita, to service copper mines established there. This station was just 19 rail miles short of Grand Canyon [Richmond, 1998, 2017].) While the Santa Fe had thus also made it possible for scientists of various sorts (such as botanists and entomologists) to visit the canyon in pursuit of gatherings in their fields, they had no vested interest in "science" *per se*. That fell to the Park Service, and it would have to entail what we today call "outside funding" and "outreach."

DIGGING IN

The industrialist and philanthropist Andrew Carnegie [1835–1919] used his billions of dollars (in today's figures) for educational and scientific projects after he retired from his business ventures in 1901. This included the founding of the Carnegie Institution of Washington, in 1902. Today, as the Carnegie Institution for Science, it is a leader in scientific discovery, in widely diverse fields. From 1920 to 1938, paleontologist and educator John Campbell Merriam [1869–1945] served as president of the institution (in 1919 he had also been president of the Geological Society of America), and Charles D. Walcott (also a GSA president, 1901) had served as an institution trustee 1902–1928 even while he directed the Geological Survey (to 1907) and the Smithsonian Institution (1907–1927). Not surprisingly, they encouraged programs of study in the earth sciences at the fledgling national park.

On recommendation, the National Park Service asked the Smithsonian's vertebrate paleontologist Charles Whitney Gilmore [1874–1945] to visit Schuchert's trackway site in the Coconino Sandstone along Hermit Trail. The purpose was to prepare a public educational exhibit. At the time, Hermit Trail had been improved by the Santa Fe so that tourists could reach Hermit Camp, the railway's tourist camp that deflected visitors from using the Bright Angel Trail that by dint of dozens of spurious "mining claims" was still largely (and illegally) "owned" by Ralph Henry Cameron [1863–1953], U.S. Senator from Arizona [1921–1927]. Gilmore went on to spend the next several field seasons in the canyon, studying and collecting from the Permian and Pennsylvanian strata along several trails. In the process, he described numerous new species and genera of vertebrate and invertebrate tracks (Gilmore, 1926, 1927, 1928) and reported the first trackway found on the north side of the canyon (Gilmore and Sturdevant, 1928).

More than relegated to stodgy scientific reports, Gilmore's work was noted in popular literature; after all, footprints are something that all can relate to, even more so that they were very old and were *in the Grand Canyon.* The prodigiously productive Merriam, too, promoted this work in his own educational publications.

Knowing that the Coconino Sandstone tracks were seen to face upslope on the fossil dunes, Gilmore (1926: 4) suggested they represented "an old trail leading to water, or possibly recording a great migration of animal life." These were additional concepts with which an engaged public could easily identify. As time went on, interest in this peculiar trait did not wane. During the 1930s and '40s, experiments on modern sand dunes and in the laboratory, sometimes using living animals, showed that the answer was more a simple process of mechanics: essentially (and a bit simplistically), upslope trackways required sure planting of feet, while downslope travel incurred more sliding and tracks were readily erased.

EDUCATION FLOWERS

Many kinds of botanical fossils are found in the Grand Canyon. Some of these early finds were based on physical forms, which proved really to be sedimentary features and thus not fossils at all; for example, a new seaweed-like species *Rivularites permiensis* was described by David White [1862–1935] in 1929, from the Permian Hermit Shale, although various species of this genus have been reassessed as microbial sedimentary features. The higher systematic plants, found in abundance particularly in the Hermit Shale, are obviously fossils; after all, if it looks like a fern it probably is a fern (figure 3). White's magnificent 1929 monograph (published by the Carnegie Institution) remains a primary guide to Grand Canyon fossil plants. (Suitably, White's grave in the Grand Canyon Cemetery is marked by a plaque in which are molded three of his new species; the figures are reproduced from his Hermit Shale monograph.) Some of White's paleobotanical taxa, such as *Supaia*, even have significance as biomarkers for the early Permian, having been found in other strata around the world. Regretfully, paleobotanical work on the vascular plants of the Grand Canyon has been sparse since White's work there.

All of this field work—ichnofossils and plants in particular—did not come cheaply. It was the Carnegie Institution that had underwritten the costs. There were the purely scientific objectives, of course, but the findings could be turned into educational projects. By the late 1920s the newly founded Grand Canyon Natural History Association (today the Grand Canyon Con-

Figure 3. *David White (left) and John C. Merriam at a fossil fern quarry in Grand Canyon (note the slab leaning against White's right leg) (NPS).*

servancy) was producing a monthly newsletter, *Nature Notes,* which frequently presented brief write-ups of the latest paleontological finds from the canyon. Glen Sturdevant [1895–1929], the only ranger–naturalist at Grand Canyon, almost single-handedly wrote the articles and news notes. After his untimely death in the Colorado River, a geology student who had been working under Merriam's programs in the canyon during recent summers, Edwin "Eddie" Dinwiddie McKee [1906–1984], stayed on as the next ranger–naturalist. As we shall see, McKee exploded into the earth sciences in the canyon and around the world.

Through the 1930s, the Carnegie Institution supported research and funded publications about many of the Grand Canyon's strata; sedimentological, stratigraphic, and paleontological studies alike. The institution's Year Book series dutifully recorded each year's support and results from its underwritten programs. In 1928, the Yavapai Observation Station was dedicated as a place where visitors could observe and learn about the geology of the canyon in a museum setting, staffed by Park Service rangers, with an observation area overlooking the canyon and displays of rocks and fossils. In 1937, David White's work was recognized by the development of a trailside exhibit in the Hermit Shale at Cedar Ridge on the South Kaibab Trail, a locale which still displays a surface with ferns (figure 4). This small glassed-over exhibit, built by the Civilian Conservation Corps, was re-dedicated in 2008 during a CCC symposium at Grand Canyon; and it is now undergoing further restoration by Grand Canyon interpretive and Volunteers-In-Parks staff.

E. D. McKee was instrumental in the development of Yavapai, staffing it himself from time to time during the late 1920s and 1930s (figure 5); that is, when he wasn't doing other naturalist duties in the park, or on one of his far-ranging geology field trips. Over the years, geological interpretation at Yavapai became rather static. The usual wear and tear on the hardware, and changing public perspectives on educational presentations, eventually called for a remodeling of Yavapai by 1980. It was a more sleek—some said "dumbed down"—exhibit now partly commandeered as a tourists' gift shop. McKee, long since having had left the canyon and by now a senior geologist in the USGS, was dismayed over this conversion. Fortunately, in the early 2000s, Yavapai was completely refitted again, this time bringing back detailed and informative modern exhibits on Grand Canyon geology, restoring the building to meet its original mission and brightening its original architecture. It was rededicated in 2007 as the Yavapai Geology Museum.

McKee would have been even more ecstatic over the most recent addition to the park's educational offerings

Figure 4. *Trailside exhibit of fossil ferns, constructed by the Civilian Conservation Corps in the Permian Hermit Shale at Cedar Ridge on South Kaibab Trail, as seen ca. 1940s? (NPS).*

Figure 5. *Ranger-Naturalist Edwin D. McKee at work in Yavapai Observation Station, ca. 1930 (NPS).*

in geology and paleontology. In 1994, geologist Karl Karlstrom from the University of New Mexico, and others, proposed the construction of a "Trail of Time" along the already existing paved Rim Trail. After many concept studies and arrangements with the park, a 4.6-km (3-mi) trail was laid with markers and rock samples from every stratigraphic formation and member in the canyon. It can be entered at several points and be informative in either direction. The trail is accessible to wheelchairs and people with strollers and is convenient to shuttle bus stops and parking areas. Best of all, trail users are encouraged to "please touch" the rock specimens.

The trail is inlaid with small bronze markers, 1 m (3 ft) apart, each "giant step" representing one million years in the history of the earth from "Today" by the Yavapai museum westward to the origin of the earth at Maricopa Point, 4,560 Ma (with one more, lone marker miles farther to the west at Pima Point that denotes the comparable "distance" to the origin of the universe, 13,750 Ma). The Trail of Time rock samples include fossils where appropriate (figure 6). They are interpreted by striking informational signs at the appropriate "ages" along the trail. Most of the rocks and slabs, far larger than geologists' usual "hand specimens," were collected along the Colorado River and taken out of the canyon by raft. In a few cases where strata are not exposed along the river, the rocks were flown out strung together like a necklace beneath a heavy-lift helicopter.

As might be expected, the project was very complex, involving dozens of people and calling for substantial funding for concept preparation, planning and on-site testing, logistics of making rock collections, preparation of specimens, designing and manufacturing signage and ground markers, and installation, not to mention administrative assistance and permitting through the park. The recently published guide to the trail by Karl Karlstrom and Laura Crossey (2019) has an engaging, exhaustive text and is richly illustrated. Though written for the interested casual audience, the guide will be seen by professionals as informative to them as well. With it, even those who cannot visit the canyon can experience and learn from the Trail of Time.

THE MCKEEIAN PERIOD

In 1927, Edwin D. McKee had been in the U.S. Naval Academy, but he was influenced by his former Boy Scout leader at Boy Scout Troop 1 in Washington, D.C.,

Figure 6. *Fossil footprints in a slab of Coconino Sandstone, displayed on the Trail of Time. This slab was retrieved from a flagstone quarry near Ash Fork, Arizona (NPS).*

to take advantage of a summer internship at the Grand Canyon with John C. Merriam. There he was the field assistant to David White and C. W. Gilmore. (Incidentally, his former troop leader was none other than Grand Canyon's plane-table cartographer, François Matthes.) He enrolled in the geology program at Cornell University and spent subsequent summers at Grand Canyon. The tragedy of Glen Sturdevant's drowning in the Colorado moved McKee into a permanent position as the park's ranger–naturalist. He never looked back.

McKee privately published *Ancient Landscapes of the Grand Canyon Region* in 1931, which of course prominently featured the fossil life found in the area. This booklet went through 30 variously revised printings until 1985. His first geological attentions were given to the large-scale cross-bedding of the Permian desert Coconino Sandstone, so prominently displayed in the canyon. The Carnegie Institution published his first major work in 1933, *The Coconino Sandstone—Its History and Origin*, that included the ichnofauna of invertebrates and vertebrates.

The canyon's other strata beckoned. McKee had become a master of minutiae, looking at sediments and fossils from one end of the canyon to the other. He became the first geologist to systematically trace key beds from one area to another, which was possible by measuring stratigraphic sections at different places in the canyon. His first monograph was yet another Carnegie publication, *The Environment and History of the Toroweap and Kaibab Formations of Northern Arizona and Southern Utah* (1938), on the Permian units that form the rim of the canyon.

Field work had been going apace in the canyon's other Paleozoic strata, too, which would produce important monographs in coming years. First up were the Cambrian formations of the Tonto Group, analyzed in another Carnegie publication in 1945 (delayed partly by the war) with paleontologist Charles Elmer Resser [1889–1943]: *Cambrian History of the Grand Canyon Region.* It was this monograph that for the first time clearly demonstrated the on- and off-lap sequencing of advancing and retreating seas on a landscape, made possible by tracing key beds. This varying, periodically reversing action of the sea, and the changing sedimentology and fossil assemblages produced by this activity, has since become the stuff of elementary geological education; diagrams printed in the book have been widely reprinted in textbooks, too.

McKee left the Grand Canyon in 1938 rather than be moved to be a ranger elsewhere in the park system. He first went to the Museum of Northern Arizona, then on to the University of Arizona where he eventually became geology department chair, and later on to the U.S. Geological Survey as a research geologist in sedimentology. During this time, in addition to publishing the occasional paper, he produced two more major monographs, effectively rounding out the Paleozoic sequence for Grand Canyon. First was the 1969 volume with Raymond Charles Gutschick [1913–2002], *History of the Redwall Limestone of Northern Arizona*, followed in 1982 by McKee's *The Supai Group of Grand Canyon.*

The Redwall and Supai yielded to McKee's quintessential methods of observation and reporting. The corresponding monographs, following on the two-author Cambrian monograph of 1945, are composed of separately authored chapters by authorities in their fields, with observations on lithologies, paleoenvironments, and fossil systematics. In paleontology, the Redwall monograph has separate chapters for crinoids (J. C. Brower), bryozoans (Helen Duncan), blastoids (Donald B. Macurda, Jr.), corals (William J. Sando), and foraminifera (Betty Skipp), with McKee and Gutschick reserving chapters on the Redwall faunas in general, brachiopods, and "miscellaneous fossil groups: algae and stromatolites, holothurians, trilobites, ostracodes, and fish."

McKee's Supai monograph of 1982 was even more comprehensive, though focusing more on lithologic analyses, including such esoteric subjects as "insoluble residue patterns" (Walter H. Peirce and others) and "stable isotope analyses" (McKee). Still, fossils were documented in the chapters on "Biostratigraphy of the Watahomigi Formation" (Mackenzie Gordon, Jr.) and "Distribution of Age and Flora" (McKee). There also was a chapter by George H. Billingsley and McKee on "Pre-Supai Buried Valleys" that announced fossil-dated Chesterian-age deposits of paleochannels in the top of the Redwall Limestone. These intermittently exposed valleys were described in 1985 as a new formation, the Surprise Canyon Formation, by Billingsley and Stanley S. Beus. (McKee had earlier named the Permian Toroweap Formation, members of the three formations in the Cambrian Tonto Group, members of the Mississippian Redwall Limestone, and divided the Permian–Pennsylvanian Supai Formation into four formations, elevating the Supai to group rank.) The Surprise Canyon Formation was afforded its own monograph (Billingsley and Beus, 1999) that followed the McKee design of separately authored chapters, which included "Megafossil Paleontology" (Beus) and "Conodont Biostratigraphy" (Harriet Martin and James E. Barrick).

Placing all of this Grand Canyon work in broader perspective, McKee focused on studying modern sediments as analogs of paleo-sediments, work that took him first to the Colorado River delta in Mexico. There, his wife, Barbara, satisfactorily explained to quizzical Yaqui Indians in whose boat they were guided through the channels that he "gets paid" to fill bags with mud. His field travels took him around the world, including to Saudi Arabia where Bedouin tribesmen appeared "out of nowhere" to watch the astonishing act of trickling a tanker truck of water into desert sand dunes (so that the dunes could be cut open to allow study of their internal structure). The tribesmen left after having had their waterbags filled. At the USGS in Denver, McKee had a laboratory where he conducted flume-sediment experiments, which he continued even in retirement. He used remote-sensing technology and Skylab observations in his studies of world sand seas as well. Not long before he died, McKee had been on South America's Rio Orinoco, surveying its sediments as an analog to the Supai's Watahomigi Formation. All this, and much more, was a remarkable series of achievements for a man with only a bachelor's degree. He and his wife are buried in the Grand Canyon Cemetery, near David White. The headstone, a water-sculpted piece of Cambrian Tapeats Sandstone, was collected by USGS geologist George Billingsley near Pumpkin Spring in western Grand Canyon.

SUPER FOSSILS, PSEUDO FOSSILS

The Proterozoic sequence of sedimentary rocks beneath the Great Unconformity that separates them from the Paleozoic strata—the Unkar and Chuar Groups, comprising the Grand Canyon Supergroup—were studied by geologists as far back as Walcott in the early 1880s, with renewed interest in the early 20th century. A flurry of additional interest came about in the late 1930s as a result of the Carnegie Institution's battery of field studies in the canyon. But first, some museum drawer-cleaning.

For years, the presumed "Precambrian" fossils that Walcott had gathered in the 1880s had been accepted without question by later workers. In the 1930s and 40s their biogenic origins were questioned, and all but *Chuaria* were relegated to the bin of pseudofossils. Even so, the Carnegie-sponsored explorations yielded more. In 1934, Clarence Edgar Van Gundy [1908–1985] examined some of the Supergroup strata exposed in easternmost Grand Canyon. In 1934 he described a new formation that he called the Nankoweap Group, stratigraphically atop the Unkar Group. (For years the Nankoweap Formation was a loner, lying unconformably between the Unkar and Chuar Groups, but more recently it has been reassigned as the basal unit of the Chuar.) He also reported finding a jellyfish (Van Gundy, 1937), which may have misled another geologist on Carnegie-sponsored canyon work, Norman Ethan Allen Hinds [1893–1961], to declare the entire Supergroup to be lower Paleozoic in age. Hinds had been working throughout the 1930s on "Algonkian" and other "Precambrian" relationships in the American West. (It should be pointed out that Carnegie was not the sole, though continuously generous, benefactor over the years. For example, in 1933 the Marsh Fund of the National Academy of Sciences provided funds to Edwin McKee for work on the Paleozoic strata; Gregory and others, 1933.)

The jellyfish was sensational news for its implications on the timing of the appearance of multicellular life. In 1941, Ray Smith Bassler [1878–1961] named Van Gundy's jellyfish *Brooksella canyonensis*. Although the title of his paper read "a supposed jellyfish" he assigned it, ironically, to a genus that had been named by C. D. Walcott (he did, though, acknowledge that the Grand Canyon specimen could be inorganic). In 1960, Preston Ercelle Cloud, Jr. [1912–1991], having examined the "problematicum" *B. canyonensis,* took Bassler to task for publishing a retouched photograph and said that the specimen is on an under, rather than upper, surface of a slab; thus it "seems to be the reverse imprint of a subradial fracture system of unknown origin in an underlying shale, bits of which are preserved in the fractures" (Cloud, 1960:44).

Van Gundy's jellyfish holds to a life of its own. Over the years it was reinterpreted—if it was organic, that is—as a starlike burrow of a filter-feeding benthic worm (a trace fossil), and in 1969 was accordingly redescribed by Martin Fritz Glaessner [1906–1989] as *Asterosoma*? *canyonensis*, which did nothing more than remove the fossil from among the medusoid taxa. It also was thought to be something possibly akin to the novel late Proterozoic Ediacaran fauna of Australia. By the 1980s, it was suggested to be a complex metazoan trace fossil, after which interest in this fossil waned, although more recently a study of phylogenetic affinities and taphonomy of the genus *Brooksella* (though from the Cambrian of Georgia and Alabama) by Ciampaglio and others (2006) "tentatively" sustained the Grand Canyon jellyfish as Glaessner's trace, *Asterosoma*? *canyonensis*. It still has not died the death of pseudofossils.

Proterozoic jellyfish in the Grand Canyon have had other, even older, representatives. In 1959 Raymond Manfred Alf [1905–1999] reported "possible fossils" from the Bass Limestone (basal unit of the Unkar Group and the oldest of Grand Canyon's sedimentary formations), which he described as jellyfish impressions. These soon were swept into the pseudofossil bin by Cloud (1960: 43, footnote) who interpreted them as "gas blisters or their impressions."

Pseudojellyfish and other wonders notwithstanding, in the Chuar Group there is a dazzling array of fossils, which even Walcott's notoriously keen eye could never have seen because scanning electron microscopy is needed to study them. In 1977, Bonnie Bloeser, while working on her Master's thesis at UCLA, published with three co-authors a paper on microfossils that she had found in the Chuar Group on Nankoweap Butte. These millimeter-sized, vase-shaped, organic-walled objects of unclear origin occur worldwide, but what she had found was a new genus, which she named *Melanocyrillium* in 1985. The known "vase-shaped microfossils" at Grand Canyon now include at least 16 species and appear to be the fossils of amoebas (Porter and others, 2003; Morais and others, 2019). Many other kinds of microfossils were observed as well, including spheroids and carbonaceous filaments; and the Grand Canyon Supergroup yields traces of various algal-like remains in many strata. Were it not so difficult to gain physical access to these strata, probably many more studies would be possible. Nonetheless, as we shall see, that does not mean that nothing has been done.

FIRE

The youngest of Grand Canyon's paleomenageries and paleoherbaria—Pleistocene faunas and flora—were completely unknown until well into the 20th century. In summer 1936, National Park Service employee Willis Evans was in far western Grand Canyon, where Hoover Dam's Lake Mead was rapidly drowning out the last of the Colorado River's rapids. There, he discovered Rampart Cave, finding inside what was called a sloth stable (Anonymous, 1936). Soon the discovery was widely reported even in popular public literature, including *Life* magazine (Anonymous, 1937). Willis had found a lair used by now-extinct giant ground sloths; specifically, the Shasta ground sloth, *Nothrotheriops shastensis* (Sinclair). They had left their bones in there, but by far the greatest trove was the abundance of fossil dung (figure 7), in layers up to 2 m (6 ft) deep. The discovery was fortuitous, because at that time there was plenty of young, able, and nearly free labor nearby: the Civilian Conservation Corps. Young men were pressed into service making excavations in the cave, gathering bones (even pieces of fur), and retrieving barrels full of dung that preserved the plant material that once grew in the western Grand Canyon—the stuff of paleoecologists' dreams.

Losing no time on the opportunity, the National Park Service thought that Rampart Cave would make an ideal public exhibit. Later they reported (Anonymous 1936), "Plans for showing the cave to the public have not been completed, but it is hoped that an exhibit in situ can be made. Tentative plans include running a trench through the cave and lining the walls of the trench with glass so that bones or any possible human artifacts may be seen." While humans seem never to have inhabited the cave, the amount of useful material there was enough to ride the same Carnegie education wagon that was making the rounds in the eastern part of the canyon, and Carnegie underwrote some of the research. The exhibit never

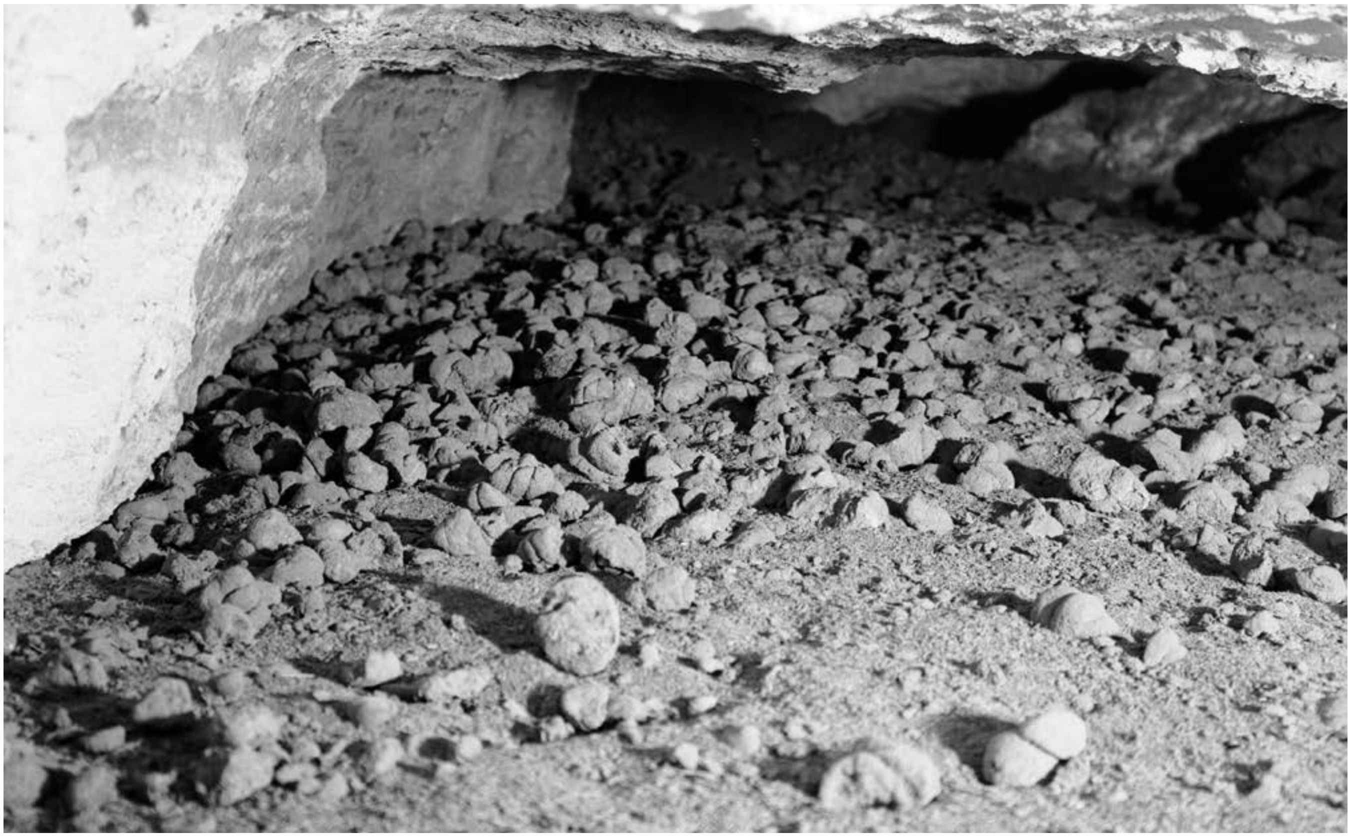

Figure 7. Castrocopros martini *Hunt and Lucas, the dung of* Nothrotheriops shastensis *(Sinclair), in Rampart Cave, September 1938 (NPS).*

came to be, even though the possibility of tourism was there. After Hoover Dam was built, tourist concessions evolved in Lake Mead National Recreation Area, which included long boat rides that stopped at Rampart Cave and ran 19 km (12 mi) up into the western part of Grand Canyon. However, the gradual silting in of the lower end of the canyon, as the "red river" slowed and dropped its sediment load in the head of the lake, ended the tours.

Even though no public exhibition ever came to Rampart Cave, studies of its contents proved quite valuable to paleontologists and paleoenvironmentalists. Archaeologist Mark Raymond Harrington [1882–1971] paid a visit soon after the discovery, commenting in part (1936: 226–227), "I have often thought the critter must have been pretty smelly for his aroma to last ten thousand years!" Soon afterward, in 1938 Jerome Douglass Laudermilk [1893–1956] and Philip Alexander Munz [1892–1974] published the first scientific studies of the flora from Rampart Cave and the nearby Muav Cave, and in 1942 Robert Warren Wilson [1909–2006] published the first comprehensive (though "preliminary") faunal study itemizing 11 vertebrate species, including the ground sloth and the mountain goat *Oreamnos harringtoni* Stock (figure 8). Both publications were Carnegie productions. In 1946 Gordon Cortis Baldwin [1908–1983] briefly updated the findings based on a 1942 survey he had done under Arthur Remington Kellogg [1892–1969]. In 1960, Loye Holmes Miller [1874–1970] reported a variety of fossil birds from Rampart Cave, including the California Condor, although the highly fragmented condition of the material was likely due to "trampling by the ponderous ground sloths." In 1961, Paul Schultz Martin [1928–2010] and colleagues produced the first paleoecological survey of the cave, extending studies to include pollen analyses of the dung.

Unfortunately, the cave was not far above a very convenient lake surface, and from time to time it attracted visitors even after it had been gated. In 1977, apparently by accident, the rich, dry dung in the cave was set on fire, probably from a home-made torch used for illumination. It was almost impossible to put out despite valiant efforts at suffocation and dumping tons of water, destroying the better part of the cave's contents; it smoldered for a year (Anonymous, 1977, 1978; U.S. National Park Service 1977). The Park Service has since put stronger safeguards in place to keep unauthorized visitors out of the cave. (Due to years of drought in the American West, the level of Lake Mead has fallen dramatically. Today, the Colorado River has reestablished itself in the lake-bottom sediments covering its original channel, where steep banks and heavy vegetation make even stopping here difficult. The lake itself is presently reached some 32 km or 20 mi farther downstream.)

Figure 8. *Skull of the extinct mountain goat,* Oreamnos harringtoni *Stock, from a Grand Canyon cave (NPS).*

ABOUT THAT ICE AGE

Despite the destruction of the valuable Rampart Cave remains, Grand Canyon is nonetheless full of caves. Many were the lairs of animals, perhaps most notably the persistent packrat, *Neotoma*. To these, one may add many more secluded, sheltered rock areas in which packrat middens have been found in abundance. Paleoenvironmental data are locked up in these middens, from which investigators have teased out a story of changing climates in the Grand Canyon since the time of the last glaciation in North America. The dateable and identifiable twigs, leaves, and pollen packed away and indurated by urine, show the coming and going of desert and woodland environments at various elevations as the advancing and receding glaciers influenced the world's atmosphere. When cooler, wetter conditions arrive, so do more plants and animals. Things are on the warmer, dry side now.

The first systematic approach to analyzing late Pleistocene environments as revealed in Grand Canyon's packrat middens was a 1974 study published by Arthur M. Phillips, III and Thomas R. Van Devender, a preamble to Phillips' 1977 doctoral dissertation on the Grand Canyon Pleistocene. This was expanded upon by Van Devender and Jim I. Mead (1976); and Van Devender (1977) identified four stages of plant community dominance in the western part of the canyon between 24,000 and 8,500 years ago. Mead's 1981 "The Last 30,000 Years of Faunal History Within the Grand Canyon" was a foundational part of work on his 1983 doctoral dissertation on the extinct Harrington's mountain goat (*Oreamnos harringtoni*) in Grand Canyon. The data from nine caves and 50 packrat middens displayed a gradual early Holocene change from woodland to desert faunal and floral communities, a change completed 8,500 years ago. Kenneth Lee Cole and Samantha T. Arundel (2006) pinpointed the Younger Dryas in Grand Canyon, an anomalous cold period in the midst of the warm-up following the last major glaciation. Most early data were from western Grand Canyon sites, but Kenneth Lee Cole's 1981 doctoral dissertation took care of the eastern part of the canyon. Cole and Mead (1981) described the animal fractions of 53 packrat middens in eastern Grand Canyon. Many regional studies corroborate and suggest refinements to the findings made in Grand Canyon; too many to practically discuss here.

"TOYS" LEAD TO FOSSILS

Stanton's Cave in the Marble Canyon section of Grand Canyon National Park is well-known to river runners. Historically, it is an important site that relates to Robert Brewster Stanton's [1846–1922] flash-in-the-pan 1889–1890 project to survey a railroad route through the canyons from Colorado to California. Scientifically, it is even more important, because it contains not only abundant fossils, but evidence of human use as well. Split-twig figurines, fashioned from a single twig (like willow) split down the middle, with its two fronds twisted and wrapped to create an animal effigy, some with stick spears in the body, were first discovered in 1933 by early river runners who thought they were aboriginal Indians' toys. They are much more than that; considering that many of them had been secreted beneath rock cairns and contain fossil dung pellets, we might see them as a sort of hunting charm. They have been dated here in the canyon to between 2,000 and 4,000 years.

Robert Clark Euler [1924–2002], archaeologist and ethnologist at Grand Canyon National Park, edited in 1978 what still stands as the comprehensive summary of studies at Stanton's Cave. The volume contains separately authored chapters; those of which pertain to paleontological studies are on ungulate remains (C. R. Harrington), zooarchaeological analysis of small vertebrates (John W. Olsen and Stanley J. Olsen), fish remains (Robert Rush Miller and Gerald R. Smith), macroscopic plant materials (Richard H. Hevly), and bird bones (Amadeo M. Rea and Lyndon L. Hargrave), with a paleoecological chapter about the cave by Eleanora I. Robbins, Paul Martin, and Austin Long, and a chapter on the cave "during and after the last ice age" by Paul Martin.

Unlike the disaster at Rampart Cave, Stanton's Cave has been well preserved and protected. A "bat gate" at the entrance prohibits unauthorized human access, while allowing the bat colony that lives in the cave easy exit and entrance.

FOSSILS GO TO SCHOOL

One might notice in this overview that federal involvement was a mainstay of geological research in the late 1800s and early 1900s. At first, geologists were a part of nationally directed surveys in the field. Some independent researchers took the field in the 1910s when the canyon was still very much an unread book. Once the National Park Service had been organized in 1916, and Grand Canyon was finally made a national park in 1919, the Park Service took the reins for a while by encouraging the involvement of the (Washington-based) Carnegie Institution to get researchers into the canyon and to develop outreach programs through museum and trailside exhibits. Almost by brute force, the Grand Canyon's geology and paleontology was being nailed down. Wartime came, with a reduction in field work, and in the post-war period researchers were striking out on their own. The deep pockets of the Carnegie were not as open to them as had been during the end of the Roaring Twenties and into the Depression, as perspectives on the nature of field work and where it was conducted shifted. More researchers were affiliated with academic institutions that sometimes offered their own funding sources for these kinds of activities, and for publication. Others, though they were working for federal agencies like the USGS, were in the same boat. Occasional research was still going on in the canyon, but the Park Service was out of the picture except in the administrative context of managing resources and issuing permits (once that became a more rigorously applied procedure).

Only a few federal geologists were studying the Grand Canyon, and it fell mostly to the universities and museums to undertake that work. Once the Baby Boom generation reached college age, there was no lack for people, though; and in some measure with the concomitant "age of environmentalism," interest in the fantastic Grand Canyon blossomed anew. Still, this was a time when computers didn't do the things they do today, and "poster sessions" at academic conferences looked like taped-together science projects on easels. Now, in just the past couple of decades, laboratory methodologies, publishing and printing techniques, and the topics of applied studies have so dramatically matured that our forebears in science surely would be as appreciatively dumbfounded as are some of us older geologists.

I take the opportunity here to update my 1984 systematic overview with a few notes that document the kinds of research conducted in the canyon since then. These are a mix of systematic, taxonomic, and paleoecological publications, selected only as a representative set rather than a complete list. (See the online bibliography for a more complete list.) From an administrative viewpoint, it's important to realize that these investigations demonstrate the value and use of resources overseen by federal agencies, and the need of these agencies to gather in data about elements of those resources that have over the past century gone into collections beyond their purview. The "bullet point"-type notes that follow are grouped taxonomically and chronologically, and they further demonstrate the shift to academic sources as well as the implementation of new technologies.

Proterozoic: Microbial mat structures in the Chuar Group have been examined by Bottjer and Hagadorn (2007) and Bohacs and others (2007). A Master's thesis on *Microfossils from the Neoproterozoic Chuar Group, Grand Canyon, Arizona: Taxonomy, paleoecological analysis and implications for life during the onset of Neoproterozoic glaciation* (Nagy, 2008). A study of systematics of organic-walled microfossils of the Chuar Group, including new taxa (Porter and Riedman, 2016). Algae in Cryogenean oceans are discussed by Brocks and others (2017). Perspectives on Ediacaran metazoan ecosystems include comparisons to the Chuar Group (Bowyer and others, 2017).

Paleozoic: An important field conference on Cambrian stratigraphy and paleontology in northern Arizona and southern Nevada (Hollingsworth and others, 2011). Brachiopods of the Redwall Limestone (Carter and others, 2014). Chondrichthyan assemblages of the Surprise Canyon and Watahomigi Formations (Hodnett and Elliott, 2018).

Ichnofossils: A new trace fossil, *Angulichnus alternipes*, described from the Bright Angel Shale of Grand Canyon (Elliott and Martin, 1987). Coconino Sandstone invertebrate trackways (Braddy, 1995). Permian tetrapod tracks from Grand Canyon (Hunt and Santucci, 1998). *Bicavichnites martini*, new ichnogenus and ichnospecies, described from the Bright Angel Shale (Lane and others, 2003). Discovery of the "oldest vertebrate trackway in Grand Canyon" (*Chelichnus*?) (Rowland, 2019, a paper presented in a symposium convened in honor of Grand Canyon National Park's 2019 centennial, Earth Day 2019, and the 150th anniversary of John Wesley Powell's 1869 pioneering Colorado River expedition). *Ichniotherium* in the Coconino Sandstone of Grand Canyon (Francischini and others, 2019).

Cave fossils: Age and diet of fossil California condors in Grand Canyon (Emslie, 1987). Mammalian biogeography (Harris, 1990; study sites include several Grand Canyon caves). Parasites in sloth dung from Rampart Cave (Schmidt and others, 1992). A Master's thesis on *Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Grand Canyon, Arizona* (Carpenter, 2003). An overview of late Pleistocene Grand Canyon cave faunas (Mead and others, 2003). A late Pleistocene bat mummy (apparently from an eastern Grand Canyon cave) (Mikesic and Chambers, 2004). An overview of 50,000 years of vegetation and climate history on the Colorado Plateau in Utah and Arizona (Coats and others, 2008). Molecular identification of the extinct mountain goat, *Oreamnos harringtoni* (Campos and others, 2010). A stable-isotope analysis of subfossil bat guano serving as a long-term environmental archive, based on material from Bat Cave in western Grand Canyon (Wurster and others, 2010). Paleoenvironment of the extinct shrub-ox *Euceratherium collinum* on the Colorado Plateau (Kropf and others, 2007, which includes references to "eastern Grand Canyon caves" that are identified only by archaeological site numbers). Larsen and others (2018) made a DNA study of "27,000-year-old papillomavirus infection and long-term codivergence with rodents" based on packrat midden collections made on Poston Butte, Grand Canyon, in 1979. Hunt and Lucas (2018) described a new ichnogenus and ichnospecies of Shasta ground sloth dung, *Castrocopros martini*, based on latrinite specimens from Rampart Cave. Delsuc and others (2019) included Rampart Cave data in DNA sequencing of fossil sloths, revealing an evolutionary history and biogeography of these animals.

If we briefly step across the boundary from Park Service to Bureau of Land Management jurisdiction, we can include a couple of interesting lines of research on the diet and health of aboriginal people living in Antelope Cave on the Uinkaret Plateau to the north of Grand Canyon. A tick found in a human coprolite was identified by Johnson and others (2008) as an adult or nymph of *Dermacentor andersoni* (Stiles), probably having passed through a digestive tract; and there is a case study by Reinhard and others (2012) on determining the pathoecological relationship between ancient diet and modern diabetes based on analyses of human coprolites from the cave. Many studies have also been made of human-made artifacts and of faunal remains here; see particularly the comprehensive overview by Janetski and others (2013).

Administrative needs: In recent years, there have been various important management projects from the National Park Service, embracing Grand Canyon, including: Vertebrate trackways in National Park Service units (Santucci and others, 1998, 2006). Paleontological resources associated with Park Service caves (Santucci and others, 2001). Paleontology as a tool for conservation (Chure, 2002). An inventory of packrat middens in Park Service lands (Tweet and others, 2012). A Master's thesis on *Late Pleistocene and Holocene Bison of Grand Canyon and Colorado Plateau: Implications from the use of paleobiology for natural resource management policy* (Martin, 2014), followed by the publication by Martin and others (2017). Application of new technologies in resource inventory and monitoring (Santucci and Wood, 2015). Concomitant archaeological and paleontological work in Grand Canyon caves (Conservation Legacy, 2016). An inventory of trilobites from Park Service lands (Norr and others, 2016). A register of name-bearing fossil specimens and taxa from National Park Service areas (Tweet and others, 2016). A history of preserving fossils in the national parks (Santucci, 2017), which includes Grand Canyon National Park and Grand Canyon–Parashant National Monument.

As these highlights of the last three decades show, paleontology, the science of the long-dead, is very much alive at Grand Canyon. It is important to realize that it was quite convenient that most of the early fossil collections from the canyon went to the Smithsonian Institution, but as the 20th century progressed more collections began to arrive in universities and independent museums. It has become all the more urgent for federal resource managers to keep up with the ever increasing, widely dispersed, collections that are made on federal lands. The means are at hand—through the diligent work of individuals, of course, but also through the use of such documentary records as digital databases.

A FINAL PALEO NOTE (OF A SORT)

The last we had heard of Joseph C. Ives' steamboat, *Explorer*, it was unmanned, adrift in a flood, heading for the Gulf of California. A survey party on the Colorado River delta during the winter of 1929–30 discovered a partially buried iron boat hull, which was investigated more closely during the following July (Sykes, 1937:90–92). The wreck was found in Sonora, Mexico, about 48 straight-line km (30 mi) from Yuma and far from an active river channel, clearly aground for a long time. Although it was nothing but a skeleton of ribs and some iron hull panels (Sykes, 1937: figure 10), its dimensions were close to those described by Ives (1861). All the wooden parts of the boat were long gone, as was its boiler, though when that had been salvaged is unknown. What made its identification possible was that there were bolts where the two massive lengthwise timbers had been affixed when *Explorer* was reassembled in December 1857, which were meant to stiffen the unnervingly flexible hull. More importantly, an iron patch on a surviving portion of the transom (Sykes, 1937: figure 11), made when the engine was raised and the drive-arm opening reconfigured, effectively confirmed the identity of *Explorer*.

Just when *Explorer* was lost is uncertain, though likely before 1865 according to Sykes. Apparently, the boat went out of control during a flood coming from the mouth of the Gila River at Yuma and was secured to the Colorado bank farther downstream. Later it broke free and disappeared. The constantly shifting channels of the Colorado delta, especially during floods, eventually stranded it in a since-abandoned slough, where it was rediscovered four decades later. There's been no report since 1930—an unceremonious end to the vessel that set in motion the first geology field trip to the Grand Canyon. Perhaps, someday, it will be a fragmentary ichnofossil of the Anthropocene.

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STRATIGRAPHY OF GRAND CANYON NATIONAL PARK

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ABSTRACT

The rocks of the Grand Canyon, which give it its signature appearance, belong to 26 sedimentary formations and a smaller number of igneous and metamorphic units. These rocks represent parts of approximately two billion years of Earth's history, and fossils are known to be present in almost all of the sedimentary units. Grand Canyon rocks are most easily simplified as three distinct packages: Precambrian Vishnu Basement rocks, Precambrian Grand Canyon Supergroup rocks, and layered sedimentary Paleozoic rocks. Major unconformities separate these major subdivisions, and numerous shorter unconformities are interspersed within these packages. Rock types are most diverse in the Vishnu Basement rocks, while the Grand Canyon Supergroup is almost entirely made up of clastic or carbonate sedimentary rocks, and the Paleozoic rocks are all sedimentary. Carbonates are more abundant in the Paleozoic package, reflecting more frequent episodes of open marine deposition, but the Paleozoic also includes several terrestrial eolian intervals. Fossils are more sporadic in the Grand Canyon Supergroup than in the Paleozoic rocks, but are locally very abundant. The fossiliferous units reveal much about the history of life on earth and are the focus of this over-arching report on Grand Canyon paleontology. There are a few Mesozoic exposures as well, but they are not the main story at Grand Canyon; only Triassic rocks are within the park itself. This article presents an overview of the stratigraphy of Grand Canyon to provide the context for a consistent stratigraphic approach utilizing the most current thinking and ages synthesized from the most recent science.

INTRODUCTION

The story that Grand Canyon tells is a spectacle of approximately two billion years of earth history (approximately one-half of the age of the earth) in its rock record, with an equally extensive paleontological component. There is no other place on Earth where the pages of Earth's story can be read so easily by the observer to reveal such a long, rich, geologic history of events that are recorded in the layers. Dr. John Strong Newberry said it best in the mid-19th century: "the most splendid exposure of stratified rocks that there is in the world" (Beus, 2003).

Grand Canyon rocks can be simplified into three main packages: Vishnu Basement rocks, Grand Canyon Supergroup rocks, and layered Paleozoic rocks. These are each separated by major unconformities and indicate formation under differing geologic conditions and during different time intervals (Mathis, 2006). Colorado Plateau uplift and recent downcutting in the canyon and volcanic activity are also responsible for younger geologic materials as well.

Grand Canyon National Park (GRCA) hosts extensive exposures of many Precambrian and Phanerozoic units ranging in age from Proterozoic to Triassic (figure 1 and tables 1 and 2). These units consist of igneous and metamorphic rocks and numerous sedimentary lithologies (siltstones, sandstones, conglomerates, limestones, and dolostones), many of which are extremely fossiliferous. Paleozoic sedimentary rocks are responsible for approximately 900 m (3,000 ft) of the stairstep topography and viewshed in the Grand Canyon. Mesozoic sedimentary rocks likely once covered the Paleozoic section, but these rocks are now only seen in rare isolated outcrops in GRCA (Billingsley and others, 2019).

This summary presents a focused overview of the stratigraphy of GRCA and does not delve into the broader and complex geologic topics and themes associated with

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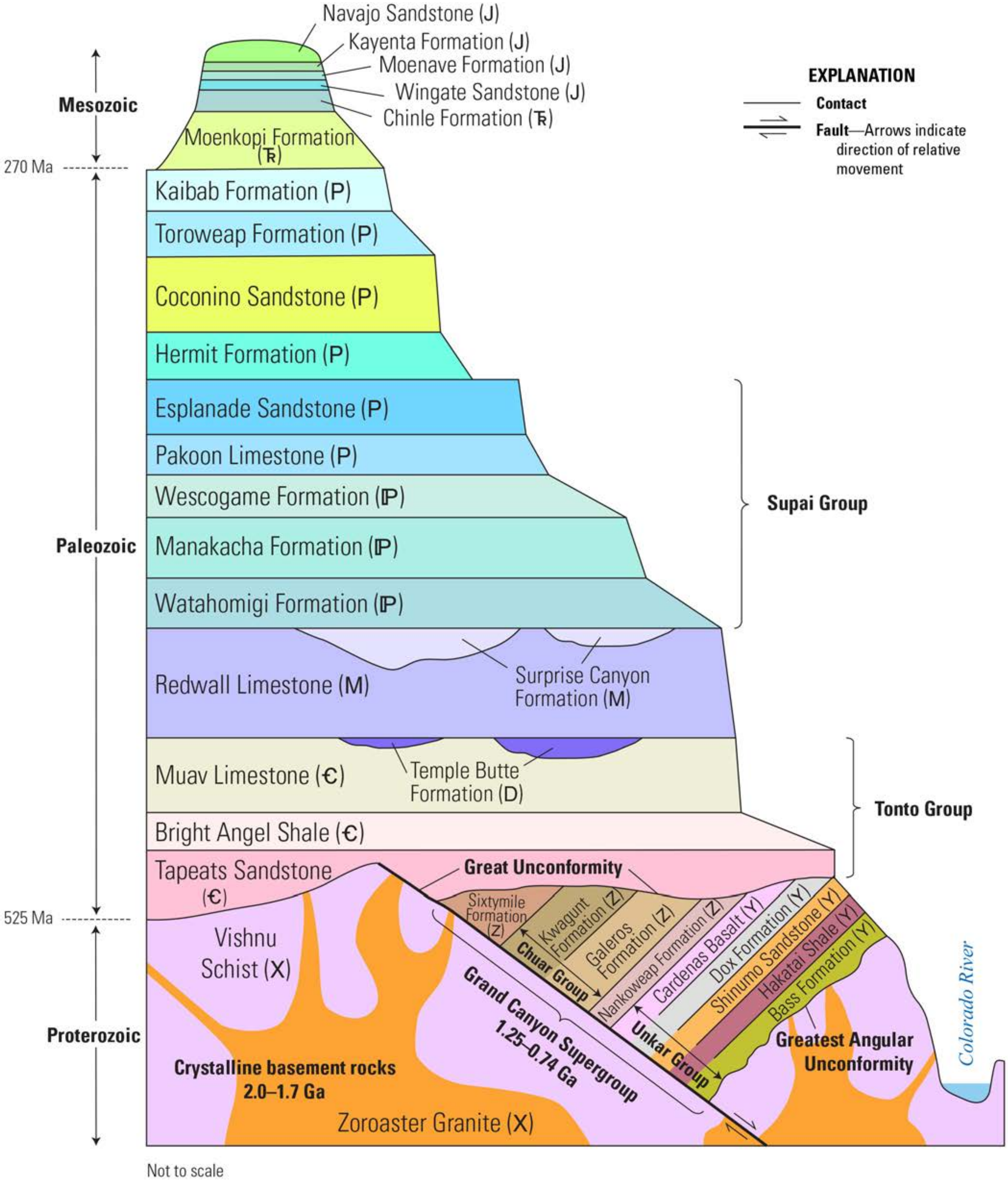

Figure 1. *Grand Canyon stratigraphy and structural relations (Billingsley and others, 2019: figure 2). Recently, the Sixtymile Formation was proposed to be Cambrian (not Proterozoic) (Karlstrom and others, 2018, 2020) and the Nankoweap was moved into the Chuar Group (Dehler and others, 2017). Mesozoic rocks younger than the Chinle Formation are not found within the boundaries of GRCA, but are present in the immediate vicinity.*

Table 1. *Grand Canyon area stratigraphy, based on Billingsley and others (2019: table 2).*

Era	Period/Subperiod	Formation	Member
Mesozoic (Mz)	Triassic (Tr)	Chinle Formation	Shinarump Member
		Moenkopi Formation	Holbrook Member Moqui Member Wupatki Member
Paleozoic (Pz)	Permian (P)	Kaibab Formation	Harrisburg Member Fossil Mountain Member
		Toroweap Formation	Woods Ranch Member Brady Canyon Member Seligman Member
		Coconino Sandstone	
		Hermit Formation	
		Esplanade Sandstone	
		Pakoon Limestone	
	Pennsylvanian (IP)	Wescogame Formation	
		Manakacha Formation	
		Watahomigi Formation	
	Mississippian (M)	Surprise Canyon Formation	
		Redwall Limestone	Horseshoe Mesa Member Mooney Falls Member Thunder Springs Member Whitmore Wash Member
	Devonian (D)	Temple Butte Formation	
	Cambrian (Ꞓ)	Frenchman Mountain Dolostone	
		Muav Limestone	Havasu Member Gateway Canyon Member Kanab Canyon Member Peach Springs Canyon Member Rampart Cave Member
		Bright Angel Shale	Flour Sack Member red-brown member
		Tapeats Sandstone	
		Sixtymile Formation	
Neoproterozoic (Z)		Kwagunt Formation	Walcott Member Awatubi Member Carbon Butte Member
		Galeros Formation	Carbon Canyon Member Jupiter Member Tanner Member
		Nankoweap Formation	
Mesoproterozoic (Y)		Cardenas Basalt	
		Dox Formation	Ochoa Point Member Comanche Point Member Solomon Temple Member Escalante Creek Member
		Shinumo Sandstone	
		Hakatai Shale	
		Bass Formation	Hotauta Conglomerate Member
Paleoproterozoic (X)		Zoroaster Granite	
		Vishnu Schist	

Table 2. *Overview of GRCA stratigraphy and paleontology. See the various articles for more paleontological information. (continued on the following page)*

Formation	**Age**	**Paleontological Resources**
Upper Cenozoic sediments	Pleistocene–Holocene	Almost entirely late Pleistocene–Holocene fossils, predominantly from dry cave and crevice deposits; horsetails, ferns, gnetales, conifers, and angiosperms (macrobotanical), driftwood, pollen, nematodes and their eggs (in dung), bivalves, aquatic and terrestrial gastropods, ostracodes, arthropods (ticks, scorpions, millipedes, beetles, flies, hemipterans, cicadas, hymenopterans, lepidopterans, antlions, grasshoppers), osteichthyans, frogs, salamanders, turtles, lizards, snakes, birds (accipitriforms, anseriforms, apodiforms, cathartiforms, charadriiforms, columbiforms, falconiforms, galliforms, gruiforms, passeriforms, pelecaniforms, piciforms, podocipediforms, strigiforms), mammals (sloths, shrews, rodents, rabbits, bats, carnivorans, proboscideans, horses, artiodactyls), dung (lizard, mammal), bird regurgitation pellets, packrat middens, ringtail middens, and bird eggshell and nests
Chinle Formation	Late Triassic	Petrified wood
Moenkopi Formation	Early–?Middle Triassic	Invertebrate trace fossils and vertebrate tracks (*Rotodactylus*)
Kaibab Formation	early Permian	Dasycladacean algae, sponges, rugose corals, conulariids, bryozoans, brachiopods, bivalves, nautiloids, gastropods, scaphopods, trilobites, crinoids, echinoids, chondrichthyans (ctenacanthiforms, hybodontiforms, euselachians, petalodontiforms, and holocephalans), platysomid actinopterygians, indeterminate actinopterygian teeth and scales, and invertebrate burrows and trails
Toroweap Formation	early Permian	Bryozoans, brachiopods, bivalves, nautiloids, gastropods, scaphopods, ostracodes, crinoids, echinoids, and stromatolites
Coconino Sandstone	early Permian	Invertebrate burrows, trails, and tracks, anamniote tracks (cf. *Amphisauropus* and *Ichniotherium*), reptile tracks (cf. *Dromopus*, *Erpetopus*, and *Varanopus*), synapsid tracks (cf. *Tambachichnium*), and undetermined tetrapod tracks
Hermit Formation	early Permian	Horsetails, “seed ferns”, ginkgoes, conifers, undetermined plants, eurypterids, insects, invertebrate burrows, trails, and tracks, anamniote tracks (*Amphisauropus*, *Batrachichnus*, and *Ichniotherium*), reptile tracks (*Dromopus*, *Erpetopus*, and *Hyloidichnus*), synapsid tracks (*Dimetropus*), undetermined tetrapod tracks, and possible microbial features
Esplanade Sandstone (in west transitions to Pakoon Limestone)	early Permian	Conifers (*Walchia*), undetermined plants, bioclasts of marine invertebrates (corals, bryozoans, pelmatozoans, and brachiopods or bivalves), invertebrate burrows and trails, and foraminifers
Wescogame Formation	Late Pennsylvanian	Undetermined plants, bioclasts of invertebrate fossils (bryozoans, pelmatozoans, and brachiopods or bivalves), holocephalan chondrichthyans, invertebrate burrows, trails, and tracks, anamniote tracks (cf. *Amphisauropus*, *Batrachichnus*, and cf. *Limnopus*), reptile tracks (*Varanopus*), undetermined tetrapod tracks, foraminifers, and microbial features
Manakacha Formation	Middle Pennsylvanian	Undetermined ferns and other plants, bioclasts of invertebrate fossils (bryozoans, ostracodes, pelmatozoans, and brachiopods or bivalves), microbial trace fossils (stromatolites), invertebrate burrows, trails, and tracks, tetrapod tracks, foraminifers, and “algal” bioclasts (calcispheres and *Girvanella*)

Table 2. *continued*

Formation	Age	Paleontological Resources
Watahomigi Formation	Early–Middle Pennsylvanian	Equisetopsids (*Calamites*), "seed ferns" (*Neuropteris*), conifers (*Cordaites* and *Walchia*), *Taeniopteris*, undetermined plants, corals including tabulates, conulariids, bryozoans, brachiopods, bivalves, gastropods, trilobites, crinoids, echinoids, conodonts, chondrichthyans (holocephalan and indeterminate dermal denticles), undetermined fish teeth, microbial trace fossils (stromatolites), invertebrate burrows and trails, foraminifers, and "algae"
Surprise Canyon Formation	Late Mississippian	*Calamites*, *Lepidodendron*, *Lepidostrobophyllum*, undetermined wood and other plant fossils, rugose and tabulate corals, bryozoans, brachiopods, bivalves, gastropods, trilobites, ostracodes, asteroids, blastoids, crinoids, echinoids, conodonts, chondrichthyans (thrinacodontids, xenacanthiforms, symmoridforms, ctenacanthiforms, hybodontiforms, euselachians, indeterminate elasmobranchs, paraselachians, orodontiforms, eugenodontiforms, petalodontiforms, and holocephalans), indeterminate actinopterygians, indeterminate tetrapods, microbial trace fossils ("algal" laminations, oncolites, stromatolites), invertebrate burrows and trails, foraminifers, and "algae"
Redwall Limestone	Early–Middle Mississippian	Rugose and tabulate corals, bryozoans, brachiopods, nautiloids, gastropods, trilobites, blastoids, crinoids, holocephalan chondrichthyans, undetermined fish teeth, invertebrate burrows and trails, foraminifers, "algae", and calcispheres
Temple Butte Formation	Middle–Late Devonian	Rugose corals, brachiopods, gastropods, conodonts, placoderms, sarcopterygians, indeterminate fish, invertebrate burrows and trails, and trace fossils or stromatoporoid sponges
Frenchman Mountain Dolostone	middle–late Cambrian	Invertebrate burrows and trails
Muav Limestone	middle Cambrian	Sponges, brachiopods, hyoliths, helcionelloids, trilobites, eocrinoids, enigmatic invertebrates (*Chancelloria*, *Scenella*), invertebrate burrows and trails, and *Girvanella*-like structures (oncolites)
Bright Angel Shale	middle Cambrian	Cryptogam spores, brachiopods, hyoliths, trilobites, bradoriids, eocrinoids, enigmatic invertebrates (*Chancelloria*, *Tontoia*), microbial wrinkle structures, invertebrate burrows and trails, leiospheres, filament mats resembling *Nematothallus*, non-marine cryptospores, terrestrial algal cell clusters, enigmatic fossils (*Margaretia*), and possibly sponges
Tapeats Sandstone	early–middle Cambrian	Brachiopods, trilobites, and invertebrate burrows and trails
Sixtymile Formation	early Cambrian	Potential undetermined fragment
Kwagunt Formation	middle Neoproterozoic (late Tonian)	Stromatolites and other microbial features, acritarchs and colonial organic-walled microfossils, microbial filaments, vase-shaped microfossils, various unspecified microfossils, "vampire traces" on microfossils, chemical evidence for possible sponges, and possible meiofaunal traces
Galeros Formation	middle Neoproterozoic (late Tonian)	Stromatolites and other microbial features, acritarchs and colonial organic-walled microfossils, microbial filaments, various unspecified microfossils, and "vampire traces"

Table 2. *continued*

Formation	Age	Paleontological Resources
Nankoweap Formation	middle Neoproterozoic (late Tonian)	None to date, unless *Brooksella canyonensis* is organic
Cardenas Basalt	late Mesoproterozoic	None to date; fossils are unlikely but not impossible
Dox Formation	late Mesoproterozoic	Stromatolites and probable microbially induced sedimentary structures; also dubiofossils
Shinumo Quartzite	late Mesoproterozoic	None confirmed; also dubiofossils
Hakatai Shale	late Mesoproterozoic	Stromatolites and other microbial features in the Bass–Hakatai transition zone; also dubiofossils
Bass Formation	middle–late Mesoproterozoic	Stromatolites and other microbial structures, possible microfossils, and possible microbial filaments; also dubiofossils
Paleoproterozoic–Mesoproterozoic basement	late Paleoproterozoic–early Mesoproterozoic	Unfossiliferous igneous and high-grade metamorphic rocks

the origin and geologic history of the Grand Canyon itself. It is a brief overview focused on the stratigraphic framework for Grand Canyon to provide a context for the rich and diverse paleontological resources presented in this report and establishes consistency for the other articles of this inventory.

PRECAMBRIAN STRATIGRAPHY OF GRAND CANYON

The Precambrian rocks of GRCA consist of igneous, metamorphic, and sedimentary rocks. Precambrian sedimentary and igneous rocks are generally only exposed in the eastern and central Grand Canyon regions along the canyon depths, while Proterozoic crystalline rocks are only exposed along the Colorado River and tributaries in eastern and western Grand Canyon (Billingsley and others, 2019).

The base of the Precambrian section is composed of various igneous and metamorphic bodies of Paleoproterozoic age, overlaid by a series of primarily sedimentary units. The "Vishnu Basement rocks" (consisting of generically the Elves Chasm Gneiss, and granites and schists) will not be treated here as they do not contain paleontological resources. The "Grand Canyon Supergroup rocks" are divided into the Mesoproterozoic Unkar Group (consisting of the Bass Formation, Hakatai Shale, Shinumo Sandstone, Dox Formation, and Cardenas Basalt), and the Neoproterozoic Chuar Group (Nankoweap Formation, Galeros Formation, and Kwagunt Formation). These sedimentary rocks are discussed in further detail in the Precambrian paleontology article by Tweet; capsule descriptions are included here.

Grand Canyon Supergroup: Unkar Group

The Unkar Group consists of the Mesoproterozoic Bass Formation, Hakatai Shale, Shinumo Sandstone, Dox Formation, and Cardenas Basalt (figures 2 and 3).

Unkar Group: Bass Formation (Mesoproterozoic)

The Bass Formation is primarily composed of dolomite, with some interbedded sandstone, mudstone, and pebble conglomerate, about 60 to 100 m (200 to 330 ft) thick. The basal part of the formation is a cobble conglomerate known as the Hotauta Member. The Bass Formation is interpreted as mostly shallow to restricted marine, with increasing clastic input over time. It grades into the overlying Hakatai Shale. The base of the formation dates to approximately 1254 Ma (million years ago) (Timmons and others, 2005, 2012). This formation is significant for preserving the oldest evidence of life in GRCA.

Unkar Group: Hakatai Shale (Mesoproterozoic)

The Hakatai Shale is a clastic unit consisting of primarily siltstone and fine-grained sandstone, with lithologies ranging from mudstone to conglomerate, varying from 137 to 300 m (450 to 980 ft) thick. The upper contact with the Shinumo Sandstone is unconformable. It is interpreted as a shallow water unit from marginal marine, tidal flat and deltaic settings, deposited at least in part after 1187 Ma (Timmons and others, 2005, 2012).

Unkar Group: Shinumo Sandstone (Mesoproterozoic)

The Shinumo Sandstone is a mostly quartzitic sandstone interpreted as a high-energy shoreface unit. It is approximately 355 to 410 m (1,160 to 1,350 ft) thick and has a gradational contact with the overlying Dox Formation (Timmons and others, 2005, 2012). It may be as old as ca. 1170 Ma (Timmons and others, 2012) or as young as 1140 Ma (Mulder and others, 2017).

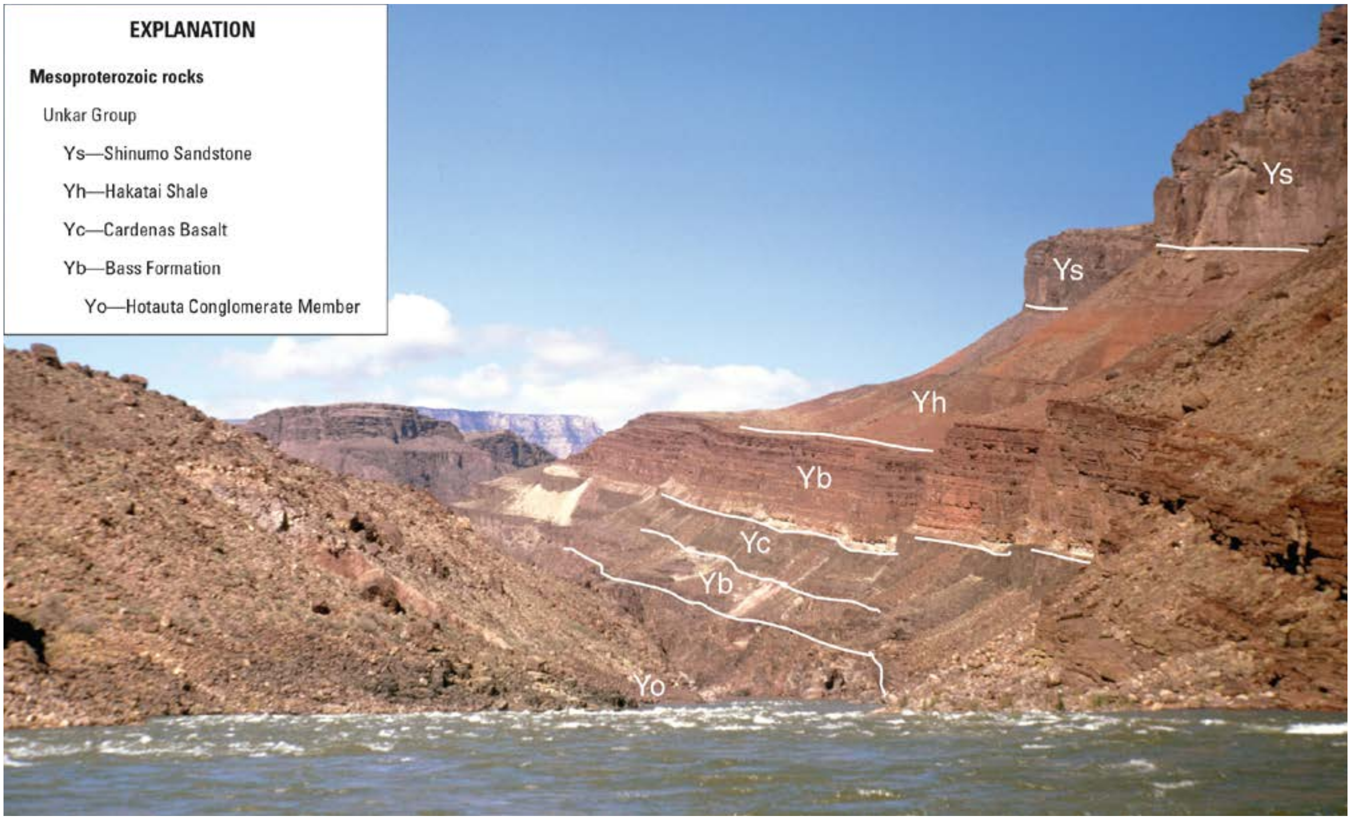

Figure 2. *Mesoproterozoic rocks of the Unkar Group (Grand Canyon Supergroup) in eastern Grand Canyon. Yo=Hotauta Conglomerate Member; Yb=Bass Formation; Yc=Cardenas Basalt; Yh=Hakatai Shale; Ys=Shinumo Sandstone (Billingsley and others, 2019: figure 3).*

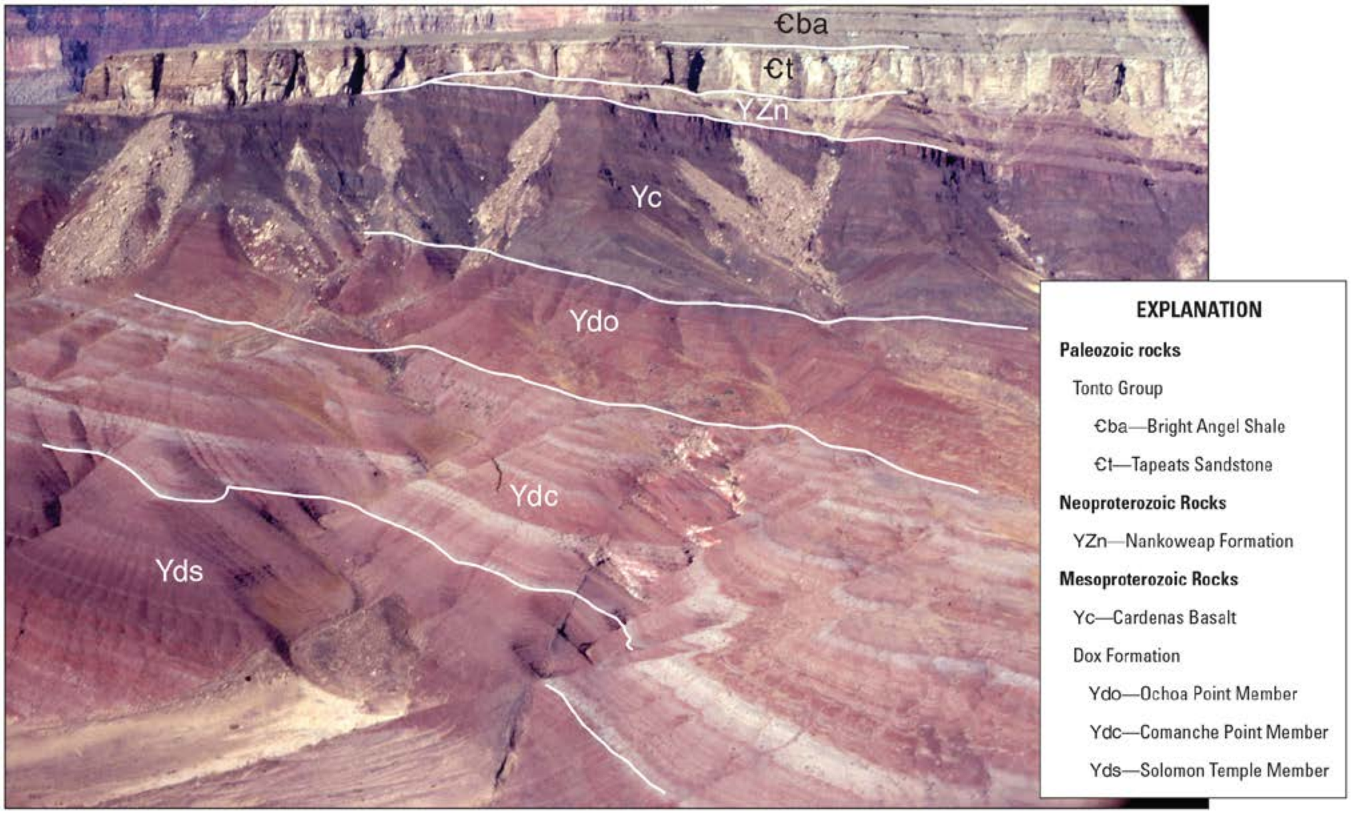

Figure 3. *Mesoproterozoic rocks in contact with lower Tonto Group (Tapeats Sandstone and Bright Angel Shale) in eastern Grand Canyon (Billingsley and others, 2019: figure 4).*

Unkar Group: Dox Formation (Mesoproterozoic)

The Dox Formation is predominantly composed of red sandstone. It is interpreted as initially a fluvial to deltaic unit, becoming more marine over time (Timmons and others, 2012; Mulder and others, 2017). It has been divided into four members, in ascending order the Escalante Creek, Solomon Temple, Comanche Point, and Ochoa Point Members, with a combined thickness of approximately 920 m (3,020 ft) (Elston, 1989a). Deposition occurred between approximately 1140 and 1104 Ma (Timmons and others, 2012; Mulder and others, 2017).

Unkar Group: Cardenas Basalt (Mesoproterozoic)

The Cardenas Basalt is an unfossiliferous basalt unit formed by eruptions that began near the end of Dox Formation deposition, as shown by interfingering Dox beds and Cardenas lava flows. It is about 300 m (980 ft) thick and dates to approximately 1104 Ma. Its upper contact with the Nankoweap Formation is unconformable (Timmons and others, 2005, 2012).

Grand Canyon Supergroup: Chuar Group

The Chuar Group consists of the Neoproterozoic Nankoweap, Galeros and Kwagunt Formations, each with their own members.

Chuar Group: Nankoweap Formation (Neoproterozoic)

The Nankoweap Formation can be divided into a lower red unit of hematite-cemented sandstone and mudstone, and an upper white unit of siltstone and sandstone (Timmons and others, 2012). These two informal members have an unconformable contact, and the overall thickness of the formation varies greatly from 113 to more than 250 m (370 to more than 820 ft) (Elston, 1989a). This unit was recently found to be much younger than previously inferred by dating detrital zircons, at less than approximately 782 Ma, and has been added to the Chuar Group (Dehler and others, 2017).

Chuar Group: Galeros Formation (Neoproterozoic)

The Galeros Formation is a dominantly clastic unit, mostly mudstones with some sandstone and dolomite beds. It is divided into four members, in ascending order the Tanner, Jupiter, Carbon Canyon, and Duppa Members. Like the similar overlying Kwagunt Formation, it is interpreted as representing primarily wave- and tidal-influenced marine deposition and supratidal. The upper contact with the Kwagunt Formation is gradational, and the two together are about 1,600 m (5,250 ft) thick (Dehler and others, 2001, 2012). It dates from after 782 Ma to approximately 751 ± 7.6 Ma (Rooney and others, 2018).

Chuar Group: Kwagunt Formation (Neoproterozoic)

The Kwagunt Formation is lithologically similar to the Galeros Formation and is also divided into several members (in ascending order the Carbon Butte, Awatubi, and Walcott Members). It was also primarily deposited in shallow subtidal to intertidal settings, with more frequent episodes of subaerial exposure than the Galeros Formation (Dehler and others, 2001, 2012). Deposition occurred after approximately 751 Ma to about 729 ± 0.9 Ma (Rooney and others, 2018).

PALEOZOIC STRATIGRAPHY OF GRAND CANYON

Outcrops of 17 distinct Paleozoic formations have been reported in GRCA, ranging in age from the Cambrian to the Permian. These rocks vary greatly in depositional environments ranging from open marine to eolian terrestrial. As discussed in the other articles, they also preserve a broad array of fossils, from Cambrian invertebrate burrows and trails, to Devonian fish, to Mississippian crinoids, to Pennsylvanian vertebrate tracks, to Permian plants and insects. GRCA boasts one of the most complete Paleozoic records in the National Park System, particularly from the Late Devonian through the end of the Permian.

Tonto Group (lower–middle Cambrian)

The Tonto Group (figures 3 and 4) consists of the Sixtymile Formation, Tapeats Sandstone, Bright Angel Shale (or Formation), Muav Limestone (or Formation), and Frenchman Mountain Dolostone (Karlstrom and others, 2020). Historically it included only the Tapeats, Bright Angel, and Muav Formations. It is misleading to consider these three units as simple “layer cake” beds. The formations are defined by lithology and because deposition occurred over many small-scale marine regressions and transgressions during the overall marine transgression, the lithologies intertongue extensively, making mapping complicated (Beus and Billingsley, 1989; Huntoon, 1989).

Tonto Group: Sixtymile Formation (lower Cambrian)

The Sixtymile Formation was thought to be Precambrian in age until recently, when dating of detrital zircons established it as Cambrian in age (Karlstrom and others, 2018). It is only found in a few areas of eastern GRCA and is composed of red- to white sandstone and siltstone with chert and interformational breccia (Elston, 1979). What had previously been described as the lowest part of the formation has been transferred to the upper Kwagunt Formation (Timmons and others, 2001). The Sixtymile Formation was deposited in lacustrine, fluvial, and shallow marine settings in fault-controlled basins. Detrital zircons indicate it was deposited between 520 and 509 Ma, making it contemporaneous in part with rocks of the lower Tonto Group in the western Grand Canyon and Lake Mead regions (Karlstrom and others, 2018). There is an angular unconformity between the Sixtymile Formation and the overlying Tapeats Sandstone (A. Mathis, pers. comm., December 2019).

Tonto Group: Tapeats Sandstone (lower–middle Cambrian)

The Tapeats Sandstone is a medium- to coarse-grained, cliff-forming conglomeratic sandstone (Beus and Billingsley, 1989). At GRCA, this unit is deposited on what had been the hilly terrain of weathered Precambrian rocks (the Grand Canyon Supergroup in eastern GRCA, the older Vishnu Basement in western GRCA) (Middleton and Elliott, 2003). The unconformity with all underlying Precambrian rocks is known as the Great Unconformity. The base of the Tapeats Sandstone is locally conglomeratic, with mudstone and fine sandstone becoming common toward the top, where the Tapeats Sandstone forms a transition zone with the overlying Bright Angel Shale (Middleton and Elliott, 2003). Three members may be apparent in the western part of the canyon, with a shale (mudstone)-rich member sandwiched between sandstone members (Elston, 1989d).

Historically, the Tapeats Sandstone and the rest of the Tonto Group were considered to span much of the Cambrian and were interpreted as a classic example of a gradual marine transgression in which the nearshore sands of the Tapeats Sandstone were replaced by successively deeper marine deposits of the Bright Angel Shale and Muav Limestone (McKee and Resser, 1945). More recent study indicates that the marine transgression responsible for the Tonto Group took place over a much shorter time frame (Karlstrom and others, 2018). West of GRCA, the upper Tapeats Sandstone includes rocks deposited approximately 508 to 504 Ma, while in eastern GRCA, the Tapeats Sandstone has a maximum depositional age of 505.4 ± 8.0 Ma (Karlstrom and others, 2018).

The Tapeats Sandstone is typically interpreted as representing shallow marine sand deposition under significant tidal influence, with more terrestrial environments toward the base (Hereford, 1977; Middleton, 1989; Middleton and Elliott, 2003). However, the formation may have been more continental overall, perhaps a fluvial braidplain (Baldwin and others, 2004). The thickness of the formation varies from very thin or absent where deposited over prominent paleotopographic highs, to 90 m (300 ft), 12 to 15 m (40 to 50 ft) of which are part of a transition zone (Beus and Billingsley, 1989).

Tonto Group: Bright Angel Shale (middle Cambrian)

The Bright Angel Shale is a mixed formation mostly composed of shale (mudstone) to fine-grained sandstone (Middleton and Elliott, 2003). The rocks are sometimes divided into numerous members (McKee, 1945; Spamer, 1984; Beus and Billingsley, 1989). It appears to have been deposited between approximately 505 to 501 Ma in Grand Canyon (Karlstrom and others, 2018). It has a complex gradational and intertonguing relationship with the overlying Muav Limestone (Middleton, 1989). To simplify matters, Elston (1989d) has suggested transferring the lower portion of the Muav Limestone to the Bright Angel Shale. The Bright Angel Shale is about 107 to 150 m (350 to 500 ft) thick (Billingsley, 2000).

The Bright Angel Shale is generally interpreted as a shallow marine shelf unit (Middleton and Elliott, 2003). The various members correspond to minor transgressions and regressions (Elston, 1989d; Beus and Billingsley, 1989). When interpreted as more continental, the rocks are instead seen as representing estuary and tidal flat settings (Baldwin and others, 2004) influenced by storm events (Elliott and Martin, 1987). The lack of acritarchs in the mudstones, the dominant lithology of the formation, may be evidence for minimal marine influence in those rocks (Baldwin and others, 2004).

Tonto Group: Muav Limestone (middle Cambrian)

The Muav Limestone is composed of limestone, dolomite, thin shale (mudstone) and siltstone, and conglomerate (Spamer, 1984; Middleton and Elliott, 2003), and forms cliffs at GRCA (Middleton and Elliott, 2003). Like the Bright Angel Shale, it can be divided into multiple members (Spamer, 1984; Middleton, 1989; Middleton and Elliott, 2003). Trilobites of the Muav Limestone can be attributed to the same part of the Cambrian as the Bright Angel Shale of eastern GRCA (Karlstrom and others, 2018), so it is likely not substantially younger. It is between 45 and 245 m (150 and 800 ft) thick (Spamer, 1984). Its upper contact is an unconformity with the unnamed dolomite unit (Beus and Billingsley, 1989).

The Muav Limestone is interpreted as representing subtidal to supratidal offshore deposits (Middleton and Elliott, 2003). The various members correspond to minor transgressions and regressions (Elston, 1989d; Beus and Billingsley, 1989). There are also some tidal flat deposits, particularly in the western part of GRCA (Wanless, 1973; Baldwin and others, 2004).

Tonto Group: Frenchman Mountain Dolostone (middle–?upper Cambrian)

Above the Muav Limestone at GRCA is a unit historically known as the "undifferentiated dolomites", now assigned to the Frenchman Mountain Dolostone by Karlstrom and others (2020). It consists of white to gray dolomite beds with thin layers of shale (mudstone) between beds, especially in the lower part of the unit. Its exact age is uncertain, due to the paucity of fossils. The thickness varies from 60 to 140 m (200 to 450 ft) (Beus and Billingsley, 1989). This unit is found in western GRCA (Middleton, 1989). It is also sometimes called the "Supra-Muav" or "Grand Wash Dolomite" in the literature (Middleton, 1989), although the latter name is precluded from formal usage because "Grand Wash" is already in use for a different unit in the area (Elston, 1989d). This unit is interpreted as shallow subtidal to possibly intertidal in depositional setting (Middleton and Elliott, 2003), deposited in a regressing sea (Spamer, 1984).

Temple Butte Formation (Middle–Upper Devonian)

The Temple Butte Formation (figure 4) is a dolomite (dolostone) and sandstone unit, becoming mostly dolomitic in western GRCA (Beus, 1989). In eastern GRCA, it is discontinuous, filling channels cut into the underlying Cambrian rocks. It becomes a thicker and continuous layer in the western part of the park, with dolomite over the channel fill (Spamer, 1984). Some descriptions have combined part of the unnamed Cambrian dolomite with the formation (Beus, 2003a). Conodont fossils have been used to date the Temple Butte Formation to the late Middle and early Late Devonian (Beus, 1980). Where present, it is up to 135 m (450 ft) thick in western GRCA (Beus and Billingsley, 1989). Both the lower contact with Cambrian rocks and the upper contact with the Redwall Limestone are unconformities (Spamer, 1984). Most of the Temple Butte Formation is interpreted as representing shallow, subtidal, open marine settings in western Grand Canyon, although some of the dolomite may be supratidal and the channel fill could correspond to tidal channels in eastern Grand Canyon (Beus, 2003a). A transgression occurred during the deposition of this unit, moving west to east (Beus, 1989).

Redwall Limestone (Lower–Middle Mississippian)

The Redwall Limestone (figures 4 and 5) is made up mostly of limestone, with some dolomite, chert, and mudstone (Beus and others, 1989). The most detailed description of the unit is McKee and Gutschick (1969a), which includes data from a number of GRCA localities. This cliff-forming unit is actually gray, but in the canyon it has been stained red on the surface by iron oxides washed from the overlying Supai Group (McKee and Gutschick, 1969b). There are four members, all present at GRCA; from oldest to youngest, they are the Whitmore Wash, Thunder Springs, Mooney Falls, and Horseshoe Mesa Members (McKee, 1963). The Whitmore Wash Member is mostly limestone and dolomite, thickening from 15 m (50 ft) in eastern GRCA to 36 m (120 ft) in western GRCA, which dates to the Early Mississippian. The Thunder Springs Member is a distinctively banded unit, due to alternating carbonate and chert beds. It is 30 m (100 ft) thick in eastern GRCA, increasing to 43 m (140 ft) in western GRCA. It is slightly younger than the Whitmore Wash Member. The Mooney Falls Member is a massive cliff-forming limestone, and spans from 76 m (250 ft) thick in eastern GRCA to 104 m (340 ft) thick in western GRCA. It dates to the early Middle Mississippian. Finally, the Horseshoe Mesa Member, composed of limestone ledges, is thinnest, ranging from 0 to 30 m (0 to 100 ft) thick. It is absent where the overlying channel-filling Surprise Canyon Formation is present. It is slightly younger than the Mooney Falls Member (Beus and Billingsley, 1989). Within the formation, there is a depositional hiatus between the Thunder Springs and Mooney Falls Members that becomes progressively greater from west to east (Beus, 1989). Shortly after its deposition, the upper part of the Redwall Limestone eroded to form a karst terrain (McKee and Gutschick, 1969d) and erodes into overhangs and caves today (McKee and Gutschick, 1969b).

The Redwall Limestone records two marine transgression-regression cycles. The older and larger cycle is represented by the transgressional Whitmore Wash Member and the regressional Thunder Springs Member, and the second cycle is represented by the transgressional Mooney Falls Member and the regressional Horseshoe Mesa Member (Beus, 1989). The marine body transgressed from west to east, forming a shallow sea (Beus, 2003b). Several types of limestone and other rocks are found throughout the members and correspond to different environments on the shelf (McKee and Gutschick, 1969c). Distinct fossil assemblages are found from these different settings. For example, featureless limestone appears to represent lime mud deposits that were not conducive to life, with the only numerous fossils being massive colonial corals. Oolitic limestone (limestone composed of small spherical particles) is probably from warm shallow water with moderate energy, and has a faunal assemblage of foraminifera, corals, ostracodes, and sea cucumbers, with algal structures (McKee and Gutschick, 1969d).

Fossil preservation in the Redwall Limestone is quite variable, depending on the matrix, organisms, and environment. Fossils found in chert are often the best,

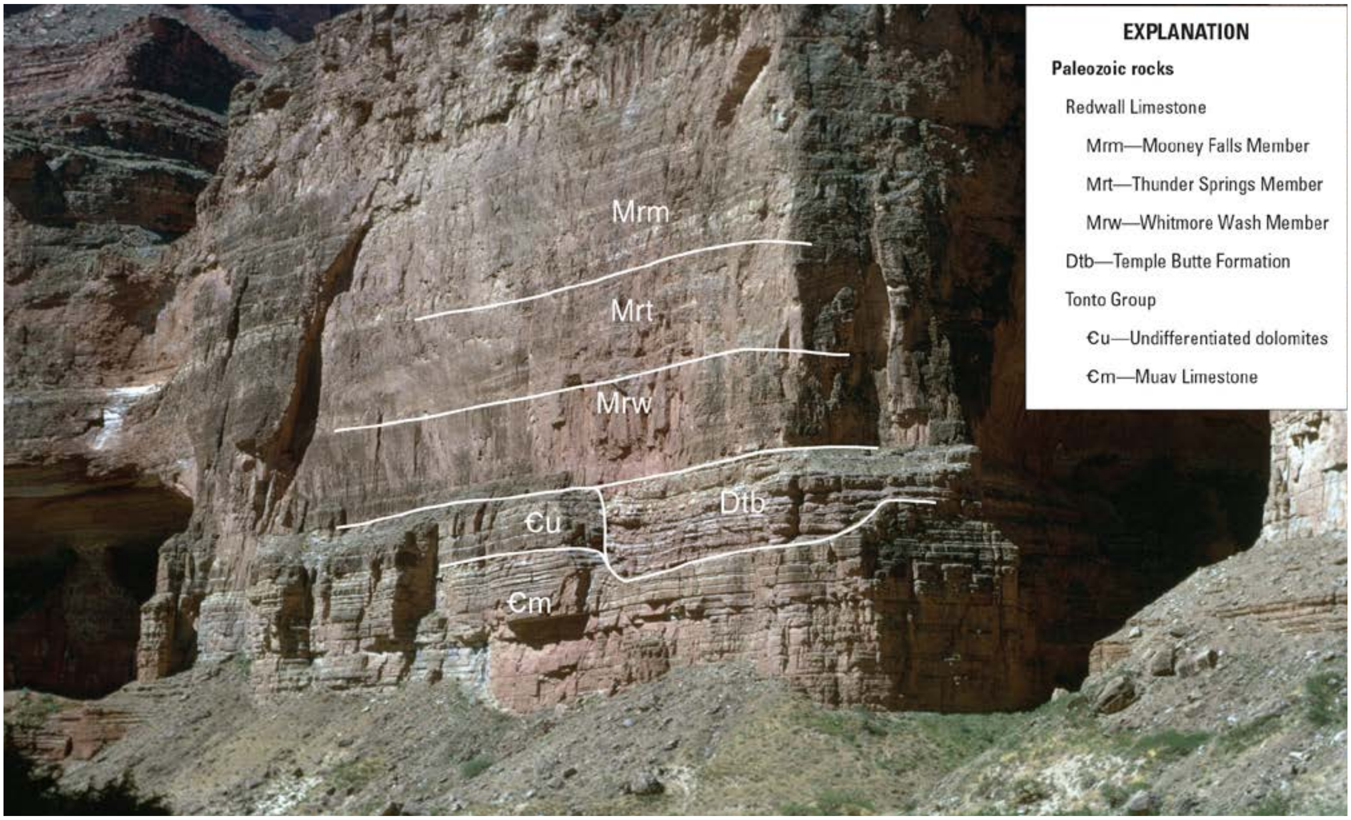

Figure 4. *Upper Tonto Group (Cm=Muav Limestone; Cu=”undifferentiated dolomites”, now the Frenchman Mountain Dolostone), Temple Butte Formation (Dtb), and Redwall Limestone (Mrw=Whitmore Wash Member; Mrt=Thunder Springs Member; Mrm=Mooney Falls Member) in eastern Grand Canyon (Billingsley and others, 2019: figure 5).*

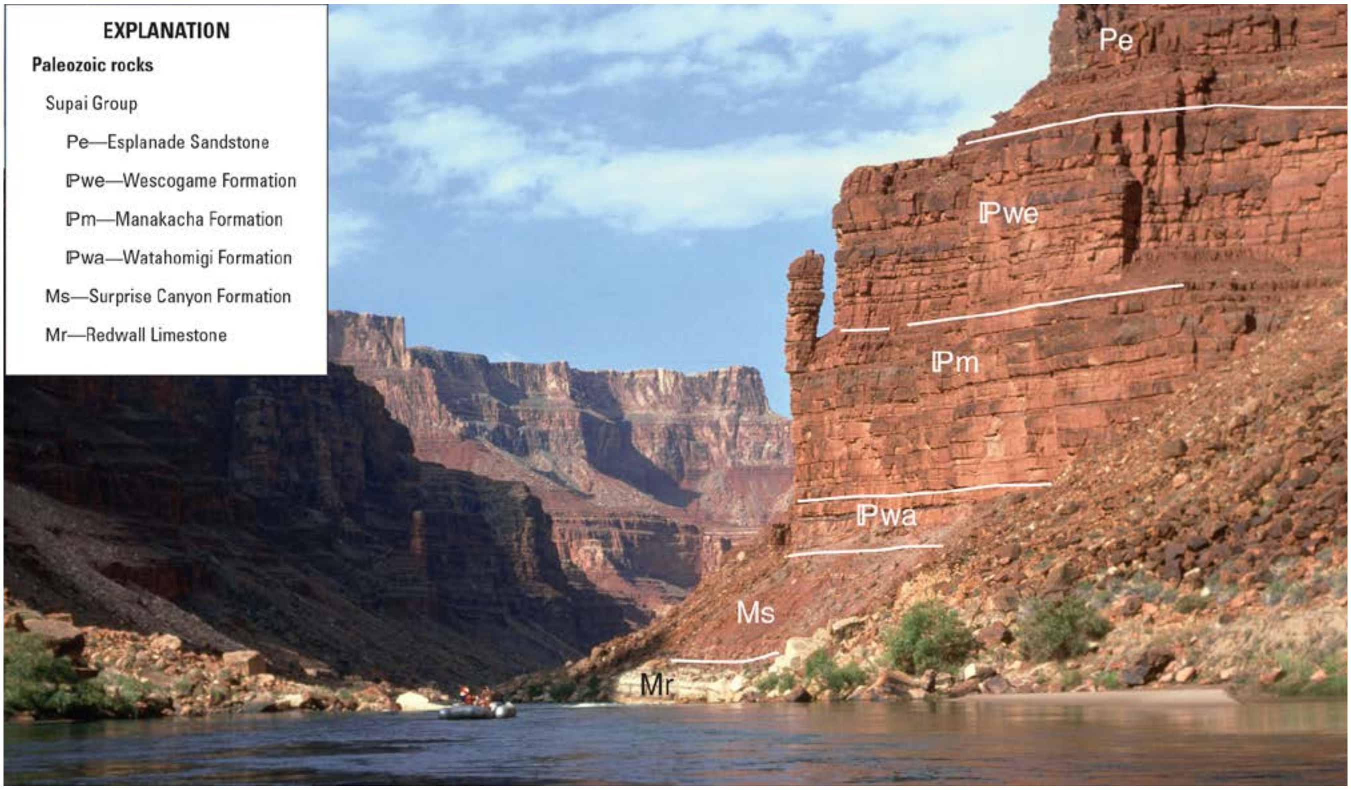

Figure 5. *Redwall Limestone (Mr), Surprise Canyon Formation (Ms), and overlying Supai Group (Pwa=Watahomigi Formation; Pm=Manakacha Formation; Pwe=Wescogame Formation; Pe=Esplanade Sandstone) (Billingsley and others, 2019: figure 6).*

though usually preserved as molds (McKee and Gutschick, 1969d). Fossils in GRCA's Whitmore Wash Member were often destroyed when limestone was altered to dolomite (Beus, 2003b), a common phenomenon in southeastern GRCA (McKee and Gutschick, 1969e). Fossils are common in the Thunder Springs and Mooney Falls members (Beus and Billingsley, 1989). The limestone beds of the Thunder Springs Member are crinoid-rich, while the chert beds are formed by silicified bryozoan limestones and mudstones (Beus and Billingsley, 1989). The best fossils are found in the chert beds (Beus, 2003b). Bryozoans dominate the Thunder Springs Member fossil assemblages in eastern GRCA, while crinoids dominate central GRCA, and a mixed bryozoan-brachiopod-gastropod-crinoid fauna is present in western GRCA. Fossils of the Mooney Falls Member are only well-preserved in a few scattered zones. Otherwise, specimens are fragmentary (McKee and Gutschick, 1969e). Fossils are rare again in the Horseshoe Mesa Member (Beus and Billingsley, 1989); however, when present, Horseshoe Mesa Member fossils are well-preserved (Beus, 2003b).

Surprise Canyon Formation (Upper Mississippian)

The Surprise Canyon Formation (figure 5) is a discontinuous unit found filling paleo-valleys and other karst features eroded in the upper Redwall Limestone. The Surprise Canyon Formation also occurs in caves in the Redwall Limestone's Mooney Falls and Horseshoe Mesa Members (Billingsley and Beus, 1985). It is found only in the Grand Canyon region. Formally named in 1985, its outcrops were first thought to be part of the Redwall Limestone or the Watahomigi Formation (Billingsley and Beus, 1985). After it was recognized as a distinct unit, but before it was formally described, it was known as the pre-Supai buried valleys or canyons (Billingsley and McKee, 1982; Spamer, 1984). The lower portion is composed of fluvial conglomerate and sandstone with some mudstone and siltstone (Beus, 2003b). The coarsest material is found near the base, grading up into sandstone (Beus and Billingsley, 1989). The middle portion is a cliff-forming marine limestone. Finally, the upper part includes marine slope-forming siltstone, sandstone, and silty to sandy limestone (Beus, 2003b). Most of the limestone of the upper unit is at the top, so there is a siltstone-sandstone slope above the middle unit's cliff leading to a cliff higher in the upper unit (Billingsley and McKee, 1982). The valleys filled by the Surprise Canyon Formation are as much as 120 m (400 ft) deep. It was deposited a few million years after the Redwall Limestone, and dates to the end of the Mississippian (Beus, 2003b). The upper contact is an unconformity with the Watahomigi Formation (Beus, 1989).

The Surprise Canyon Formation forms a dendritic drainage system that can be traced through GRCA (Billingsley and others, 1999). Flow moved from east to west (Beus, 2003b). The three parts of the formation formed under different conditions. In general, the lower sandstone/conglomerate portion is interpreted as fluvial, the middle limestone portion is interpreted as marine, and the upper silty portion is interpreted as estuary. The eastern depositional area may have been fluvial during its entire deposition (Beus, 2003b). An alternate paleoenvironmental interpretation for the entire formation is as a more widespread shallow sea. This interpretation would be more consistent with the distribution of some of the marine fossils, but is not favored (Beus, 2003b).

Supai Group

The Supai Group (figure 5) was recognized for many years as the Supai Formation in the Grand Canyon. It was designated as a group and divided into four formations in 1975. In ascending order, these are the Watahomigi Formation, Manakacha Formation, Wescogame Formation, and Esplanade Sandstone (McKee, 1975). The coeval Pakoon Limestone intertongues with the Esplanade Sandstone in western GRCA (Blakey and Knepp, 1989). The Supai Group as a whole is thought of as a broad coastal plain, over which the sea advanced from the west and retreated several times. The four formations represent different stages of several transgressive-regressive cycles, with the depositional setting oscillating between continental (particularly eolian) and shallow marine environments (Blakey, 2003).

Supai Group: Watahomigi Formation (Lower–Middle Pennsylvanian)

The Watahomigi Formation (figure 5) is composed of mudstone, siltstone, limestone, and dolostone. The lower and upper portions are slope-forming red beds, and the middle is a ledge-forming carbonate (Blakey, 2003). These parts can be recognized throughout the Grand Canyon (Beus and Billingsley, 1989). Carbonates dominate western GRCA and mudstone dominates the eastern outcrops in the park, with very little of the middle unit present (McKee, 1982b). It is 24 to 91 m (80 to 300 ft) thick at GRCA, becoming thicker from east to west (Beus and Billingsley, 1989). The formation mostly dates to the Early Pennsylvanian. An erosional horizon represented by a conglomerate marks both the base of the upper section and the Early–Middle Pennsylvanian boundary (McKee, 1982b). It was deposited after a short hiatus following the deposition of the Surprise Canyon Formation (Beus, 1989). The upper contact with the Manakacha Formation may be another unconformity (Blakey and Knepp, 1989), or conformable (Blakey, 2003).

The Watahomigi Formation is interpreted as a shoreline unit, deposited in shallow marine to coastal plain settings (Blakey and Knepp, 1989). It is part of a marine transgression (McKee, 1982c). The upper portion had more marine influence than the lower portion (Blakey, 2003). During the Early Pennsylvanian, a sea was present west of the modern Little Colorado River, which expanded to the east during the early Middle Pennsylvanian (McKee, 1982a). Fossils in the Watahomigi Formation suggest low energy conditions (McKee, 1982d), but possibly too energetic or with too much sand and silt for extensive coral growth (Gordon, 1982).

Supai Group: Manakacha Formation (Middle Pennsylvanian)

The Manakacha Formation (figure 5) is primarily a mix of sandstone and limestone, with some mudstone, conglomerate, and dolostone (Blakey and Knepp, 1989). It is usually exposed as a lower cliff and upper slope, with a conglomeratic zone between the two. Unlike other Supai Group formations, there is not a basal conglomerate (Beus and Billingsley, 1989). Carbonates are prominent in western GRCA, grading to sandstone and mudstone in central GRCA, and then mudstone and sandstone in eastern GRCA. The top of the unit is a widely recognized channeled surface that marks an unconformity (McKee, 1982b). Its thickness is relatively consistent throughout the park, ranging from 61 to 84 m (200 to 275 ft) thick (Beus and Billingsley, 1989). The Manakacha Formation dates to the early Middle Pennsylvanian.

The Manakacha Formation was initially interpreted as a dominantly marine formation (McKee, 1982c), representing marine shelf to open marine environments, with mudstone limited to restricted marine environments and the dominant sandstone and limestone deposited under high energy (Blakey and Knepp, 1989). More recently, it has been interpreted as dominantly eolian. Eolian deposition began encroaching from the north into the area that had been submerged by the marine transgression of the Watahomigi Formation (Blakey, 2003).

Supai Group: Wescogame Formation (Upper Pennsylvanian)

The Wescogame Formation (figure 5) is a mixed unit, with limestones prominent in extreme western GRCA, sandstones dominant in central GRCA, and mudstones increasing in prominence in eastern GRCA. It is exposed as a lower cliff and upper slope (Blakey, 2003). It is the most complex of the Supai Group formations, with rapidly shifting rock types (Blakey and Knepp, 1989). The thickness is between 30 and 69 m (100 and 225 ft) at GRCA (Beus and Billingsley, 1989). Both the upper and lower contact are unconformities (Blakey, 2003). The Wescogame Formation dates to the end of the Late Pennsylvanian.

The Wescogame Formation is interpreted as predominately eolian, representing one or more large dune fields (Blakey, 2003). Fluvial, coastal plain, shoreline, shelf, and open marine settings are also likely represented in its various rock types (Blakey and Knepp, 1989).

Supai Group: Esplanade Sandstone (lower Permian)

The Esplanade Sandstone (figures 5 and 6) is a quartz-rich sandstone, with basal and upper slope-forming beds of finer sediments (McKee, 1982c). It was deposited during the early Permian (McKee, 1982d). The lower portion of the Esplanade Sandstone intertongues with the Pakoon Limestone in western GRCA (Blakey and Knepp, 1989). The combined Esplanade Sandstone–Pakoon Limestone thickens from east to west, going from 91 m (300 ft) thick in eastern GRCA to more than 137 m (450 ft) in the western part of the park (Billingsley, 1997). The lower contact with the Wescogame Formation and the upper contact with the Hermit Formation are unconformable. The base of the unit in eastern and central GRCA is a conglomerate that fills paleochannels in the Wescogame Formation (Beus and Billingsley, 1989).

The depositional environment of this formation has been interpreted in multiple ways. The marine interpretation sees the Esplanade Sandstone as mostly high-energy marine sandstone with more terrestrial beds at the top and bottom (McKee, 1982c; Blakey and Knepp, 1989). The more current interpretation is that it is an eolian unit (Beus and Billingsley, 1989; Blakey, 2003), or part of a large coastal plain (Blakey, 2003). The base was probably less eolian than the rest of the unit (Blakey, 2003). Marine influence increased to the west, as evidenced by the change into the Pakoon Limestone (McKee, 1982c). Some gypsum is also present (Blakey, 2003).

Pakoon Limestone (lower Permian)

The Pakoon Limestone is a heterogeneous unit including dolomite, limestone, sandstone, mudstone, and gypsum (Blakey and Knepp, 1989). It is mostly dolomite and limestone in the Grand Canyon region (Blakey, 2003). It intertongues with the lower Esplanade Sandstone in western GRCA (Blakey and Knepp, 1989), and dates to the earliest Permian (Blakey, 2003). The Pakoon Limestone is interpreted as a clear water, shallow marine unit (Blakey, 2003). It is not mapped separately from the Esplanade Sandstone within GRCA (Billingsley and Wellmeyer, 2004; Billingsley and others, 2006a).

Hermit Formation (lower Permian)

The Hermit Formation (figure 6; formerly known as Hermit Shale) is a mixed red bed unit composed of very fine-grained sandstone, siltstone, and minor mudstone. At GRCA, it is known as a reddish-brown, slope-forming unit (Blakey, 2003). Its common alternate name is a misnomer, as it includes very little true shale. The thickness varies greatly from 49 m (160 ft) in eastern GRCA to 244 m (800 ft) in western GRCA (Beus and Billingsley, 1989). It dates to the late early Permian (Blakey, 2003). Although there is an unconformity between the Hermit Formation and the underlying Esplanade Sandstone with deep channel cuts, there was probably little time between the two (White, 1927). The upper contact, with the Coconino Sandstone, is also disconformable, but is sharp (Beus and Billingsley, 1989). The Hermit Formation is interpreted as a broad coastal plain and fluvial, but was also deposited as loess and scattered eolian dunes (Blakey and Middleton, 2012). The climate was probably semi-arid, with long hot dry seasons (White, 1929).

Coconino Sandstone (lower Permian)

The Coconino Sandstone (figure 6) is a fine-grained eolian sandstone, changing from white and tan, to brown or red in western GRCA (Beus and Billingsley, 1989). This unit is bracketed by other units dated to the late early Permian (Blakey and Knepp, 1989). From east to west, the unit thickens rapidly in eastern GRCA to 210 m (700 ft) and then thins to practically nothing in western GRCA. Its base forms a sharp unconformity with the Hermit Formation (Beus and Billingsley, 1989). The upper contact with the Toroweap Formation intertongues (Blakey and Knepp, 1989). The Coconino Sandstone is interpreted as an eolian unit formed as an erg (Hunt and others, 2005). Sand was deposited by wind action (Blakey and Knepp, 1989).

Toroweap Formation (lower Permian)

The Toroweap Formation (figure 6) has been studied extensively and offers striking lateral and vertical changes in lithofacies over a relatively small area. Members with carbonate and evaporite lithologies are more easily discerned in western outcrops and these distinctions become absent in the eastern phase that is mostly cross-bedded sandstone (Turner, 2003).

In the west it can be divided into three members in the GRCA area; in ascending order these are the Seligman, Brady Canyon, and Woods Ranch Members. The relatively thin Seligman Member appears to intertongue and be conformable with the underlying Coconino Sandstone and is no thicker than 15 m (45 ft) at GRCA (Turner, 2003). Above the Seligman Member is the overlying

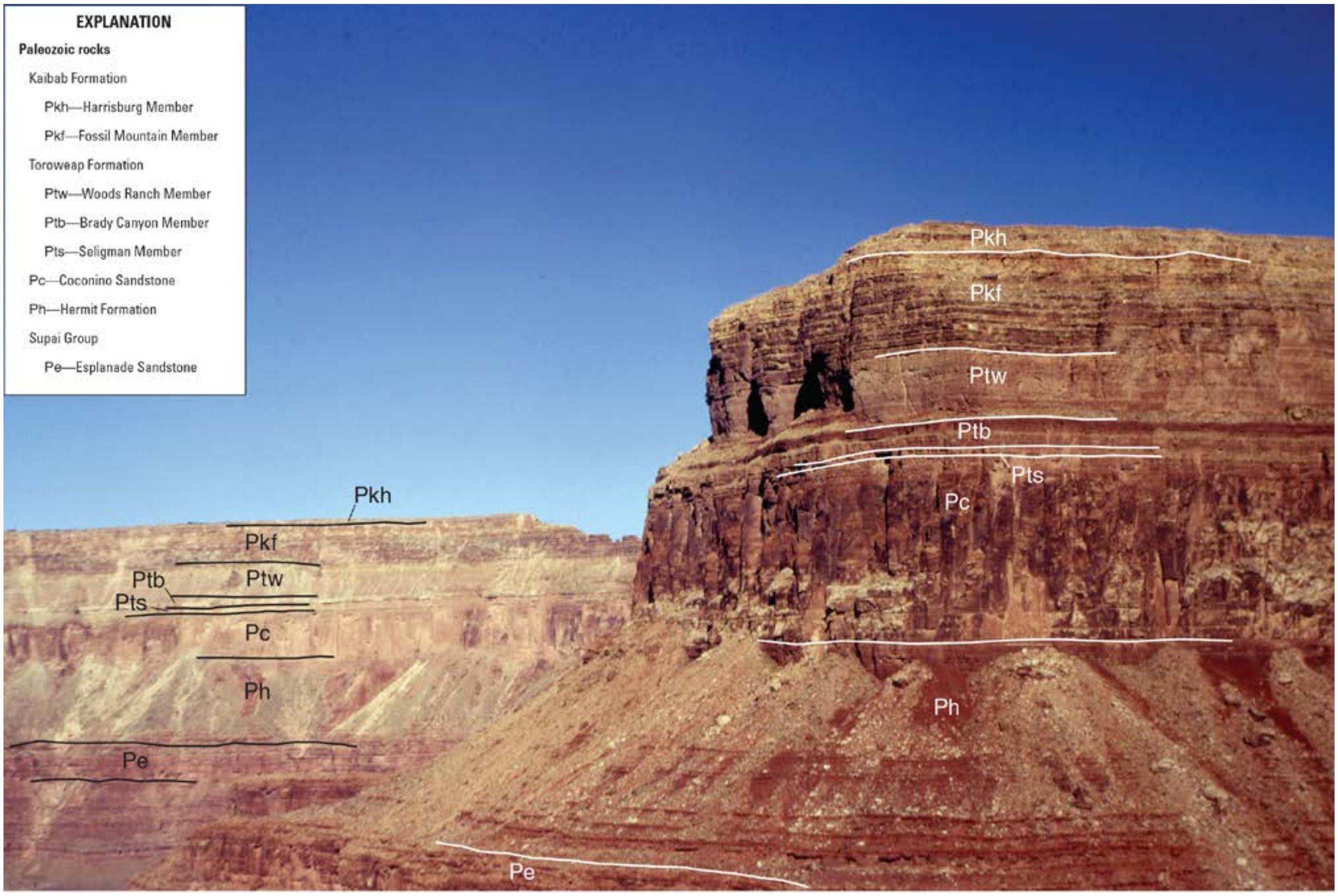

__Figure 6.__ Uppermost Supai Group (Pe=Esplanade Sandstone), Hermit Formation (Ph), Coconino Sandstone (Pc), Toroweap Formation (Seligman Member=Pts; Brady Canyon Member=Ptb; Woods Ranch Member=Ptw), and Kaibab Formation (Fossil Mountain Member=Pkf; Harrisburg Member=Pkh) (Billingsley and others, 2019: figure 7).

Brady Canyon Member, a cliff-forming carbonate unit composed of limestone and mixed dolostone in western GRCA. The Brady Canyon Member is thickest in western GRCA, up to 93 m (280 ft) thick. The Brady Canyon Member thins uniformly to the east to its depositional edge near Marble Canyon and grades into the overlying Woods Ranch Member, mostly made of repetitive evaporites, limestone, and sandstone. The Woods Ranch Member forms distinctive slopes and attains a maximum thickness of about 60 m (180 ft) (Turner, 2003). The Woods Ranch Member is interpreted as a shallow evaporitic marine shelf. The climate during deposition of the Toroweap Formation is thought to have been semi-arid to arid (Turner, 2003). At GRCA, gypsum and/or contorted sandstones of the Woods Ranch Member always underlie the Kaibab Formation. (Hopkins and Thompson, 2003).

Most fossils in the Toroweap Formation are from the Brady Canyon Member, with fossils in the Woods Ranch Member limited to an unusual *Schizodus* bed near the top of the member (McKee, 1938; Rawson and Turner, 1974).

Kaibab Formation (lower–middle Permian)

The Kaibab Formation (figure 6) is a complex sedimentary package of numerous lithologies. At GRCA, it forms the canyon rim and is 90 to 120 m (300 to 400 ft) thick (Hopkins and Thompson, 2003). Early workers divided the Kaibab Formation into the Gamma, Beta, and Alpha Members (McKee, 1938), which have since been subsumed into the Fossil Mountain and overlying Harrisburg members. The Fossil Mountain Member is the equivalent of the Gamma and Beta Members, and the Harrisburg Member is the equivalent of the Alpha Member (Blakey and Knepp, 1989). Chert is a major feature of the Fossil Mountain Member at GRCA, and it is quite voluminous and varied in character and weathers to form distinct recesses along cliff faces. It is mostly attributed to the original distribution and abundance of siliceous sponges and spicules. In the west, the Fossil Mountain Member is more carbonate-rich (fossiliferous limestone) but becomes more siliciclastic eastward (sandstone, sandy carbonate, and dolomite) (Hopkins and Thompson, 2003). It thickens westward and ranges from 75 to 205 m (250 to 300 ft) thick, to approximately 60 m (200 ft) at the type section at Fossil Mountain along the south rim. The Harrisburg Member constitutes the uppermost cliffs and ledges at GRCA and is a mixed unit including gypsum, dolostones, sandstone, redbeds, chert, and minor limestone. Thicknesses range from 25 to 90 m (80 to 300 ft) at GRCA, and numerous subunits are discernable in its overall extent (Hopkins and Thompson, 2003).

The Kaibab Formation is evidence of an ancient seaway covering the GRCA area in the Permian. A complex depositional history is evidenced by the mixing of carbonates and siliciclastics with numerous variations of subtidal to shallow-marine settings. The Fossil Mountain Member documents a west to east shift of fossiliferous open-marine limestones to restricted-marine sandy dolostones and the Harrisburg records retreat of the Kaibab Sea (Hopkins and Thompson, 2003).

MESOZOIC STRATIGRAPHY OF GRAND CANYON

Limited exposures of Mesozoic formations are found at Cedar Mountain near Desert View in GRCA, including the Lower–Middle Triassic Moenkopi Formation and the Upper Triassic Chinle Formation. These units were evaluated for paleontological resources during the 2019 GRCA PaleoBlitz and are discussed in the contribution by Marsh and others of this inventory. Additionally, the Lower Jurassic Wingate Sandstone, Moenave Formation, Kayenta Formation (and Springdale Sandstone Member), and Navajo Sandstone are known in the surrounding Grand Canyon region (Billingsley and others, 2019) but not within GRCA.

Moenkopi Formation (Lower–Middle Triassic)

The Moenkopi Formation (figure 7) is a continental redbed unit found across the American Southwest (McKee, 1954; Stewart and others, 1972a) that includes marginal marine depositional facies in its western exposures (Nevada and Utah) and regressive freshwater fluvial and lacustrine facies in its eastern exposures (Arizona and New Mexico). The only complete section of Moenkopi Formation exposed within GRCA occurs at Cedar Mountain, adjacent to the far eastern boundary near Desert View. This 2 km (1.2 mi) wide feature is largely covered by loose talus and juniper trees, but includes the Wupatki, Moqui, and Holbrook Members, all of which are also exposed along the nearby Little Colorado River Valley from Cameron to Holbrook, Arizona. Noble (1922) determined that the Moenkopi Formation at Cedar Mountain is nearly 150 m (490 ft) thick. The Wupatki Member at Cedar Mountain is characterized by low mounds of ripple-laminated sandstone, the Moqui Member is a slope-former with interbedded evaporite/channel complexes, and the Holbrook Member includes the cliff-forming "upper massive sandstone". Fossils have been reported from the Moenkopi Formation at GRCA (Marsh and others, this inventory) and similar sections nearby are known for producing actinopterygian fish, mastodonsauroid, trematosaurian, and brachyopid temnospondyl amphibians, tanystropheid reptiles, and pseudosuchian archosaurs (Welles, 1947, 1969; Nesbitt, 2000, 2005a, 2005b). Terrestrial vertebrate (Lucas, 2010; Martz and Parker, 2017), ichnological biochronology (McKee, 1954; Klein and Lucas, 2010; Henderek and others, 2017), and U-Pb detrital zircon geochronology (Dickinson and Gehrels, 2009) suggest that at least the uppermost part of the Moenkopi Formation is Middle Triassic in age.

Chinle Formation (Upper Triassic)

The only exposure of the Chinle Formation (figure 7) within eastern GRCA caps the Moenkopi Formation section at Cedar Mountain and is represented by the Shinarump Member (formerly the "Shinarump Conglomerate"; Noble, 1922; Repenning and others, 1969; Stewart and others, 1972b). It is approximately 8 m (26 ft) thick here and is characterized by well-cemented channel conglomerates with mud rip-up clasts and pieces of (or entire) petrified conifer trees. No vertebrate fossils are known from the Chinle Formation (Shinarump Member) at GRCA, but terrestrial vertebrate biochronology and U-Pb detrital zircon geochronology of overlying and/or equivalent units constrain the entire Chinle Formation to the Late Triassic (Lucas, 2010; Atchley and others, 2013; Riggs and others, 2016; Martz and Parker, 2017; Kent and others, 2019).

CONCLUSIONS

The Grand Canyon serves as a geologic and paleontologic window into the past. The park contains colorful, awe-inspiring rocks and traces of life that showcase spectacular stratigraphy and tell a vast story of almost two billion years of earth history and organism evolution, making it one of the geologic wonders on Earth. The Vishnu Basement rocks, Grand Canyon Supergroup rocks, and layered Paleozoic rocks combine to present a story like no place on Earth. These old rocks contrast nicely with the geologically "young" age of the canyon. Magmatism, volcanism, metamorphism, deposition, and erosion are all visible on a grand scale at Grand Canyon, leaving their evidence for the viewer to decipher this planet's rich geologic history and record of organism evolution over the eons.

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Figure 7. *Mesozoic rocks in eastern GRCA at Cedar Mountain (NPS/DIANA BOUDREAU).*

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STROMATOLITE

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Stromatolite
Scientific Name: *??????*
Geologic Age: 1.255 billion years ago (Precambrian)
Geologic Formation: Grand Canyon Supergroup

Interactive 3D model

Laminations form as sediment is trapped by cyanobacteria mats.

Stromatolites are the oldest fossils. They are laminated structures formed mostly by colonial blue-green bacteria (cyanobacteria) in ancient shallow oceans when Earth's atmosphere was forming. Stromatolites helped power the Cambrian explosion of life and are still alive today.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

5 of 9

Grand Canyon National Park Fossil Trading Card featuring a fossil stromatolite from the Precambrian Grand Canyon Supergroup (NPS).

PRECAMBRIAN PALEONTOLOGY OF GRAND CANYON NATIONAL PARK

Justin S. Tweet[1]

ABSTRACT

Grand Canyon National Park (GRCA) has a rich assemblage of Precambrian fossils pertaining to two general time frames: approximately 1250 to 1100 million years ago, from rocks of the Mesoproterozoic Unkar Group; and approximately 780 to 730 million years ago, from rocks of the Neoproterozoic Chuar Group. These fossils include a variety of microbial structures, especially stromatolites, and microfossils. Microbial structures are present in several formations of both the Unkar and Chuar Groups and represent the oldest known fossils of the park, but microfossils are to date only well known from the Galeros and Kwagunt Formations of the Chuar Group. Among the park's Precambrian microfossils are various acritarchs, filaments, sheaths, and vase-shaped microfossils. GRCA is part of several firsts in Precambrian paleontology, including the initial description of the megascopic acritarch *Chuaria circularis* by Charles Doolittle Walcott in the late 19th century; the discovery and initial description of vase-shaped microfossils in the 1970s and 1980s; and the discovery of the oldest direct evidence of predation on eukaryotes in the form of "vampire traces". Also intertwined with the history of study of Precambrian microfossils are a number of examples of pseudofossils and dubiofossils, beginning with Walcott's work (and in fact predating his discovery of the legitimate fossil *Chuaria*). The most famous of these is the putative jellyfish *Brooksella canyonensis,* but a variety of other objects have been misinterpreted. GRCA provides detailed views of life during two stages of the Proterozoic, and bodes fair as a source of further discoveries illuminating this time in the development of life.

INTRODUCTION

The Precambrian paleontology of Grand Canyon National Park (GRCA) is fundamentally unlike the paleontology of any other portion of the park's substantial stratigraphic column. There are no shells, teeth, bones, footprints, leaves, or similar large fossils. The only fossils visible to the naked eye are layered structures left by microbial mats and the very largest of a diverse assemblage of microfossils **(appendix A)**. The tools of choice are not shovels and picks, but chemical treatments and powerful microscopes. Very few visitors would be able to spot a Precambrian fossil. Notwithstanding the humble, inconspicuous nature of these fossils, they offer important glimpses at two stages in the development of life, approximately 1250 to 1100 million years ago (Ma) and 780 to 730 Ma, long before the appearance of familiar multicellular organisms with hard parts. The Precambrian fossils of GRCA are the oldest fossils of the park and include type specimens for 18 taxa **(appendix B)**, such as the organic-walled microfossil *Chuaria circularis* and species of *Melanocyrillium*, the first described vase-shaped microfossil, as well as the notable pseudofossil (resembling a fossil but inorganic in origin) *Brooksella canyonensis*, first described as a possible jellyfish. They also have a place in the history of Precambrian paleontology, from Charles Walcott's early explorations to the present.

HISTORY OF RESEARCH

An excellent summary of the early Precambrian paleontology of GRCA can be found in Spamer (1984). Although Powell (1876) and White (1876) briefly mentioned potential fossils in the Grand Canyon Supergroup (at that time defined as a group), the study of Precambrian fossils at GRCA was pioneered by Charles Doolittle Walcott in the 1880s and 1890s. The study of Precambrian fossils in general was just beginning, and Walcott made several misidentifications among his more last-

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Tweet, J.S., 2021, Precambrian Paleontology of Grand Canyon National Park, *in* Santucci, V.L., and Tweet, J.S., editors, Grand Canyon National Park Centennial Paleontological Resources Inventory—A Century of Fossil Discovery and Research: Utah Geological Association Special Publication 1, p. 55-72.

ing discoveries (see also "Notable Pseudofossils and Dubiofossils" below). For example, his erroneous identifications of several "fossils" led him to initially regard the Chuar Group as Cambrian in age (Walcott, 1883). Of his initial assemblage, only the "stromatoporoids" (stromatolites) and some of the "brachiopods" (*Chuaria*) proved to be legitimate fossils, and he retreated on several of the identifications later (Walcott, 1899). Walcott (1899) includes stratigraphic descriptions of the Grand Canyon Supergroup and the description of *Chuaria circularis* (figure 1). Dawson (1897) also gave the name *Cryptozoon occidentale* to an example of Walcott's "stromatoporoids" during this time frame.

After the 1890s Walcott's attention turned to other topics, including the overlying Cambrian strata at GRCA, and little research on Precambrian fossils at GRCA was conducted until the 1920s. Toward the end of the 1920s, David White briefly mentioned some fossils and potential fossils from the Precambrian rocks of GRCA alongside his research on later Paleozoic plant fossils from the canyon (White, 1927, 1928a, 1928b, 1929). Because of White's paleobotanical focus, the Precambrian fossils and pseudofossils he described were primarily stromatolites, due to their "algal" origin, and "fucoids", a now-obsolete term for what were then thought to be seaweeds. "Fucoids" as a whole are now known to include various invertebrate burrows and burrow-like sedimentary features such as mud cracks, and the Precambrian "fucoids" appear to be inorganic features.

Between the 1920s and 1970s, most of the work on GRCA Precambrian paleontology focused on objects now generally regarded as pseudofossils. The most significant of these is the long-controversial *Brooksella canyonensis* from the Nankoweap Formation, which was first interpreted as a potential jellyfish (Van Gundy, 1937, 1951; Bassler, 1941). A running dialog on the interpretation of various enigmatic features took place in the literature (e.g., Seilacher, 1956; Alf, 1959; Cloud, 1968; Glaessner, 1969; Nitecki, 1971). Toward the end of the 1960s, Ford and others (1969) published initial work toward a complete stratigraphic re-evaluation of the Chuar Group, and Downie (1969) published a brief discussion of microfossils from these rocks, an area of research that would become increasingly significant.

Figure 1. Chuaria circularis *depicted in Walcott (1899: plate 27:12).* C. circularis *specimens are up to 5 mm (0.2 in) across, making them the largest of GRCA's Precambrian body fossils.*

Beginning with the late 1960s publications, paleontological work in the Precambrian of GRCA has focused on the microfossils of the Kwagunt and Galeros formations of the Chuar Group. Many advances and discoveries were published during the 1970s, including: the formal division of the Chuar Group (Ford and Breed, 1973a); the redescription of *Chuaria circularis* (Ford and Breed, 1973b, 1977); the first report of GRCA filamentous fossils (Schopf and others, 1973); and the initial description of vase-shaped microfossils (Bloeser and others, 1977). Since the 1970s, Precambrian research at GRCA has documented fossils including acritarchs and other organic-walled microfossils (Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016), filaments (Horodyski and Bloeser, 1983), vase-shaped microfossils (Bloeser, 1985; Porter and Knoll, 2000; Porter and others, 2003), and apparent puncture traces (Porter, 2016a). Chemical biomarkers have also been studied (Summons and others, 1988; Brocks and others, 2016). In recent years there have also been re-assessments of the Nankoweap Formation (Dehler and others, 2017) and Sixtymile Formation (Karlstrom and others, 2018), finding both to be younger than originally thought. In the case of the Sixtymile Formation, it is now known to be Cambrian in age, but it will be included briefly in this article due to the recency of its reassessment and long historical placement in the Proterozoic.

STRATIGRAPHIC DISTRIBUTION OF FOSSILS

The Precambrian rocks of GRCA include crystalline Paleoproterozoic basement rocks and a sequence of Mesoproterozoic and Neoproterozoic sedimentary rocks known as the Grand Canyon Supergroup. The Supergroup is divided into the Mesoproterozoic Unkar Group and the Neoproterozoic Chuar Group, which in turn are both divided into several formations. The Unkar Group includes, in ascending order (oldest first), the Bass Formation, Hakatai Shale, Shinumo Quartzite, Dox Formation, and Cardenas Basalt. The Chuar Group includes the Nankoweap, Galeros, and Kwagunt formations. As mentioned above, the Sixtymile Formation was previously thought to be a Precambrian formation, but is now known to be Cambrian in age.

Although the crystalline rocks beneath the Grand Canyon Supergroup can be found near the western end of GRCA, the rocks of the Supergroup are exposed only in eastern GRCA, from roughly Nankoweap Canyon in the east to Deer Creek Falls in the west; all of their outcrops are limited to GRCA. The Unkar Group is more widely exposed, being found from a short distance below the Little Colorado River to Deer Creek Falls. The Chuar Group is limited to the stretch of the canyon between approximately Nankoweap Canyon and Unkar Creek, and except for outcrops of the Nankoweap Formation on the south/east side of the Colorado River within a few km or mi of the Tanner Trail, is only exposed west or north of the river (figure 2). Outcrops are discontinuous, and it is not uncommon for rocks of the overlying Tonto Group to overlie the ancient crystalline rocks without the Supergroup between them, indicating erosion between the Paleoproterozoic and Cambrian. Fossils are confirmed from the Bass Formation, Dox Formation, Galeros Formation, and Kwagunt Formation. More controversial reports have come from the Hakatai Shale, Shinumo Quartzite, and Nankoweap Formation (table 1).

Formations are discussed below in ascending order. See table 1 for a brief summary. The following information is also included in tabular form in **appendix A.**

Figure 2. *An aerial view showing several topographic features west of the Colorado River in eastern GRCA. The distant mesa is Nankoweap Mesa. Nankoweap Butte is to the left. Kwagunt Butte is near the center of the photo. Awatubi Crest is in the foreground (NPS).*

Table 1. *Summary of GRCA Precambrian stratigraphy, fossils, and depositional settings in descending order of age, from youngest to oldest; Sixtymile Formation included based on historical classification. Details and references can be found in the text. (continued on the following page)*

Formation	Age	Fossils Within GRCA	Depositional Environment
Sixtymile Formation	early Cambrian	Potential undetermined fragment	Lacustrine, fluvial, and shallow marine
Kwagunt Formation	middle Neoproterozoic (late Tonian)	Stromatolites and other microbial features, acritarchs and colonial organic-walled microfossils, microbial filaments, vase-shaped microfossils, various unspecified microfossils, “vampire traces” on microfossils, chemical evidence for possible sponges, possible meiofaunal traces	Primarily subtidal to intertidal with active tectonism
Galeros Formation	middle Neoproterozoic (late Tonian)	Stromatolites and other microbial features, acritarchs and colonial organic-walled microfossils, microbial filaments, various unspecified microfossils, “vampire traces”	Primarily subtidal to supratidal, intermittently restricted with active tectonism

Table 1. *Continued.*

Formation	Age	Fossils Within GRCA	Depositional Environment
Nankoweap Formation	middle Neoproterozoic (late Tonian)	None to date, unless *Brooksella canyonensis* is organic	Primarily marine shoreface with active tectonism
Cardenas Basalt	late Mesoproterozoic	None to date; fossils are unlikely but not impossible	Extrusive igneous
Dox Formation	late Mesoproterozoic	Stromatolites and probable microbially induced sedimentary structures; dubiofossils	Fluvial and deltaic to estuarine to marine over time
Shinumo Quartzite	late Mesoproterozoic	None confirmed; dubiofossils	Marine shoreface
Hakatai Shale	late Mesoproterozoic	Stromatolites and other microbial features in the Bass–Hakatai transition zone; dubiofossils	Marginal marine, tidal, and deltaic
Bass Formation	middle–late Mesoproterozoic	Stromatolites and other microbial structures, possible microfossils and microbial filaments; dubiofossils	Subtidal to supratidal, intermittently restricted with active tectonism
Paleoproterozoic–Mesoproterozoic basement	late Paleoproterozoic–early Mesoproterozoic	Unfossiliferous igneous and high-grade metamorphic rocks	Various; igneous rocks that formed at depth, sedimentary rocks with origins obscured by metamorphism

Paleoproterozoic–Mesoproterozoic basement rocks (upper Paleoproterozoic–lower Neoproterozoic)

The sedimentary rocks of the Grand Canyon Supergroup are deposited on igneous and high-grade metamorphic rocks that include the oldest known rocks in southwestern North America (the Elves Chasm gneiss of 1840 ± 1 Ma; Holland and others, 2015). These crystalline basement rocks are unfossiliferous and included here for geologic completeness.

Unkar Group: Bass Formation (middle–upper Mesoproterozoic)

The Bass Formation is a mixed unit dominated by dolomite, interpreted as altered original limestone, with interbedded sandstone, mudstone, and pebble conglomerate, and a basal cobble conglomerate known as the Hotauta Member. The depositional environment is interpreted as shallow and sometimes restricted marine with fluvio-tidal clastic input from active tectonism, becoming more clastic in the transition to the Hakatai Shale (Timmons and others, 2005, 2012). The base of the formation dates to approximately 1254.8 ± 1.6 Ma (Timmons and others, 2005), although some contested detrital zircons date to around 1200 Ma (Timmons and others, 2012).

The Bass Formation preserves the oldest evidence of life in GRCA. The most abundant and obvious fossils in the formation are various forms of stromatolites (figure 3). "Algal reefs" were reported in the formation by White (1927, 1928a), who identified tabular stromatolites, lenticular stromatolites, winding or knobby masses, and *Collenia*-type columnar forms (White, 1928a). The *Collenia* forms can be divided into *C. undosa, C. symmetrica,* and *C. frequens* (Beus and others, 1974). More recently, Lathrop (2018) observed crinkly, domal, small domal, conical, and pseudo-conical stromatolites, and noted that stromatolites were sometimes ripped up and redeposited by mass flows. Stromatolites persist into the transition to the Hakatai Shale; stromatolitic carbonate beds typical of the Bass Formation are found interbedded with clastic beds typical of the Hakatai Shale, to the extent that sometimes Hakatai-type clasts of sandstone and conglomerate are encrusted by stromatolites (Timmons and others, 2012). Possible microbial filaments have been observed in thin sections of Bass Formation stromatolites (Dalton, 1972; Beus and others, 1974; Ford and Breed, 1977), as well as calcispheres (calcitic microfossils) (Dalton, 1972; Lathrop, 2018). Lathrop's calcispheres were found in conical stromatolites and have been replaced by silica.

Other types of potential fossils from the Bass Forma-

Figure 3. *Bass Limestone stromatolites (not in life position) (NPS/CASSI KNIGHT).*

tion are tantalizing but unconfirmed or considered to be pseudofossils. In the former category, there are: "algal" scales and vertical plates (White, 1928a); mysterious *Chuaria*-like objects first mentioned by White (1928a); objects first reported as potential bivalved animals (Smith, 1966) that may be microbial oncoids (Ford and Breed, 1977); branching structures resembling brown algae (Nitecki, 1971); ovoid pellets resembling fecal pellets, associated with potential calcispheres, stromatolites, and potential filaments (Ford and Breed, 1977); and organic detritus (Vidal and Ford, 1985). In the latter category are: possible animal traces (White, 1927); "fusiform remains" in dark red beds transitional into the Hakatai Shale (White, 1929); and potential sponges and medusae (Alf, 1959), now widely regarded as pseudofossils (Cloud, 1968; Glaessner, 1969; Nitecki, 1971; Ford and Breed, 1977). The *Chuaria*-like objects reported by White (1928a) cannot be evaluated, because no locality information or specimens exist (Ford and Breed, 1977), but Nitecki (1971) did report finding *Chuaria*-like microfossils after dissolving an apparently inorganic siliceous "biscuit" concretion.

Unkar Group: Hakatai Shale (upper Mesoproterozoic)

The Hakatai Shale is primarily composed of siltstone and fine-grained sandstone, although beds range from mudstone to conglomerate (figure 4). It is interpreted as the result of shallow water deposition in marginal marine, tidal flat, and deltaic settings. Detrital zircons indicate at least some deposition occurred after 1187 Ma (Timmons and others, 2012).

Fossils are unconfirmed from the Hakatai Shale. Aside from stromatolites found in the transition with the Bass Formation, mentioned above, most records appear to be pseudofossils. The GRCA museum has records of Hakatai "algal" structures, although in the absence of more detailed provenance information, these could be from Bass Formation beds in the transitional zone. White (1929) reported potential "algal thalli" impressions in this formation. Seilacher (1956) reported features he compared to the trilobite trace fossil known as *Rusophycus*, but they were regarded as inorganic in Cloud

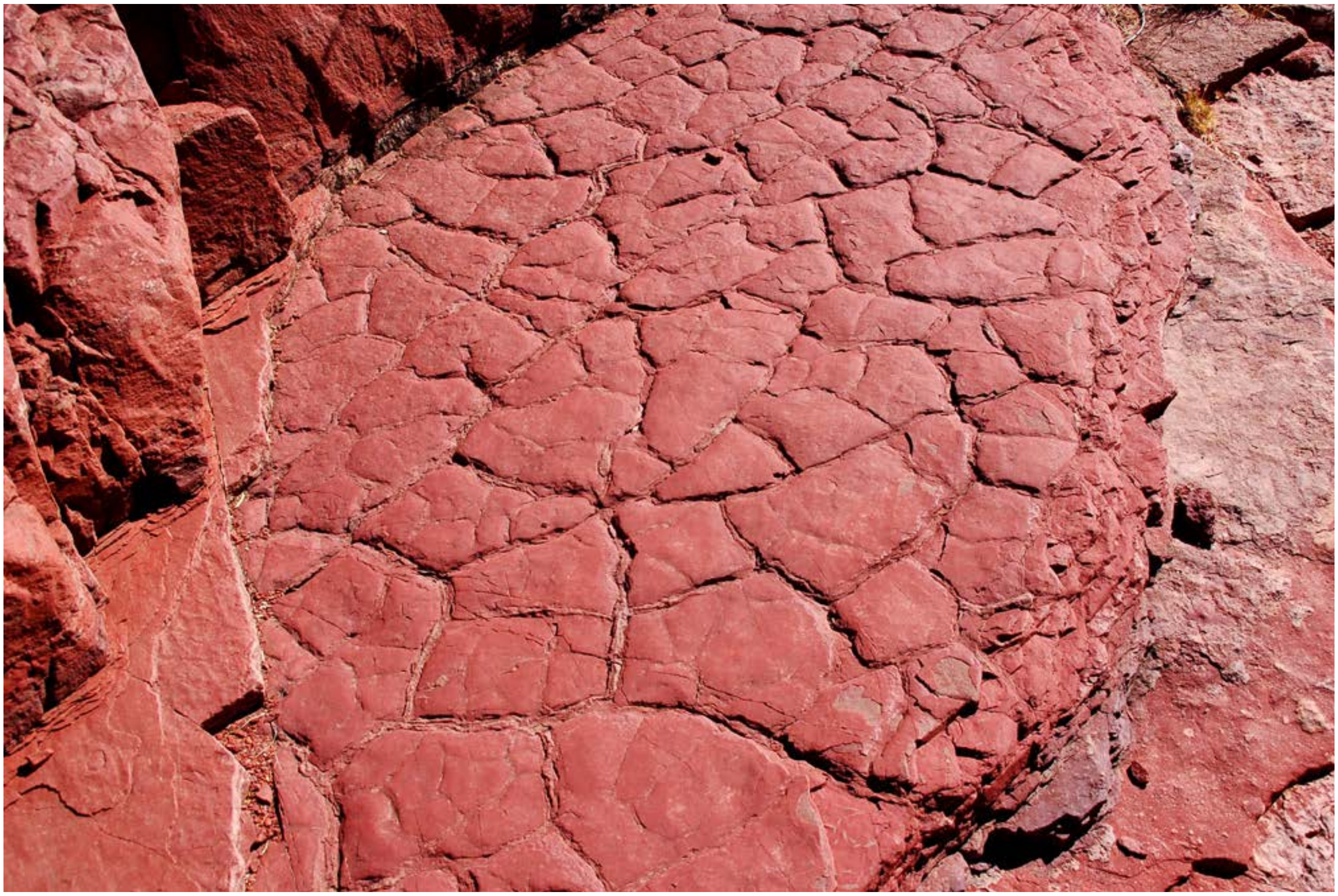

Figure 4. *A mud-cracked surface in the Hakatai Shale. Mud cracks are sometimes mistaken for burrows (NPS/CARL BOWMAN).*

(1968). Other "fucoids" were reported by White (1928a). Nitecki (1971) noticed "worm burrows" in the Hakatai Shale, which he regarded as possibly sedimentary.

Unkar Group: Shinumo Quartzite (upper Mesoproterozoic)

The Shinumo Quartzite or Sandstone is primarily composed of quartz sandstone, with some feldspar-rich sandstone in the lower part of the formation and a lag deposit at the unconformable contact with the underlying Hakatai Shale. It is interpreted as a high-energy shoreface unit. Laterally continuous contorted beds, resulting from soft-sediment deformation, are found in this unit (Timmons and others, 2012). Detrital zircons indicate it was deposited ca. 1170 Ma (Timmons and others, 2012), but it could be as young as 1140 Ma (Mulder and others, 2017).

Fossils have not been confirmed from the Shinumo Quartzite. White (1929) mentioned features that could be "fucoids" or inorganic near the base of the formation. Miller and Byers (1984) described the Shinumo Quartzite as "heavily burrowed" in a table based on a personal communication, without further discussion. As noted by Spamer (1984), burrows in the Shinumo Quartzite would be very significant, but to date this observation has not been replicated. Many of the features interpreted to be potentially biogenic in origin could be explained by the dynamic soft-sediment deformation in the unit (C. Dehler, pers. comm., May 2019).

Unkar Group: Dox Formation (upper Mesoproterozoic)

The Dox Formation is a clastic unit dominated by red sandstone, with lesser quantities of siltstone and other mudrocks. Deposition began in fluvial and deltaic settings, becoming more marine over time, with rivers becoming estuaries and nearshore marine to possibly intertidal deposition setting in. Deposition occurred between approximately 1140 and 1104 Ma (Timmons and others, 2012; Mulder and others, 2017).

The Dox Formation, like the Bass Formation, is noted for stromatolites. Stromatolites were first noted in passing by Ford and Breed (1977), and are found in the Comanche Point Member (Stevenson and Beus, 1982; Hendricks and Stevenson, 1990; Timmons and others, 2012), the second highest of four members recognized in the formation. Dox Formation stromatolites have not been described in detail to date. McKee (1932) pointed out Dox Formation "fucoids" that appear to be microbially induced sedimentary structures (Tweet and Lucas, in press) (figure 5). Park collections attribute one of the specimens (GRCA 11442, the right object) to the ichnogenus *Teichichnus*, but it is not clear why this ichnogenus was invoked because the features do not have the distinctive "stacked" appearance of *Teichichnus*.

Unkar Group: Cardenas Basalt (upper Mesoproterozoic)

The volcanic Cardenas Basalt began erupting before the end of Dox Formation deposition, as shown by interfingering beds of the two units. Eruption occurred approximately 1104 Ma (Timmons and others, 2012). Although extrusive igneous units sometimes include fossils, such as tree molds in volcanic flows and organisms buried by tuffs and other pyroclastic deposits, no fossils have been reported from the Cardenas Basalt.

Chuar Group: Nankoweap Formation (middle Neoproterozoic: late Tonian age)

The Nankoweap Formation includes a lower red unit of hematite-cemented sandstone and mudstone, and an upper white unit of siltstone and thin-bedded sandstone, separated by a local lag deposit (Timmons and others, 2012). It is interpreted as indicating shoreface and mudflat deposition (C. Dehler, pers. comm., May 2019), perhaps marine or lacustrine (Timmons and others, 2005). The Nankoweap Formation was recently found to be younger than previously suspected, at most approximately 782 Ma, making it very similar in age to the established formations of the Chuar Group (Dehler and others, 2017). Because of this, and the apparent absence of a pronounced unconformity with the overlying Galeros Formation, Dehler and others (2017) moved the Nankoweap Formation into the Chuar Group as the lowest unit.

No uncontroversial fossils have been reported from the Nankoweap Formation. A famous likely pseudofossil, *Brooksella canyonensis*, was named from a Nankoweap Formation specimen (Bassler, 1941); its lengthy history is discussed under "Notable Pseudofossils and Dubiofossils" below. As with other Grand Canyon Supergroup units, the Nankoweap Formation has features that resemble sinuous trace fossils, but which are more likely truncated mud cracks (Ford, 1990).

Chuar Group: Galeros Formation (middle Neoproterozoic: late Tonian age)

The Galeros Formation is primarily clastic, with variegated and organic-rich mudstones to sandstones represented, but a small percentage of dolomite is also present. Four members are recognized, in ascending

Figure 5. *Left: Dox Formation "fucoids" as shown in McKee (1932); the original caption is "Peculiar casts and moulds in Dox Formation. Photo by Grant". No scale was provided. Right: The specimens as relocated in 2019, placed in a similar setting and photographed with a scale. The two pieces are actually part and counterpart, with the left piece having concave equivalents of the convex features on the right piece (the large light gray redox spot is a tie point) (NPS/JUSTIN TWEET).*

order the Tanner, Jupiter, Carbon Canyon, and Duppa members. Deposition occurred in subtidal to supratidal environments, and possibly terrestrial environments as well (Dehler and others, 2001, 2012, 2017). Until recently, the formation had not been directly dated. The lower part of the formation is younger than the <782 Ma Nankoweap Formation (Dehler and others, 2017). An organic-rich dolomite in the lower Carbon Canyon Member has been dated using the Re-Os system to 757 ± 6.8 Ma, and a marcasite nodule in the basal Awatubi Member of the Kwagunt Formation has been dated to 751 ± 7.6 Ma (Rooney and others, 2018). Therefore, the Galeros Formation spans no more than about 25 million years, and likely less.

All four members of the Galeros Formation are fossiliferous (Porter and Riedman, 2016). Most fossils are microfossils, but there are two prominent stromatolitic horizons, not only notable for their fossils but also for being carbonate beds in a primarily clastic formation. The lower horizon, the *Stratifera/Inzeria* horizon, is at the base of the Jupiter Member. The upper horizon, the *Baicalia* horizon, is near the top of the Carbon Canyon Member (Ford and Breed, 1973a; Dehler and others, 2001, 2012, 2017). The Galeros Formation has also yielded significant microfossils, primarily acritarchs (Ford and Breed, 1973b; Bloeser and others, 1977; Vidal and Ford, 1985; Nagy and others, 2009; Dehler and others, 2012, 2017; Porter and Riedman, 2016). Filaments and sheaths (Vidal and Ford, 1985; Porter and Riedman, 2016) and organic detritus (Downie, 1969; Vidal and Ford, 1985) have also been reported. Puncture marks, described as "vampire traces", have been identified on some microfossils (Porter, 2016a, 2016b, 2017).

Chuar Group: Kwagunt Formation (middle Neoproterozoic: late Tonian age)

Similar to the underlying Galeros Formation, the Kwagunt Formation is primarily a fine-grained organic-rich and variegated clastic unit with occasional dolomite beds, and is divided into several members. In ascending order, the members of the Kwagunt Formation are the Carbon Butte, Awatubi, and Walcott members. The Kwagunt Formation was primarily deposited in subtidal to intertidal environments, although with more episodes of subaerial exposure, especially in the upper Walcott Member (Dehler and others, 2001, 2012, 2017). The majority of the formation is younger than a ca. 751 Ma marcasite nodule in the basal Awatubi Member (Rooney and others, 2018). A tuff at the top of the formation, formerly dated to 742 ± 6 Ma (Karlstrom and others, 2000), has been re-dated via a higher precision U-Pb method to 729 ± 0.9 Ma (Rooney and others, 2018).

The Awatubi and Walcott members of the Kwagunt Formation are notably fossiliferous, but no fossils have yet been reported from the Carbon Butte Member. There is a prominent stromatolitic horizon, the *Baicalia–Boxonia* horizon, at the base of the Awatubi Member. At the base of the Walcott Member is the "flaky dolomite bed", which is thought to be composed of microbial laminations that have been reworked and altered by soft-sediment deformation (Ford and Breed, 1973a; Dehler and others, 2001, 2012, 2017). As in the Galeros Formation, most fossils are microfossils, including acritarchs and colonial organic-walled microfossils (Bloeser and others, 1977; Vidal and Ford, 1985; Horodyski, 1993; Nagy and others, 2009; Dehler and others, 2012, 2017; Porter and Riedman, 2016), filaments and sheaths (Schopf and others, 1973; Horodyski and Bloeser, 1983; Vidal and Ford, 1985; Horodyski, 1993; Porter and Knoll, 2000; Dehler and others, 2012, 2017; Porter and Riedman, 2016), and vase-shaped microfossils (Bloeser and others, 1977; Bloeser, 1985; Vidal and Ford, 1985; Porter and Knoll, 2000; Porter and others, 2003). Acritarchs are abundant and diverse in the Awatubi Member but disappear within the Walcott Member, while vase-shaped microfossils are primarily found in the Walcott Member (Porter and Riedman, 2016; Dehler and others, 2017).

The Kwagunt Formation has also yielded more obscure fossils in GRCA. "Vampire traces" continue into this formation, and larger circular or semi-circular punctures have been found on vase-shaped microfossils (Porter, 2016a, 2016b, 2017). Chemical analysis of Kwagunt Formation rocks has yielded steranes, a type of biomarker (Summons and others, 1988; Dehler and others, 2012; Brocks and others, 2016), including a sterane profile that is typical of some groups of sponges (Brocks and others, 2016). Possible traces smaller than a millimeter (0.04 in) have also been reported by Horodyski (1988, 1993), who interpreted them as trace fossils made by meiofauna.

Sixtymile Formation (lower Cambrian)

The Sixtymile Formation has recently been shown to be Cambrian in age (Karlstrom and others, 2018), but it is included here because of its traditional Precambrian placement. It is only found in a few areas of eastern GRCA, and is composed of red sandstone with chert and breccia (Elston, 1979). What had previously been described as the lowest part of the formation has been transferred to the upper Kwagunt Formation (Timmons and others, 2001; Kenny, 2017). The Sixtymile Formation was deposited in lacustrine, fluvial, and shallow marine settings. Detrital zircons indicate it was deposited between 520 and 509 Ma, making it contemporaneous in part with rocks of the lower Tonto Group in the western Grand Canyon–Lake Mead region (Karlstrom and others, 2018). Karlstrom and others (2020) have included it in the Tonto Group as the basalmost formation. The supplementary information for Karlstrom and others

(2018) included a figure of an object in a chert nodule, described as "akin to a lithistid demosponge or perhaps a coralomorph", representing the first published report of a potential fossil in the Sixtymile Formation

TYPES OF FOSSILS

The Precambrian fossil record of GRCA can be divided into two major categories: stromatolites and other microbial structures, which are apparent to the naked eye; and microfossils, which have only been studied since the late 1960s, with the notable exception of *Chuaria*. The Galeros and Kwagunt formations have significant microfossil assemblages. The search for fossils in the park's Precambrian rocks has also led to the description of inorganic features as fossils; some of these pseudofossils (non-fossils) or dubiofossils (unclear if fossils or not) have been the subjects of lengthy debate in the literature and are documented here for completeness.

Stromatolites and Other Microbial Structures

The most visible uncontroversial fossils in the Precambrian rocks of GRCA are stromatolites, which at this time are known from four formations (Bass, Dox, Galeros, and Kwagunt). The stromatolites from the Bass Formation are the oldest fossils known from the park (figures 3 and 6), between 1.25 and 1.2 billion years old. Stromatolites and related structures such as oncolites and thrombolites are trace fossils produced by microbial colonies. In the past, they were frequently described as "algal", but with the refinement of the definition of algae, it is more appropriate to describe the producers under the generalized term "microbes". Stromatolites form from cycles of sediment being trapped on the surface of a microbial mat; the colony grows over the layer of sediment to have access to the outside environment, and a new layer of sediment begins to form. The colonies can have a variety of forms, related to environmental conditions and the type of microbes. Morphologies include flat layers, crinkly layers, groups of columns, domes, and cones. Oncolites show concentric layers around objects, and thrombolites show "clotted" structures instead of layers. There may also be microbial laminations not divisible into distinct colonies. Brecciated and folded microbial laminations are thought to be the source of the "flaky dolomite bed" of the Kwagunt Formation (Ford and Breed, 1973a).

Some researchers have applied scientific names to stromatolites, but this is controversial; describing them in terms of morphology is more common. Taxonomic names applied to GRCA stromatolites include the following: stromatolites from the Bass Formation have been identified as *Collenia* (White, 1928a; Beus and others, 1974; Ford and Breed, 1977); *Baicalia*-type

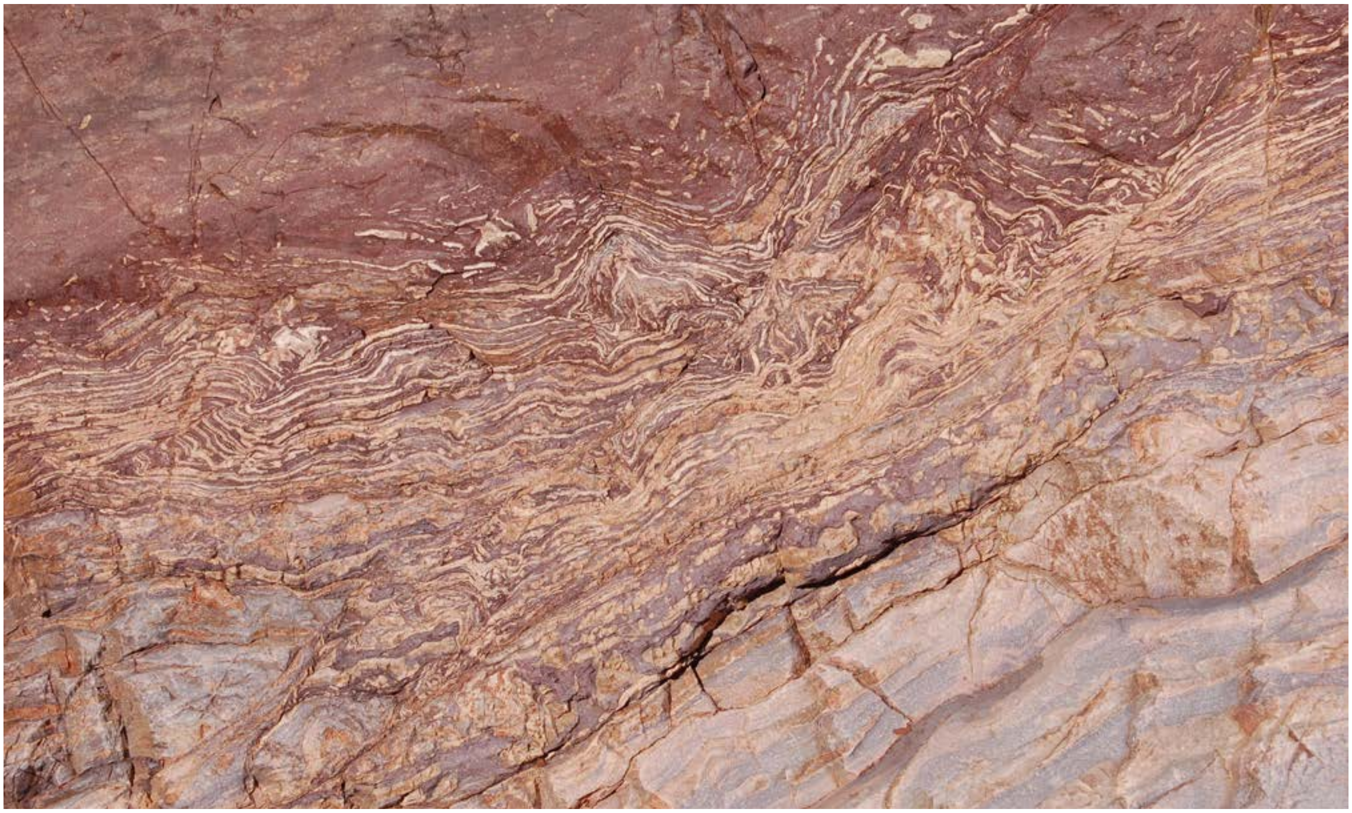

Figure 6. *Another view of a Bass Limestone stromatolitic horizon just below the Hakatai Shale (NSP/CARL BOWMAN).*

stromatolites have been identified from the Galeros and Kwagunt formations (Ford and Breed, 1973a; Dehler and others, 2001, 2012); *Inzeria*-type and *Stratifera*-type stromatolites have been identified from the Galeros Formation (Ford and Breed, 1973a; Dehler and others, 2001, 2012, 2017); *Boxonia*-type stromatolites have been reported from the Kwagunt Formation (Ford and Breed, 1973a; Dehler and others, 2001, 2012); and the stromatolite taxon *Cryptozoon occidentale* was named from what was later identified as most likely the Awatubi Member of the Kwagunt Formation (Dawson, 1897; Ford and Breed, 1973a). As mentioned above, stromatolites form distinct horizons in the Galeros and Kwagunt formations. White (1928a) and Lathrop (2018) identified diverse morphologies in the Bass Formation stromatolites, but in general it has been more typical to report the presence of stromatolites in passing.

Acritarchs and Other Organic-Walled Microfossils

Many of the Precambrian microfossils of GRCA are organic-walled structures. They include acritarchs, colonial forms, and filaments and sheaths. "Acritarch" is a term for a non-colonial microfossil of uncertain origin with a central cavity and organic walls rather than mineralized walls. The term should be considered a category rather than a taxonomic group, because many different organisms produce structures that could be described as acritarchs (Evitt, 1963). GRCA's Precambrian acritarchs include forms with smooth or ornamented walls, generally spherical to elliptical, mostly ranging in size from a few tens of µm to a few hundred µm in diameter (Porter and Riedman, 2016). Aside from the *Chuaria*-like Bass Formation microfossils described by White (1928a), which have not been subsequently relocated, and Nitecki's microfossils from the same formation (Nitecki, 1971), Precambrian acritarchs at GRCA are limited to the Galeros and Kwagunt formations. They are most diverse in the Galeros Formation (Nagy and others, 2009). A number of taxa have been recognized (Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016; Dehler and others, 2017), five of which were named from GRCA fossils. The taxonomy differs in each report, so following specific finds from report to report can be confusing. Leiosphaerids are another distinct type of acritarch. They have simple smooth walls and are found in abundance higher in section than most of the acritarchs, in the Awatubi Member of the Kwagunt Formation. There are also colonial forms, such as aggregates of small round cells known as *Bavlinella* (*Sphaerocongregus* of older reports), also abundant in the Awatubi and overlying Walcott members (Nagy and others, 2009; as the authors noted, not all occurrences of *Bavlinella* are necessarily fossils).

Chuaria circularis is the most historically notable Precambrian microfossil from GRCA, and like many Precambrian fossils described in the 19th century or early 20th century has had a long history of controversy. It is unusual for its great size, being visible to the naked eye: *C. circularis* fossils are generally 2 to 3 mm (0.08 to 0.1 in) across, up to 5 mm (0.2 in) (Ford, 1990). It has also had an outsized impact: the work that led to the division of the Chuar Group and helped initiate the study of microfossils in these rocks was begun at the request of the National Museum of Natural History to relocate Walcott's type locality for *Chuaria circularis* (Ford and Breed, 1973a). Aside from size, *C. circularis* can be described as "flattened carbonaceous spheroids, now discs," lacking pores or other openings, or regular surficial ornamentation, but with wrinkles or cracks (figure 1). In the field, they can be seen as black shiny discs on bedding laminae, although when prepared they look yellowish and translucent (Ford and Breed, 1973b).

Although the report in White (1876) of "*Lingulella* and *Obolella*" from Kwagunt Valley sounds superficially like *Chuaria*, it is unlikely that these objects were *Chuaria* (Spamer, 1988). The first definite report of *Chuaria* is the "small Discinoid shell" of Walcott (1883). Walcott formally described it some years later as *Chuaria circularis* (Walcott, 1899). Over the next few decades *Chuaria* was the subject of numerous attempts at classification and was reported from many other places across the world (see summaries in Spamer, 1984 and 1988), although many of these reports are questionable (Vidal and Ford, 1985). Authors suggested everything from brachiopods, to hyolith operculae, to gastropods, to ostracodes, to foraminifera, to algae, to trilobite eggs, to pseudofossils (Ford and Breed, 1973b; Spamer, 1984). By the 1960s, opinion had crystallized around an algal identification (Ford and Breed, 1973b). Ford and Breed (1973a, 1973b, 1977) redescribed *Chuaria circularis* from GRCA material. Because of the diversity of fossils from numerous locations that have been described as *Chuaria*, caution should be exerted when applying interpretations to GRCA *Chuaria* that are based on fossils from other locations: they may not represent the same organisms. At some locations outside of GRCA, such as in India, fossils described as *Chuaria* are linked to fossils known as *Tawuia*, perhaps as two parts of the same structure (e.g., Kumar, 2001; Sharma and others, 2009). Although *Tawuia* is apparently only found with *Chuaria* (Xiao and Dong, 2006), the opposite is not the case, as *Tawuia* has never been reported from GRCA. Therefore, *Chuaria circularis* of GRCA is not necessarily the same kind of fossil as the "*Chuaria-Tawuia* complex".

Filaments and Sheaths

Potential filamentous structures have been reported from the Bass Formation (Dalton, 1972; Beus and others, 1974; Ford and Breed, 1977), but uncontroversial filaments are only known from the Galeros and Kwagunt formations. Filaments and sheaths were first reported by Schopf and others (1973) from a cherty pisolite bed in the Walcott Member of the Kwagunt Formation. Several taxa have since been reported from shale beds (Vidal and Ford, 1985; Horodyski, 1993; Porter and Riedman, 2016).

GRCA Precambrian filaments can be divided into several groups. The most abundant forms are narrow, non-branching, non-tapering, and non-tubular, between one and several µm across (Horodyski, 1993). This group was divided by Porter and Riedman (2016) into several species of *Siphonophycus* based on size. They are found both isolated and as parts of fragments of filamentous mats. Similar but larger tubular filaments up to several tens of µm across have been found, but are rarer. There are also rare non-tubular filaments from 10 to >100 µm across. One carbonaceous form is apparently limited to a 0.1-mm-thick (0.004 in) interval near the top of the Awatubi Member of the Kwagunt Formation, in which it is very abundant. They are most likely from eukaryotic algae, but could be prokaryotic (Horodyski, 1993).

Vase-Shaped Microfossils

Vase-shaped microfossils (VSMs) are non-colonial fossils shaped like a simple vase with a wider "base" and narrower "upper" end featuring an opening. They were first reported from GRCA and are now known from a number of formations across the world, but flourished only between approximately 760 Ma and the onset of the first Snowball Earth glaciation at 717 Ma (MacDonald and others, 2010). They are frequently preserved as siliceous or calcareous casts, sometimes coated by organic material or oxides, probably replacing an original organic material. Some feature a "honeycomb" appearance, derived from an original scaled surface. Most are straight, but some have curved necks. In some forms there is a distinct "neck", while in others the shape tapers without an obvious break. Some have a "collar" or other distinct apertural feature, while others do not. They range in size from approximately 20 to 300 µm long and 10 to 200 µm wide (Porter and Knoll, 2000). A few features previously reported in the literature appear to have been mistaken. Bloeser (1985) interpreted some features as opercula, but these appear to be sediment plugs instead (Porter and Knoll, 2000). The internal vesicles of Horodyski (1993) appear to be crystalline precipitates (Porter and Knoll, 2000). As of this writing, a dozen species of VSMs have been named from GRCA fossils, all from the Kwagunt Formation (Porter and others, 2003). They can be exceedingly abundant in certain beds, up to 4000/mm^3 in some nodules (Porter and Knoll, 2000). They are interpreted as the fossils of testate amoebas ("testate" meaning they form a structure, a test, around the body) (Porter and Knoll, 2000), apparently ancient examples of arcellinid amoebas (Lahr and others, 2019).

VSMs are first found in the uppermost Awatubi Member, where they overlap with *Chuaria*, leiosphaerids, and *Sphaerocongregus* (=*Bavlinella*). These other groups disappear higher in the Awatubi Member or in the lower half of the Walcott Member, leaving the VSMs as the dominant group. This pattern has been interpreted as the result of prolonged eutrophication, in which nutrient-rich water promotes "algal" blooms, and the increased productivity depletes oxygen from the water, disrupting the existing phytoplankton ecosystem while providing an opportunity for protozoans to thrive (Nagy and others, 2009).

VSMs were first reported in Bloeser and others (1977) as "tear- and flask-shaped microfossils", attributed to chitinozoans (a type of flask-shaped organic-walled microfossil of uncertain origin otherwise known from Paleozoic rocks). At that time two forms were distinguished: flask-shaped with a short "neck" with pronounced "collar"; and slightly longer, thinner tear-shaped forms lacking a distinct neck. The initial genus, *Melanocyrillium*, was mentioned several times before formal publication (e.g., Spamer, 1984; Vidal and Ford, 1985). Bloeser (1985) formally described *Melanocyrillium* and separated the fossils into three species: *M. fimbriatum* for the tear-shaped form, and *M. hexodiadema* and *M. horodyskii* for flask-shaped forms with two different "necks" and "collars". She also removed them from the chitinozoans, suggesting that they were cysts of an unknown alga. Porter and Knoll (2000) first proposed the testate amoeba hypothesis, which is now widely accepted. Porter and others (2003) provided a description of the GRCA VSM assemblage, naming a number of new taxa and transferring *Melanocyrillium fimbriata* and *M. horodyskii* to a new genus, *Trigonocyrillium*. Additional taxa were reported from GRCA in Morais and others (2019).

Other Fossils

Some researchers have explored hydrocarbons in the Precambrian rocks. This line of research was initiated by Summons and others (1988), who identified biomarkers including steranes and neohopanes that indicate eukaryotes. Brocks and others (2016), continuing this work, identified a new sterane they called cryostane, which they linked to a group of sponges known as demosponges (with the caveat that other eukaryotes could have produced it). They interpreted this as a type of sterol evolved to protect cells against toxins released by protist predators.

Holes have been observed in some of the microfossils, such as semi-circular and circular holes in VSMs. They are thought to represent predation and/or scavenging (Porter and others, 2003; Porter, 2016a). One unusual class of these perforations consists of minute circular holes, 0.1 to 3.4 µm across, found in the walls of at least seven species of GRCA organic-walled microfossils. They are believed to represent "vampire-like" predation behavior as exhibited today by several groups of eukaryotes and are, to date, the oldest direct evidence for predation on eukaryotes (Porter, 2016a).

In addition, some other types of fossils have been reported, but generally in passing or otherwise in such little detail that it is not possible to evaluate the report or to be sure that they do not belong to one of the other categories. They include various unspecified cellular fossils in the Chuar Group (Schopf and others, 1973; Bloeser and others, 1977; Vidal and Ford, 1985; Ford, 1990; Dehler and others, 2012), Bass Formation calcispheres (Dalton, 1972; Ford and Breed, 1977; Lathrop, 2018), and the possible Kwagunt meiofaunal traces mentioned by Horodyski (1988, 1993). Undefined organic detritus has also been reported from the Bass Formation (Vidal and Ford, 1985) and Chuar Group (Downie, 1969).

Notable Pseudofossils and Dubiofossils

Reports of pseudofossils (resembling a fossil but inorganic in origin) and dubiofossils (potentially a fossil, but origin unclear) in the Precambrian rocks of GRCA go back to the "*Lingulella* and *Obolella*" of White (1876). Walcott (1883) reported finding a "small Discinoid shell, a couple of specimens of a Pteropod allied to *Hyolithes triangularis* and an obscure Stromatopora-like group of forms" in rocks of the Chuar Group. A few years later, he added a possible trilobite fragment and a *Lingula*-like shell to the lot (Walcott, 1886). By 1899, he'd reevaluated the "hyolith" as potentially of mechanical origin and decided that the trilobite fragment could have been misinterpreted, but had also added an *Acrothele*-like brachiopod (Walcott, 1899). After observing some of Walcott's specimens, Horodyski (1993) interpreted the *Acrothele*-like brachiopod (USNM 33801) as an "apparently mineralic precipitate along a fracture or bedding surface", and the trilobite fragment (USNM 33802) as "probably a fortuitously exposed portion of a carbonaceous layer". Ford and Breed (1977) suspected that the lingulid shell could also be dismissed in a similar way. The only fossils from Walcott's assemblage are the "discinoid shell", which he named *Chuaria circularis* in 1899, and the "Stromatopora", actually stromatolites. "Stromatopora", now used for certain layered sponges, is a term that in the 19th century was not firmly distinguished from the various terms then used for what are now recognized as stromatolites.

The most significant of the various Precambrian pseudofossils and dubiofossils is the lobed object known as *Brooksella canyonensis*. It first came to attention in the 1930s, a putative jellyfish uncovered in the course of work on what became named the Nankoweap Formation (Van Gundy, 1937). Bassler (1941) formally created the name *Brooksella canyonensis* for Van Gundy's specimen (USNM 99438), although he was hesitant to declare it a jellyfish, arguing that it could also be algal or inorganic. Although the jellyfish hypothesis has long been out of favor, there have been decades of arguments and counter-arguments, split between organic (e.g., Glaessner, 1969; Kauffman and Steidtmann, 1981; Kauffman and Fursich, 1983) and inorganic (e.g., Cloud, 1968; Ford and Breed, 1977; Ford, 1990) camps. The organic camp favors a trace-fossil origin, such as a worm-like burrowing sediment feeder (Glaessner, 1969) or an advanced metazoan burrow produced by complex feeding behavior (Kauffman and Fursich, 1983). The inorganic camp has suggested such origins as gas-escape structures or compactions (Cloud, 1968), similar to "sand volcanoes" formed by fluid escape (Ford and Breed, 1977; Ford, 1990), or an aggregation of mud rolls (Fedonkin and Runnegar, 1992).

Another category of Precambrian pseudofossils is the "fucoids". White (1928a, 1929) and McKee (1932) reported "fucoids" in several of the Grand Canyon Supergroup units. "Fucoid", from Fucaceae, an order of brown algae, is an obsolete term applied to what were once thought to be fossil seaweeds, but which are now known to be invertebrate burrows or various burrow-like sedimentary features such as mud cracks (figure 4). McKee (1932) recognized that most "fucoids" were not seaweed fossils and used the term in a general fashion to encompass anything with that general shape, including a photographed slab of Dox Formation "fucoids" (figure 5). Mud cracks are thought to be responsible for putative "trace fossils" in the Nankoweap Formation (Ford, 1990).

Several other pseudofossils and dubiofossils are worth noting. Seilacher (1956) reported the presence of bilobed features 1 mm (0.04 in) across in the Hakatai Shale, which he compared to the trilobite resting trace *Rusophycus*. Cloud (1968) considered them inorganic. Alf (1959) reported several potential fossils from near the Bass–Hakatai transition interval, including vermiform markings, more putative jellyfish (figure 7), and a possible sponge. Cloud (1968) regarded one of the "jellyfish" varieties as more likely marks left by water drops and the other variety as gas-escape structures or compactions, and the "sponge" as a silica nodule. Glaessner (1969) disagreed with the water drop interpretation of some of Alf's "jellyfish", which he thought might be algal colonies instead, but agreed with the silica nodule identification of the "sponge", and regarded the vermiform markings as filled mud cracks. Ford and Breed (1973a, 1977) disagreed with Glaessner's algal interpretation, and returned to a gas escape structure explanation. Nitecki (1971) reported similar nodules to the "sponge" and considered them inorganic, but was able to produce apparent microfossils by dissolving one of them in hydrofluoric acid.

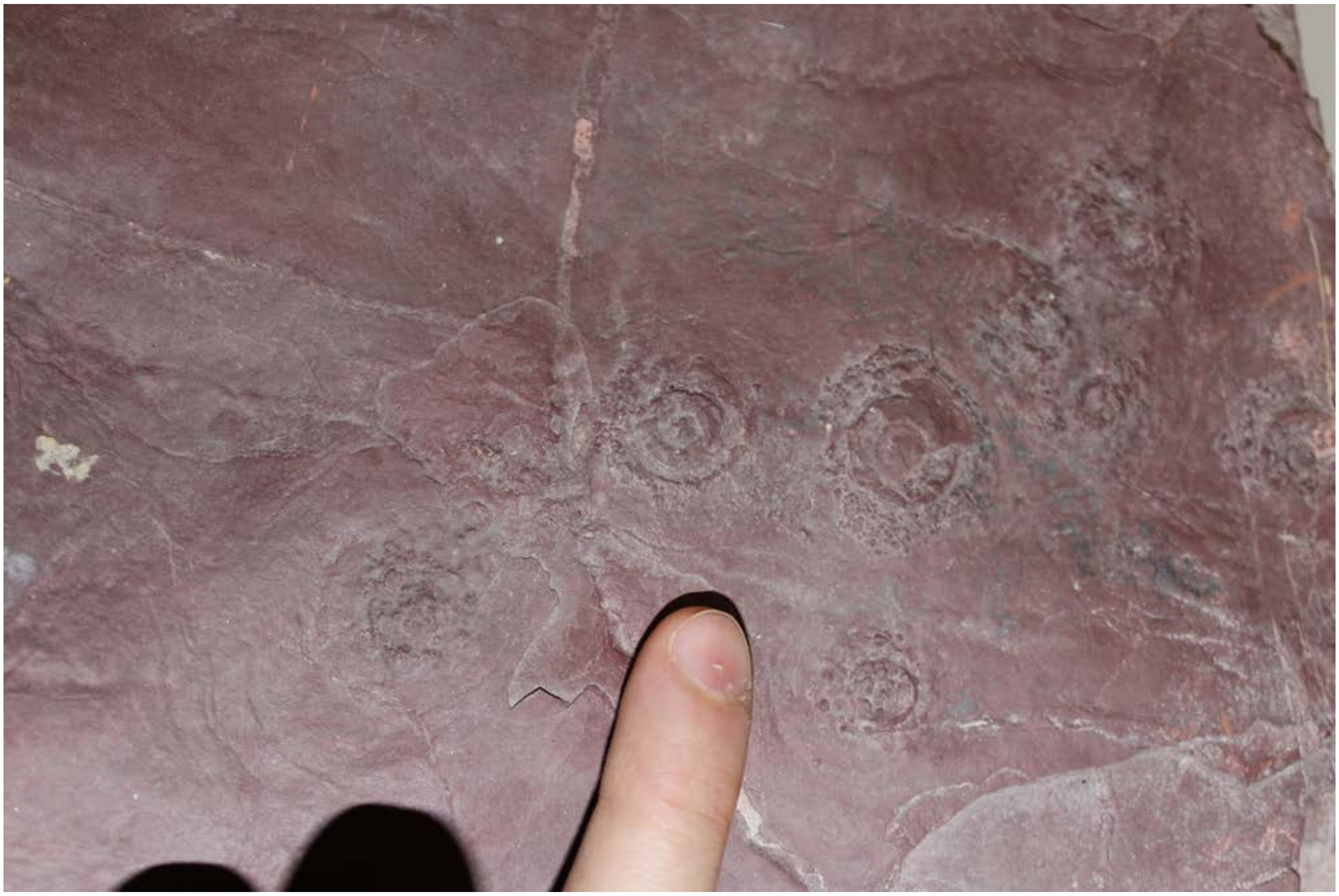

Figure 7. *Examples of Alf's circular structures from the Bass–Hakatai transition interval (RAYMOND M. ALF MUSEUM/ DON LOFGREN).*

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Appendix A

Precambrian Taxa From GRCA

It was not possible to critically evaluate every cited occurrence. There are undoubtedly instances below where the same taxon is listed more than once due to differing interpretations or general changes in taxonomic usage. This is not limited to choices of genera and species; one author may describe a find as [*Genus*] [*species*], where another may prefer [*Genus*] sp. In addition, it was not within the scope of the project to evaluate every potential synonymy and genus-species combination. The most recent name is generally used, with other combinations included in notes following the tables to allow translation between different references. Some cited taxa have outdated names, but the author did not provide enough information to determine more appropriate names. In these cases, the taxonomy is left as the author gave it. Records are marked stratigraphically with "Y" in the corresponding formation column; questionable records are marked with "?".

GCM = Grand Canyon museum collections (only unique results unreported in the literature are included)

Due to the number of taxa and formations, entries have been split into two tables, incorporating the following formations in ascending order:

Appendix table A-1: Unkar Group
Yud = Dox Formation
Yus = Shinumo Quartzite
Yuh = Hakatai Shale
Yub = Bass Formation

Appendix table A-2: Chuar Group
Zck = Kwagunt Formation
Zcg = Galeros Formation
Zcn = Nankoweap Formation

Appendix Table A-1. *Unkar Group fossil taxa.*

Category	Taxon	Yub	Yuh	Yus	Yud	References
Structures of microbial origin	Various “algal” structures	Y	Y	–	–	White, 1928a; GCM
	Possible microbial laminations	–	–	–	Y	Stevenson and Beus, 1982
	Possible microbially induced sedimentary structures	–	–	–	Y	Tweet and Lucas, in press
	Stromatolites: *Collenia frequens*	Y	–	–	–	Beus and others, 1974; Ford and Breed, 1977
	Stromatolites: *Collenia symmetrica*	Y	–	–	–	Beus and others, 1974; Ford and Breed, 1977
	Stromatolites: *Collenia undosa*	Y	–	–	–	Beus and others, 1974; Ford and Breed, 1977
	Stromatolites: *Collenia*-type	Y	–	–	–	White, 1928a
	Stromatolites: general	Y	?[1]	–	Y	Nitecki, 1971; Ford and Breed, 1977; Stevenson and Beus, 1982; Beus, 1987; Hendricks and Stevenson, 1990; Timmons and others, 2012; Lathrop, 2018
Acritarchs	*Chuaria*-like microfossils	Y	–	–	–	White 1928a, Nitecki 1971
Filaments and sheaths	Possible “algal” filaments	Y	–	–	–	Dalton, 1972; Beus and others, 1974; Ford and Breed, 1977
	Enigmatic branching structures	Y	–	–	–	Nitecki, 1971
Miscellaneous fossils	Calcispheres (Calcitarcha)	Y	–	–	–	Dalton, 1972; Ford and Breed, 1977; Lathrop, 2018
	Organic detritus	Y	–	–	–	Vidal and Ford, 1985
	Ovoid pellets	Y	–	–	–	Ford and Breed, 1977
Select pseudofossils and dubiofossils	Apparent algal thalli impressions	–	Y	–	–	White, 1929
	Apparent bivalved fossils (?oncolites)	Y	–	–	–	Smith, 1969; Ford and Breed, 1977
	“Jellyfish”	Y	–	–	–	Seilacher, 1956; Alf, 1959; Cloud, 1968; Glaessner, 1969; Ford and Breed, 1977
	“*Rusophycus*”	–	Y	–	–	Seilacher, 1956; Cloud, 1968; Glaessner, 1969; Webby, 1970
	“Sponge”	Y	–	–	–	Alf, 1959; Cloud, 1968; Ford and Breed, 1977
	Various “fucoids” and other putative invertebrate trace fossils	Y	Y	Y	Y	White, 1927, 1928a, 1929; McKee, 1932; Alf, 1959; Cloud, 1968; Glaessner, 1969; Nitecki, 1971; Ford and Breed, 1977

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[1] Stromatolites are noted in the Bass–Hakatai transition zone, but are limited to beds of the Bass facies (Timmons and others, 2012)

Appendix Table A-2. *Chuar Group fossil taxa. (continued on following page)*

Category	Taxon	Zcn	Zcg	Zck	Zcu	References
Invertebrate trace fossils	Possible meiofaunal traces	–	–	Y	–	Horodyski, 1988, 1993
Fossils and structures of microbial origin	Circular and semi-circular holes in vase-shaped microfossils	–	–	Y	–	Porter and others, 2003; Porter, 2016a
	“Cryptalgal” features	–	Y	–	–	Ford, 1990
	“Microbial mats”	–	–	Y	–	Bohacs and Junium, 2007
	Stromatolites: *Baicalia*-type	–	Y	Y	–	Ford and Breed, 1973a; Bloeser and others, 1977; Ford, 1990; Dehler and others, 2001, 2012, 2017
	Stromatolites: *Boxonia*-type	–	–	Y	–	Ford and Breed, 1973a; Bloeser and others, 1977; Ford, 1990; Dehler and others, 2001, 2012
	Stromatolites: *Cryptozoon occidentale*	–	–	Y	–	Dawson, 1897; Ford and Breed, 1973a
	Stromatolites: *Inzeria*-type	–	Y	–	–	Ford and Breed, 1973a; Bloeser and others, 1977; Ford, 1990; Dehler and others, 2001, 2012, 2017
	Stromatolites: *Stratifera*-type	–	Y	–	–	Ford and Breed, 1973a; Bloeser and others, 1977; Ford, 1990; Dehler and others, 2001, 2012, 2017
	Stromatolites: general	–	Y	Y	–	Ford and Breed, 1973a; Horodyski and Bloeser, 1983; Ford, 1990; Porter and Knoll, 2000; Dehler and others, 2001, 2017; Porter and Riedman, 2016
	“Vampire traces”	–	Y	Y	Y	Porter, 2016a, 2016b, 2017
Acritarchs and colonial organic-walled microfossils	**Overall acritarchs and colonial organic-walled microfossils**	**–**	**Y**	**Y**	**Y**	**–**
	Bavlinella faveolata	–	–	Y	–	Nagy and others, 2009; Dehler and others, 2012
	Caelatimurus foveolatus	–	Y	–	–	Porter and Riedman, 2016
	Cerebrosphaera globosa	–	Y	Y	Y	Nagy and others, 2009; Porter and Riedman, 2016; Dehler and others, 2017
	Cerebrosphaera sp.	–	Y	–	–	Dehler and others, 2017
	Chuaria circularis	–	Y	Y	–	Ford and Breed, 1973a, 1973b; Bloeser and others, 1977; Vidal and Ford, 1985; Ford, 1990; Porter and Knoll, 2000; Nagy and others, 2009; Dehler and others, 2012, 2017; Porter and Riedman, 2016
	Culcitulisphaera revelata	–	Y	Y	–	Nagy and others, 2009; Porter and Riedman, 2016
	Galerosphaera walcottii	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016

Appendix Table A-2. *Continued.*

Category	Taxon	Zcn	Zcg	Zck	Zcu	References
Acritarchs and colonial organic-walled microfossils (continued)	*Kaibabia gemmulella*	–	Y	Y	–	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016
	Kildinosphaera chagrinata	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009
	Lanulatisphaera laufeldii	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016; Dehler and others, 2017
	Leiosphaeridia asperata	–	Y	Y	–	Vidal and Ford, 1985
	Leiosphaeridia crassa	–	Y	Y	–	Porter and Riedman, 2016
	Leiosphaeridia jacutica	–	Y	Y	–	Porter and Riedman, 2016
	Leiosphaeridia minutissima	–	Y	Y	–	Porter and Riedman, 2016
	Leiosphaeridia tenuissima	–	Y	Y	–	Porter and Riedman, 2016
	Leiosphaeridia sp.	–	Y	Y	–	Vidal and Ford, 1985; Porter and Riedman, 2016
	Unspecified leiosphaerids	–	Y	Y	–	Dehler and others, 2017
	Microlepidopalla mira	–	Y	–	–	Porter and Riedman, 2016
	Navifusa majensis	–	Y	–	–	Porter and Riedman, 2016
	Palaeastrum dyptocranum	–	Y	–	–	Porter and Riedman, 2016
	Squamosphaera colonialica	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016
	Cf. *Stictosphaeridium* sp.	–	Y	Y	–	Vidal and Ford, 1985; Dehler and others, 2012
	Clustered cf. *Stictosphaeridium* sp.	–	Y	–	–	Vidal and Ford, 1985
	Synsphaeridium sp.	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016; Dehler and others, 2017
	Tasmanites rifejicus	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009
	Trachysphaeridium timofeevi	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009
	Corroded *Trachysphaeridium* spp.	–	Y	–	–	Vidal and Ford, 1985
	Valeria lophostriata	–	Y	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009; Porter and Riedman, 2016
	Vidalopalla cf. *verrucata*	–	Y	Y	–	Vidal and Ford, 1985; Porter and Riedman, 2016
	Volleyballia dehlerae	–	Y	–	–	Nagy and others, 2009; Porter and Riedman, 2016
	Unnamed Form A (Porter and Riedman 2016)	–	Y	–	–	Porter and Riedman, 2016
	Unnamed Form B (Porter and Riedman 2016)	–	Y	–	–	Porter and Riedman, 2016

Appendix Table A-2. *Continued.*

Category	Taxon	Zcn	Zcg	Zck	Zcu	References
Acritarchs and colonial organic-walled microfossils (continued)	Unnamed Form C (Porter and Riedman 2016)	–	Y	–	–	Porter and Riedman, 2016
	Unnamed Form D (Porter and Riedman 2016)	–	Y	Y	–	Porter and Riedman, 2016
	Unnamed Form E (Porter and Riedman 2016)	–	Y	–	–	Porter and Riedman, 2016
	Clusters of small cells, possibly *Eoentophysalis* sp. (cyanobacteria?)	–	Y	–	–	Vidal and Ford, 1985
	Unspecified organic-walled microfossils	–	Y	Y	–	Bloeser and others, 1977; Vidal and Ford, 1985; Horodyski, 1993; Porter and Knoll, 2000; Dehler and others, 2012, 2017
Filaments and sheaths	**Overall filaments and sheaths**	**–**	**Y**	**Y**	**–**	**–**
	Archaeotrichion spp.	–	–	Y	–	Horodyski, 1993
	Rugosoopsis tenuis	–	Y	–	–	Porter and Riedman, 2016
	Siphonophycus robustum	–	Y	Y	–	Porter and Riedman, 2016
	Siphonophycus septatum	–	Y	Y	–	Porter and Riedman, 2016
	Siphonophycus typicum	–	Y	Y	–	Porter and Riedman, 2016
	Siphonophycus sp.	–	Y	Y	–	Horodyski, 1993; Porter and Riedman, 2016
	Taeniatum sp.	–	–	Y	Y	Vidal and Ford, 1985; Nagy and others, 2009
	"Algal" filaments	–	Y	Y	–	Ford and Breed, 1973a; Schopf and others, 1973; Bloeser and others, 1977; Ford, 1990
	Bacterial filaments and filamentous bacteria	–	–	Y	–	Porter and Knoll, 2000; Dehler and others, 2012
	Carbonaceous filaments	–	–	Y	–	Horodyski and Bloeser, 1983
	Eukaryotic? filaments	–	–	Y	–	Porter and Knoll, 2000; Dehler and others, 2012
	Filamentous sheaths, cyanobacteria?	–	Y	–	–	Vidal and Ford, 1985
	Filamentous sheaths, septate?, possibly oscillatoriacean	–	–	Y	–	Vidal and Ford, 1985
	Filamentous sheaths, similar to *Eomycetopsis*	–	–	Y	–	Schopf and others, 1973
	Nontubular filament fragments	–	–	Y	–	Horodyski, 1993
	Unspecified filaments	–	–	Y	–	Dehler and others, 2017
Vase-shaped microfossils	**Overall vase-shaped microfossils**	**–**	**–**	**Y**	**–**	**–**
	Bombycion micron	–	–	Y	–	Porter and others, 2003

Appendix Table A-2. *Continued.*

Category	Taxon	Zcn	Zcg	Zck	Zcu	References
Vase-shaped microfossils (continued)	*Bonniea dacruchares*	–	–	Y	–	Porter and others, 2003
	Bonniea pytinaia	–	–	Y	–	Porter and others, 2003
	Cycliocyrillium simplex	–	–	Y	–	Porter and others, 2003
	Cycliocyrillium torquata	–	–	Y	–	Porter and others, 2003
	Hemisphaeriella ornata	–	–	Y	–	Porter and others, 2003
	Limeta lageniformis	–	–	Y	–	Morais and others, 2019
	Melanocyrillium hexodiadema	–	–	Y	–	Bloeser, 1985; Porter and others, 2003
	Melanocyrillium sp.	–	–	Y	–	Vidal and Ford, 1985
	Melicerion poikilon	–	–	Y	–	Porter and others, 2003
	Obelix rootsii	–	–	Y	–	Morais and others, 2019
	Pakupaku kabin	–	–	Y	–	Morais and others, 2019
	Palaeoamphora urucumense	–	–	Y	–	Morais and others, 2019
	Palaeoarcella athanata	–	–	Y	–	Porter and others, 2003
	Trachycyrillium pudens	–	–	Y	–	Porter and others, 2003
	Trigonocyrillium fimbriatum	–	–	Y	–	Bloeser, 1985; Porter and others, 2003
	Trigonocyrillium horodyskii	–	–	Y	–	Bloeser, 1985; Porter and others, 2003
	Unspecified vase-shaped microfossils	–	–	Y	–	Bloeser and others, 1977; Porter and Knoll, 2000; Dehler and others, 2012, 2017; Porter and Riedman, 2016
Miscellaneous fossils	**Overall miscellaneous fossils**	**–**	**Y**	**Y**	**Y**	**–**
	“Algae”	–	–	–	Y	GCM
	Organic detritus	–	Y	Y	–	Downie, 1969
	Steranes	–	–	Y	–	Summons and others, 1988; Vogel and others, 2005; Dehler and others, 2012; Brocks and others, 2016
	Unspecified spheroids / unicells	–	Y	Y	–	Schopf and others, 1973; Bloeser and others, 1977; Vidal and Ford, 1985; Ford, 1990; Dehler and others, 2012
	Unspecified microfossils	–	Y	Y	–	Downie, 1969; Ford, 1990
Select pseudofossils and dubiofossils	“*Brooksella canyonensis*”	Y	–	–	–	Van Gundy, 1937, 1951; Bassler, 1941; Cloud, 1968; Glaessner, 1969; Kauffman and Steidtmann, 1981; Kauffman and Fursich, 1983; Ford, 1990
	Various “fucoids” and other putative invertebrate trace fossils	Y	–	–	–	Ford, 1990

Taxonomic Notes

Porter and Riedman (2016) should be considered the most authoritative account of GRCA's Precambrian organic-walled microfossils. A few taxa not cited in that report are included in the table here; a few taxa cited in Nagy and others (2009) are exceptions. Some of the identifications in Nagy and others (2009) were provisional, and because they were presented only in a list, they are difficult to evaluate (S. Porter, pers. comm., April 2019). It is likely they represent specimens later re-evaluated by Porter and Riedman (2016), so they were omitted from the table. An obvious overlap is the four forms of *Leiosphaeridia* differentiated by vesicle thickness in Nagy and others (2009), which doubtless correspond to the four *Leiosphaeridia* species in Porter and Riedman (2016) (*L. crassa* and *L. jacutica* have thick vesicles and *L. minutissima* and *L. tenuissima* have thin vesicles). For reference, omitted taxa are:

- *Cerebrosphaera* sp. cf. *C. ananguae* (Zcg);
- *Eosynechococcus moorei* (Zcu);
- *Leiosphaeridia* sp. (very thin vesicle) (Zcg, Zck);
- *Leiosphaeridia* sp. (thin vesicle) (Zcg, Zck);
- *Leiosphaeridia* sp. (thick vesicle) (Zcg, Zck);
- *Leiosphaeridia* sp. (very thick vesicle) (Zcg, Zck);
- *Ostiana microcystis* (Zcu);
- *Pterospermopsimorpha insolita* (Zcg);
- *Trachysphaeridium levis* (Zcu);
- Unnamed Form B (Zcg, Zck)

Other taxonomic notes:

- *Cerebrosphaera buickii* of Nagy and others (2009) = *Cerebrosphaera globosa*
- Clusters of micron-sized scales (Porter and others, 2013) = *Microlepidopalla mira*
- Cf. *Cymatiosphaeroides kullingii* of Vidal and Ford (1985) = possibly *Kildinosphaera verrucata* of Nagy and others (2009) = *Lanulatisphaera laufeldii*
- *Collenia occidentale* = *Cryptozoon occidentale*; this also includes the so-called "Stromatopora" of some of Walcott's literature
- *Kildinosphaera lophostriata* = *Valeria lophostriata*
- *Kildinosphaera verrucata* of Vidal and Ford (1985) = *Vidalopalla* cf. *verrucata*
- *Melanocyrillium fimbriatum* = *Trigonocyrillium fimbriatum*
- *Melanocyrillium horodyskii* = *Trigonocyrillium horodyskii*
- *Leiosphaeridia* sp. A of Vidal and Ford (1985) and Nagy and others (2009) = *Kaibabia gemmulella*
- *Satka colonialica* = *Squamosphaera colonialica*
- *Sphaerocongregus variabilis* = *Bavlinella faveolata*
- *Trachysphaeridium* sp. A of Vidal and Ford (1985), *Trachysphaeridium laminaritum* of Nagy and others (2009) = *Culcitulisphaera revelata*
- *Trachysphaeridium laminaritum* of Vidal and Ford (1985) = *Lophosphaeridium laufeldi* of Nagy and others (2009) = *Lanulatisphaera laufeldii*

Species of *Trachysphaeridium* in general have been transferred to other genera (Porter and Riedman, 2016), but some listed taxa are retained under *Trachysphaeridium* because it is not apparent where they should go

- Unnamed form A of Nagy and others (2009) = *Volleyballia dehlerae*
- *Vandalosphaeridium walcottii* = *Galerosphaera walcottii*

Appendix B

Precambrian Taxa Named From GRCA

Appendix Table B-1. *Precambrian taxa named from specimens found within GRCA.*

Taxon	Citation	Age, Formation	Type Specimen	Notes
Cryptozoon? *occidentale*	Dawson, 1897	Neoproterozoic, Kwagunt	USNM 33799 (USNM 60710 and 60711 per Rezak, 1957)	Stromatolite
Chuaria circularis	Walcott, 1899	Neoproterozoic, Kwagunt	Lectotype USNM 33800	Organic-walled microfossil
Kaibabia gemmulella	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36082a	Organic-walled microfossil
Microlepidopalla mira	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36104b	Organic-walled microfossil
Vandalosphaeridium walcottii	Vidal and Ford, 1985	Neoproterozoic, Kwagunt	LO 5661	Organic-walled microfossil
Volleyballia dehlerae	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36080d	Organic-walled microfossil
Bombycion micron	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62988	Vase-shaped microfossil
Bonniea dacruchares	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64409	Vase-shaped microfossil
Bonniea pytinaia	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64410	Vase-shaped microfossil
Cycliocyrillium simplex	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64455	Vase-shaped microfossil
Cycliocyrillium torquata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64453	Vase-shaped microfossil
Hemisphaeriella ornata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62990	Vase-shaped microfossil
Melanocyrillium fimbriatum	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58968 (now LACM?)	Vase-shaped microfossil
Melanocyrillium hexodiadema	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58959 (now LACM?)	Vase-shaped microfossil
Melanocyrillium horodyskii	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58976 (now LACM?)	Vase-shaped microfossil
Melicerion poikilon	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62990	Vase-shaped microfossil
Palaeoarcella athanata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62988	Vase-shaped microfossil
Trachycyrillium pudens	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64413	Vase-shaped microfossil

TRILOBITE

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Trilobite

Scientific Name: *Dolichometopus productus*

Geologic Age: 506 million years ago (Cambrian)

Geologic Formation: Bright Angel Shale

Interactive 3D model

Rusophycus, or resting trace, of a trilobite

Trilobites crawled along ancient seafloors searching for food with their primitive eyes. These arthropods thrived for over 300 million years until the great Permian mass extinction 252 million years ago. Trilobites are related to modern spiders, scorpions and horseshoe crabs.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

4 of 9

Grand Canyon National Park Fossil Trading Card featuring the fossil trilobite Dolichometopus *productus and trilobite trace* Rusophycus *from the Cambrian Bright Angel Shale (NPS).*

PALEOZOIC INVERTEBRATE PALEONTOLOGY OF GRAND CANYON NATIONAL PARK

Linda Sue Lassiter[1], Justin S. Tweet[2], Frederick A. Sundberg[3], John R. Foster[4], and P. J. Bergman[5]

ABSTRACT

Our planet has a rich paleontologic history of life and environments that is uniquely captured in the brilliant rocks on display at Grand Canyon National Park (GRCA). The span of the Paleozoic fossil record at GRCA encompasses over about 250 million years of snapshots of ancient invertebrate life. Invertebrates discovered here include mostly marine brachiopods, bivalves, crinoids, corals, and arthropods like the familiar trilobite, but GRCA is also home to significant terrestrial invertebrate discoveries. *Tupus*, an early relative of modern dragonflies, was discovered at the park. Over 7,300 specimens listed in this work include almost 5,800 cataloged at the GRCA museum. Cambrian and Mississippian fossils have been extensively studied but most of the other period inventories are lacking. Significant stretches of GRCA can reveal much about the community of life before and after several of Earth's major extinction events of the Cambrian, end-Devonian, and Permian. The Sinsk extinction event of the early Cambrian precedes the deposits of the Tonto Group and the rich fossil history within these transgressional units. The Devonian Temple Butte Formation is Frasnian age and immediately precedes the Hangenberg extinction event but very few fossils have been documented. Finally, most of the surface deposits of GRCA contain communities of aquatic fossils that represent life in healthy Permian oceans just before the largest extinction event on our planet. There is much work yet to be done, much that remains to be learned, and much left to discover at our wonderful Grand Canyon.

INTRODUCTION

As impressive as the Grand Canyon is to any observer from the rim, the river, or even from space, these cliffs and slopes are much more than an array of colors above the serpentine majesty of the Colorado River. The erosive forces of the Colorado River and feeder streams took millions of years to carve more than 290 million years of Paleozoic Era rocks. These exposures of Paleozoic Era sediments constitute 85% of the almost 5,000 km^2 (1,903 mi^2) of the Grand Canyon National Park (GRCA) and reveal important chronologic information on marine paleoecologies of the past. This expanse of both spatial and temporal coverage is unrivaled anywhere else on our planet. While many visitors stand on the rim and peer down into the abyss of the carved canyon depths, few realize that they are also staring at the history of life from almost 520 million years ago (Ma) where the Paleozoic rocks cover the great unconformity (Karlstrom and others, 2018) to 270 Ma at the top (Sorauf and Billingsley, 1991). The Paleozoic rocks visible from the South Rim Visitors Center, are mostly from marine and some fluvial sediment deposits (figure 1).

This report covers the most abundant group of fossils in GRCA, the skeletal remains of invertebrates, of which more than 99% are marine organisms. Invertebrate fossils include well-known groups such as arthropod trilobites, two-valved brachiopods and mollusk bivalves, corals, echinoderms, mollusk gastropods and cephalopods, sponges, microfossil foraminifera, and other taxonomic groups preserved because of their biomineralized tissues in calcitic, chitinophosphatic, silicic, and other durable body parts. There are more than 80 fossil invertebrate species named from GRCA.

The Paleozoic history of invertebrate life ranges from the Cambrian Period (541 Ma) and ends in the Permian

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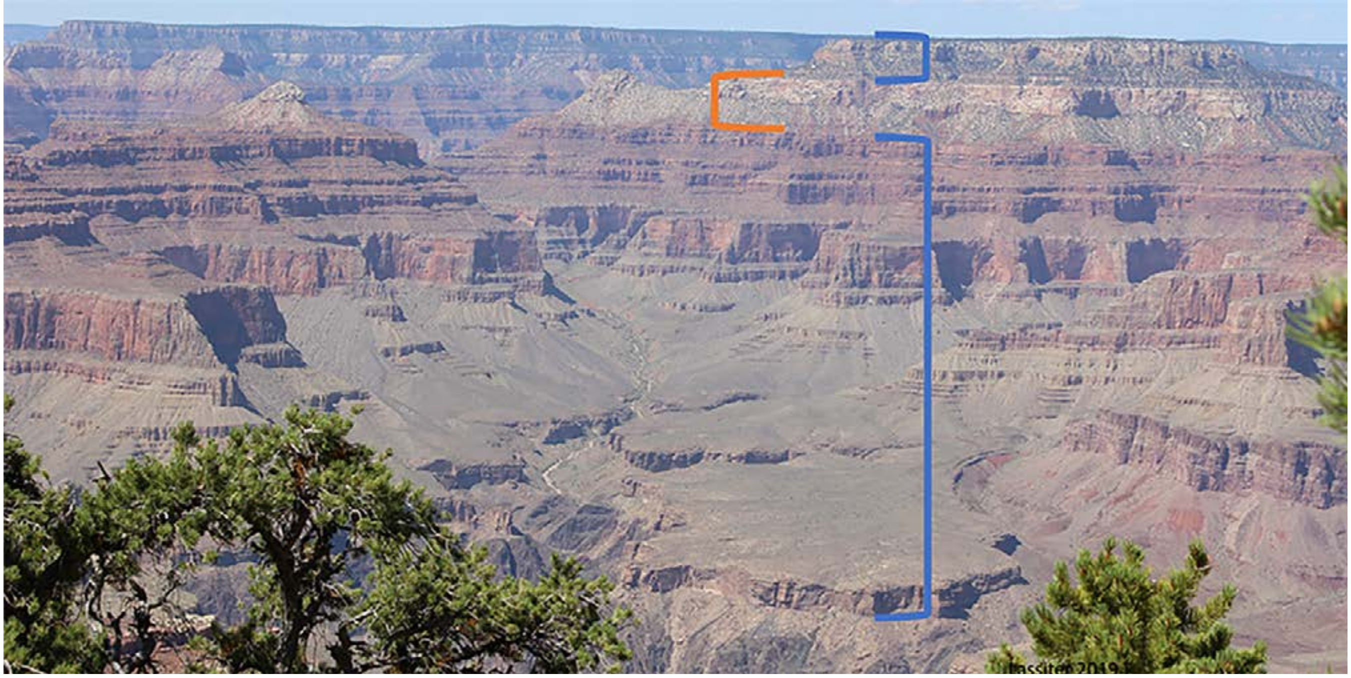

Figure 1. *Grand Canyon view from South Rim Visitors Center with Paleozoic stratigraphic units marked within blue and orange bands. Blue bands delimit mostly marine and fluvial deposits that contain invertebrate body fossils; orange, terrestrial deposits with no invertebrate body fossils (LINDA S. LASSITER).*

Period (252 Ma), but the GRCA geologic strata cover approximately 520–270 My. The GRCA invertebrate fossil record starts in the Cambrian Tonto Group, then is interrupted for 70 My during the Ordovician, Silurian, and Early Devonian periods. This is a significant unconformity and gap in the Paleozoic fossil record at GRCA but should not be confused with the "Great Unconformity" (Elston and others, 1989). The record resumes in the Mississippian and continues with minor pauses into the middle Permian.

The Paleozoic faunal record of GRCA invertebrates offers glimpses of fossil communities important to the identification of fossil assemblages before and after major global extinction events. GRCA Cambrian fossils document assemblages after the early Cambrian (Stage 4) Sinsk Event of about 513 Ma (Zhuravlev and Wood, 2018). Other GRCA assemblages predate (Late Devonian Temple Butte Formation) and postdate (Early Mississippian Redwall Limestone) the Devonian Frasnian–Famennian global extinction event (Raup and Sepkoski, 1982; Bond and Wignall, 2005). Significant fossil assemblages are also recorded at GRCA before the Permian–Triassic mass extinction event (Kaibab Formation).

Even though the significance of the Paleozoic fossil record at GRCA is potentially as vast as the thousands of square kilometers within the park boundaries, a mere fraction of the park has been surveyed for invertebrate body fossils. Due to the rugged terrain of GRCA, most Paleozoic specimens inventoried are reported from near maintained trails, in the most-traveled inner corridor areas, and along the 277 river miles of the Colorado River. There is therefore an enormous untapped reservoir of information at GRCA, especially pertaining to invertebrate body fossils of the Paleozoic Era.

METHODS

More than 7,000 specimens **(appendix A)** and almost 270 species **(appendix B)** have been identified from the literature and museum records of the Grand Canyon National Park Museum (GRCA), Museum of Northern Arizona (MNA), and National Museum of Natural History (USNM). The GRCA museum has more than 5,800 fossil specimens interpreted as Paleozoic invertebrate body fossils, more than 4,600 of which were accessioned before 1980. The MNA has 214 invertebrate specimens known to be from GRCA localities. USNM online listings include more than 500 GRCA invertebrate body fossil specimens, with 42 specimens noted as holotypes. 80 species of Paleozoic invertebrates have been named from fossils found within GRCA **(appendix C)**, and another 11 are based on fossils that may have been found in the park **(appendix D)**. A number of other institutions reposit smaller collections of GRCA fossils, and it was not possible to document them all to the same extent as the GRCA, MNA, and USNM collections. The literature acts as a partial proxy for these institutions; about 590 specimens have been identified from GRCA in the literature.

Localities were assessed as much as possible to verify that only those within park boundaries were included. It is inevitable that some reports have been omitted or overlooked, because of the long history of research, varying standards of locality reporting, and other factors. Conversely, some records that actually came from outside of GRCA may be included. Stratigraphy and taxonomy are also uncertain in some cases.

All taxonomic names have been updated to use currently accepted classifications and genus/species names. The original name in the literature or accession records was checked against several paleontology databases including the Global Biodiversity Information Facility (GBIF at gbif.org), the Paleobiology Database (PBDB at paleobiodb.org), and the World Foraminifera Database (marinespecies.org; Hayward and others, 2019). For additional details of the review process for this report, see the section on taxonomic uncertainty in **appendix A.**

INVERTEBRATE BODY FOSSILS

The Paleozoic history of Grand Canyon is recorded in the lineages of many phyla (table 1), including the Arthropoda (trilobites, bradoriids, and insects), Brachiopoda (inarticulate and articulate brachiopods), Cnidaria (tabulate and rugosa corals), Echinodermata (eocrinoids, crinoids, sea stars, and sea urchins), Mollusca (bivalves, gastropods, cephalopods, and scaphopods), Porifera (sponges and sponge-like animals), Foraminifera (microfossils), and other groups (Problematica) of uncertain taxonomic affinity (*Chancelloria*, Hyolithida, *Margaretia*, *Scenella*, and *Tontoia*). The Paleozoic history of invertebrates at GRCA covers more than 180 million years, 13 named geologic formations, more than 7,000 collected fossils held at numerous repositories, and literature reports of more than 260 taxa.

Early Paleozoic faunas at GRCA are preserved in the Cambrian Tonto Group and are dominated by trilobite arthropods (Trilobita), but also contain phosphatic brachiopods (Linguliformea), calcitic brachiopods (Rhynchonelliformea), bradoriid arthropods (Bradoriida), eocrinoid echinoderms (Eocrinoidea), and the problematic chancelloriids (Chancelloriida) and hyoliths (Hyolithida). After the fossil record hiatus of the Ordovician to Early Devonian, GRCA fossil communities in the middle Paleozoic of the Temple Butte Formation are sparse and rarely identified beyond class, including Trilobita, Rhynchonellata, Anthozoa, Gastropoda, and potentially Stromatoporoidea. The Mississippian (Redwall and Surprise Canyon formations) invertebrates include a diverse assemblage of brachiopods, stenolaemate bryozoans (Bryozoa), echinoderms, rugose and tabulate corals (Anthozoa), and mollusks, primarily bivalves and gastropods but also cephalopods. Additionally, an extensive study of foraminifera has been done for these Carboniferous units (Skipp and others, 1966; Skipp, 1969). The Pennsylvanian stratigraphic units (Supai Group formations of the Watahomigi, Manakacha, and Wescogame) are less fossiliferous due in part to the eolian and shallow water environments of deposition (Blakey, 1990) but do have examples of lingulid, rhynchonellid, and strophomenid brachiopods, bivalves, gastropods, and crinoids. The Permian strata of GRCA includes the Supai Group Esplanade and Coconino Sandstone formations of primarily eolian, wind-driven origin (Blakey, 1990) which lack macroscopic body fossils. The Hermit Formation is better known for flora but has a few noteworthy instances of arthropod insect body fragments and a possible eurypterid (Carpenter, 1927, 1928; White, 1929; Spamer, 1984). With the return of shallow marine environments during the deposition of the Toroweap and Kaibab formations, GRCA invertebrate body fossils include brachiopods, bryozoans,

Table 1. *The number of Paleozoic invertebrate body fossils of GRCA by phylum as reported from the literature or as listed in the museum collections included in this report. Specimens in the collections that are not assigned to a phylum, or are composite blocks of undetermined specimens, comprise the undetermined category.*

Phylum/Period	Cambrian	Devonian	Mississippian to Pennsylvanian	Permian	Total
Arthropoda	1419	2	10	45	1476
Brachiopoda	370	4	951	1062	2387
Bryozoa	0	0	96	113	209
Cnidaria	0	4	144	51	199
Echinodermata	9	0	39	139	187
Foraminifera	0	0	263	3	266
Mollusca	8	1	230	1260	1499
Porifera	7	0	0	40	47
Problematica	70	0	0	0	70
Undetermined	33	29	116	538	716
Total	1916	40	1849	3251	7056

corals, gastropods, bivalves, scaphopods, cephalopods, crinoids, echinoids, sponges, and a few proetid trilobites.

STRATIGRAPHIC DISTRIBUTION OF FOSSILS

The following sections document invertebrate body fossils found from the Paleozoic stratigraphic units of GRCA. Invertebrate body fossils have been confirmed from all Paleozoic formations at GRCA except for the Sixtymile Formation (recently found to be Cambrian in age and placed in the Tonto Group; Karlstrom and others, 2018, 2020), the Frenchman Mountain Dolostone, the Pakoon Limestone, and the Coconino Sandstone.

Cambrian Fauna

The early Paleozoic fossil record at GRCA is represented by the Cambrian Tonto Group, from which many invertebrate body fossils have been reported although Cambrian exposures cover only 13% of the park. The extensive Cambrian fauna of GRCA includes species from the groups Bradoriida, Brachiopoda, Echinodermata, Hyolithida, Porifera, and Trilobita. The Tonto Group includes five named formations (Karlstrom and others, 2020): the Sixtymile Formation, Tapeats Sandstone (Tapeats Formation), Bright Angel Shale (Bright Angel Formation), Muav Limestone (Muav Formation), and Frenchman Mountain Dolostone. No definite invertebrate body fossils have been reported from the Sixtymile Formation and Frenchman Mountain Dolostone at GRCA. Detailed geologic descriptions of the Tonto Group and other Paleozoic units of GRCA are discussed in the contribution by Connors and others of this inventory. However, it is worth noting that the transition between the Tapeats Sandstone and Bright Angel Shale is difficult to distinguish, and for this report, the traditional interpretations and names of the stratigraphic units have been retained.

Tonto Group: Undifferentiated Geologic Unit Fauna

Species from the Tonto Group (Ctu, Cu) that are not assigned to one of the constituent geologic units include asaphid, corynexochid, olenellid, and ptychopariid trilobites, brachiopods of the Kutorginata, Lingulata, Paterinata, Rhynchonellata and Strophomenata, and hyoliths (Hyolitha). The GRCA brachiopods of the Cambrian are dominated by phosphatic types (Linguliformea) that first appeared globally during Series 2 (Stage 3) of the Cambrian (Kouchinsky and others, 2012).

Most arthropods from undifferentiated Cambrian rocks at GRCA are trilobites, represented by several orders. Corynexochids include *Anoria, Athabaskia kanabensis, Glossopleura* (*G. boccar*), *Kootenia* (*K. mckeei*), and *Ptarmigania*. Ptychopariids (figure 2) include *Elrathia, Kochina angustata, Parehmania kwaguntensis, P. nitida, Proehmaniella hebes, Spencella* (*S. diligens*), and *Trachycheilus typicale* (Walcott, 1890, 1916a; Schuchert, 1918a; Noble, 1922; Schenk and Wheeler, 1942; Resser, 1945; Foster, 2011; Bonde and others, 2018). The asaphid *Glyphaspis kwaguntensis* (Resser, 1945) and the corynexocid *Olenoides* (*Olenellus*?) (Walcott, 1890) have also been reported from undifferentiated Cambrian rocks at GRCA. Although there are specimens in the GRCA collections listed as agnostid trilobites, these are considered to be misidentified ptychoparioids as agnostids are more typical of open ocean environments not found at GRCA. Additionally, there are fossils reported as ostracods by Walcott (1890) from the Cambrian Tonto Group, but these are presumably bradoriids.

Brachiopod species listed as from undifferentiated Tonto Group units include representatives from the inarticulate and phosphatic Linguliformea, and articulate calcitic Rhynchonelliformea (Williams and others, 1996). Brachiopods today still have these two kinds of biomineralization in their shells, a trait established during the early Cambrian (Zhuravlev and Wood, 2018). Extant crinoids (Echinodermata), like brachiopods, may be called "Articulata" (Wright and others, 2017), adding confusion to the continued use of this term. Linguliforms (Lingulata) include *Acrothele*, several species of *Lingulella*, and *Lingulepis perattenuatus*. The paterinate linguliform species include *Iphidella pannula*, *Micromitra* (*Paterina*) *crenistria*, and *Iphidea ornatella*. Rhynchonelliforms include the kutorginid *Nisusia* (*N. kanabensis* and *N. obscura*), and protorthid *Protorthis* (Walcott, 1890, 1912a, 1916a; Resser, 1945).

Tonto Group: Tapeats Sandstone Fauna

The Tapeats Sandstone (Ctt) is mapped as covering about 88 km^2 (34 mi^2) or approximately 2% of the Paleozoic units exposed in GRCA (13% of the Tonto Group exposures). The characteristics of the depositional environment and multiple facies of the Tapeats Sandstone yield bioturbated surfaces better known for trace fossils than body fossils (Rose, 2006). Thirteen invertebrate taxa are reported from the Tapeats Sandstone in various sources, primarily museum collections. At least some of these may be mistaken records or from the transition zone with the Bright Angel Shale instead. Arthropods include the redlichiid *Olenellus* (Resser, 1945) and ptychopariid *Spencella*, and the bradoriids *Indianites* (*I. curta*, *I. impressa*) and *Walcottella*. The brachiopods are represented by five species of the lingulate genus *Lingula* (*L. chuarensis*, *L. euglypha*, *L. lineolata*, *L. spatulus*, and *L. zetus*), and two species of paterinate brachiopods, *Iphidella pannula* and *Paterina* (*Iphidea*) *crenistria*. Schuchert (1918a) reported an unidentified obolellid.

Figure 2. *Cambrian trilobite fragments of* Solenopleurella porcata *(USNM 108626; now* Spencella porcata *Rasetti, 1963) from undifferentiated Tonto Group, possibly the Muav Limestone. Scale bar 1 cm (0.4 in) (NPS/ANNE MILLER).*

Tonto Group: Bright Angel Shale Fauna

The Bright Angel Shale (Ctba) produces proportionately more fossils per area in the Tonto Group and covers 5% of the GRCA geologic area (33% of the Tonto Group), about 266 km^2 (103 mi^2). This unit has locally abundant corynexochid and ptychopariid trilobites (Foster, 2011) and chitinophosphatic brachiopods. As many as 59 species of fossil invertebrates have been named from the Bright Angel Shale of GRCA **(appendix C)**, although not all of them are currently considered valid. These 59 taxa include 23 bradoriids, 22 trilobites, 13 brachiopods, and the eocrinoid *Eocrinus multibrachiatus* (now classified in *Gogia*). The bradoriids were collected from only two localities within the park boundaries and include species from the genera *Dielymella*, *Indiana*, and *Walcottella* (Ulrich and Bassler, 1931). The named trilobites from GRCA are in the genera *Acrocephalops*, *Albertella*, *Alokistocare* (=*Amecephalus*), *Anoria*, *Ehmaniella*, *Elrathia*, *Glossopleura*, *Glyphaspis*, *Kootenia*, *Pachyaspis*, *Parehmania*, *Proehmaniella*, and *Spencia* (Walcott, 1916a, 1916b; Resser, 1945). The brachiopods named from GRCA are in the genera *Billingsella*, *Dictyonina*, *Iphidea*, *Lingulella*, *Nisusia*, and *Paterina* (Walcott, 1897, 1898, 1902, 1905; Resser, 1945).

Arthropoda: Trilobite specimens collected from GRCA are abundant but are often only fragments of the exoskeleton (figure 3). GRCA fossil records capture some of the diversity of Cambrian trilobite assemblages (Schenk and Wheeler, 1942; Resser, 1945; Foster, 2011). Trilobite genus and species taxonomy, and family-level assignments, are frequently revised. For example, ptychopariid trilobites of the genus *Amecephalus* (figure 4A) are taxonomically listed as kochaspids (Sundberg, 2004).

Olenellid trilobites (Redlichiida: Olenellidae) have been found in the western portion of the Grand Canyon in the transition zone between the Tapeats Sandstone and Bright Angel Formation and within the Bright Angel Formation (Schenk and Wheeler, 1942; Resser, 1945). The olenellids are the earliest trilobites reported from GRCA in what is sometimes called the *Olenellus–Antagmus* horizon (McKee and Resser, 1945).

Ptychopariid (Ptychopariida) trilobites differ from olenellids by possessing librigenae sutures, fewer thorax segments, and a distinct, but sometimes small pygidium (micropygous to subisopygous). Overall, ptychopariids are smaller than olenellids, particularly in the early Cambrian. A common ptychopariid of the Bright Angel Shale is *Amecephalus althea* (figure 5B). Other ptychopariids in this unit are from the genera *Alokistocare* (*A. lepida*), *Antagmus* (*A. arizonaensis*), *Bolaspis* (*B. aemula*), *Ehmaniella*, *Elrathia* (*E. nitens*), *Elrathiella* (*E. decora*), *Kochina*, *Pachyaspis*, *Parehmania* (*P. kwaguntensis*, *P. tontoensis*), *Proehmaniella* (*P. basilica*), *Spencella* (*S. porcata*), and *Spencia* (*S. tontoensis*) (Walcott, 1916a, 1916b; Schuchert, 1918a; Noble, 1922; Schenk and

Figure 3. *Trilobite fragments including olenellid genal spines of unidentified species, and a probable ptychopariid pygidium boxed in red from the Cambrian Bright Angel Shale (GRCA 6598). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

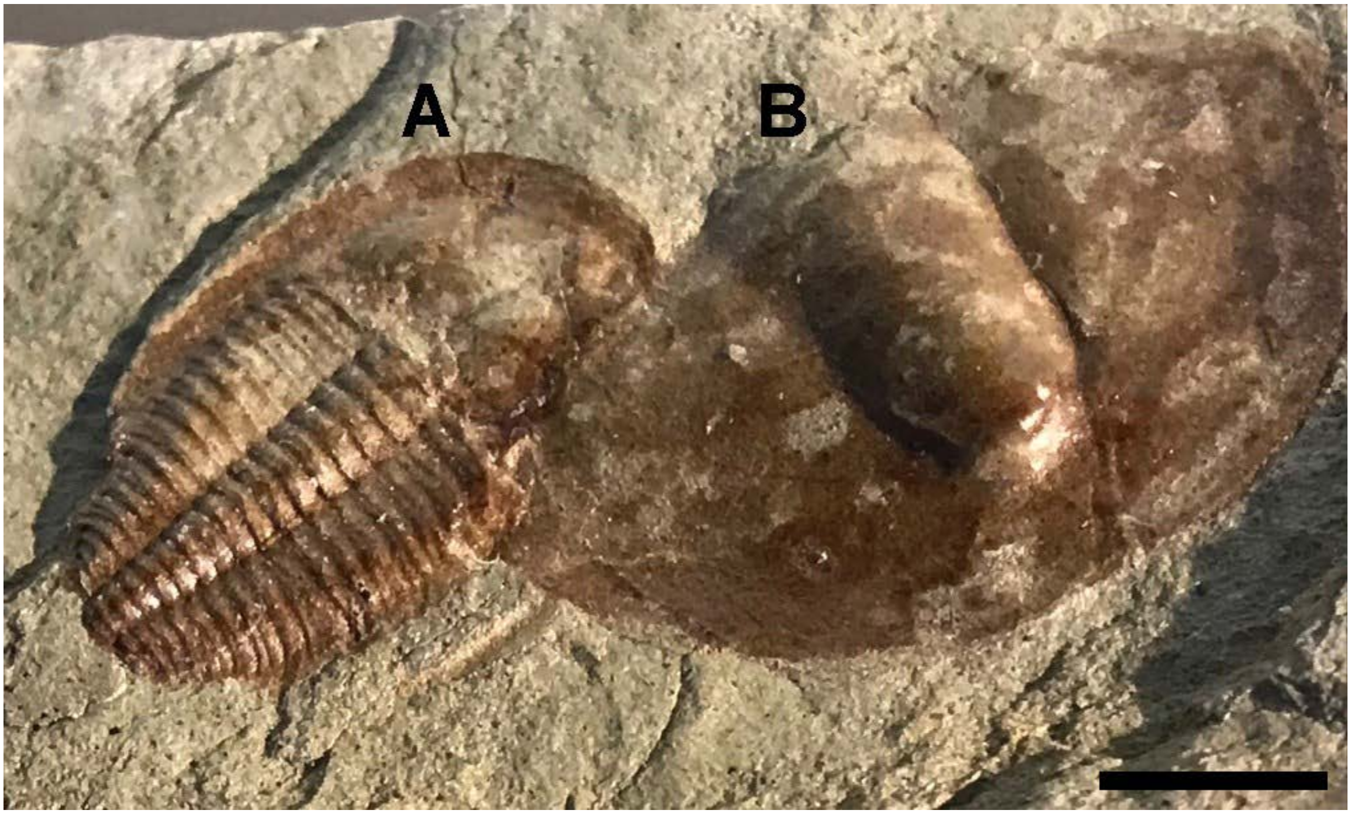

Figure 4. *The Cambrian trilobites (GRCA 9529)* Amecephalus althea ***A.*** *and a dolichometopid* ***B.*** *from the Bright Angel Shale. Scale bar 1 cm (0.4 in) (JOHN FOSTER).*

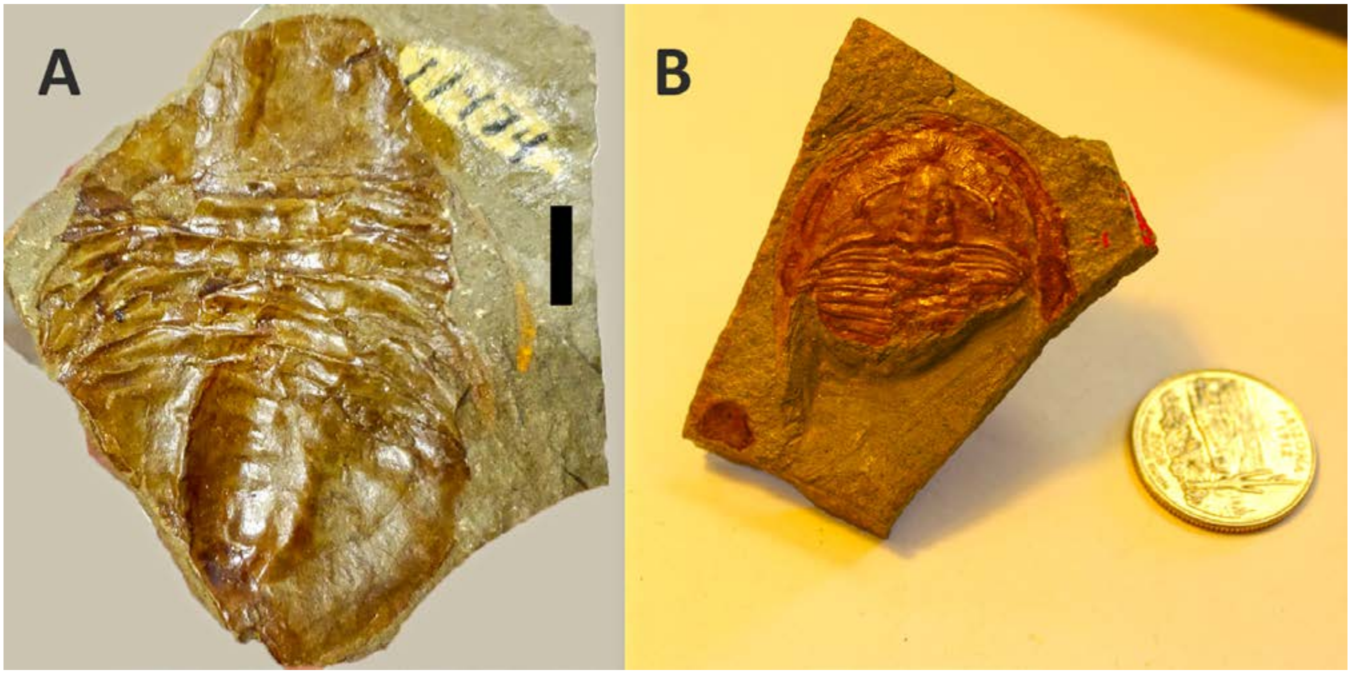

Figure 5. *Examples of common, well-preserved Bright Angel Shale ptychopariid trilobites.* ***A.*** Anoria tontoensis *(GRCA 11474) (LINDA S. LASSITER) with 1 cm (0.4 in) scale bar.* ***B.*** Amecephalus althea *(GRCA 11612) (LINDA S. LASSITER) with quarter (diameter 24.26 mm or 0.955 in).*

Wheeler, 1942; McKee and Resser, 1945; Resser, 1945; Bonde and others, 2018).

Bright Angel Shale corynexochids are the most abundant trilobites of GRCA with more than 530 specimens in the GRCA museum collections (versus 221 specimens of ptychopariids). Corynexochid trilobites are represented at GRCA most commonly by the genera *Anoria* (*A. tontoensis* of figure 5A), and *Glossopleura* (*G. boccar*, *G. mckeei*, *G. meriwitica*, *G. productus*) (Walcott, 1916a; Schuchert, 1918a; Noble, 1922; Schenk and Wheeler, 1942; Resser, 1945). Other trilobite genera of this order from GRCA include *Albertella* (*A. schenki*), *Kootenia* (*K. schenki*, *K. simplex*), *Olenoides*, *Prozacanthoides*, *Ptarmigania*, and *Zacanthoides* (Schenk and Wheeler, 1942; Resser, 1945; Bonde and others, 2018).

Another group of arthropods that are common in the Bright Angel Shale are the bradoriids. Bradoriids are extinct bivalved, phosphatic arthropods generally less than 20 mm (0.8 in) long and appear morphologically similar to the calcitic ostracods (figure 6). Bradoriids can be quite common in some locations in the Bright Angel Shale. Recent phylogenetic analyses of all arthropods now place bradoriids as a basal member of the Euarthropoda, distinct from sister clades of the trilobites, chelicerates, and the derived clade of Mandibulata (Legg and others, 2013). However, some databases still place bradoriids in the class Ostracoda (GBIF) or resolved as a basal arthropod clade (PBDB).

Figure 6. *Bradoriids from the Bright Angel Shale of GRCA. Scale bar 1 cm (0.4 in) (JOHN FOSTER).*

Bradoriids have been described globally only from the Cambrian (Topper and others, 2011) and on the surface appear to have been highly endemic in eastern GRCA. Nearly two dozen bradoriid species have been named and described from the Bright Angel Shale of eastern GRCA by Ulrich and Bassler (1931) **(appendix C)**. It would not be surprising if this figure is inflated by over-splitting. Fitting the GRCA bradoriids into the biogeography and distributions of other Cambrian faunal assemblages might be useful as bradoriids became common worldwide before trilobites (Hou and others, 2010). GRCA bradoriids have been assigned to the genera *Bradoria*, *Dielasma*, *Indianites*, and *Walcottella* (Ulrich and Bassler, 1931; Resser, 1945); species are listed in **appendix tables A-1** and **B-1**.

Brachiopoda: Bright Angel Shale brachiopods from GRCA include phosphatic linguliform lingulids and paterinids, and examples of several orders of calcitic forms **(appendix tables A-1** and **B-1)**. The similarity in size and chitinophosphatic composition make linguliform brachiopods easily confused with bradoriids in Cambrian stratigraphic units. Lingulid specimens are from *Acrotreta*, *Lingulella*, and *Lingula* (Frech, 1893; Walcott, 1898, 1902, 1912a, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1945). Paterinids represented in the Bright Angel Shale include *Dictyonina*, *Iphidella*, *Micromitra*, and *Paterina* (Walcott, 1897, 1912a, 1916a; Noble, 1922; Resser, 1945).

Calcitic-valved brachiopods of the Bright Angel Shale include obolellides, kutorginates (*Nisusia*), the rhynchonellid orthid *Wimanella*, an unidentified thecideid (*Diraphora*?), and the strophomenid *Billingsella* (Frech, 1893; Schenk and Wheeler, 1942; Resser, 1945). Obolellides, such as *Obolella*, have oval, biconvex valves and a minute foramen opening at the tip of the pedicle valve. Kutorginates of the genus *Nisusia* have a strophic hinge, a prominent, extended, curved beak over the interarea and can reach lengths of 1 to 2 cm (0.4 to 0.8 in). The only species of *Nisusia* from GRCA identified to a specific unit is *Nisusia noblei* from the Bright Angel Shale (Walcott, 1924; Resser, 1945). The orthid *Wimanella* is only about 4 mm (0.2 in) wide, can be poorly preserved and difficult to identify (figure 7). Three specimens from the GRCA collections of the Bright Angel Shale have been incorrectly assigned to the genus *Composita*, which has no fossil record before the Devonian (Grinnell and Andrews, 1964). Therefore, these specimens require reidentification; it is probable that they are orthids.

The strophomenids *Billingsella* (Bright Angel Shale) and *Clitambonites* (Muav Limestone) are small brachiopods less than 2 cm (0.8 in) wide with strophic hinge lines and calcitic valves. *Billingsella* is unique in possessing features that are associated with both strophomenids and orthids as a basal configuration, which could warrant placement in a distinct clade (Congreve and others, 2015).

Echinodermata: Eocrinoids (Eocrinoidea), a type of early stalked echinoderm, are reported from the Bright Angel Shale of GRCA (Kirk, 1945; Robison, 1965; Sprinkle, 1973). *Eocrinus multibrachiatus*, named from a GRCA specimen in Kirk (1945), is now assigned to the genus *Gogia* **(appendix C)**. *Gogia longidactylus* (GRCA 2641) is also known from Bright Angel Shale (figure 8) and was illustrated in Sprinkle (1973). An undetermined cystoid (GRCA 2479) has been identified as a rhombiferid but has not been re-examined. An ascocystitid, *Eocystites*, was reported from this unit by Walcott (1916a) and Noble (1922), but the fossil was not in the collections surveyed for this report.

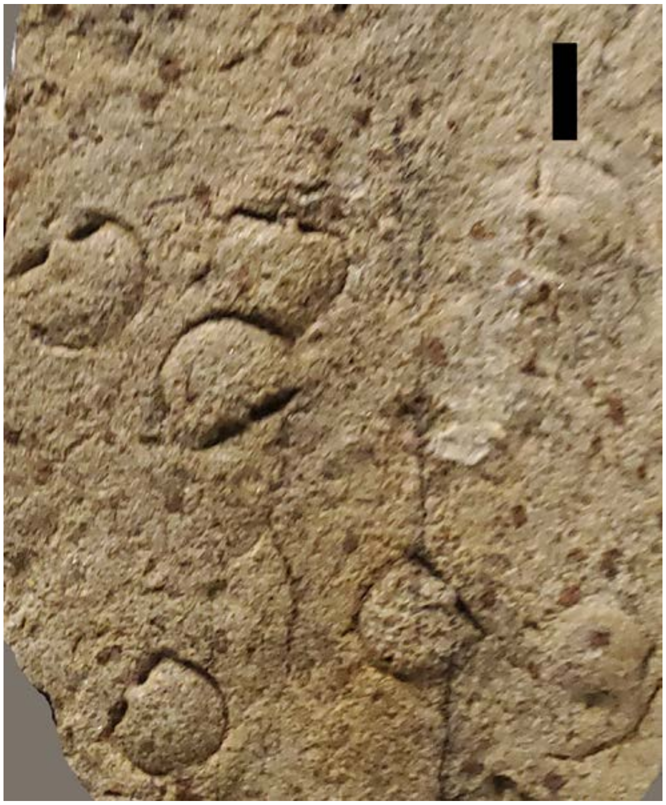

Figure 7. *The phosphatic orthid brachiopod* Wimanella *(GRCA 8423) preserved mostly as outlines of the valves in a slab from the Bright Angel Shale. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Figure 8. *An eocrinoid,* Gogia longidactylus *(GRCA 2641), from the Bright Angel Shale. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Mollusca: Several Bright Angel Shale specimens in GRCA collections are identified to the molluscan classes Bivalvia (four specimens) and Gastropoda (three). Given the rarity of Cambrian mollusks in general, it is likely that these are misidentified.

Porifera: Three specimens (GRCA 2532, 2533, and 2537) are listed doubtfully as the archaeocyathid *Ethmophyllum chankensis*. However, archaeocyathids are not known later than the early Cambrian Series 3 (Lee and others, 2016) and other Bright Angel Shale fossils indicate a middle Cambrian age. If these fossils are confirmed as archaeocyaths, they would be among the youngest reported archaeocyathids in the world. Archaeocyaths were also reported in Resser (1945). There are a few other sponges listed but not identified at the GRCA museum.

Incertae Sedis: Several specimens of uncertain classification are reported from the Bright Angel Shale at GRCA. One (USNM 57660) is the holotype of *Tontoia kwaguntensis* (figure 9), reported as a possible trilobite by Walcott (1912b). *Margaretia*, a stalked organism sometimes misspelled *Margaritia*, was described from the Burgess Shale as a fossil of algal or hemichordate affinities and is also reported from the Bright Angel Shale of GRCA (Schenk and Wheeler, 1942). *Margaretia* specimens are listed in the GRCA collections with one specimen noted as having "thin fronds" or as possibly dolichometopid trilobite fragments (GRCA 598, 605, 609, and 630). *Margaretia* is a genus used for algae, but the Burgess Shale specimens have recently interpreted as the tube enclosure of a hemichordate (Nanglu and others, 2016). This organism is of uncertain affinity and only listed in this invertebrate body fossil summary as a placeholder until taxonomic placement is resolved.

Chancelloria (several GRCA and MNA specimens) is a sponge-like animal of uncertain affinity (Elliott and Martin, 1987), described as calcareous spicules of a sponge by Walcott (1920). It is interpreted as a sack-shaped animal with a spicular body (Elliott and Martin, 1987). This animal is now considered to be related to *Wiwaxia* and halkieriids (Bengtson and Collins, 2015) although it is incertae sedis at the phylum level. *Chancelloria* is associated with the class Coeloscleritophora (Elliott and Martin, 1987). The spicules or sclerites from the Bright Angel Shale have a ring of five spines that are about 0.5 to 6.0 mm (0.02 to 0.2 in) in length with short central spines of 0.5 to 1 mm (0.02 to 0.04 in) length (Elliott and Martin, 1987). The shapes of the hollow sclerites are interpreted as similar to, but distinct from, those of *Chancelloria pentacta*, not found at GRCA.

There are 38 specimens of hyoliths (figure 10) in the collections at GRCA museum, all identified as *Hyolithes* sp. Hyoliths are an extinct group of animals with shells composed of aragonite. Their classification has long been debated, as *incertae sedis*, in their own phylum (Hyolitha), a class within Mollusca, or most recently as an ancestral lophophorate (Moysiuk and Caron, 2017). Hyoliths from GRCA (figure 10) are listed as in the genus *Hyolithes*. The specimens at GRCA superficially resemble the Burgess Shale and Spence Shale hyolith *Haplophrentis* (Babcock and Robison, 1988) and may belong to that genus. Most of the time, these fossils are found disarticulated and the operculum may be mistaken for an inarticulate brachiopod.

Figure 9. *An illustration of* Tontoia kwaguntensis *(USNM 57660), which is described as a 25 mm (1 in) long animal of trilobite or other arthropod affinity (Walcott, 1912b: plate 24).*

Figure 10. *Two hyoliths from the Bright Angel Shale (GRCA numbers uncertain). The hyolith on the right retains the operculum cap. Scale bar 1 cm (0.4 in) and U.S. quarter (diameter 24.26 mm or 0.955 in) (LINDA S. LASSITER).*

Tonto Group: Muav Limestone Fauna

Outcrops of the Muav Limestone (Ctm) in GRCA represent the largest area of the Tonto Group (40%) and about 6% of the park (300 km^2 or 116 mi^2). However, the invertebrate body fossil assemblage is not as diverse as that found in the Bright Angel Shale. As with the other Tonto Group members, the Muav Limestone is trilobite-dominated with ptychopariid and corynexochid species. There are also several enigmatic fossils from the Muav Limestone including hyoliths, the single-shelled mollusk *Helcionella*, and *Scenella hermitensis*, which is named from GRCA (Resser, 1945). The hyoliths are discussed in more detail in the Bright Angel Shale section.

Seven fossil invertebrate taxa have been named from specimens found in the Muav Limestone of GRCA, with another 12 to 14 collected either from the Bright Angel Shale or Muav Limestone (appendix C). Those definitely from the Muav Limestone include *Scenella hermitensis*, the trilobite species *Bolaspis aemula*, *Glyphaspis tecta*, *Kootenia schenki*, *Spencella erosa*, and *S. porcata* (Resser, 1945), and the brachiopod *Nisusia noblei* (Walcott, 1924). Trilobites of the Muav Limestone may be attributed to similar assemblage zones as those in the Bright Angel Shale (Stage 5, Series 3), although this is still under current study.

Arthropoda: Identified trilobites of the Muav Limestone include the corynexochid genera *Anoria*, *Athabaskia*, *Dorypyge*, *Glossopleura*, *Kootenia*, *Neolenus*, and *Zacanthoides*; the asaphid *Glyphaspis*; and the ptychopariids *Alokistocare*, *Anomocarella*, *Bolaspis*, *Pachyaspis*, *Parehmania*, *Saukia*, and *Spencella* (Noble, 1922; Stoyanow, 1936; Schenk and Wheeler, 1942; Resser, 1945). Specimens identified to the species level include *Bolaspis aemula*, *Glossopleura meriwitica*, *Glyphaspis kwaguntensis*, *G. tecta*, *G. vulsa*, *Kootenia havasuensis*, *K. mckeei*, *K. schenki*, *K. simplex*, *Pachyaspis moorei*, *Parehmania kwaguntensis*, *Spencella porcata*, and *S. erosa* (Schenk and Wheeler, 1942; Resser, 1945). There are more than 60 unidentified or tentatively identified specimens of trilobites in the GRCA museum collections, including some identified tentatively as *Elrathiella*.

Brachiopoda: The strophomenid *Clitambonites* is found in the Muav Limestone (Noble, 1922). The kutorginates are of the same diversity as in the Bright Angel Shale (*Nisusia*). Other Muav Limestone brachiopods are chintophosphatic forms in the genera *Dictyonina*, *Discina*, *Lingula*, *Lingulella* (*Lingulepis*), *Trematis*, and possibly *Acrotreta* (Walcott, 1883, 1890; Noble, 1922; Resser, 1945). *Syntrophia* was identified by Noble (1922) but is typically found in Lower Ordovician to Silurian rocks which are missing from GRCA.

Echinodermata: Three undetermined cystoids (GRCA 2174, 11842, 11843) have been cataloged from the Muav Limestone in the GRCA museum collections but are doubtful in their identification and were excluded from the final listing **(appendix A)**. Although James Sprinkle (UT-Austin) has interpreted one as surface impressions likely from a set of burrows, the other specimens have yet to be re-examined.

Mollusca: Helcionelloida is a class of snail-like mollusks that appeared in the Cambrian and went extinct in the Ordovician. *Helcionella* has been informally identified from the Muav Limestone (A. Palmer, USGS, written comm. to M. B. Ingham, 1963). The specimen from the Muav Limestone of GRCA is held at Lake Mead NRA (LAKE 2243), having been collected from a part of GRCA once within the recreation area.

Porifera: Resser (1945) indicated the presence of archaeocyathids in the Muav Limestone. However, these have most likely been misidentified.

Incertae Sedis: *Hyolithes* is reported from the Muav Limestone (Resser, 1945) and in the collections at GRCA. Additionally, the Muav also has an unusual invertebrate fossil named *Scenella* (Resser, 1945). First reported as a gastropod and classified in current databases (PBDB) as a monoplacophoran mollusk, *Scenella* is a simple, cap-shaped shell that resembles the modern limpet. *Scenella* from GRCA is generally 1 to 1.5 cm (0.4 to 0.6 in) long, oval in outline, and composed of either calcium phosphate or calcium carbonate. So far, it has only been reported from the Muav Limestone at GRCA (*Scenella hermitensis*, MNA 1640 and USNM 108568a, named in Resser, 1945). Re-interpretations of similar shaped objects from other Cambrian localities have suggested that *Scenella* is an internal float device used by soft-bodied cnidarias (hydrozoans) (Yochelson and Cid, 1984). *Chancelloria* may also be found in the Muav Limestone as mentioned by Schenk and Wheeler (1942) and Resser (1945).

Devonian Fauna

Temple Butte Formation Fauna

Two percent of the park has been marked as exposures of the Devonian Temple Butte Formation (Dtb) (95 km^2 or 37 mi^2), which is limestone or more commonly dolomitized (Rowland and others, 1995). This formation can be found as isolated channel-fills cut into the underlying Muav Limestone with many larger exposures of limestone and dolostone in the western GRCA (Beus, 1990). The Temple Butte Formation has probably not been sufficiently surveyed for fossils as reflected in the sparse number of specimens in the collections at the GRCA museum. Out of more than 7,000 Paleozoic invertebrate body fossils in GRCA collections, only about 40 are from the Temple Butte Formation and 30 of those are not even identified to phylum **(appendix table A-2)**. A few fossils, one brachiopod and one coral, are reported from locations of uncertain Devonian or Mississippian age from the literature (Beus, 1990) that are believed to be from the Temple Butte Formation. Beus (1990) also noted the presence of possible stromatoporoids, but no further information on locality or current location is known. Otherwise, unidentified specimens of the Temple Butte Formation include a few rugose corals, gastropods, crinoids, and brachiopods (Beus, 1990) but none are identified beyond genus level.

Arthropoda: There are unidentified trilobites associated with the Temple Butte Formation (GRCA 2668, 2669) that appear to be similar to *Elrathia*.

Brachiopoda: Spiriferids are the only named group of brachiopods reported from the Temple Butte Formation and are only identified as *Spirifer* sp. in the GRCA museum collections. Other unidentified brachiopods are mentioned in Walcott (1883) and Stoyanow (1936).

Cnidaria: Corals first appear in GRCA in the Temple Butte Formation. Only three specimens assigned to the order Stauriida have been identified from the literature (Walcott, 1883; Noble, 1922; Schenk and Wheeler, 1942). One has been identified as *Streptelasma* sp. (Schenk and Wheeler, 1942) but the location data is uncertain, and it may not have been within the current park boundaries.

Mollusca: One unidentified gastropod was mentioned by Walcott (1883) as being from unnamed Devonian rocks and is presumably from the Temple Butte Formation.

Mississippian Fauna

Mississippian units at GRCA include the Redwall Limestone and Surprise Canyon Formation (McKee and Gutschick, 1969a; Beus, 1990), which are thickest in western GRCA. These units cover deposition from the Early Mississippian (Kinderhookian, 360–355 Ma) in western GRCA to Late Mississippian (Chesterian) (McKee and Gutschick, 1969b). These strata have had significant studies of the microfossil Foraminifera and macroscopic invertebrate body fossils.

Redwall Limestone Fauna

The Mississippian-age Redwall Limestone (Mr) has exposures covering about 7% or 342 km^2 (132 mi^2) of the park but has produced about 20% of the specimens from the Paleozoic units of GRCA. There are four members present at GRCA, in ascending order the Whitmore Wash, Thunder Springs, Mooney Falls, and Horseshoe Mesa members (McKee, 1963). The oldest member dates to the Early Mississippian (late Kinderhookian, equivalent to the middle Tournaisian), and the youngest, as Middle Mississippian (middle Meramecian, equivalent to the middle Visean) (McKee and Gutschick, 1969b). The Redwall Limestone records two marine transgression-regression cycles, one in the Whitmore Wash to Thunder Springs members, and one in the Mooney Falls to Horseshoe Mesa members (Beus, 1989). These cycles created an intermittent shallow sea (Beus, 2003) reflected in variations of the limestone that indicate changes in water depths and energy levels (McKee and Gutschick, 1969c).

The Redwall Limestone faunal assemblages are dominated by rhynchonellid and strophomenid brachiopods. Besides the brachiopods, other invertebrate fossils include rugose and tabulate corals, bivalve and gastropod mollusks, and fenestrate and branching bryozoans. There are also a few trilobites, blastoids, and crinoids (chapters in McKee and Gutschick, 1969a). A large study of foraminifera identified more than 360 specimens from the Redwall Limestone (Skipp and others, 1966; Skipp, 1969).

Arthropoda: Trilobite presence is limited in the middle Paleozoic and this reduction in diversity and abundance is noted at GRCA with only a few species in the Redwall Limestone. Trilobites include the proetids *Aprathia, Breviphillipsia* and *Phillipsia peroccidens* (identified as *P. tuberculata* in GRCA collections; GRCA 9994) (McKee and Gutschick, 1969d, 1969f; Cisne, 1971; Brezinski, 2017).

Brachiopoda: Most brachiopods of the Redwall Limestone are spiriferids (Rhynchonellata: Spiriferida) although by this time the orthotetids (Strophomenata) like *Derbyia* have also become common (figure 11; **appendix tables A-2** and **B-2**). Carter and others (2014) reported a number of brachiopod taxa from the Redwall Limestone of Arizona, based on specimens originally to have been described for McKee and Gutschick (1969a). Few of the studied specimens came from within GRCA itself, but it is likely that the taxa can also be found in the park.

Spiriferids represent more than 90% of Rhynchonellata specimens and the most frequently reported taxon is *Spirifer* sp. Rhynchonellata brachiopods besides the Spiriferida include representatives from the orders Athyridida, Orthida, Rhynchonellida, Spiriferinida, and Terebratulida (Frech, 1893; Schuchert, 1918b; Noble, 1922; McKee and Gutschick, 1969d; Carter and others, 2014; Bonde and others, 2018). Most reported taxa are only identified to the genus level **(appendix tables A-2** and **B-2)** (Noble, 1922; McKee and Gutschick, 1969d; Carter and others, 2014). This may be indicative of the poor preservation observed for most of the Redwall Limestone specimens, or relatively little study of the collections.

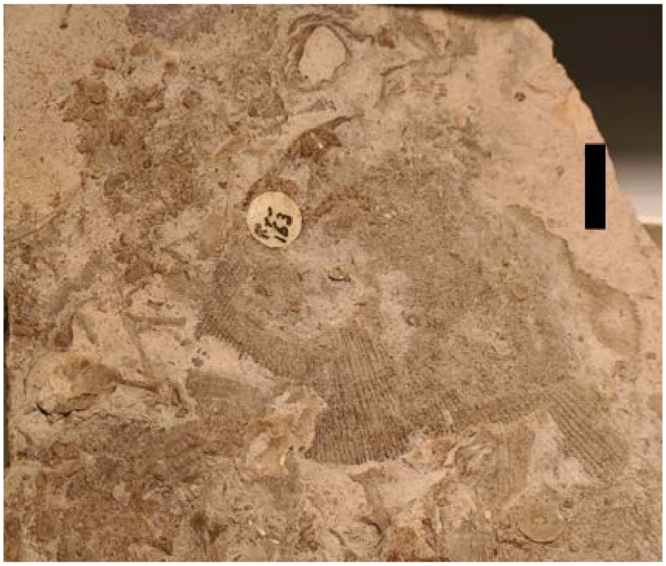

Figure 11. *An unidentified brachiopod with fine costae like the common* Derbyia *(Strophomenata: Orthotetida) on a fossiliferous slab from the Redwall Limestone (GRCA 11065). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Of the 255 specimens of Strophomenata listed in the GRCA museum collections from the Redwall Limestone, 229 are identified as the orthid *Derbyia* sp. Aside from orthotetids, productids and strophomenids are also represented but in small numbers.

Bryozoa: Most bryozoans from the Redwall Limestone are fenestrate (Fenestrata and Fenestrida) or cystoporids (Cystoporida). Although there are several trepostome specimens at USNM reported from the Mooney Falls Member of the Redwall Limestone (Duncan, 1969), none have been identified beyond order (Trepostomatida). Generally, bryozoans are fragmentary and molds with the best specimens are found in the oolitic limestone of the Mooney Falls Member (McKee and Gutschick, 1969d). Encrusting, ramose, fenestrate, and branching bryozoan forms have been reported from GRCA, although most are not otherwise identified (Schuchert, 1918b; McKee and Gutschick, 1969d). Duncan (1969) did extensive work documenting the Redwall Limestone bryozoan assemblages and provides a helpful resource.

Fossil specimens of the Fenestrata include the genera *Fenestralia*, *Lyroporella*, *Neoreteporina*, and *Polyporella* (Duncan, 1969; McKee and Gutschick, 1969d). The Fenestrida from GRCA include *Fenestella* (*F. compressa, F. serratula*), *Penniretepora*, and *Polypora* (Schuchert, 1918b; Duncan, 1969; McKee and Gutschick, 1969d). These are net-like, or lacy, zooaria with openings, or fenestrules, between the longitudinal sections of the overall colony form. The genera are distinguished by the shapes of the fenestrules between sections or by the position and numbers of the zooecium. For example, the genus *Polypora* (Fenestrida) has three to eight rows of autopore apertures on only one side (obverse) of the zoarium, and fenestrules are long and sometimes oval (Miller, 1963). *Polypora* is helpful for stratigraphic correlation. It is rare in the Redwall but is also found in the Kaibab Formation. *Fenestralia* (Fenestrata) is found throughout the Redwall Limestone and has four zooecia per row that are divided by a keel into two rows on one side, and fenestrules are oval to rectangular (Burckle, 1960). Most commonly, bryozoans are preserved so that the only visible diagnostic feature is the spacing and distribution of the fenestrules as the obverse side with zooecia not exposed (Duncan, 1969). *Neoreteporina* is only reported from the Thunder Springs Member.

Cystoporids are found in the Redwall Limestone including *Cheilotrypa*, *Coscinotrypa*, *Dichotrypa*, and *Ramiporalia* (Duncan, 1969; McKee and Gutschick, 1969d). A distinctive middle Paleozoic bryozoan from GRCA is *Cystodictya*, which has lunaria in bifoliate colonies that may appear leaf-shaped when well-preserved.

Cnidaria: Redwall Limestone corals have been reviewed in detail in Sando (1969) and the GRCA fossils can be compared to specimens outside of GRCA (Sando and Bamber, 1985). Tabulate corals are more diverse and abundant in the Redwall Limestone than other geologic units at GRCA, although many specimens are difficult to identify (figure 12). There are specimens from the auloporids *Syringopora* (*S. aculeata*, *S. surcularia*), and *Cladochonus* (*Monilipora* of Noble, 1922) (Schuchert, 1918b; Noble, 1922; Sando, 1969; Sando and Bamber, 1985; Bonde and others, 2018). *Syringopora* (figure 13) has cylindrical tubes in irregular patterns with transverse connections at random locations. If the top is visible, these corals do not form the appearance of a chain but appear as masses of circular openings. Other tabulate forms include another Redwall Limestone species that may form small branches or look similar to *Syringopora* as a massive coral with conical tubes with thick, dividing walls and a classic “honeycomb” appearance on the surface. Favositid corals are represented in the GRCA collections (*Cladopora*).

Rugose corals were more abundant than tabulates during the Mississippian and this is also reflected in GRCA fossil distributions. Solitary rugose corals are easily identified by their curved, ceratoid or horn-shape structure. In both individual and colonial rugosa, each polyp forms septa that radiate from the peripheral outer edge in towards the central axis. The rugose (Stauriida) coral *Vesiculophyllum incrassatum* is the most frequently reported coral from this unit (Easton and Gutschick, 1953; McKee and Gutschick, 1969d; Sando, 1969; Bonde and others, 2018), but several other taxa are present in the Redwall of GRCA as well **(appendix tables A-2** and **B-2)**.

Echinodermata: Crinoid columnals are common but have limited diagnostic features for classification. In general, columnals are not usually diagnostic to genus or species, so it is usually not possible to classify isolated columnals. This helps to explain why nearly all crinoid specimens are only defined to the class level (Crinoidea). The blastoid *Pentremites* has been reported from the Redwall Limestone at GRCA (Macurda, 1969); see the more detailed description in the Surprise Canyon Formation section.

Mollusca: Mollusks reported from the Redwall Limestone at GRCA include gastropods and a single cephalopod, *Rayonnoceras* (Breed, 1969). A few specimens of bivalves have also been reported from the Redwall Limestone and are in GRCA collections, but were collected from localities outside of GRCA.

Many river guide texts refer to the nautiloid fossils found in abundance at Nautiloid Canyon in outcrops of the Whitmore Wash Member of the Redwall Limestone. At Nautiloid Canyon, the erosion surfaces create a false appearance of tentacles on the fossils (Billingsley and Breed, 1976). They are attributed to *Rayonnoceras* sp.,

Figure 12. *A coral from the Redwall Limestone of GRCA (GRCA 4470) with poor preservation for clear diagnosis beyond phylum. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Figure 13. *Tabulate phaceloid coral (*Syringopora *sp.) from the Redwall Limestone of GRCA showing a massive form with individual corallites (GRCA 11055). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

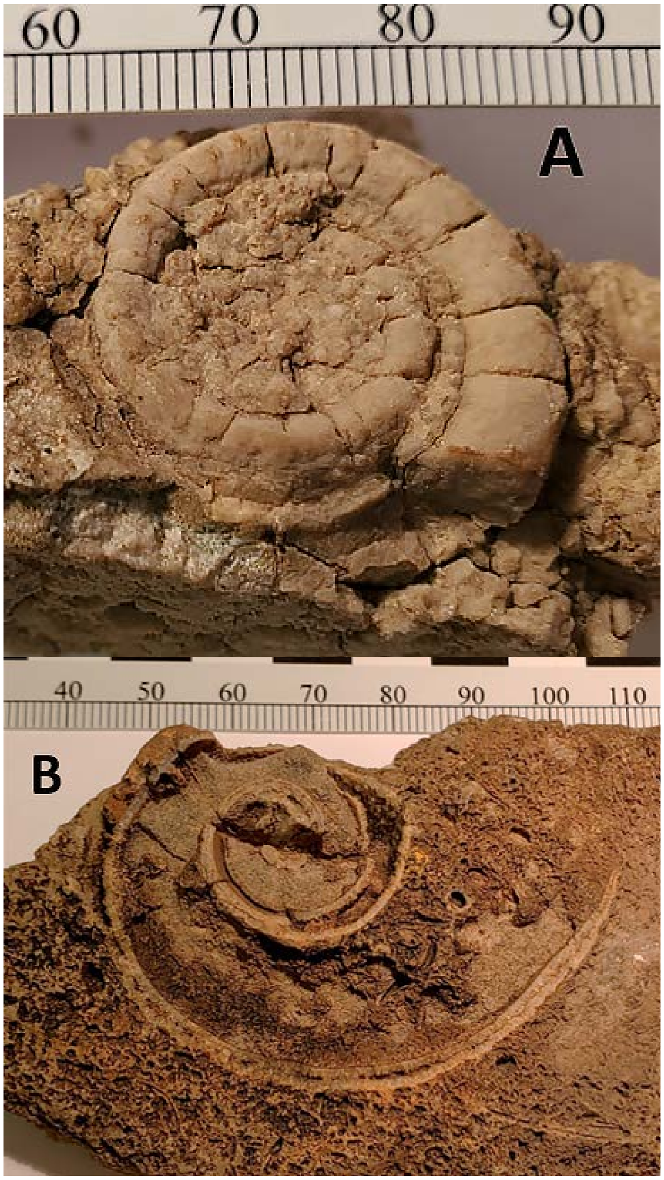

Figure 14. *Gastropods showing poor preservation common in fossils from the Redwall Limestone of the families Euomphalidae (GRCA 7641)* ***A.*** *and Bellerophontidae (GRCA 7628)* ***B.*** *Ruler scale in millimeters (LINDA S. LASSITER).*

a longiconic orthocone (Breed, 1969; Billingsley and Breed, 1976). An undetermined coiled nautiloid was also briefly noted by Billingsley and Breed (1976).

Gastropods in the Redwall Limestone are often fragmented, worn, or may only be internal molds (steinkerns) (figure 14), making species-level identification difficult (Yochelson, 1969). Genera of the Euomphalina (figure 14A) and Bellerophontida (figure 14B) orders are the most common. Euomphalids at GRCA in the Redwall include the genera *Euomphalus*, *Platyceras*, and *Straparollus* (Noble, 1922; Yochelson, 1969). *Euomphalus* has a slight raised edge or shoulder or carinae on the whorls. *Platyceras* is a common gastropod of the middle Paleozoic with an asymmetrical spire and whorls that may not contact in later growth (evolute). *Straparollus* is similar to *Euomphalus* and distinguishing between these genera requires good preservation of the fossils. Bellerophonts include specimens of *Bellerophon* (Noble, 1922) and *Euphemites*, with the most common specimens at the GRCA museum being *E. subpapillosus*. *Bellerophon* is somewhat globular with unsculptured whorls. However, this genus has a distinctive band on the outer rim of the shell called a selenizone band. The aperture is flared, forming the widest part of the coiled shell. Bellerophon is about 2 cm (0.8 in) wide and found in Redwall Limestone and Kaibab Formation deposits (figure 14).

Foraminifera: Fusulinids (Fusulinata), the "giant" calcareous foraminifera of the late Paleozoic, are well-represented in the Redwall Limestone at GRCA. Mississippian fusulinids were more commonly described from Russian literature before the studies conducted at GRCA (Skipp and others, 1966). Fusulinids of the order Endothyrida represent most of the diversity and are useful for biostratigraphy and zoning as with *Endothyra* found in the Horseshoe Mesa Member and *Tuberendothyra* in the Mooney Falls Member. The foram genera from GRCA include *Endothyra*, *Eoendothyranopsis*, *Septaglomospiranella*, and *Tournayella*. Foraminifera collected from GRCA and held at the USNM are listed in table 2. There are a few specimens of the fusulinid *Schubertella* at the GRCA museum.

Table 2. *Foraminifera from the Redwall Limestone of the Grand Canyon in USNM collections. Continued on following page.*

Class	Order	Species	#
Fusulinata	Archaediscida	*Pohlia henbesti*	18
Fusulinata	Archaediscida	*Septatournayella* cf. *S. pseudocamerata*	3
Fusulinata	Archaediscida	*Septatournayella?* cf. *"S. minuta"*	1
Fusulinata	Archaediscida	*Tournayella* aff. *"T. subangulata"*	6
Fusulinata	Archaediscida	*Tournayella discoidea*	18
Fusulinata	Earlandiida	*Earlandia* sp.	4
Fusulinata	Earlandiida	*Paracaligella?* sp.	4
Fusulinata	Endothyrida	*Brunsiina?* sp.	1
Fusulinata	Endothyrida	*Chernyshinella?* aff. "*C. anteflexa"*	4
Fusulinata	Endothyrida	*Endothyra kleina*	1
Fusulinata	Endothyrida	*Endothyra* aff*. Spinothyra pauciseptata*	3
Fusulinata	Endothyrida	*Endothyra* cf*. E. incrassata*	2
Fusulinata	Endothyrida	*Endothyra gutschicki*	11
Fusulinata	Endothyrida	*Endothyra* sp.	12
Fusulinata	Endothyrida	*Endothyra tantula*	8
Fusulinata	Endothyrida	*Endothyra trachida*	15
Fusulinata	Endothyrida	*Endothyra?* aff. *"E. excellens"*	1
Fusulinata	Endothyrida	*Endothyra?* cf*. Plectogyra plectogyra*	4
Fusulinata	Endothyrida	*Eoendothyranopsis hinduensis*	4
Fusulinata	Endothyrida	*Eoendothyranopsis macra*	2
Fusulinata	Endothyrida	*Eoendothyranopsis scitula*	8
Fusulinata	Endothyrida	*Eoendothyranopsis* sp.	2
Fusulinata	Endothyrida	*Eoendothyranopsis spiroides*	15
Fusulinata	Endothyrida	*Eoendothyranopsis?* cf*. Banffella banffensis*	7
Fusulinata	Endothyrida	*Globoendothyra baileyi*	10
Fusulinata	Endothyrida	*Globoendothyra baileyi* subsp*. bridgensis*	4
Fusulinata	Endothyrida	*Globoendothyra baileyi* subsp*. poloumera*	6
Fusulinata	Endothyrida	*Granuliferelloides?* sp.	1
Fusulinata	Endothyrida	*Inflatoendothyra* aff*. I. nordvikensis*	1
Fusulinata	Endothyrida	*Inflatoendothyra eospiroides*	7
Fusulinata	Endothyrida	*Neoseptaglomospiranella dainae*	10
Fusulinata	Endothyrida	*Plectogyra turgida*	1
Fusulinata	Endothyrida	*Plectogyranopsis* aff*. P. eocompressa*	1

Table 2. *Continued.*

Class	Order	Species	#
Fusulinata	Endothyrida	*Plectogyranopsis eocompressa*	8
Fusulinata	Endothyrida	*Quasiendothyra turbida*	3
Fusulinata	Endothyrida	*Septabrunsiina* (*Spinobrunsiina*) *parakrainica*	12
Fusulinata	Endothyrida	*Septabrunsiina mckeei*	12
Fusulinata	Endothyrida	*Septaglomospiranella chernoussovensis*	17
Fusulinata	Endothyrida	*Septaglomospiranella primaeva* subsp. *noda*	11
Fusulinata	Endothyrida	*Septaglomospiranella rossi*	2
Fusulinata	Endothyrida	*Skippella redwallensis*	12
Fusulinata	Endothyrida	*Spinobrunsiina torquida*	11
Fusulinata	Endothyrida	*Spinoendothyra bellicosta*	3
Fusulinata	Endothyrida	*Spinoendothyra spinosa*	13
Fusulinata	Endothyrida	*Spinoendothyra spinosa*	1
Fusulinata	Endothyrida	*Spinoendothyra?* aff. *S. paraspinosa*	2
Fusulinata	Endothyrida	*Tuberendothyra* aff. *"Tuberendothyra tumulosa"*	2
Fusulinata	Endothyrida	*Tuberendothyra paratumula*	27
Fusulinata	Endothyrida	*Tuberendothyra safonovae*	8
Fusulinata	Endothyrida	*Tuberendothyra tuberculata*	22
Fusulinata	Lituolida	*Spiroplectamminoides?* cf. *Palaeospiroplectammina tchernyshinensis*	2
Fusulinata	Lituolida	*Spiroplectamminoides?* cf. *Spiroplectammina parva*	3
Fusulinata	Parathuramminida	*Calcisphaera* sp.	1
Fusulinata	Parathuramminida	*Tuberitina* sp.	5
Globothalamea	Lithuolida	*Glomospira? sp.*	1
Tubothalamea	Miliolida	*Cornuspira?* sp.	1

Surprise Canyon Formation Fauna

The Surprise Canyon Formation (Msc) covers only 20 km^2 (8 mi^2) as mapped but is a significant source of invertebrate body fossils (Beus, 1999). The Surprise Canyon Formation is interpreted as a dendritic drainage system (Beus, 2003). The formation is thickest in the western Grand Canyon, where the valleys eroded into the Redwall Limestone are deepest. The eastern GRCA exposures of the Surprise Canyon Formation are interpreted as fluvial with tidal influences only seen in the western GRCA deposits (Beus, 1989). An alternate paleoenvironmental interpretation for the entire formation is a widespread shallow sea (Beus, 2003).

Invertebrate body fossils have been reported from the marine-influenced middle and upper facies of the Surprise Canyon Formation (figure 15) and include abundant and diverse brachiopods, bryozoans of ramose, fenestrate, and encrusting forms, echinoderms, corals, and a few bivalves and gastropods (Beus, 1999; Billingsley and Beus, 1999a). However, not all specimens collected and recorded in Beus (1999) from the Surprise Canyon Formation are from within GRCA or available for study from the museums.

Figure 15. A composite sample of unidentified brachiopods, crinoids and coral fragments from the Surprise Canyon Formation (GRCA 57636). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).

Arthropoda: Trilobite diversity continued to wane in the Surprise Canyon Formation, with only the proetid *Pala-*

din documented (M. Gordon, USGS, written comm. to E. D. McKee, 1979). Ostracods are also present (Billingsley and Beus, 1999a).

Brachiopoda: Most of the brachiopods from the Surprise Canyon Formation belong to Rhynchonellata, with Strophomenata representing about one third of the brachiopod sample, but the museum collections are sparse **(appendix tables A-2 and B-2)**. Rhynchonellate genera are diverse with a few kinds of orthids, *Rhipidomella* and *Schizophoria* (Billingsley and McKee, 1982), spiriferinids *Punctospirifer transversus* and *Reticulariina*, and terebratulids *Beecheria* and *Cranaena* (Billingsley and McKee, 1982). The rhynchonellids are represented by *Cupularostrum*, *Leiorhynchoidea*, *Macropotamorhynchus*, *Rotaia neogenes*, and *Pugnoides* (Billingsley and McKee, 1982). Notably absent when compared to the older Redwall Limestone assemblages are the formerly dominant *Derbyia* and *Spirifer*. The spiriferids of the Surprise Canyon Formation at GRCA include *Anthracospirifer*, *Brachythyris*, *Cleiothyridina*, *Composita*, and *Torynifer* (Billingsley and McKee, 1982; Beus, 1999). The Strophomenata are primarily productids (*Antiquatonia*, *Flexaria*, *Inflatia*, *Ovatia*) and the orthotetid *Orthotetes*.

Bryozoa: As is typical for a Carboniferous stratigraphic unit, the distinctive corkscrew-like bryozoan *Archimedes* is present (Beus, 1999). *Archimedes* is only recorded from the Surprise Canyon Formation at GRCA. Currently, there are no formal reports of the other common bryozoan of this period, *Polypora*, although it is reported from the Redwall Limestone (Duncan, 1969; McKee and Gutschick, 1969d).

Cnidaria: The corals include favositid tabulates and stauriid rugose corals. The tabulate coral *Michelinia* (figure 16) has hexagonal patterns on the surface of the corallum with a raised center node in well-preserved specimens. Reported rugose corals include *Amplexus* and *Barytichisma* (Beus, 1999).

Figure 16. *Fragments of the coral* Michelinia *(Favositida) from the Surprise Canyon Formation (GRCA 7647). U.S. quarter for scale (diameter 24.26 mm or 0.955 in) (LINDA S. LASSITER).*

Echinodermata: Few echinoderms are reported from Mississippian units at GRCA and almost all of the specimens identified beyond class are from the Surprise Canyon Formation. The only identified specimens of Asteroidea from GRCA come from this formation, with two specimens from GRCA (MNA N4010 and N4011) assigned to the order Uractinida (Uractinina in PBDB) (Beus, 1999). Two additional unpublished blocks with asteroids are also in MNA collections (J. Tweet, pers. obs.). Blastoids (Blastoidea), represented by *Pentremites*, are uncommon. The only GRCA specimens in museum collections are from the Surprise Canyon Formation. Blastoids are extinct, stemmed echinoderms that have pentametric ambulacra distributed around the pear-shaped 1 to 2 cm (0.4 to 0.8 in) wide calyx or theca, thus explaining the name of *Pentremites*. The only Surprise Canyon crinoid attributed to a genus is *Cymbiocrinus*, although crinoid fragments are common (Beus, 1999).

Mollusca: Few mollusks have been reported from the Surprise Canyon Formation, but the oldest definite bivalves at GRCA are found in this unit (Billingsley and McKee, 1982). Bivalves include myalinids *Aviculopecten* and *Septimyalina* (M. Gordon, USGS, written comm. to E. D. McKee, 1979) and the trigoniid *Schizodus* (Billingsley and McKee, 1982). The gastropods are typical of Mississippian assemblages, with *Bellerophon* (*Bellerophon*), *Euomphalus*, *Bellazona*, and *Straparollus* (M. Gordon, USGS, written comm. to E. D. McKee, 1979; Billingsley and McKee, 1982).

Foraminifera: Only undetermined foraminifera have been reported from the Surprise Canyon Formation of GRCA (M. Gordon, USGS, written comm. to E. D. McKee, 1979). "Chesterian" foraminifera-producing sites on the Bright Angel Trail cited in McKee and Gutschick (1969b) are probably from the Horseshoe Mesa Member of the Redwall Limestone (Billingsley and Beus, 1999b).

Pennsylvanian Fauna

Pennsylvanian geologic units at GRCA include three of the four formations of the Supai Group and represent different stages of several transgressive-regressive cycles, with the depositional setting fluctuating between continental eolian and shallow marine environments of a broad coastal plain (Blakey, 2003). These units were deposited beginning in the latest Mississippian (Martin and Barrick, 1999; Hodnett and Elliott, 2018) and continuing through the Pennsylvanian. These strata have scattered areas of fossiliferous units with invertebrate body fossils in the carbonates most prominent in western GRCA (McKee, 1982a). For convenience, the lower Permian Esplanade Sandstone of the Supai Group will also be considered here. It is a sparsely fossiliferous eolian sandstone, and invertebrates are only represented by microscopic bioclasts (fragments of fossils) (McKee, 1982a). McKee (1982a) reported foraminifera, unspecified invertebrate fossils, and bioclasts of corals, bryozoans, bivalves or brachiopods, and echinoderms in thin-section from the Esplanade Sandstone. The bioclasts are possibly reworked materials from other units such as the Pakoon Limestone or may indicate that these samples were part of the Pakoon Limestone. Refinement of the presence of invertebrate body fossils in this unit would require a review of the slides but the repository for those specimens is unknown. The Pakoon Limestone, a fossiliferous marine limestone, intertongues to a limited extent with the lower Esplanade Limestone in western GRCA but has not been documented as producing fossils within the park and will not be considered further here. Outside of the park it has a fauna including corals, gastropods, brachiopods, fusulinids, and bryozoans (Spamer, 1984).

Supai Group Fauna

The Supai Group (IPsu) has locally abundant marine fossils in the formations with limestone beds and covers about 14% of the park (700 km^2 or 270 mi^2). The rocks mostly date to the Pennsylvanian, and are divided into four formations, from oldest to youngest the Watahomigi Formation (IPswa), Manakacha Formation (IPsm), Wescogame Formation (IPswe), and Esplanade Sandstone (Pse) (McKee, 1975, 1982; Blakey, 1990). The Supai Group lies unconformably on the Surprise Canyon Formation indicating a short hiatus in deposition (Beus, 1989). Of more than 500 specimens and about 80 genera identified from the Supai Group formations, 66 genera are listed from the Watahomigi Formation. Fossils in the Watahomigi Formation suggest low energy conditions (McKee, 1982a) but possibly too energetic or with too much sand and silt for extensive coral growth (Gordon, 1982), which explains the dominance of brachiopods in the assemblages. Fossils are sparse in the overlying Manakacha, Wescogame, and Esplanade formations at GRCA, only containing a few foraminifera, unspecified marine fossils, and bioclasts of unspecific bryozoans, brachiopods, bivalves, pelmatozoan echinoderms, and foraminifera (Gordon, 1982; McKee, 1982a). Larger but still not notably diverse faunas are known for the Manakacha and Wescogame formations from areas just outside of GRCA in the western Grand Canyon area, where the marine influence was more pronounced.

The most abundant invertebrate specimens from the Supai Group within GRCA reflect a shallow marine, nearshore environment of brachiopods and bivalve mollusks (figure 17). Less abundant taxa include gastropods (*Euomphalus*), disarticulated corals and crinoids. There are many unidentified specimens in the GRCA museum collections including some tentatively identified as ostracods.

Figure 17. *Examples of brachiopods and bivalves from the Supai Group (GRCA 11326) including prominent examples of* Anthracospirifer tanoensis *(center and right), with the bivalves* Promytilus *and* Permophorus *reported as present as well. U.S. quarter for scale (diameter 24.26 mm or 0.955 in) (LINDA S. LASSITER).*

Arthropoda: The arthropod community is primarily a scattered number of proetid trilobites (Gordon, 1982; McKee, 1982a) of the genus *Paladin* at GRCA. This genus is a common Mississippian to early Permian trilobite with an oval shape and isopygous form (Cisne, 1967). The reduction of trilobite diversity at GRCA is reflected in global patterns and may also be indicative of the paleoenvironment of the time. Ostracods are recognized in bioclasts from the Manakacha Formation within GRCA (McKee, 1982a).

Brachiopoda: Brachiopods from the Supai Group include species from the classes Lingulata, Rhynchonellata, and Strophomenata **(appendix tables A-3 and B-3)** (Gordon, 1982; McKee, 1982a, 1982b). The lingulids *Orbiculoidea* (figure 18A) and *Lingula* are not as common as other brachiopods and include the species *Orbiculoidea meekana* (McKee, 1982a). The cone-like shape of orbiculoids supports interpretations of high-energy environments where collected (Gordon, 1982; Spamer, 1984).

The most common Supai Group brachiopods from GRCA include the spiriferid *Composita*, and, as was true in the Redwall Limestone, the ubiquitous strophomenate *Derbyia* (figure 18B). There are also a few productids, but they are not as dominant as in the Permian Period. Spiriferids are classified based upon their internal lophophores with the typical, wide, hinge line and tapered points seen in *Spirifer* and *Anthracospirifer* (figure 17). *Composita*, however, looks more like a terebratulid in external morphology and is abundant in the Watahomigi Formation (McKee, 1975).

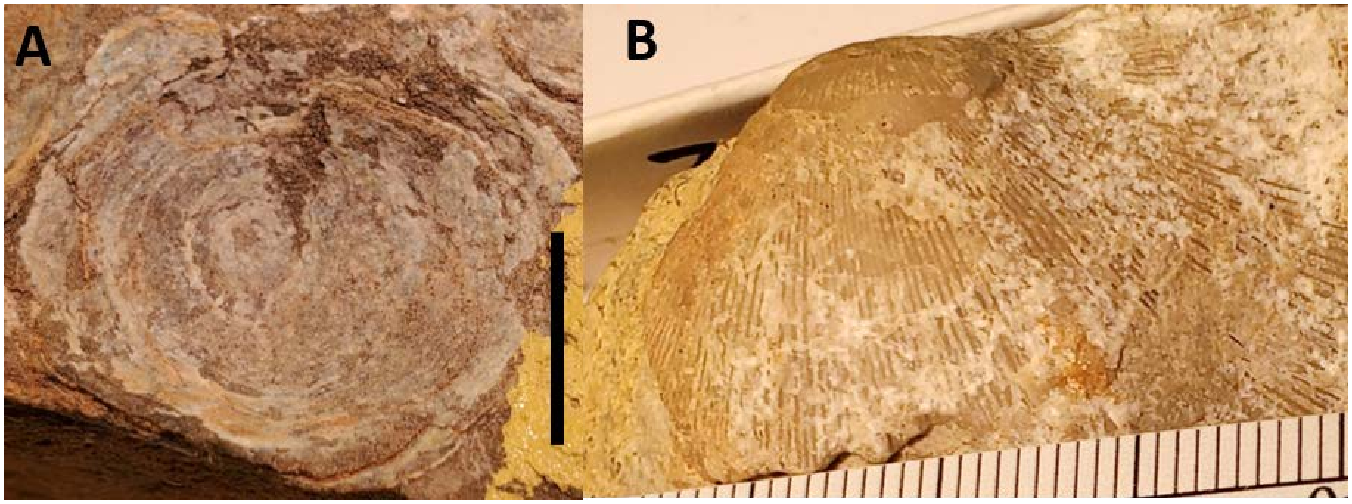

Figure 18. Supai Group brachiopods with reasonable preservation (LINDA S. LASSITER). A. Orbiculoidea *(Lingulida) (GRCA 1126) showing concentric growth lines. B.* Derbyia *(GRCA 20577) with fine costae. Scale bar 1 cm (0.4 in).*

Bryozoa: A small bryozoan fauna has been reported from the Watahomigi Formation (Gordon, 1982; McKee, 1982a). Encrusting bryozoans are reported on the surface of brachiopods (Gordon, 1982) and assist interpretations of paleoenvironments accordingly. Higher in the Supai Group, poor environmental conditions for bryozoans has resulted in only bioclasts recording their presence at GRCA for the Supai Group, primarily in the Wescogame Formation (McKee, 1982a). As McKee (1982a) points out, the sandy beds created an "unfavorable" environment.

Cnidaria: Conulariids have been reported from the Watahomigi Formation (Gordon, 1982; McKee, 1982a). Conulariids have a unique herringbone surface pattern and four sides. The morphological features have led to many different interpretations for phylogenetic placement of conulariids. Most recently, conulariids are considered to be ancestral cnidarians related to sea jellies of the class Scyphozoa (Van Iten and others, 2006) or medusozoans (Staurozoa) with a stalk (Marques and Collins, 2004).

Tabulate and rugose corals are uncommon. Undetermined corals and the favositid *Michelinia* have been reported from the Watahomigi Formation (McKee, 1982a, 1982b), and a few other taxa have been found near but outside of GRCA (McKee, 1982a) and so may eventually be found within the park. These fossils are typical of quieter environments. Above the Watahomigi, the only cnidarian remains reported from the Supai Group within GRCA are coral bioclasts in the Esplanade Sandstone (McKee, 1982a).

Echinodermata: There are literature references that indicate echinoid spines and crinoid columnals are found in the Watahomigi Formation (Gordon, 1982; McKee, 1982a). Several GRCA museum specimens may be echinoderms but were not in the collections surveyed in this report.

Mollusca: The Watahomigi Formation is dominated by myalinid bivalves, including *Aviculopecten* (*A. gravidus*), *Myalina* (*M. cuneiformis*, *M. perattenuata*), and *Septimyalina* **(see appendix tables A-3** and **B-3).** Outside of GRCA, there are reports of cardiids of *Oriocrassatella*, *Wilkingia terminalis*, and *Permophorus* in the Wescogame Formation (Gordon, 1982; McKee, 1982a).

The only other class of mollusks known from the Supai Group of GRCA is Gastropoda, but cephalopods and rostroconchs have been found near the park (Gordon, 1982). All of the Supai gastropods reported from within GRCA are from the Watahomigi Formation, but large bellerophontid gastropods are known outside of the park in the Manakacha and Wescogame formations (McKee, 1982a). The Watahomigi gastropods include bellerophontids and euomphalinids (*Euomphalus* and *Straparollus*) (Gordon, 1982; McKee, 1982a).

Foraminifera: Foraminifera or foraminiferal bioclasts are known from all of the formations of the Supai Group at GRCA, with the most taxa reported from the Manakacha Group (McKee, 1982a, 1982b). McKee (1975, 1982a) used fusulinids to determine the age of the Manakacha Formation (Atokan, Middle Pennsylvanian) and Wescogame Formation (Virgilian, Late Pennsylvanian).

Permian Fauna

Permian invertebrate body fossils are known from the Esplanade Sandstone (mentioned above), the Hermit Formation, the Toroweap Formation, and the Kaibab Formation within GRCA. The Hermit Formation is dated to the early Permian (Cisuralian epoch) and represents low-energy, fluvial deposition across a broad coastal plain (Blakey, 2003), in a semi-arid climate with long hot and dry seasons (White, 1929). The overlying eolian Coconino Sandstone (Cisuralian) interrupts the invertebrate body fossil history of the Permian Period at GRCA with a lack of body fossils but does have invertebrate trace fossils (Miller and others, this inventory). Invertebrate body fossils are once again reported in the Toroweap Formation (McKee, 1938). The Toroweap records another transgression-regression cycle, with deposition varying from tidal flat, evaporites, eolian, and shallow-marine environments in a semi-arid to arid climate (Rawson and Turner, 1974; Turner, 1990). The Kaibab Formation forms the cap of the Grand Canyon rim at GRCA and most of the surface exposures, and was formed by a shallow sea (Noble, 1914; McKee, 1938).

Hermit Formation Fauna

The Hermit Formation (Ph), which covers 8% of the surface area of the park (397 km^2 or 153 mi^2), is significant because it contains the only specimens of pre-Quaternary insects from GRCA (Spamer, 1984). Although sometimes called the Hermit Shale, most of the formation is sandstone, siltstone, and mudstone in a reddish-brown slope-forming unit (Blakey, 2003). Invertebrate body fossils are uncommon and often poorly preserved due to the terrestrial and arid conditions of preservation in a fluvial to deltaic environment, and the unfavorable grain size (Spamer, 1984).

Arthropoda: Two fossil insect wings from the Hermit Formation of GRCA have been described as species of *Tupus: T. gilmorei* (Carpenter, 1927), *T. whitei* (figure 19) and *T. permianus* (Carpenter, 1928), originally under the obsolete spelling "*Typus*". Both species are meganeurids, members of an extinct clade resembling modern dragonflies (Odonata). The finds are significant for GRCA and for dating the Hermit Formation to the early Permian (Spamer, 1984).

Other fossils reported as Insecta are a partial wing of an odonate (now lost) and a forewing of an unnamed blattoid or cockroach (USNM 71712, collected by David White in 1927) (Spamer, 1984). The only reported eurypterid, *Hastimima*, from GRCA is from this unit, but details are limited as the fossil is only an external mold (White, 1929) with insufficient detail to be included in recent Eurypterida phylogenetic analyses (Lamsdell and others, 2010).

Figure 19. *Hermit Formation insect wing of* Tupus whitei *(GRCA 3090). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Toroweap Formation Fauna

The Toroweap Formation (Pt) was included in the Kaibab Formation before McKee (1938) distinguished it as a separate formation. The Toroweap is dated to the late early Permian (approximately 273 Ma) (McKee and Breed, 1969; Mathis and Bowman, 2007) and is divided into three members, from oldest to youngest the Seligman, Brady Canyon, and Woods Ranch members. The Toroweap represents about 4% or 189 km^2 (73 mi^2) of exposures at the park. In the Grand Canyon, western faunal assemblages are typical of open but shallow marine environments with corals, bryozoans, brachiopods, and crinoids. The eastern areas are interpreted as a restricted-marine environment with a molluscan assemblage of bivalves, gastropods, a few nautiloid cephalopods, and scaphopods (Rawson and Turner, 1974). The Brady Canyon Member is the most fossiliferous, with bryozoans, brachiopods, bivalves, nautiloids, gastropods, scaphopods, ostracods, crinoids, and sea urchins (McKee, 1938). The Seligman Member has poorly preserved mollusks (McKee, 1938), and the top, thin beds of the Woods Ranch Member have abundant specimens of the smooth-surfaced clam *Schizodus*, leading McKee (1938) to refer to the unit as the *Schizodus* limestone. The three members formed during a transgression-regression cycle, with the Seligman Member as the early part of the transgression and tidal flat, the Brady Canyon Member as the maximum transgression of low-energy, shallow marine deposits, and the Woods Ranch Member as the regressive phase of an evaporitic marine shelf (Rawson and Turner, 1974).

Figure 20. *Toroweap Formation slab with unidentified bivalves (GRCA 15324). Scale bar is 1 cm (0.4 in) (LINDA S. LASSITER).*

Many fossil specimens from the Toroweap Formation of GRCA are not identified to the genus level, as with the assemblage of bivalves shown in figure 20, although some brachiopods, bivalves, gastropods, scaphopods and others have been (McKee, 1938; Spamer, 1984; Sorauf and Billingsley, 1991). There are bryozoans and sponges identified only to phylum in MNA and GRCA museum collections. Some mollusks and ostracods were not identified fully in McKee (1938). Spamer (1992) summarized assemblages with sponges, corals, bryozoans, brachiopods, bivalves, nautiloid cephalopods, gastropods, scaphopods, trilobites, and echinoids from across the Grand Canyon area. There are also fossils from the GRCA area reported from undifferentiated Toroweap Formation/Kaibab Formation rocks in the museum collections. These include the bivalve *Wilkingia wyomingensis*, the gastropod *Glyptospira cristulata*, spiriferid *Squamularia*, orthotetid *Meekella occidentalis*, productid *Rugatia paraindica*, and a trepostomatid bryozoan of the genus *Rhombotrypella*.

Arthropoda: Ostracods are uncommon at GRCA, having only been reported from the Toroweap Formation (McKee, 1938), Surprise Canyon Formation (Billingsley and Beus, 1999a), and as bioclasts from the Manakacha Formation (McKee, 1982a). The relative absence of ostracods from Devonian and later units at GRCA is puzzling. Leperditicopids are common in Devonian stratigraphic units elsewhere, as are palaeocopids from the Devonian through the Permian.

Brachiopoda: Brachiopods identified to genus or species from the Toroweap of GRCA are the productid *Peniculauris bassi* and the common spiriferid *Composita* (Schuchert, 1918b; McKee, 1938). A species of brachiopod (*Productus ivesi*, now *Peniculauris ivesi)* was named from a specimen found in the Toroweap Formation or Kaibab Formation at a location possibly within the park (Newberry, 1861) **(appendix D)**.

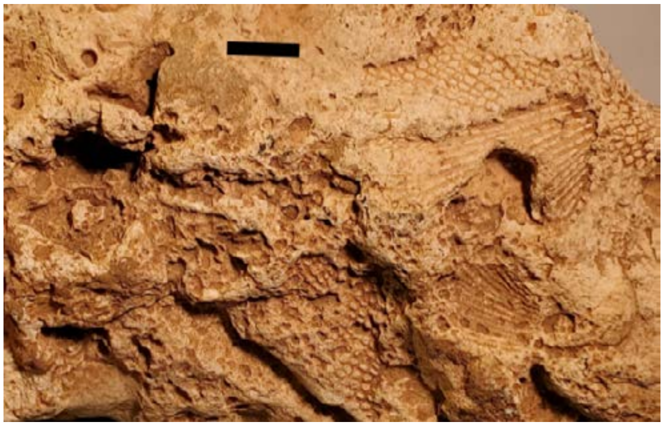

Figure 21. *Example of impressions of fenestrate-type bryozoan colonies (GRCA 11373) from the Toroweap Formation. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

Bryozoa: Unidentified fenestrate forms are recorded in composite blocks collected from the Toroweap Formation of GRCA (figure 21). McKee (1938) identified multiple beds with bryozoans in Toroweap limestone beds, but the fossils are poorly preserved.

Echinodermata: The echinoid *Archaeocidaris* (sometimes reported under the suppressed name *Echinocrinus*) has been reported or collected from the Toroweap Formation (Newberry, 1861; McKee, 1938; Sorauf and Billingsley, 1991; GRCA Museum records). Many specimens are cataloged at GRCA. Three echinoid species, *Archaeocidaris gracilis*, *A. longispinus*, and *A. ornatus* (now *A. coloradensis*), were possibly named from the Toroweap or Kaibab formations of the park **(appendix D)**. Echinoids are preserved as disarticulated spines. Crinoids are noted in Toroweap Formation limestone lenses at GRCA (McKee, 1938) but are mostly columnal fragments and otherwise not identifiable to genus or species.

Mollusca: The Toroweap Formation has a widespread bed in the upper Woods Ranch Member with abundant fossils of the bivalve *Schizodus* in limestone lenses (McKee, 1938). The Toroweap bivalve community includes the pholadomyid *Allorisma*, the ostreid *Pteria*, the adapedont *Edmondia*, the protobranch *Solemya,* and the trigoniid *Schizodus* (McKee, 1938). There are also some scallops (*Deltopecten*) and the asymmetrically valved *Nuculana* (including *Leda* and *Nucula* of McKee, 1938). Gastropods are represented by several genera not defined to species (McKee, 1938). McKee (1938) mentions the cephalopod *Domatoceras*.

There are scaphopods in the Toroweap Formation, but unlike the Kaibab forms, the specimens have not been identified beyond genus. Scaphopods in the museum collections at GRCA from the Toroweap are labeled as *Dentalium* and show longitudinal ridges (costate). Scaphopods are known informally as tusk shells due to their elongate, conical shells, which have openings at both ends. Scaphopods from the museum collections are fragments about 1 to 2 cm (0.4 to 0.8 in) in length and a few millimeters in diameter.

Kaibab Formation Fauna

The Kaibab Formation (Pk), also known as the Kaibab Limestone, covers more than 1,057 km^2 (408 mi^2) or more than 21% of the surface of the GRCA park and provides evidence of Permian life from a vast, shallow sea. The Kaibab Formation has proven difficult to date precisely but appears to include both the late early Permian (McKee and Breed, 1969) and early middle Permian (Thompson, 1995; Blakey and Middleton, 2012). This predates the Permian–Triassic boundary, when a major extinction event wiped out about 95% of marine life (Sepkoski, 1997). Within GRCA, Kaibab Formation fossils document marine life before the extinction event. Invertebrate body fossils reported in the literature from the Kaibab Formation of GRCA include sponges, rugose corals, conulariids, bryozoans, brachiopods, bivalves, nautiloids, gastropods, scaphopods, trilobites, crinoids, and echinoids (McKee, 1935, 1938; Griffin, 1966; Cisne, 1971).

The two members of the Kaibab Formation are the Fossil Mountain Member (formerly the gamma and beta units) and the younger Harrisburg Member (formerly alpha unit) (McKee, 1938; Blakey and Knepp, 1989). The Fossil Mountain Member is a cliff-forming unit of limestone, dolomite, and sandy limestone, with some fossiliferous chert nodules. The overlying Harrisburg Member is a slope-former with some ledges and is a mixed unit of limestone, dolomite, siltstone, sandstone, gypsum, and chert. There are differences in the faunal assemblages between the Fossil Mountain Member and the overlying Harrisburg Member. The Fossil Mountain Member includes sponges, rugose corals, conulariids, and echinoids, all of which are missing in the Harrisburg Member. The Fossil Mountain Member is more fossiliferous in western GRCA than eastern GRCA, corresponding to the predominance of limestone instead of dolomite (Beus and Billingsley, 1989). The Harrisburg Member also has a gypsiferous facies with brachiopods in western GRCA, but non-gypsiferous facies are dominated by mollusks in eastern GRCA. The Harrisburg Member nautiloids have not been reported from the Fossil Mountain Member assemblages (McKee, 1938; Miller and Unklesbay, 1942; Miller and Youngquist, 1949).

At least nine fossil invertebrates have been named from specimens found in the Kaibab Formation of GRCA, including four brachiopods, three bryozoans, a conulariid, and a trilobite **(appendix C)**. In addition, five Kaibab brachiopod species (*Avonia dorsoconcava*, *Chonetes kaibabensis*, *Marginifera meridionalis*, *Productus bassi*, and *Productus paraindicus*; all now under different genera) have been named from specimens possibly found within GRCA and three sea urchins (*Archaeocidaris gracilis*, *A. longispinus*, and *A. ornatus*) may have been named from the Toroweap or Kaibab formations of GRCA **(appendix D)**.

Arthropoda: Arthropods are only represented by trilobites at GRCA in the Kaibab Formation. These proetids include the genera *Ameura*, *Ditomopyge*, *Paladin*, and the species *Delaria macclintocki*, *D. sevilloidia*, *D. snowi*, *Ditomopyge scitulus*, and *Novoameura mckeei* (McKee, 1938; Cisne, 1971). *Delaria macclintocki* was named from GRCA (Cisne, 1971).

Brachiopoda: Brachiopods are diverse and abundant in the Kaibab Formation, with a number of taxa represented at GRCA **(appendix tables A-4** and **B-4)**. The most common brachiopods from the Kaibab Formation are the productids (figure 22), which are abundant at many Permian localities. The common *Peniculauris bassi* was also known formerly as *Productus bassi* or *Dictyoclostus bassi*, and many GRCA museum specimens still carry the original name in the catalog. *Avonia subhorrida newberryi* (McKee, 1938), *Chonetes quadratus* (King, 1931), *Composita arizonica* (McKee, 1938), and *Derbyia arizonensis* (McKee, 1941) are brachiopods named from GRCA's Kaibab Formation **(appendix C)**.

The diverse brachiopod orders of the Kaibab Formation include Athyridida (McKee, 1938), Rhynchonellida (McKee, 1938; Sorauf and Billingsley, 1991), Spiriferida (McKee, 1938; Sorauf and Billingsley, 1991), Spiriferinida (McKee, 1938), Terebratulida (McKee, 1938), Orthida (Condra and Elias, 1944; McKee, 1938), Orthotetida (McKee, 1938; Sorauf and Billingsley, 1991), and Productida (McKee, 1938; Sorauf and Billingsley, 1991; Thayer, 2009). GRCA museum collections have hundreds of Kaibab Formation productids of the genera *Chonetes*, "*Productus*", and *Rugatia* and the equally common spiriferid genera *Composita* and *Squamularia*. The once-dominant strophomenid orthotetid *Derbyia* (*D. arizonensis, D. multistriata, D. nasuta*) is still common but not present in the quantities seen in the earlier stratigraphic units of the Carboniferous. In a section described by McKee (1938) along the Hermit Trail, assemblages of *Avonia*, *Chonetes*, "*Productus*", *Ruga-*

Figure 22. *Kaibab Limestone productids from GRCA (LINDA S. LASSITER).* ***A.*** Peniculauris bassi *(GRCA 21372).* ***B.*** *A drawer full of productid brachiopods (GRCA 11055). Scale bar 1 cm (0.4 in).*

Figure 23. *An unidentified fenestrate bryozoan from the Kaibab Formation. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

tia, *Composita*, *Squamularia*, and *Derbyia* are visible with bivalves, crinoids, and bryozoans.

Bryozoa: Three bryozoan species, *Bicorbis arizonica*, originally *Bicorbula* (Condra and Elias, 1945a), *Bascomella subsphaerica* (Condra and Elias, 1944), and *Girtypora maculata* (McKinney, 1983), have been named from the GRCA Kaibab Formation **(appendix C)**. Fenestrate bryozoans (figure 23) with characteristic fan shapes and other forms can be seen in many GRCA Kaibab exposures but are only identifiable to species by destructive analysis of the zooecia. Identified fenestrate bryozoans from the Kaibab include the genera *Bicorbis, Chasmatopora, Fenestella,* and *Septopora*. The most common genus is *Septopora*, which has oval fenestrules with three to four zooecia per row on the obverse side. The reverse side is smooth with some pores. *Fistulipora* are distinctive in that the zooecium has a raised, horseshoe shaped area on one side of the aperture called a lunarium. Another common cystoporidan of the Kaibab Formation is *Meekopora*, which lacks the lunarium, although discerning these features is difficult without preparation and magnification of the specimen.

Several genera of cryptostome (Cryptostomida) bryozoans have been reported from the Kaibab Formation of GRCA. *Rhombopora* forms cylindrical zooaria that may or may not be branched and have acanthopore ridges in polygonal raised areas around the zooecium. Other cryptostomid bryozoans include *Girtypora, Rhabdomeson,* and *Streblotrypa* (McKinney, 1983).

Trepostome bryozoans form ramose, or erect, branching zooaria. The most common trepostome is *Stenopora*, but there are also specimens from the genera *Stenodiscus* and *Bascomella*. The bryozoan *Bascomella subsphaerica* (Condra and Elias, 1944) is named from GRCA **(appendix C)**.

Cnidaria: The only true coral reported from the Kaibab Formation is the solitary rugosan genus *Lophophyllum* (McKee, 1938; Sorauf and Billingsley, 1991).

Conulariids have been reported from the Kaibab Formation. McKee (1935) named the Kaibab species *Conularia kaibabensis* (figure 24) for a GRCA specimen **(appendix C)**. This conulariid is also sometimes referred to as *Paraconularia kaibabensis* (Sinclair, 1948; McKee and Breed, 1969, in which it is described as a coral, perhaps because of the then-recent placement of conulariids within Cnidaria). The specimen was first thought to be a fish, as described in Spamer (1984).

Echinodermata: Echinoids are often only represented by spines that are about 2 cm (0.8 in) long (McKee, 1938; Sorauf and Billingsley, 1991) and at GRCA are found primarily in the Kaibab Formation. Crinoid columnals are found in many Kaibab Formation rocks along the rim trail (figure 25). Multiple specimens identified as the genus *Archaeocidaris* (superseded name "*Echinocrinus*" of some references) are reported from the Kaibab Formation. Three species of echinoids potentially from the Kaibab Formation of GRCA were described in Newberry (1861) as *Archaeocidaris gracilis, A. longispinus,* and *A. ornatus.* An additional undescribed specimen (GRCA 20263) may also be *Archaeocidaris*.

Mollusca: Most bivalve specimens from GRCA are from the Permian and some became quite large (figure 26). This is a typical population distribution as bivalves grew in diversity and numbers during the late Paleozoic (Clapham and Bottjer, 2007). The trigoniid bivalve

Figure 24. *Conulariid* Conularia kaibabensis *holotype from the Kaibab Formation (USNM 102289). Scale bar 1 cm (0.4 in) (NPS/ANNE MILLER).*

Figure 25. *Crinoid stems and individual columnals found in the Kaibab Formation (GRCA 11468). Ruler includes mm tick marks and cm boxes (LINDA S. LASSITER).*

Figure 26. *A large bivalve of the Kaibab Formation,* Allorisma capax *(GRCA 13501). U.S. quarter for scale (diameter 24.26 mm or 0.955 in) (LINDA S. LASSITER).*

Schizodus and the pectinid *Aviculopecten* are common in the Kaibab Formation, with about 170 specimens of the former in GRCA collections. *Aviculopecten* (figure 27) can be distinguished by the coarse costae which *Schizodus* lacks. Along the Hermit Trail, fossil assemblages often include representatives of the bivalves *Schizodus, Aviculopecten,* and *Solemya* (=obsolete *Solenomya*) (McKee, 1938).

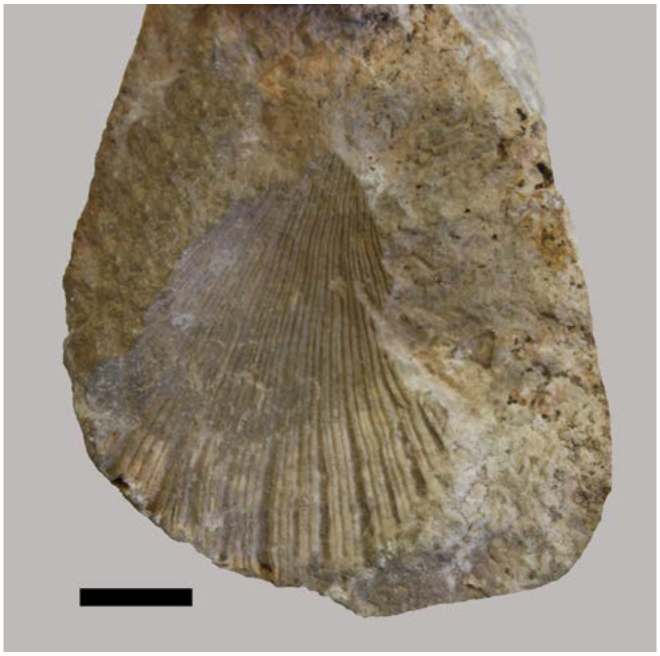

Figure 27. *A common pectinid bivalve,* Aviculopecten *(GRCA 3621), from the Kaibab Formation. Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

The Kaibab bivalve community consists of scallop-like pectinids of the genera *Acanthopecten coloradoensis*, *Deltopecten* (*D. caneyanus*), *Pecten*, *Pseudomonotis*, and *Pterinopecten*. Other bivalves are the nuculanids *Nucula* (*N. levatiforme*), *Nuculana*, *Yoldiella lucida*, the pholadomyid *Allorisma* (*A. capax*), the ostreids *Bakewellia parva* and *Pteria*, and the modiomorphid *Modiomorpha* (Shimer, 1919; McKee, 1938). *Nuculana* valves have an asymmetrical, swept appearance and are easily recognized. The cardiid bivalves are *Astartella* (*A. gurleyi, A. subquadrata*), *Permophorus* (*P. albequus*), and *Wilkingia wyomingensis* (Shimer, 1919; McKee, 1938).

There are gastropods from GRCA of the orders Bellerophontida, Cycloneritida, Euomphalina, Murchisoniina, and Pleurotomariida (Shimer, 1919; McKee, 1938). The most common gastropods of the GRCA museum collections from the Kaibab Formation are bellerophontids (*Bellerophon, Bucanopsis, Euphemites*), but other taxa are also present **(appendix tables A-4** and **B-4)**. Specimens are better preserved in the Kaibab Formation but may still be difficult to identify as they are often preserved as steinkerns which preserve no external details.

Scaphopods also occur in the Kaibab Formation of GRCA. Shimer (1919) and McKee (1938) reported *Prodentalium canna* (figure 28). This species is distinguished by a straight shape to the shell and ribbing which is not obvious, but concentric growth rings may be. Permian scaphopods are also sometimes referred to under the names *Dentalium* and *Plagioglypta*, and many specimens are still labeled under either name at the GRCA museum. Scaphopods from the Kaibab Formation are small fragments often no wider than a millimeter and no longer than 1 cm (0.4 in).

Coiled Permian cephalopods are rare at GRCA and the lack of ammonoids was noted by McKee (1938). For the Kaibab Formation, there are reports and museum records of the genera *Domatoceras, Metacoceras,* and *Stearoceras* (formerly *Titanoceras*) (Miller and Unklesbay, 1942; Miller and Youngquist, 1949). The orthoconic nautiloid *Orthoceras* was reported from the Kaibab Formation in McKee (1938), but this is a wastebasket identification for a longiconic form. Several specimens of possible nautiloids are also mentioned (McKee, 1938; Miller and Unklesbay, 1942; Miller and Youngquist, 1949).

Porifera: One sponge species is identified from the Kaibab Formation of GRCA, the lithistid demosponge *Actinocoelia maeandrina* (GRCA 3592) (Griffin, 1966; Thayer, 2009). This sponge is frequently preserved in silica nodules and is relatively common. It is considered an index fossil for age-comparable stratigraphic units to the Kaibab Formation (Finks and others, 1961). Many other Kaibab sponge specimens at the GRCA museum have not been assigned to a genus (figure 29). Six demosponges at MNA are from the Kaibab Formation at GRCA, one of which has been attributed to *Actinocoelia* (MNA 7248), the other five only identified to phylum.

SUMMARY OF THE PALEOZOIC INVERTEBRATE BODY FOSSILS

More than 6,500 specimens were reviewed from catalog listings from museum collections (GRCA, MNA, USNM), and another 592 were identified from the literature. Only 269 species from GRCA are documented as being from a known and verified species. The Grand Canyon Museum (GRCA) has more than 5,800 specimens identified as invertebrate body fossils from the Paleozoic. More than 5,400 of those specimens were collected before 1980 and some of the localities may now be from outside of the current park boundaries. The Smithsonian (USNM) paleobiology collections have more than 500 specimens from the Grand Canyon and the Museum of Northern Arizona (MNA) has more than 240 specimens. Although a determined effort was made to check locations against the current park boundaries, there is much more work to be done to refine and correct the summary of invertebrate body fossils from GRCA. The numbers of specimens per species or entry from literature reports only documents that the kind of organism was reported. Within the text of the literature are more accurate numbers of specimens, in most cases. There are more specimens, more museums, and probably more records that need review and incorporation into this survey. The GRCA compilation of Paleozoic invertebrate

Figure 28. *A specimen of the scaphopod* Prodentalium canna *(GRCA 14373) showing the conical shape and small size. It was collected from the Kaibab Limestone outside of the park boundaries. U.S. quarter for scale (diameter 24.26 mm or 0.955 in) (LINDA S. LASSITER).*

Figure 29. *An unidentified sponge from the Kaibab Formation (GRCA 3590). Scale bar 1 cm (0.4 in) (LINDA S. LASSITER).*

body fossils and documentation of this report is only a starting point.

Some discrepancies in these findings require further investigation. For example, the record of archaeocyathid sponges in the Tonto Group, if confirmed, could indicate a refugia of this group otherwise assumed to have gone extinct during the Sinsk extinctions (Zhuravlev and Wood, 2018). There are enigmatic fossils from the Bright Angel Shale that may be resolved by comparison with records from Cambrian lagerstätten localities outside of GRCA. The GRCA fossil record is remarkably limited for cephalopods, ostracods, and rostroconchs. The limited occurrence of key bryozoans *Archimedes* and *Polypora* is odd. There are other puzzles that may be solved using the GRCA resources of exposed Paleozoic units and specimens in the collections; these are but a few.

CONCLUSIONS

The Grand Canyon records life on our planet immediately before or after several of Earth's major extinction events. Globally, the Sinsk extinction event of the Stage 4 early Cambrian (513 Ma) (Zhuravlev and Wood, 2018) preceded the rocks of the Tonto Group (510–505 Ma). The depositional record of marine fossils at GRCA resumes only after the Ordovician radiation and during the final convergence of the paleocontinents of Laurentia, Baltica, and Avalonia into Laurasia. The GRCA Devonian fossil record during the Frasnian stage immediately precedes the Hangenberg extinction event of the Frasnian–Famennian (372 Ma) (Caplan and Bustin, 1999). The major extinctions of the middle and end-Permian took place after the deposition of the Kaibab Formation. The invertebrate body fossils reported here are only those collated from three museums and the literature. Admittedly, there are other fossils in inventories at other museums and private collections that are not yet identified. There are many undiscovered clues about how life evolved and changed in the marine environments during the Paleozoic as captured in these rocks. As more work is done, the final story will be epic, just like the views from the top, and even from space.

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Appendix A

Grand Canyon (GRCA) Paleozoic Invertebrate Specimens List

This appendix lists identified specimens of GRCA fossils from Paleozoic geologic units of GRCA in tables. The information was assembled from four sources: three museums and the literature. The three museums surveyed for this report are the Grand Canyon Museum (GRCA), Museum of Northern Arizona (MNA), and the Smithsonian Museum (USNM). Some entries listed in museum catalogs may be specimens reported from the literature, creating some duplication. While reviewing listings, species names were reviewed for consistency and current usage; the methods are listed in the following section on taxonomic uncertainty. Further work to resolve duplicates or underreported numbers of specimens is needed and recognized. To aid navigation and readability, the full list has been split into four shorter tables: appendix table A-1, Cambrian; appendix table A-2, Devonian and Mississippian; appendix table A-3, Supai Group; and appendix table A-4, post-Supai Permian. Additional electronic updates and details of this appendix will be published in a digital repository (DRYAD) at a later date.

Taxonomic Uncertainty

Taxonomic uncertainty is a common issue for museum curators and researchers. Out of more than 7,000 entries reviewed for this appendix, only about 5,500 had valid genus and/or species names that could be verified in an online, searchable database of paleontologic specimens or in the global names index (gni.globalnames.org). Most of the specimens had names that could not be verified in the databases, indicating that GRCA specimens are difficult to verify.

For this report, the following uncertainty notations were used after Bengtson (1988) and are as follows. When a specimen was originally labeled with "aff." or "cf." and the species name is not currently valid, the inventory interpretation for the genus and/or species will include the questionable name in quotes ("). The name was also revised to include the full genus name in lieu of using an initial abbreviation for clarity for all species names, including those following aff. or cf. If the original entry was noted as n. sp., this was interpreted as a new species to be defined at a future time if the name could not be confirmed by any other means. This notation was difficult to interpret if the specimen noted with n. sp. had not been formally described or listed with a reference for the source of the notation. For example, a specimen listed in an inventory as *Composita* n. sp. could be considered equivalent to sp.? or simply sp. with the second notation preferred. If a museum catalog entry had n. sp. for a museum specimen, the specimen name herein is referred to by the valid genus name followed by "sp." to indicate the uncertain interpretation of this specimen to species level. Taxonomists use "?" as a prefix or suffix identifier for a taxon name that appears similar to a genus known to the person making the entry. However, for this inventory, the question mark is appended consistently at the end of the genus or species name for ease in spreadsheet sorting filters and consistency. Taxonomists of the past were not subject to the interpretations of software protocols that use the question mark as an individual character placeholder. For example, *Composita* sp. for a museum specimen would indicate that the specimen matched the criteria for the genus, but further diagnosis to species level was not made by the author or collector. *Composita*? sp. uses a valid genus name but may not be the best genus match for this specimen. *Composita* n. sp. was found as the listed species name for many museum catalog entries but is confusing. This notation (n. sp.) would mean that the specimen does not meet the diagnosis criteria for any known species of the genus according to the definitions available at the time the specimen was cataloged. However, unless a reference was linked to the entry that actually described a new species (n. sp.), the entry was changed to sp.? for this inventory. Otherwise, the lack of a published description associated with a new species would make the name a *nomem nudum*.

Conforming to Bengtson (1988), the use of sp. is sufficient for this report of known specimens and their species interpretations. A question mark after the genus name would therefore be similar to some uses of cf. but indicates a tentative identification to that genus and is preferred. Generally, *Composita* sp. should be interpreted herein as a specimen probably of the *Composita* genus, but further identification has not been made with certainty. The specimen may be able to be refined to a species name, require a new description as n. sp., or may be too difficult to ascertain due to the preservation of the fossil. The use of cf. and aff. is also difficult to interpret as cf. means to "compare to" and aff. may mean "compare with", but both were retained as the original source applied if a species was provided for comparison.

Institutional Abbreviations—**GRCA**, Grand Canyon National Park Museum, Grand Canyon, Arizona; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **Other**, from literature sources; **USNM**, National Museum of Natural History Paleobiology Collections, Washington, D.C.

Geologic Unit Abbreviations—**Cambrian: Ctu**, Tonto Group undifferentiated; **Ctt**, Tonto Group, Tapeats Sandstone; **Ctba**, Tonto Group, Bright Angel Shale; **Ctm**, Tonto Group, Muav Limestone; **Cu**, Cambrian undifferentiated; **Devonian: Dtb**, Temple Butte Formation; **Mississippian: Mr**, Redwall Limestone; **Msc**, Surprise Canyon Formation; **Pennsylvanian: IPsu**, Supai Group undifferentiated (most records are probably from the Watahomigi Formation); **IPswa**, Supai Group: Watahomigi Formation; **IPsm**, Supai Group: Manakacha Formation; **IPswe**, Supai Group: Wescogame Formation; **Permian: Pse**, Supai Group: Esplanade Sandstone; **Ph**, Hermit Formation; **Pt**, Toroweap Formation; **Pk**, Kaibab Formation; **Pu**, Permian undifferentiated.

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Taxonomic Notes

Because taxonomic updates have been applied, a list of changes is appended to make it simpler to translate from historic usage to what is presented here. This is by no means exhaustive. It is broken into four sections, for the four stratigraphic blocks (Cambrian, Devonian–Mississippian, Supai Group, and post-Supai Permian). The usage favored in the tables is on the right. These lists are also applicable to appendix B.

Cambrian

- *Alokistocare althea* = *Amecephalus althea*
- *Billingsella obscura* = *Nisusia obscura*
- *Clavaspidella kanabensis* = *Athabaskia kanabensis*
- *Clavaspidella enucleata* possibly = *Clavaspidella* sp. =*Athabaskia*
- *Dolichometopus productus* (in part) = *Dolichometopus tontoensis* (in part) = *Glossopleura mckeei* = *Glossopleura boccar*
- *Dolichometopus tontoensis* (in part) = *Anoria tontoensis*
- *Ehmaniella basilica* = *Proehmaniella basilica*
- *Ehmaniella hebes* = *Proehmaniella hebes*
- *Eocrinus* = *Gogia*
- *Finkelnburgia noblei* = *Nisusia noblei*
- *Glossopleura mckeei* = *Glossopleura boccar*
- *Indiana* = *Indianites*
- *Iphidea crenistria* = *Micromitra* (*Paterina*) *crenistria*
- *Iphidea superba* = *Micromitra* (*Paterina*) *superba*
- *Kootenia* n. sp. of Schenk and Wheeler (1942) = *Kootenia schenki*
- *Lingulella perattenuata* ("*attenuata*" of Resser, 1945) = *Lingulella spatula*
- *Micromitra* (*Iphidella*) *pannula* (in part) = *Dictyonina arizonaensis*
- *Nisusia*? (*Jamesella*) *kanabensis* = *Nisusia kanabensis*
- *Obolus* (*Lingulella*) *chuarensis* = *Obolus* (*Westonia*) *chuarensis* = *Lingulella chuarensis*

- *Obolus* (*Lingulella*) *euglyphus* = *Obolus* (*Westonia*) *euglyphus* = *Lingulella euglypha*
- *Obolus* (*Lingulella*) *lineolatus* = *Lingulella lineolata*
- *Obolus* (*Lingulella*) *spatulus* = *Lingulella attenuata* (in part) = *Lingulella* (*Lingulepis*) *spatula* = *Lingulepis spatula* = *Lingulella spatula*
- *Obolus* (*Lingulella*) *zetus* = *Lingulella zetus*
- *Obolus* (*Westonia*) *themis* = *Lingulella themis*
- *Orthisina* = *Clitambonites*
- *Solenopleurella diligens* = *Spencella diligens*
- *Solenopleurella erosa* = *Spencella erosa*
- *Solenopleurella porcata* = *Spencella porcata*
- *Solenopleurella* n. sp. of Schenk and Wheeler (1941) = *Solenopleurella porcata* = *Spencella porcata*

Devonian–Mississippian

- *Caninophyllum incrassatum* = *Vesiculophyllum incrassatum*
- *Endothyra baileyi* = *Globoendothyra baileyi*
- *Endothyra baileyi poloumera* = *Globoendothyra baileyi poloumera*
- *Endothyra eospiroides* = *Inflatoendothyra eospiroides*
- *Endothyra spinosa* = *Spinoendothyra spinosa*
- *Endothyra torquida* = *Spinobrunsiina torquida*
- *Eomillerella spiroides* = *Eoendothyranopsis spiroides*
- *Lithostrotion* (*Diphyphyllum*) *inconstans* = *Dorlodotia inconstans*
- *Monilipora*? sp. = *Cladochonus* sp.
- *Phillipsia sampsoni* = *Aprathia* sp.
- *Phillipsia tuberculata* = *Phillipsia peroccidens*
- *Schuchertella chemungensis* = *Floweria chemungensis*
- *Septaglomospiranella primaeva* = *Septaglomospiranella chernoussovensis*
- *Septatournayella henbesti* = *Pohlia henbesti*
- *Spirifer striatus* = *Neospirifer striatus*
- *Straparollus* (*Euomphalus*) = *Euomphalus*
- *Triplophyllites* (*Homalophyllites*) *paucicinctus* = *Homalophyllites paucicinctus*

Supai Group

- *Anthracospirifer curvilateralis* subsp. *tanoensis* = *Anthracospirifer tanoensis*
- *Derbyia* may also be spelled *Derbya* in some references
- *Straparollus* (*Euomphalus*) = *Euomphalus*

Post-Supai Permian

- *Anisopyge mckeei* = *Novoameura mckeei*
- *Avonia dorsoconcava* = *Echinauris dorsoconcava*
- *Avonia subhorrida newberryi* = *Echinauris newberryi*
- *Bicorbula arizonica* = *Bicorbis arizonica*
- *Chonetes hillanus* = *Dyoros hillanus*
- *Chonetes kaibabensis* = *Quadrochonetes kaibabensis* = *Dyoros kaibabensis*
- *Chonetes* (*Lissochonetes*) *subliratus* = *Dyoros subliratus*
- *Chonetes quadratus* = *Dyoros tetragonus*
- *Delaria macclintocki* = *Delaria sevilloidia*
- *Dentalium canna* = *Plagioglypta canna* = *Prodentalium canna*

- *Derbyia* may also be spelled *Derbya* in some references
- *Derbyia regularis* = *Derbyia arizonensis*
- *Echinocrinus* = *Archaeocidaris* (suppressed for *Archaeocidaris*)
- *Euphemus* = *Euphemites*
- *Griffithides scitulus* = *Ditomoyge scitulus*
- *Marginifera meridionalis* = *Kozlowskia meridionalis* = *Kutorginella meridionalis*
- *Marginifera popei* = *Liosotella popei*
- *Leda* sp. and *Nucula* sp. of McKee (1938) = *Nuculana*? sp.
- *Pleurophorus* = *Permophorus*
- *Productus irginae* = *Waagenoconcha irginae*
- *Productus subhorridus* = *Avonia subhorrida* = *Echinauris subhorrida*
- *Productus* (*Dictyoclostus*) *bassi* = *Peniculauris bassi*
- *Productus* (*Dictyoclostus*) *ivesi* = *Dictyoclostus ivesi* = *Peniculauris ivesi*
- *Productus* (*Dictyoclostus*) *occidentalis* = *Dictyoclostus occidentalis* = *Rugatia occidentalis*
- *Productus* (*Dictyoclostus*) *paraindicus* = *Rugatia paraindicus*
- *Productus montpelierensis* = *Waagenoconcha montpelieriensis* = *Bathymyonia nevadensis*
- *Pugnoides pinguis* = *Wellerella pinguis* = *Phrenophoria pinguis*
- *Retzia meekana* = *Hustedia meekana*
- *Squamularia guadalupensis* = *Phricodothyris guadalupensis*
- *Spiriferina hilli* = *Spiriferellina hilli*
- *Straparollus* (*Euomphalus*) = *Euomphalus*
- *Titanoceras rotundatum* = *Stearoceras rotundatum*
- *Titanoceras sanandreasense* = *Stearoceras sanandreasense*
- *Typus gilmorei* = *Tupus gilmorei*
- *Typus whitei* = *Tupus whitei*

Appendix Table A-1. *Specimens of invertebrate body fossils from GRCA Cambrian units as reported from the Grand Canyon Museum (GRCA), Museum of Northern Arizona (MNA), Smithsonian Institution (USNM), or otherwise listed in the literature (Other). Specimens reported are listed with the stratigraphic unit as reported by the sources, if available, although some reports may have been based on superseded stratigraphic interpretations as described in the methods section. Continued on following page.*

Unit	Source	Phylum	Class	Order	Species	#
Ctu	Other	Arthropoda	Ostracoda	Leperditicopida	Undetermined	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis kwaguntensis*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Athabaskia kanabensis*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura boccar*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia mckeei*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Olenoides* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Ptarmigania* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Elrathiella?* aff. *E. insueta*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Kochina angustata*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Parehmania kwaguntensis*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Parehmania nitida*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Proehmaniella hebes*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Ptychoparia* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencella diligens*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencella* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Trachycheilus typicale*	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia kanabensis*	1
	USNM	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Acrothele* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella kanabensis*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella winona* aff. *L. winona* subsp. *convexa*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella zetus*	1

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctu (continued)	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulepis perattenuatus*	1
	Other	Brachiopoda	Paterinata	Paterinida	*Iphidea ornatella*	1
	USNM	Brachiopoda	Paterinata	Paterinida	*Iphidella pannula*	3
	Other	Brachiopoda	Paterinata	Paterinida	*Micromitra (Paterina) crenistria*	1
	Other	Brachiopoda	Rhynchonellata	Protorthida	*Protorthis* sp.	1
	Other	Problematica	Hyolitha	Hyolithida	*Hyolithes* sp.	1
Ctt	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites* cf. *I. faba*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites curta*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites impressa*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella* sp.	1
	MNA	Arthropoda	Trilobita	Ptychopariida	*Spencella* sp.	1
	Other	Arthropoda	Trilobita	Redlichiida	*Olenellus* sp.	1
	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulella chuarensis*	21
	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulella euglypha*	2
	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulella lineolatus*	5
	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulella spatulus*	3
	USNM	Brachiopoda	Lingulata	Lingulida	*Lingulella zetus*	4
	Other	Brachiopoda	Obolellata	Obolellida	Undetermined	1
	USNM	Brachiopoda	Paterinata	Paterinida	*Iphidella pannula*	1
	USNM	Brachiopoda	Paterinata	Paterinida	*Paterina (Iphidea)? crenistria*	7
Ctba	Other	Arthropoda	Bradoriida clade	Bradoriida	*Bradoria tontoensis*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Bradoria tontoensis*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites* aff. *I. faba?*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Indianites curtus*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Indianites faba*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites faba*	5
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Indianites faba* subsp. *intermedia*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Indianites impressus*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Indianites intermedius*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella apicalis*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella apicalis*	5

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella breviuscula*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella breviuscula*	2
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella concentrica*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella concentrica*	3
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella leperditoides*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella leperditoides*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella limatula*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella limatula*	3
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella longula*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella longula*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella nitida*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella nitida*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella oblonga*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella oblonga*	2
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella obsoleta*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella obsoleta*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella pulchella*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella pulchella*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella scitula*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella scitula*	1
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella subtruncata*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella subtruncata*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella subtruncata*	2
	Other	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella ventrosa*	1
	USNM	Arthropoda	Bradoriida clade	Bradoriida	*Walcottella ventrosa*	1
	Other	Arthropoda	Bradoriida clade	Indianidae	*Dielymella appressa*	1
	USNM	Arthropoda	Bradoriida clade	Indianidae	*Dielymella appressa*	3
	Other	Arthropoda	Bradoriida clade	Indianidae	*Dielymella dorsalis*	1
	USNM	Arthropoda	Bradoriida clade	Indianidae	*Dielymella dorsalis*	1
	Other	Arthropoda	Bradoriida clade	Indianidae	*Dielymella nasuta*	1
	USNM	Arthropoda	Bradoriida clade	Indianidae	*Dielymella nasuta*	3

Appendix Table A-1. Continued

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	Other	Arthropoda	Bradoriida clade	Indianidae	*Dielymella recticardinalis*	1
	USNM	Arthropoda	Bradoriida clade	Indianidae	*Dielymella recticardinalis*	5
	Other	Arthropoda	Bradoriida clade	Indianidae	*Dielymella recticardinalis* aff. *D. recticardinalis* subsp. *angustata*	1
	USNM	Arthropoda	Bradoriida clade	Indianidae	*Dielymella recticardinalis* aff. *D. recticardinalis* subsp. *angustata*	1
	GRCA	Arthropoda	Trilobita	Asaphida	*Glyphaspis* sp.	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis* sp.	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis vulsa*	1
	GRCA	Arthropoda	Trilobita	Composite	Composite of *Alokistocare* sp. and *Glossopleura mckeei*	1
	GRCA	Arthropoda	Trilobita	Composite	Composite of *Amecephalus althea* and *Glossoplerua producta*	3
	GRCA	Arthropoda	Trilobita	Composite	Composite of *Anoria tontoensis* and *Amecephalus althea*	2
	Other	Arthropoda	Trilobita	Corynexochida	*Albertella schenki*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Albertella* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	29
	MNA	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	3
	Other	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	2
	GRCA	Arthropoda	Trilobita	Corynexochida	*Anoria tontoensis*	149
	MNA	Arthropoda	Trilobita	Corynexochida	*Anoria tontoensis*	2
	Other	Arthropoda	Trilobita	Corynexochida	*Anoria tontoensis*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Athabaskia* sp.	2
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura* aff. *"G. walcotti"*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura boccar*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura mckeei*	134
	MNA	Arthropoda	Trilobita	Corynexochida	*Glossopleura mckeei*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura meriwitica*	27
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura productus*	48
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp.	55
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp.	1

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp. or *Anoria* sp.	24
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp. or *Clavaspidella* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Kootenia* aff. *"K. simplia"*	3
	GRCA	Arthropoda	Trilobita	Corynexochida	*Kootenia schenki*	2
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia simplex*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Kootenia* sp.	13
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Olenoides* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Prozacanthoides* sp.	2
	Other	Arthropoda	Trilobita	Corynexochida	*Ptarmigania* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	Undetermined	2
	Other	Arthropoda	Trilobita	Corynexochida	*Zacanthoides* cf. *Z. walapai*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Zacanthoides* sp.	42
	Other	Arthropoda	Trilobita	Corynexochida	*Zacanthoides* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Acrocephalops?* cf. *A. arizonaensis*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Alokistocare lepida*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Alokistocare* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Alokistocare* sp. or *Ehmaniella* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Alokistocare?* sp.	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Amecephalus althea*	76
	MNA	Arthropoda	Trilobita	Ptychopariida	*Amecephalus althea*	6
	Other	Arthropoda	Trilobita	Ptychopariida	*Amecephalus althea*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Amecephalus* cf. *A. althea*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Amecephalus* cf. *A. packi*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Amecephalus* sp.	86
	MNA	Arthropoda	Trilobita	Ptychopariida	*Amecephalus* sp.	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Antagmus arizonaensis*	2
	Other	Arthropoda	Trilobita	Ptychopariida	*Antagmus arizonaensis*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Antagmus* sp.	3
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Bolaspis aemula*	6
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Ehmaniella* aff. "*E. arizonaensis*"	21

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	Other	Arthropoda	Trilobita	Ptychopariida	*Ehmaniella* aff. “*E. arizonaensis*”	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Ehmaniella* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Elrathia nitens*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Elrathia* sp.	24
	Other	Arthropoda	Trilobita	Ptychopariida	*Elrathia* sp.	2
	MNA	Arthropoda	Trilobita	Ptychopariida	*Elrathiella?* aff. *E. insueta*	1
	MNA	Arthropoda	Trilobita	Ptychopariida	*Kochina* aff. “*K. adunca*”	1
	MNA	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis* aff. *“P. arenosa”*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis* cf. *P. fonticola*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis fonticola*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis moorei*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Parehmania kwaguntensis*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Parehmania* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Parehmania tontoensis*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Proehmaniella basilica*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Spencella porcata*	2
	MNA	Arthropoda	Trilobita	Ptychopariida	*Spencia tontoensis*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencia tontoensis*	1
	GRCA	Arthropoda	Trilobita	Redlichiida	*Olenellus* sp.	113
	Other	Arthropoda	Trilobita	Redlichiida	*Olenellus* sp.	1
	Other	Arthropoda	Trilobita	Redlichiida	Undetermined	1
	GRCA	Arthropoda	Trilobita	Undetermined	Undetermined	258
	MNA	Arthropoda	Trilobita	Undetermined	Undetermined	3
	Other	Arthropoda	Trilobita	Undetermined	Undetermined	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* aff. *N. noblei*	1
	GRCA	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* aff. *N. obscura*	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* aff. *N. obscura*	1
	GRCA	Brachiopoda	Kutorginata	Kutorginida	*Nisusia noblei*	1
	GRCA	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* sp.	22
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* sp.	1

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia?* sp.	1
	GRCA	Brachiopoda	Lingulata	Lingulida	*Acrotreta* sp.	6
	GRCA	Brachiopoda	Lingulata	Lingulida	*Lingula* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingula* sp.	2
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella acutangula*	1
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella* aff. *“L. noblei”*	1
	GRCA	Brachiopoda	Lingulata	Lingulida	*Lingulella chuarensis*	98
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella chuarensis*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella chuarensis*	1
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella euglypha*	5
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella euglypha*	1
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella lineolata*	5
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella lineolata*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella mckeei*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella* sp.	1
	GRCA	Brachiopoda	Lingulata	Lingulida	*Lingulella spatula*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella spatula*	1
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella spatula*	5
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella themis*	2
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella zetus*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella?* aff. *O. themis*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella?* cf. *L. monticula*	1
	GRCA	Brachiopoda	Lingulata	Lingulida	*Lingulella?* sp.	4
	MNA	Brachiopoda	Lingulata	Lingulida	*Lingulella?* sp.	2
	GRCA	Brachiopoda	Lingulata	Lingulida	*Obolus* sp.	21
	Other	Brachiopoda	Obolellata	Obolellida	*Obolella aff. O. polita*	1
	MNA	Brachiopoda	Obolellata	Obolellida	*Obolella* sp.	1
	Other	Brachiopoda	Obolellata	Obolellida	*Obolella* sp.	2
	Other	Brachiopoda	Paterinata	Paterinida	*Dictyonina arizonaensis*	1
	MNA	Brachiopoda	Paterinata	Paterinida	*Iphidella arizonaensis*	1

***Appendix Table A-1**. Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	GRCA	Brachiopoda	Paterinata	Paterinida	*Iphidella pannula* aff. *I. pannula* subsp. *aladensis*	2
	GRCA	Brachiopoda	Paterinata	Paterinida	*Iphidella* sp.	4
	Other	Brachiopoda	Paterinata	Paterinida	*Micromitra (Paterina) crenistria*	1
	Other	Brachiopoda	Paterinata	Paterinida	*Micromitra (Paterina) superba*	1
	Other	Brachiopoda	Paterinata	Paterinida	*Micromitra pealei*	1
	MNA	Brachiopoda	Paterinata	Paterinida	*Micromitra superba*	4
	GRCA	Brachiopoda	Paterinata	Paterinida	*Paterina?* sp.	3
	Other	Brachiopoda	Paterinata	Paterinida	*Paterina?* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Orthida	*Wimanella* sp.	4
	Other	Brachiopoda	Rhynchonellata	Thecideida	*Diraphora?* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Undetermined	Undetermined	3
	GRCA	Brachiopoda	Strophomenata	Billingsellida	*Billingsella* sp.	13
	GRCA	Brachiopoda	Undetermined	Undetermined	Undetermined	51
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	5
	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	GRCA	Composite	Composite	Composite	Composite of *Billingsella highlandensis* and *Glossopleura* or *Anoria*	2
	GRCA	Composite	Composite	Composite	Composite of *Billingsella highlandensis* and *Glossopleura* sp.	2
	MNA	Composite	Composite	Composite	Composite of *Hyolithes* and *Anoria tontoensis* and *Amecephalus althea*	1
	GRCA	Echinodermata	Cystoidea?	Undetermined	Undetermined	1
	Other	Echinodermata	Eocrinoidea	Ascocystitida	*Eocystites* sp.	1
	GRCA	Echinodermata	Eocrinoidea	Gogiida	*Gogia longidactylus*	1
	Other	Echinodermata	Eocrinoidea	Gogiida	*Gogia multibrachiatus*	1
	USNM	Echinodermata	Eocrinoidea	Gogiida	*Gogia multibrachiatus*	1
	Other	Echinodermata	Eocrinoidea	Gogiida	*Gogia?* aff. *G. longidactylus*	1
	GRCA	Echinodermata	Eocrinoidea	Gogiida	Undetermined	1
	GRCA	Echinodermata	Not assigned	Rhombifera	Undetermined	1
	GRCA	Echinodermata	Undetermined	Undetermined	Undetermined	1
	GRCA	Mollusca	Bivalvia	Undetermined	Undetermined	4

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctba (continued)	GRCA	Mollusca	Gastropoda	Undetermined	Undetermined	3
	GRCA	Porifera	Archaeocyatha	Ajacicyathida	*Ethmophyllum chankensis*	3
	Other	Porifera	Archaeocyatha	Undetermined	Undetermined	1
	GRCA	Porifera	Undetermined	Undetermined	Undetermined	2
	GRCA	Problematica	Coeloscleritophora	Chancelloriida	*Chancelloria* cf. *C. eros*	3
	MNA	Problematica	Coeloscleritophora	Chancelloriida	*Chancelloria* sp.	7
	Other	Problematica	Hyolitha	Hyolithida	*Hyolithes* sp.	3
	GRCA	Problematica	Hyolitha	Hyolithida	*Hyolithes?* sp.	38
	MNA	Problematica	Hyolitha	Hyolithida	*Hyolithes?* sp.	3
	Other	Problematica	Undetermined	Undetermined	*Margaretia?* sp.	2
	Other	Problematica	Undetermined	Undetermined	*Tontoia kwaguntensis*	1
	USNM	Problematica	Undetermined	Undetermined	*Tontoia kwaguntensis*	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	27
Ctm	GRCA	Arthropoda	Trilobita	Asaphida	*Glyphaspis kwaguntensis*	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis kwaguntensis*	1
	GRCA	Arthropoda	Trilobita	Asaphida	*Glyphaspis* sp.	4
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis* sp.	1
	GRCA	Arthropoda	Trilobita	Asaphida	*Glyphaspis tecta*	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis tecta*	1
	GRCA	Arthropoda	Trilobita	Asaphida	*Glyphaspis vulsa*	1
	Other	Arthropoda	Trilobita	Asaphida	*Glyphaspis?* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Anoria* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Athabaskia* sp.	2
	Other	Arthropoda	Trilobita	Corynexochida	*Dorypyge* sp.	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura meriwitica*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Glossopleura* sp. or *Anoria* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia havasuensis*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia mckeei*	1

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctm (continued)	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia schenki*	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia simplex*	1
	GRCA	Arthropoda	Trilobita	Corynexochida	*Kootenia* sp.	3
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Kootenia?* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Neolenus* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Pagodia?* sp.	1
	Other	Arthropoda	Trilobita	Corynexochida	*Zacanthoides* sp.	1
	Other	Arthropoda	Trilobita	Proetida	*Bathyurus?* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Alokistocare* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Anomocarella* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Bolaspis aemula*	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Bolaspis*? sp.	1
	USNM	Arthropoda	Trilobita	Ptychopariida	*Elrathiella?* aff. *E. insueta*	3
	Other	Arthropoda	Trilobita	Ptychopariida	*Pachyaspis moorei*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Parehmania kwaguntensis*	3
	Other	Arthropoda	Trilobita	Ptychopariida	*Ptychoparia* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Ptychoparia?* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Saukia* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencella erosa*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Spencella porcata*	10
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencella porcata*	1
	GRCA	Arthropoda	Trilobita	Ptychopariida	*Spencella* sp.	1
	MNA	Arthropoda	Trilobita	Ptychopariida	*Spencella* sp.	1
	Other	Arthropoda	Trilobita	Ptychopariida	*Spencella* sp.	1
	GRCA	Arthropoda	Trilobita	Undetermined	Undetermined	68
	MNA	Arthropoda	Trilobita	Undetermined	Undetermined	1
	Other	Arthropoda	Trilobita	Undetermined	Undetermined	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia noblei*	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia noblei*	1
	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia* sp.	1

Appendix Table A-1. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Ctm (continued)	Other	Brachiopoda	Kutorginata	Kutorginida	*Nisusia?* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Acrotreta?* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Discina* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingula* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulella (Lingulepis)* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingulepis prima*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Trematis* sp.	1
	Other	Brachiopoda	Paterinata	Paterinida	*Dictyonina* sp.	1
	USNM	Brachiopoda	Rhynchonellata	Kutorginida	*Nisusia noblei*	3
	Other	Brachiopoda	Rhynchonellata	Orthida	*Finkelnburgia* sp.	1
	Other	Brachiopoda	Rhynchonellata	Pentamerida	*Syntrophia* sp.	1
	Other	Brachiopoda	Strophomenata	Billingsellida	*Clitambonites* sp.	1
	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	MNA	Composite	Composite	Composite	Composite unidentified	1
	Other	Mollusca	Helcionelloida	Helcionelliformes	*Helcionella* sp.	1
	Other	Porifera	Archaeocyatha	Undetermined	Undetermined	1
	Other	Problematica	Coeloscleritophora	Chancelloriida	*Chancelloria* cf. *C. eros*	1
	Other	Problematica	Coeloscleritophora	Chancelloriida	*Chancelloria?* sp.	1
	Other	Problematica	Hyolitha	Hyolithida	*Hyolithes* aff. *H. primordialis*	1
	Other	Problematica	Hyolitha	Hyolithida	*Hyolithes* sp.	1
	GRCA	Problematica	Hyolitha	Hyolithida	*Hyolithes?* sp.	4
	Other	Problematica	Hyolitha	Hyolithida	*Hyolithes?* sp.	1
	MNA	Problematica	Monoplacophora?	Cyrtonellida?	*Scenella hermitensis*	1
	Other	Problematica	Monoplacophora?	Cyrtonellida?	*Scenella hermitensis*	1
Cu	USNM	Brachiopoda	Kutorginata	Kutorginida	*Nisusia obscura*	1

Appendix Table A-2. *Specimens of invertebrate body fossils from GRCA Devonian and Mississippian units as reported from the Grand Canyon Museum (GRCA), Museum of Northern Arizona (MNA), Smithsonian Institution (USNM), or otherwise listed in the literature (Other). Specimens reported are listed with the stratigraphic unit as reported by the sources, if available, although some reports may have been based on superseded stratigraphic interpretations as described in the methods section. Continued on following page.*

Unit	Source	Phylum	Class	Order	Species	#
Dtb	GRCA	Arthropoda	Trilobita	Undetermined	Undetermined	2
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	2
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	Other	Cnidaria	Anthozoa	Stauriida	*Streptelasma?* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	Undetermined	1
	Other	Cnidaria	Anthozoa	Stauriida	Undetermined	1
	Other	Cnidaria	Anthozoa	Undetermined	Undetermined	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	28
	Other	Undetermined	Undetermined	Undetermined	Undetermined	1
Mr	Other	Arthropoda	Trilobita	Proetida	*Aprathia* sp.	1
	Other	Arthropoda	Trilobita	Proetida	*Breviphillipsia* sp.	1
	GRCA	Arthropoda	Trilobita	Proetida	*Phillipsia tuberculata*	1
	GRCA	Arthropoda	Trilobita	Undetermined	Undetermined	1
	USNM	Brachiopoda	Rhynchonellata	Athyridida	*Cleiothyridina* sp.	1
	Other	Brachiopoda	Rhynchonellata	Orthida	*Rhipidomella* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Camarotoechia* aff. "*C. nutallica*"	2
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Camarotoechia* sp.	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Camarotoechia?* sp.	2
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnax osagensis*	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnax* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnoides* sp.	5
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnoides* sp.	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	Undetermined	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita?* sp.	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Mirifusella* cf. *M. fortunata*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Neospirifer striatus*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Prospira* sp.	2
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Punctospirifer kentuckyensis*	4
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* aff. *S. incertus*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer centronatus*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer centronatus*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* cf. *Elivina occidentalis*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer redwallensis*	4
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	325
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	3
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Torynifer* cf. *T. setiger*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Unispirifer minnewankensis*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Unispirifer minnewankensis*	3
	Other	Brachiopoda	Rhynchonellata	Spiriferinida	*Syringothyris?* sp.	1
	USNM	Brachiopoda	Rhynchonellata	Terebratulida	*Dielasma* sp.	1
	Other	Brachiopoda	Rhynchonellata	Terebratulida	Undetermined	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.	229
	Other	Brachiopoda	Strophomenata	Orthotetida	*Floweria chemungensis*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Meekella* sp.	1
	MNA	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Streptorhynchus* sp.	5
	GRCA	Brachiopoda	Strophomenata	Productida	*Chonetes* sp.	7
	GRCA	Brachiopoda	Strophomenata	Productida	*Productus* sp.	4
	USNM	Brachiopoda	Strophomenata	Productida	*Tomiproductus gallatinensis*	2
	GRCA	Brachiopoda	Strophomenata	Productida	Undetermined	2
	Other	Brachiopoda	Strophomenata	Productida	Undetermined	1
	Other	Brachiopoda	Strophomenata	Strophomenida	*Leptagonia* sp.	1
	Other	Brachiopoda	Strophomenata	Undetermined	Undetermined	1

Appendix Table A-2*. Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	GRCA	Brachiopoda	Undetermined	Undetermined	Undetermined	12
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	USNM	Brachiopoda	Undetermined	Undetermined	Undetermined	2
	Other	Bryozoa	Stenolaemata	Cryptostomida	Undetermined	1
	USNM	Bryozoa	Stenolaemata	Cystoporida	*Cheilotrypa* sp.	2
	USNM	Bryozoa	Stenolaemata	Cystoporida	*Coscinotrypa* sp.	1
	Other	Bryozoa	Stenolaemata	Cystoporida	*Cystodictya* sp.	1
	Other	Bryozoa	Stenolaemata	Cystoporida	*Dichotrypa* sp.	2
	USNM	Bryozoa	Stenolaemata	Cystoporida	*Dichotrypa* sp.	6
	USNM	Bryozoa	Stenolaemata	Cystoporida	*Dichotrypa?* sp.	3
	USNM	Bryozoa	Stenolaemata	Cystoporida	*Ramiporalia* sp.	2
	GRCA	Bryozoa	Stenolaemata	Fenestrata	*Fenestralia* sp.	1
	USNM	Bryozoa	Stenolaemata	Fenestrata	*Fenestralia* sp.	2
	Other	Bryozoa	Stenolaemata	Fenestrata	*Fenestralia?* sp.	1
	USNM	Bryozoa	Stenolaemata	Fenestrata	*Lyroporella* sp.	8
	USNM	Bryozoa	Stenolaemata	Fenestrata	*Lyroporella?* sp.	1
	USNM	Bryozoa	Stenolaemata	Fenestrata	*Neoreteporina?* sp.	1
	USNM	Bryozoa	Stenolaemata	Fenestrata	*Polyporella* sp.	3
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* aff. *F. albida*	1
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* aff. *F. cingulata*	2
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* aff. *F. compressa*	4
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* aff. *F. serratula*	4
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* aff. *F. subflexuosa*	2
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* cf. *F. cingulata*	1
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* cf. *F. compressa*	2
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* cf. *F. serratula*	1
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella compressa*	5
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Fenestella serratula*	1
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* sp.	2
	Other	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* sp.	8

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	Other	Bryozoa	Stenolaemata	Fenestrida	*Penniretepora* sp.	1
	Other	Bryozoa	Stenolaemata	Fenestrida	*Polypora* sp.	1
	USNM	Bryozoa	Stenolaemata	Fenestrida	*Polypora* sp.	1
	Other	Bryozoa	Stenolaemata	Fenestrida	*Polypora*? sp.	1
	Other	Bryozoa	Stenolaemata	Fenestrida	Undetermined	1
	USNM	Bryozoa	Stenolaemata	Trepostomatida	Undetermined	5
	GRCA	Bryozoa	Undetermined	Undetermined	Undetermined	2
	MNA	Bryozoa	Undetermined	Undetermined	Undetermined	2
	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	Other	Cnidaria	Anthozoa	Auloporida	*Cladochonus?* sp.	1
	Other	Cnidaria	Anthozoa	Auloporida	*Syringopora aculeata*	1
	Other	Cnidaria	Anthozoa	Auloporida	*Syringopora* aff. *S. surcularia*	1
	Other	Cnidaria	Anthozoa	Auloporida	*Syringopora* cf. *S. surcularia*	1
	GRCA	Cnidaria	Anthozoa	Auloporida	*Syringopora* sp.	1
	MNA	Cnidaria	Anthozoa	Auloporida	*Syringopora* sp.	2
	Other	Cnidaria	Anthozoa	Auloporida	*Syringopora* sp.	1
	Other	Cnidaria	Anthozoa	Auloporida	*Syringopora surcularia*	1
	GRCA	Cnidaria	Anthozoa	Auloporida	*Syringopora surcularia*	13
	USNM	Cnidaria	Anthozoa	Auloporida	*Syringopora surcularia*	1
	GRCA	Cnidaria	Anthozoa	Favositida	*Cladopora* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Amplexizaphrentis* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Clisiophyllum* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Diphyphyllum?* cf. *Lithostrotion* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Diphyphyllum?* sp.	1
	USNM	Cnidaria	Anthozoa	Stauriida	*Dorlodotia* cf. *D. arizelum*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Dorlodotia* cf. *D. inconstans*	1
	GRCA	Cnidaria	Anthozoa	Stauriida	*Dorlodotia inconstans*	3
	MNA	Cnidaria	Anthozoa	Stauriida	*Dorlodotia inconstans*	1
	USNM	Cnidaria	Anthozoa	Stauriida	*Dorlodotia inconstans*	2
	Other	Cnidaria	Anthozoa	Stauriida	*Dorlodotia inconstans*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Dorlodotia* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	USNM	Cnidaria	Anthozoa	Stauriida	*Ekvasophyllum* cf. *E. inclinatum*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Homalophyllites paucicinctus*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Homalophyllites subcrassus*	1
	USNM	Cnidaria	Anthozoa	Stauriida	*Homalophyllites subcrassus*	2
	GRCA	Cnidaria	Anthozoa	Stauriida	*Lithostrotion* (*Diphyphyllum*)*? inconstans*	3
	Other	Cnidaria	Anthozoa	Stauriida	*Menophyllum excavatum*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Sychnoelasma* sp.	1
	GRCA	Cnidaria	Anthozoa	Stauriida	*Triplophyllites* (*Triplophyllites*) *persimilia*	2
	GRCA	Cnidaria	Anthozoa	Stauriida	*Triplophyllites* sp.	2
	Other	Cnidaria	Anthozoa	Stauriida	Undetermined	1
	GRCA	Cnidaria	Anthozoa	Stauriida	*Vesiculophyllum incrassatum*	20
	Other	Cnidaria	Anthozoa	Stauriida	*Vesiculophyllum incrassatum*	1
	USNM	Cnidaria	Anthozoa	Stauriida	*Vesiculophyllum incrassatum*	2
	Other	Cnidaria	Anthozoa	Stauriida	*Vesiculophyllum* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Zaphrentites persimilis*	1
	Other	Cnidaria	Anthozoa	Undetermined	Undetermined	1
	GRCA	Cnidaria	Undetermined	Undetermined	Undetermined	51
	Other	Echinodermata	Blastoidea	Spiraculata	*Pentremites* sp.	1
	GRCA	Echinodermata	Crinoidea	Undetermined	Undetermined	13
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	USNM	Foraminifera	Fusulinata	Archaediscida	*Pohlia henbesti*	18
	Other	Foraminifera	Fusulinata	Archaediscida	*Pohlia henbesti*	2
	Other	Foraminifera	Fusulinata	Archaediscida	*Septatournayella*? sp.	1
	Other	Foraminifera	Fusulinata	Archaediscida	*Tournayella* sp.	1
	Other	Foraminifera	Fusulinata	Archaediscida	*Tournayella?* sp.	1
	Other	Foraminifera	Fusulinata	Earlandiida	*Earlandia* sp.	1
	USNM	Foraminifera	Fusulinata	Earlandiida	*Earlandia* sp.	4
	Other	Foraminifera	Fusulinata	Earlandiida	*Paracaligella?* sp.	1
	USNM	Foraminifera	Fusulinata	Earlandiida	*Paracaligella?* sp.	4
	Other	Foraminifera	Fusulinata	Earlandiida	*Paramillerella?* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* aff. *E. gutschicki*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* aff. *E. tantala*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* aff. *E. trachida*	2
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra kleina*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Endothyra kleina*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* sp.	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* sp.	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Endothyra* sp.	2
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra tantula*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Endothyra tantula*	8
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra trachida*	2
	USNM	Foraminifera	Fusulinata	Endothyrida	*Endothyra trachida*	15
	USNM	Foraminifera	Fusulinata	Endothyrida	*Endothyra?* aff. *"E. excellens"*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Eoendothyranopsis* aff. *E. spiroides*	2
	USNM	Foraminifera	Fusulinata	Endothyrida	*Eoendothyranopsis* sp.	2
	Other	Foraminifera	Fusulinata	Endothyrida	*Eoendothyranopsis spiroides*	2
	USNM	Foraminifera	Fusulinata	Endothyrida	*Eoendothyranopsis spiroides*	15
	Other	Foraminifera	Fusulinata	Endothyrida	*Globoendothyra baileyi*	2
	USNM	Foraminifera	Fusulinata	Endothyrida	*Globoendothyra baileyi*	10
	Other	Foraminifera	Fusulinata	Endothyrida	*Globoendothyra baileyi* subsp*. poloumera*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Globoendothyra baileyi* subsp*. poloumera*	6
	Other	Foraminifera	Fusulinata	Endothyrida	*Inflatoendothyra eospiroides*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Inflatoendothyra eospiroides*	7
	Other	Foraminifera	Fusulinata	Endothyrida	*Septabrunsiina* (*Spinobrunsiina*) *parakrainica*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Septabrunsiina* (*Spinobrunsiina*) *parakrainica*	12
	Other	Foraminifera	Fusulinata	Endothyrida	*Septabrunsiina* sp.	2
	Other	Foraminifera	Fusulinata	Endothyrida	*Septaglomospiranella chernoussovensis*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Septaglomospiranella chernoussovensis*	17
	Other	Foraminifera	Fusulinata	Endothyrida	*Septaglomospiranella rossi*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Septaglomospiranella rossi*	2
	Other	Foraminifera	Fusulinata	Endothyrida	*Septaglomospiranella* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	Other	Foraminifera	Fusulinata	Endothyrida	*Spinobrunsiina* aff. *S. torquida*	2
	USNM	Foraminifera	Fusulinata	Endothyrida	*Spinobrunsiina torquida*	11
	Other	Foraminifera	Fusulinata	Endothyrida	*Spinoendothyra* aff. *S. spinosa*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Spinoendothyra spinosa*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Spinoendothyra spinosa*	13
	Other	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra paratumula*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra paratumula*	27
	Other	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra* sp.	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra* sp.*?*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra tuberculata*	1
	USNM	Foraminifera	Fusulinata	Endothyrida	*Tuberendothyra tuberculata*	22
	Other	Foraminifera	Fusulinata	Endothyrida	*Spinobrunsiina torquida*	1
	GRCA	Foraminifera	Fusulinata	Fusulinida	*Schubertella* sp.	4
	Other	Foraminifera	Fusulinata	Lituolida	*Spiroplectamminoides?* cf. *Spiroplectammina parva*	1
	USNM	Foraminifera	Fusulinata	Lituolida	*Spiroplectamminoides?* cf. *Spiroplectammina parva*	3
	Other	Foraminifera	Fusulinata	Parathuramminida	*Calcisphaera* sp.	1
	USNM	Foraminifera	Fusulinata	Parathuramminida	*Calcisphaera* sp.	1
	Other	Mollusca	Cephalopoda	Actinocerida	*Rayonnoceras* sp.	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* sp.	2
	Other	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* sp.	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Euphemites subpapillosus*	17
	Other	Mollusca	Gastropoda	Bellerophontida	*Euphemites?* sp.	1
	Other	Mollusca	Gastropoda	Bellerophontida	Undetermined	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	3
	Other	Mollusca	Gastropoda	Euomphalina	*Euomphalus?* sp.	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Straparollus* sp.	15
	GRCA	Mollusca	Gastropoda	Euomphalina	Undetermined	7
	Other	Mollusca	Gastropoda	Euomphalina	Undetermined	1
	GRCA	Mollusca	Gastropoda	Murchisoniina	*Loxonema* sp.	1

Appendix Table A-2. Continued

Unit	Source	Phylum	Class	Order	Species	#
Mr (continued)	Other	Mollusca	Gastropoda	Murchisoniina	Undetermined	1
	Other	Mollusca	Gastropoda	Pleurotomariida	*Euconospira* aff. *“E. montezuma”*	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	60
	Other	Undetermined	Undetermined	Undetermined	Undetermined	1
Msc	Other	Arthropoda	Trilobita	Proetida	*Paladin* cf. *P. chesterensis*	1
	Other	Arthropoda	Trilobita	Proetida	*Paladin* sp.	1
	Other	Brachiopoda	Rhynchonellata	Athyrida	*Cleiothyridina* sp.	1
	Other	Brachiopoda	Rhynchonellata	Athyrida	*Eumetria* sp.	1
	Other	Brachiopoda	Rhynchonellata	Orthida	*Rhipidomella nevadensis*	1
	GRCA	Brachiopoda	Rhynchonellata	Orthida	*Rhipidomella* sp.	1
	Other	Brachiopoda	Rhynchonellata	Orthida	*Schizophoria* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Cupularostrum* aff. *“C. purduie”*	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Leiorhynchoidea carbonifera*	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Leiorhynchoidea* sp.	2
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Macropotamorhynchus* cf. *M. purduei*	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Macropotamorhynchus* sp.	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnoides* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Rotaia neogenes*	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Rotaia neogenes*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer* aff. *A. curvilateralis*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer bifurcatus*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer* cf. *A. curvilateralis*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer curvilateralis*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer curvilateralis*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Brachythyris (Spirifer) subcardiiformis*	1
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Cleiothyridina orbicularis*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita gibbosa*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita laevis*	1
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita laevis*	2

Appendix Table A-2. Continued

Unit	Source	Phylum	Class	Order	Species	#
Msc (continued)	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita laevis*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita ovata*	1
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subquadrata*	2
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subquadrata*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subquadrata*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Torynifer* aff. *T. setiger*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Torynifer* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	Undetermined	2
	MNA	Brachiopoda	Rhynchonellata	Spiriferinida	*Punctospirifer transversus*	2
	GRCA	Brachiopoda	Rhynchonellata	Spiriferinida	*Reticulariina* sp.	1
	Other	Brachiopoda	Rhynchonellata	Terebratulida	*Beecheria* cf. B. *arkansanum*	1
	Other	Brachiopoda	Rhynchonellata	Terebratulida	*Beecheria* sp.	1
	Other	Brachiopoda	Rhynchonellata	Terebratulida	*Cranaena* sp.	1
	MNA	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	1
	Other	Brachiopoda	Strophomenata	Orthotetida	Undetermined	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Antiquatonia* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Flexaria* sp.	3
	Other	Brachiopoda	Strophomenata	Productida	*Flexaria* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Inflatia* aff. *I. clydensis*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Inflatia* sp.	2
	Other	Brachiopoda	Strophomenata	Productida	*Inflatia* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Inflatia* sp. or *Sandia* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Inflatia?* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Ovatia* sp.	2
	Other	Brachiopoda	Strophomenata	Productida	Undetermined	2
	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	2
	MNA	Bryozoa	Stenolaemata	Fenestrida	*Archimedes* sp.	1
	Other	Bryozoa	Stenolaemata	Fenestrida	*Archimedes* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Msc (continued)	Other	Bryozoa	Undetermined	Undetermined	Undetermined	4
	GRCA	Cnidaria	Anthozoa	Favositida	*Michelinia* sp.	2
	Other	Cnidaria	Anthozoa	Favositida	*Michelinia* sp.	1
	GRCA	Cnidaria	Anthozoa	Stauriida	*Amplexus* aff. *“Barytchisma” zaphrentiformis*	1
	Other	Cnidaria	Anthozoa	Stauriida	*Amplexus* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	*Barytichisma* sp.	1
	Other	Cnidaria	Anthozoa	Stauriida	Undetermined	1
	Other	Cnidaria	Anthozoa	Undetermined	Undetermined	1
	MNA	Echinodermata	Asteroidea	Uractinida	Undetermined	4
	GRCA	Echinodermata	Blastoidea	Spiraculata	*Pentremites* sp.	2
	MNA	Echinodermata	Blastoidea	Spiraculata	*Pentremites* sp.	1
	Other	Echinodermata	Blastoidea	Undetermined	Undetermined	1
	MNA	Echinodermata	Crinoidea	Ampelocrinida	*Cymbiocrinus* sp.	1
	Other	Echinodermata	Crinoidea	Ampelocrinida	*Cymbiocrinus* sp.	1
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	Other	Echinodermata	Echinoidea	Undetermined	Undetermined	2
	Other	Echinodermata	Undetermined	Undetermined	Undetermined	1
	Other	Echinodermata	Undetermined	Undetermined	Undetermined	1
	Other	Foraminifera	Undetermined	Undetermined	Undetermined	1
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	1
	Other	Mollusca	Bivalvia	Myalinida	*Septimyalina* sp.	1
	Other	Mollusca	Bivalvia	Myalinida	*Septimyalina*? sp.	1
	Other	Mollusca	Bivalvia	Pectinida	Undetermined	1
	Other	Mollusca	Bivalvia	Pholadomyida	*Edmondia* sp.	1
	Other	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	1
	GRCA	Mollusca	Bivalvia	Undetermined	Undetermined	1
	Other	Mollusca	Bivalvia	Undetermined	Undetermined	1
	MNA	Mollusca	Gastropoda	Archaeogastropoda	Undetermined	1
	Other	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* (*Bellerophon*) sp.	1
	Other	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* spp.	1
	Other	Mollusca	Gastropoda	Eotomarioidea	*Glabrocingulum* sp.	1

Appendix Table A-2. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Msc (continued)	Other	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	1
	Other	Mollusca	Gastropoda	Euomphalina	*Straparollus?* sp.	1
	MNA	Mollusca	Gastropoda	Murchisoniina	*Bellazona* sp.	1
	Other	Mollusca	Gastropoda	Murchisoniina	*Bellazona* sp.	1
	Other	Mollusca	Gastropoda	Murchisoniina	*Loxonema* sp.	1
	Other	Mollusca	Undetermined	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	2
	Other	Undetermined	Undetermined	Undetermined	Undetermined	1
	Other	Undetermined	Undetermined	Undetermined	Undetermined	1

Appendix Table A-3. *Specimens of invertebrate body fossils from the Supai Group of GRCA as reported from the Grand Canyon Museum (GRCA), Museum of Northern Arizona (MNA), Smithsonian Institution (USNM), or otherwise listed in the literature (Other). Specimens reported are listed with the stratigraphic unit as reported by the sources, if available, although some reports may have been based on superseded stratigraphic interpretations as described in the methods section. Continued on following page.*

Unit	Source	Phylum	Class	Order	Species	#
IPsu	GRCA	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea* sp.	28
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	94
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	25
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.	41
	GRCA	Brachiopoda	Strophomenata	Productida	*Linoproductus* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Productus* sp.	6
	GRCA	Cnidaria	Undetermined	Undetermined	Undetermined	3
	GRCA	Echinodermata	Crinoidea	Undetermined	Undetermined	5
	GRCA	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	2
	GRCA	Mollusca	Bivalvia	Myalinida	*Myalina* aff. *M. swallovi*	6
	GRCA	Mollusca	Bivalvia	Myalinida	*Myalina cuneiformis*	2
	GRCA	Mollusca	Bivalvia	Myalinida	*Myalina perattenuata*	6
	GRCA	Mollusca	Bivalvia	Myalinida	*Myalina* sp.	73
	GRCA	Mollusca	Bivalvia	Mytilida	*Modiolus* sp.	4
	GRCA	Mollusca	Bivalvia	Ostreida	*Cornellites* sp.	2
	GRCA	Mollusca	Bivalvia	Undetermined	Undetermined	30
	GRCA	Mollusca	Gastropoda	Euomphalina	*Euomphalus?* sp.	4
	MNA	Mollusca	Gastropoda	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	50
IPswa	Other	Arthropoda	Trilobita	Proetida	*Paladin* sp.	1
	Other	Arthropoda	Trilobita	Proetida	*Paladin?* aff. “*Librogenae*”	1
	Other	Arthropoda	Trilobita	Proetida	*Paladin?* sp.	1
	Other	Brachiopoda	Lingulata	Lingulida	*Lingula* sp.	2
	Other	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea* aff. *O. meekana*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea meekana*	1
	USNM	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea meekana*	1
	Other	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea* sp.	1

Appendix Table A-3. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
IPswa (continued)	Other	Brachiopoda	Rhynchonellata	Orthida	*Schizophoria* aff. S. *altirostris*	1
	USNM	Brachiopoda	Rhynchonellata	Orthida	*Schizophoria* aff. S. *altirostris*	2
	Other	Brachiopoda	Rhynchonellata	Orthida	*Schizophoria altirostris*	2
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Cupularostrum?* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer newberryi*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer newberryi*	2
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer occiduus*	4
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer tanoensis*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Anthracospirifer tanoensis*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita ovata*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Composita ovata*	3
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subtilita*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subtilita*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spiriferina?* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferinida	*Punctospirifer transversus*	1
	USNM	Brachiopoda	Rhynchonellata	Spiriferinida	*Punctospirifer transversus*	3
	Other	Brachiopoda	Rhynchonellata	Spiriferinida	*Reticulariina gonionota*	2
	Other	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* aff. *D. robusta*	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.	1
	USNM	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.?	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	1
	USNM	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	Undetermined	1
	USNM	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	Other	Bryozoa	Stenolaemata	Cystoporata	Undetermined	1
	Other	Bryozoa	Stenolaemata	Cystoporida	*Cystiodictya?* sp.	1
	Other	Bryozoa	Stenolaemata	Cystoporida	Undetermined	1
	Other	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* sp.	1

Appendix Table A-3. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
IPswa (continued)	Other	Bryozoa	Stenolaemata	Trepostomatida	Undetermined	1
	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	Other	Cnidaria	Anthozoa	Favositida	*Michelinia* sp.	1
	Other	Cnidaria	Anthozoa	Undetermined	Undetermined	1
	Other	Cnidaria	Staurozoa?	Conulatae	Undetermined	1
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	Other	Echinodermata	Undetermined	Undetermined	Undetermined	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Fusulinella* sp.	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Pseudostaffella* sp.	1
	Other	Mollusca	Bivalvia	Cardiida	*Oriocrassatella* sp.	1
	Other	Mollusca	Bivalvia	Cardiida	*Permophorus* sp.	1
	USNM	Mollusca	Bivalvia	Cardiida	*Permophorus* sp.	1
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten* aff. *A. gravidus*	1
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten gravidus*	1
	USNM	Mollusca	Bivalvia	Pectinida	*Aviculopecten gravidus*	1
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	1
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	1
	USNM	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	1
	USNM	Mollusca	Bivalvia	Myalinida	*Myalina (Myalina)* sp.	1
	Other	Mollusca	Bivalvia	Myalinida	*Myalina* sp.	2
	Other	Mollusca	Bivalvia	Myalinida	*Septimyalina* sp.	1
	USNM	Mollusca	Bivalvia	Myalinida	*Septimyalina* sp.	2
	Other	Mollusca	Bivalvia	Myalinida	Undetermined	1
	Other	Mollusca	Bivalvia	Ostreida	*Leptodesma* sp.	1
	Other	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	1
	USNM	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	2
	Other	Mollusca	Bivalvia	Unionida	*Promytilus* sp.	1
	USNM	Mollusca	Bivalvia	Unionida	*Promytilus* sp.	1
	Other	Mollusca	Gastropoda	Bellerophontida	Undetermined	1
	Other	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	1
	Other	Mollusca	Gastropoda	Euomphalina	*Straparollus* sp.	1

Appendix Table A-3. *Continued*

Unit	**Source**	**Phylum**	**Class**	**Order**	**Species**	**#**
IPswa (continued)	Other	Mollusca	Gastropoda	Pleurotomariida	Undetermined	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
IPsm	Other	Arthropoda	Ostracoda	Undetermined	Undetermined	1
	Other	Echinodermata	Undetermined	Undetermined	Undetermined	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra media*	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra* sp.	1
	Other	Foraminifera	Fusulinata	Endothyrida	*Endothyra teres*	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Eoschubertella* sp.	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Fusulinella* sp.	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Pseudostaffella* sp.	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Schubertella* sp.	2
	Other	Foraminifera	Fusulinata	Fusulinida	Undetermined	1
	Other	Foraminifera	Undetermined	Undetermined	Undetermined	1
	Other	Undetermined	Undetermined	Undetermined	Calcisphere bioclasts	1
IPswe	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	Other	Foraminifera	Fusulinata	Fusulinida	Undetermined	1
	Other	Foraminifera	Undetermined	Undetermined	Undetermined	1
Pse	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	Other	Cnidaria	Undetermined	Undetermined	Undetermined	1
	Other	Echinodermata	Undetermined	Undetermined	Undetermined	1
	Other	Foraminifera	Fusulinata	Fusulinida	*Schubertella* sp.	2
	Other	Foraminifera	Undetermined	Undetermined	Undetermined	1

Appendix Table A-4. *Specimens of invertebrate body fossils from post-Supai Permian units at GRCA as reported from the Grand Canyon Museum (GRCA), Museum of Northern Arizona (MNA), Smithsonian Institution (USNM), or otherwise listed in the literature (Other). Specimens reported are listed with the stratigraphic unit as reported by the sources, if available, although some reports may have been based on superseded stratigraphic interpretations as described in the methods section. Continued on following page.*

Unit	Source	Phylum	Class	Order	Species	#
Ph	Other	Arthropoda	Subphylum Chelicerata	Eurypterida	*Hastimima?* sp.	1
	USNM	Arthropoda	Subphylum Chelicerata	Eurypterida	*Hastimima?* sp.	2
	USNM	Arthropoda	Insecta	Blattodea	Undetermined	1
	USNM	Arthropoda	Insecta	Meganisoptera	*Tupus gilmorei*	1
	USNM	Arthropoda	Insecta	Meganisoptera	*Tupus whitei*	1
	Other	Arthropoda	Insecta	Odonata	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	10
	USNM	Undetermined	Undetermined	Undetermined	Undetermined	1
Pt	Other	Arthropoda	Ostracoda	Undetermined	Undetermined	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	25
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Peniculauris bassi*	7
	MNA	Brachiopoda	Strophomenata	Productida	*Peniculauris ivesi*	1
	Other	Brachiopoda	Strophomenata	Productida	*Peniculauris ivesi*	1
	MNA	Bryozoa	Undetermined	Undetermined	Undetermined	1
	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	GRCA	Echinodermata	Crinoidea	Undetermined	Undetermined	2
	MNA	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	GRCA	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp.	1
	MNA	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp.	3
	Other	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp.	1
	GRCA	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp. (*Echinocrinus* sp.)	24
	MNA	Echinodermata	Echinoidea	Undetermined	Undetermined	1
	Other	Mollusca	Bivalvia	Adapedonta	*Edmondia* sp.	1
	Other	Mollusca	Bivalvia	Cardiida	*Permophorus* sp.	1
	GRCA	Mollusca	Bivalvia	Nuculanida	*Nuculana* sp.	3

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pt (continued)	Other	Mollusca	Bivalvia	Nuculanida	*Nuculana?* sp.	1
	Other	Mollusca	Bivalvia	Ostreida	*Pteria* sp.	1
	GRCA	Mollusca	Bivalvia	Pectinida	*Deltopecten* sp.	1
	MNA	Mollusca	Bivalvia	Pectinida	*Pecten* sp.	1
	GRCA	Mollusca	Bivalvia	Pholadomyida	*Allorisma* sp.	1
	MNA	Mollusca	Bivalvia	Pholadomyida	*Allorisma* sp.	1
	Other	Mollusca	Bivalvia	Pholadomyida	*Allorisma* sp.	1
	Other	Mollusca	Bivalvia	Protobranchia	*Solemya* sp.	1
	GRCA	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	5
	MNA	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	1
	Other	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	1
	GRCA	Mollusca	Bivalvia	Undetermined	Undetermined	1
	Other	Mollusca	Bivalvia	Undetermined	Undetermined	1
	Other	Mollusca	Cephalopoda	Nautilida	*Domatoceras?* sp.	1
	Other	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* sp.	2
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Euphemites* sp.	2
	Other	Mollusca	Gastropoda	Bellerophontida	*Euphemites* sp.	1
	Other	Mollusca	Gastropoda	Cycloneritida	*Naticopsis* sp.	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	3
	Other	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	1
	Other	Mollusca	Gastropoda	Murchisoniina	*Aclisina* sp.	1
	Other	Mollusca	Gastropoda	Murchisoniina	*Goniospira* sp.	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
	GRCA	Mollusca	Scaphopoda	Dentaliida	*Dentalium* sp.	2
	Other	Mollusca	Undetermined	Undetermined	Undetermined	1
	GRCA	Porifera	Undetermined	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	23
Pk	GRCA	Arthropoda	Trilobita	Proetida	*Ameura* sp.	3
	GRCA	Arthropoda	Trilobita	Proetida	*Anisopyge* (=*Novoameura*) *mckeei*	1
	GRCA	Arthropoda	Trilobita	Proetida	*Delaria macclintocki*	1
	Other	Arthropoda	Trilobita	Proetida	*Delaria sevilloidia*	1

Appendix Table A-4. Continued

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	GRCA	Arthropoda	Trilobita	Proetida	*Delaria snowi*	2
	Other	Arthropoda	Trilobita	Proetida	*Delaria snowi*	1
	GRCA	Arthropoda	Trilobita	Proetida	*Ditomopyge scitulus*	1
	GRCA	Arthropoda	Trilobita	Proetida	*Ditomopyge* sp.	1
	Other	Arthropoda	Trilobita	Proetida	*Ditomopyge* sp.	1
	Other	Arthropoda	Trilobita	Proetida	*Novoameura mckeei*	1
	GRCA	Arthropoda	Trilobita	Undetermined	Undetermined	23
	Other	Arthropoda	Trilobita	Undetermined	Undetermined	1
	GRCA	Brachiopoda	Lingulata	Lingulida	*Orbiculoidea* sp.	5
	GRCA	Brachiopoda	Rhynchonellata	Athyridida	*Hustedia* aff. *H. meekana*	2
	Other	Brachiopoda	Rhynchonellata	Athyridida	*Hustedia* aff. *H. meekana*	1
	Other	Brachiopoda	Rhynchonellata	Athyridida	*Hustedia* sp.	1
	Other	Brachiopoda	Rhynchonellata	Orthida	*Rhipidomella hessensis*	1
	Other	Brachiopoda	Rhynchonellata	Orthida	*Rhipidomella transversa*	1
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Phrenophoria pinguis*	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnax osagensis*	6
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnax* sp.	3
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnoides* sp.	21
	Other	Brachiopoda	Rhynchonellata	Rhynchonellida	*Pugnoides* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Rhynchonella* sp.	6
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Stenoscisma hueconianum*	1
	GRCA	Brachiopoda	Rhynchonellata	Rhynchonellida	*Stenoscisma* sp.	9
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita arizonica*	11
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita arizonica*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita arizonica*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	62
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subtilita*	3
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita subtilita*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Composita?* sp.	1

Appendix Table A-4. Continued

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Neophricadothyris* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Phricodothyris guadalupensis*	2
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Phricodothyris guadalupensis*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spirifer* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Spiriferina* sp.	7
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Spiriferina?* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Squamularia* sp.	105
	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Squamularia* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferida	*Squamularia* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferida	*Timaniella pseudocameratus*	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferinida	*Punctospirifer* sp.	1
	Other	Brachiopoda	Rhynchonellata	Spiriferinida	*Punctospirifer?* sp.	1
	GRCA	Brachiopoda	Rhynchonellata	Spiriferinida	*Spiriferellina hilli*	1
	MNA	Brachiopoda	Rhynchonellata	Spiriferinida	*Spiriferellina hilli*	1
	Other	Brachiopoda	Rhynchonellata	Spiriferinida	*Spiriferellina hilli*	1
	MNA	Brachiopoda	Rhynchonellata	Terebratulida	*Dielasma bovidens*	1
	GRCA	Brachiopoda	Rhynchonellata	Terebratulida	*Dielasma phosphoriense*	1
	Other	Brachiopoda	Rhynchonellata	Terebratulida	*Dielasma phosphoriense*	1
	GRCA	Brachiopoda	Rhynchonellata	Terebratulida	*Dielasma* sp.	6
	Other	Brachiopoda	Strophomenata	Orthotetida	*Derbyia arizonensis*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia arizonensis*	4
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia multistriata*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia nasuta*	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Derbyia nasuta*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.	22
	MNA	Brachiopoda	Strophomenata	Orthotetida	*Derbyia sp.*	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Derbyia* sp.	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Meekella occidentalis*	5
	USNM	Brachiopoda	Strophomenata	Orthotetida	*Meekella occidentalis*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Meekella pyramidalis*	14
	MNA	Brachiopoda	Strophomenata	Orthotetida	*Meekella pyramidalis*	2

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	Other	Brachiopoda	Strophomenata	Orthotetida	*Meekella pyramidalis*	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Meekella* sp.	41
	MNA	Brachiopoda	Strophomenata	Orthotetida	*Meekella sp.*	1
	Other	Brachiopoda	Strophomenata	Orthotetida	*Meekella* sp.	1
	GRCA	Brachiopoda	Strophomenata	Orthotetida	*Orthotetes* sp.	16
	MNA	Brachiopoda	Strophomenata	Productida	*Antiquatonia* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Avonia* sp.	57
	MNA	Brachiopoda	Strophomenata	Productida	*Avonia* sp.	3
	Other	Brachiopoda	Strophomenata	Productida	*Avonia* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Bathymyonia nevadensis*	1
	MNA	Brachiopoda	Strophomenata	Productida	*Bathymyonia nevadensis*	2
	GRCA	Brachiopoda	Strophomenata	Productida	*Chonetes* aff. "*C. hillianus*"	12
	GRCA	Brachiopoda	Strophomenata	Productida	*Chonetes permianus*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Chonetes* sp.	141
	MNA	Brachiopoda	Strophomenata	Productida	*Chonetes* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Chonetes* sp.	2
	GRCA	Brachiopoda	Strophomenata	Productida	*Dictyoclostus semireticulatus*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Dictyoclostus* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Dyoros* (*Tetragonetes*) *tetragonus*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Dyoros kaibabensis*	1
	Other	Brachiopoda	Strophomenata	Productida	*Dyoros kaibabensis*	1
	Other	Brachiopoda	Strophomenata	Productida	*Dyoros subliratus*	1
	MNA	Brachiopoda	Strophomenata	Productida	*Dyoros subliratus*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Echinauris dorsoconcava*	1
	Other	Brachiopoda	Strophomenata	Productida	*Echinauris dorsoconcava*	1
	Other	Brachiopoda	Strophomenata	Productida	*Echinauris newberryi*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Echinauris newberryi*	1
	Other	Brachiopoda	Strophomenata	Productida	*Echinauris* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Kozlowskia* sp.	1
	MNA	Brachiopoda	Strophomenata	Productida	*Kutorginella meridionalis*	5
	Other	Brachiopoda	Strophomenata	Productida	*Liosotella popei*	1

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	GRCA	Brachiopoda	Strophomenata	Productida	*Liosotella popei*	3
	MNA	Brachiopoda	Strophomenata	Productida	*Marginifera* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Marginifera* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Peniculauris bassi*	66
	MNA	Brachiopoda	Strophomenata	Productida	*Peniculauris bassi*	2
	MNA	Brachiopoda	Strophomenata	Productida	*Peniculauris bassi*	4
	Other	Brachiopoda	Strophomenata	Productida	*Peniculauris bassi*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Peniculauris ivesi*	43
	Other	Brachiopoda	Strophomenata	Productida	*Peniculauris ivesi*	1
	USNM	Brachiopoda	Strophomenata	Productida	*Peniculauris ivesi*	3
	MNA	Brachiopoda	Strophomenata	Productida	*Peniculauris* sp.	1
	Other	Brachiopoda	Strophomenata	Productida	*Peniculauris* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Productus* aff. *"P. iiginac"*	2
	GRCA	Brachiopoda	Strophomenata	Productida	*Productus* sp.	87
	GRCA	Brachiopoda	Strophomenata	Productida	*Rugatia occidentalis*	133
	Other	Brachiopoda	Strophomenata	Productida	*Rugatia occidentalis*	1
	USNM	Brachiopoda	Strophomenata	Productida	*Rugatia occidentalis*	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Rugatia paraindica*	2
	MNA	Brachiopoda	Strophomenata	Productida	*Rugatia paraindica*	2
	Other	Brachiopoda	Strophomenata	Productida	*Rugatia paraindica*	1
	USNM	Brachiopoda	Strophomenata	Productida	*Rugatia paraindica*	3
	Other	Brachiopoda	Strophomenata	Productida	*Rugatia* sp.	1
	GRCA	Brachiopoda	Strophomenata	Productida	Undetermined	1
	GRCA	Brachiopoda	Strophomenata	Productida	*Waagenoconcha irginae*	9
	GRCA	Brachiopoda	Strophomenata	Productida	*Waagenoconcha* sp.	5
	Other	Brachiopoda	Strophomenata	Productida	*Waagenoconcha* sp.	1
	GRCA	Brachiopoda	Undetermined	Undetermined	Undetermined	9
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	MNA	Brachiopoda	Undetermined	Undetermined	Undetermined	2

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	Other	Brachiopoda	Undetermined	Undetermined	Undetermined	1
	Other	Bryozoa	Stenolaemata	Cryptostomida	*Girtypora maculata*	1
	Other	Bryozoa	Stenolaemata	Cryptostomida	*Rhabdomeson* sp.	1
	GRCA	Bryozoa	Stenolaemata	Cryptostomida	*Rhombopora lepidodendroides*	3
	Other	Bryozoa	Stenolaemata	Cryptostomida	*Rhombopora lepidodendroides*	1
	Other	Bryozoa	Stenolaemata	Cryptostomida	*Streblotrypa sp.*	1
	GRCA	Bryozoa	Stenolaemata	Cystoporida	*Dichotrypa* sp.	1
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Fistulipora* aff. *“F. arizonensis”*	1
	GRCA	Bryozoa	Stenolaemata	Cystoporida	*Fistulipora* sp.	3
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Fistulipora* sp.	2
	Other	Bryozoa	Stenolaemata	Cystoporida	*Fistulipora* sp.	2
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* aff. “*M. robusta”*	13
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* aff. *M. tenuis*	1
	Other	Bryozoa	Stenolaemata	Cystoporida	*Meekopora parilis*	1
	GRCA	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* sp.	2
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* sp.	3
	Other	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* sp.	1
	MNA	Bryozoa	Stenolaemata	Cystoporida	*Meekopora* sp. aff. *M. tenuis*	1
	Other	Bryozoa	Stenolaemata	Fenestrida	*Bicorbis arizonica*	1
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Chasmatopora* sp.	2
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Fenestella* sp.	1
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Polypora* aff. *P. spinulifera*	5
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Polypora* sp.	2
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Polypora spinulifera*	4
	Other	Bryozoa	Stenolaemata	Fenestrida	*Polypora spinulifera*	1
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Septopora biserialis*	3
	Other	Bryozoa	Stenolaemata	Fenestrida	*Septopora biserialis*	1
	GRCA	Bryozoa	Stenolaemata	Fenestrida	*Septopora* sp.	9
	Other	Bryozoa	Stenolaemata	Fenestrida	*Septopora* sp.	1
	Other	Bryozoa	Stenolaemata	Fenestrida	Undetermined	1
	MNA	Bryozoa	Stenolaemata	Trepostomatida	*Bascomella subsphaerica*	3

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	Other	Bryozoa	Stenolaemata	Trepostomatida	*Bascomella subsphaerica*	1
	Other	Bryozoa	Stenolaemata	Trepostomatida	*Stenodiscus* sp.	1
	MNA	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora* aff. *“S. diagonalis”*	4
	MNA	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora* aff. “*S. kaibabensis”*	9
	MNA	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora* aff. *“S. polygona”*	5
	MNA	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora intercalaris*	1
	GRCA	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora* sp.	6
	Other	Bryozoa	Stenolaemata	Trepostomatida	*Stenopora* sp.	2
	Other	Bryozoa	Undetermined	Fenestrida	Undetermined	1
	MNA	Bryozoa	Undetermined	Undetermined	*Timanodyctia* sp.	1
	MNA	Bryozoa	Undetermined	Undetermined	Undetermined	5
	Other	Bryozoa	Undetermined	Undetermined	Undetermined	1
	GRCA	Cnidaria	Anthozoa	Stauriida	*Lophophyllum* sp.	12
	Other	Cnidaria	Anthozoa	Stauriida	*Lophophyllum* sp.	2
	Other	Cnidaria	Anthozoa	Stauriida	Undetermined	1
	USNM	Cnidaria	Staurozoa?	Conulatae	*Conularia kaibabensis*	1
	GRCA	Cnidaria	Undetermined	Undetermined	Undetermined	32
	MNA	Cnidaria	Undetermined	Undetermined	Undetermined	2
	GRCA	Echinodermata	Crinoidea	Undetermined	Undetermined	79
	MNA	Echinodermata	Crinoidea	Undetermined	Undetermined	3
	Other	Echinodermata	Crinoidea	Undetermined	Undetermined	1
	GRCA	Echinodermata	Echinoidea	Not assigned	“*Echinocrinus*?” aff. *“E. coloradensis”*	1
	MNA	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp.	1
	Other	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp.	1
	GRCA	Echinodermata	Echinoidea	Not assigned	*Archaeocidaris* sp. (including *Echinocrinus* sp.)	10
	GRCA	Echinodermata	Undetermined	Undetermined	Undetermined	8
	Other	Mollusca	Bivalvia	Cardiida	*Astartella gurleyi*	1
	GRCA	Mollusca	Bivalvia	Cardiida	*Astartella* sp.	12
	GRCA	Mollusca	Bivalvia	Cardiida	*Astartella subquadrata*	10
	MNA	Mollusca	Bivalvia	Cardiida	*Astartella subquadrata*	1

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	GRCA	Mollusca	Bivalvia	Cardiida	*Permophorus albequus*	4
	MNA	Mollusca	Bivalvia	Cardiida	*Permophorus albequus*	1
	GRCA	Mollusca	Bivalvia	Cardiida	*Permophorus* sp.	12
	Other	Mollusca	Bivalvia	Cardiida	*Permophorus* sp.	1
	USNM	Mollusca	Bivalvia	Cardiida	*Wilkingia wyomingensis*	1
	GRCA	Mollusca	Bivalvia	Modiomorphida	*Modiomorpha* sp.	2
	GRCA	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	23
	Other	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	3
	MNA	Mollusca	Bivalvia	Pectinida	*Aviculopecten* sp.	2
	MNA	Mollusca	Bivalvia	Pectinida	*Aviculopecten? (Pseudomonotis?)* sp.	1
	MNA	Mollusca	Bivalvia	Myalinida	*Myalina* (*Myalina*) sp.	2
	GRCA	Mollusca	Bivalvia	Nuculanida	*Nucula levatiforme*	1
	GRCA	Mollusca	Bivalvia	Nuculanida	*Nuculana* sp.	1
	Other	Mollusca	Bivalvia	Nuculanida	*Nuculana?* sp.	1
	GRCA	Mollusca	Bivalvia	Nuculanida	*Yoldiella lucida*	6
	Other	Mollusca	Bivalvia	Ostreida	*Bakewellia parva*	1
	GRCA	Mollusca	Bivalvia	Ostreida	*Pteria* sp.	3
	Other	Mollusca	Bivalvia	Ostreida	*Pteria* sp.	1
	Other	Mollusca	Bivalvia	Pectinida	*Acanthopecten coloradoensis*	1
	GRCA	Mollusca	Bivalvia	Pectinida	*Acanthopecten coloradoensis*	5
	GRCA	Mollusca	Bivalvia	Pectinida	*Deltopecten caneyanus*	17
	GRCA	Mollusca	Bivalvia	Pectinida	*Deltopecten* sp.	11
	GRCA	Mollusca	Bivalvia	Pectinida	*Pecten* sp.	9
	MNA	Mollusca	Bivalvia	Pectinida	*Pseudomonotis* sp.	3
	GRCA	Mollusca	Bivalvia	Pectinida	*Pseudomonotis* sp.	1
	GRCA	Mollusca	Bivalvia	Pectinida	*Pterinopecten* sp.	1
	MNA	Mollusca	Bivalvia	Pectinida	Undetermined	1
	GRCA	Mollusca	Bivalvia	Pholadomyida	*Allorisma capax*	12
	GRCA	Mollusca	Bivalvia	Pholadomyida	*Allorisma* sp.	6
	Other	Mollusca	Bivalvia	Protobranchia	*Solemya* sp.	1
	GRCA	Mollusca	Bivalvia	Protobranchia	*Solemya trapezoides*	32

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	GRCA	Mollusca	Bivalvia	Trigoniida	*Kaibabella curvilenata*	1
	GRCA	Mollusca	Bivalvia	Trigoniida	*Schizodus canalis*	1
	GRCA	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	176
	Other	Mollusca	Bivalvia	Trigoniida	*Schizodus* sp.	1
	GRCA	Mollusca	Bivalvia	Undetermined	Undetermined	447
	MNA	Mollusca	Bivalvia	Undetermined	Undetermined	4
	Other	Mollusca	Bivalvia	Undetermined	Undetermined	1
	Other	Mollusca	Cephalopoda	Nautilida	*Domatoceras bradyi*	1
	Other	Mollusca	Cephalopoda	Nautilida	*Domatoceras simplex*	1
	GRCA	Mollusca	Cephalopoda	Nautilida	*Domatoceras* sp.	2
	GRCA	Mollusca	Cephalopoda	Nautilida	*Metacoceras* sp.	1
	GRCA	Mollusca	Cephalopoda	Nautilida	*Stearoceras rotundatum*	5
	Other	Mollusca	Cephalopoda	Nautilida	*Stearoceras rotundatum*	1
	GRCA	Mollusca	Cephalopoda	Nautilida	*Stearoceras sanandreasense*	8
	Other	Mollusca	Cephalopoda	Nautilida	*Stearoceras sanandreasense*	1
	GRCA	Mollusca	Cephalopoda	Nautilida	*Stearoceras* sp.	13
	GRCA	Mollusca	Cephalopoda	Orthocerida	*Orthoceras* sp.	1
	Other	Mollusca	Cephalopoda	Orthocerida	*Orthoceras* sp.	1
	GRCA	Mollusca	Cephalopoda	Undetermined	Undetermined	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Bellerophon deflectus*	24
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Bellerophon majusculus*	1
	Other	Mollusca	Gastropoda	Bellerophontida	*Bellerophon majusculus*	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Bellerophon* sp.	90
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Bucanopsis* sp.	40
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Euphemites aequisulcatus*	1
	Other	Mollusca	Gastropoda	Bellerophontida	*Euphemites* cf. *E. carbonarius*	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Euphemites* sp.	36
	Other	Mollusca	Gastropoda	Bellerophontida	*Euphemites* sp.	1
	GRCA	Mollusca	Gastropoda	Bellerophontida	*Warthia* sp.	1
	GRCA	Mollusca	Gastropoda	Cycloneritida	*Naticopsis kaibabensis*	3
	GRCA	Mollusca	Gastropoda	Cycloneritida	*Naticopsis* sp.	2

Appendix Table A-4. *Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	Other	Mollusca	Gastropoda	Cycloneritida	*Naticopsis* sp.	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Euomphalus kaibabensis*	2
	MNA	Mollusca	Gastropoda	Euomphalina	*Euomphalus kaibabensis*	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	25
	MNA	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	1
	Other	Mollusca	Gastropoda	Euomphalina	*Euomphalus* sp.	1
	GRCA	Mollusca	Gastropoda	Euomphalina	*Glyptospira cristulata*	6
	GRCA	Mollusca	Gastropoda	Murchisoniina	*Ananias franciscanus*	6
	GRCA	Mollusca	Gastropoda	Murchisoniina	*Ananias franciscanus*	14
	GRCA	Mollusca	Gastropoda	Murchisoniina	*Goniospira* sp.	1
	Other	Mollusca	Gastropoda	Murchisoniina	*Goniospira* sp.	1
	GRCA	Mollusca	Gastropoda	Not assigned	*Orthonema* sp.	1
	GRCA	Mollusca	Gastropoda	Not assigned	*Orthonema striatonodosum*	4
	GRCA	Mollusca	Gastropoda	Pleurotomariida	*Murchisonia geminocarinata*	2
	Other	Mollusca	Gastropoda	Pleurotomariida	*Murchisonia?* cf. *M. terebra*	1
	GRCA	Mollusca	Gastropoda	Pleurotomariida	*Pleurotomaria* sp.	8
	Other	Mollusca	Gastropoda	Pleurotomariida	*Pleurotomaria* sp.	1
	GRCA	Mollusca	Gastropoda	Undetermined	Undetermined	1
	MNA	Mollusca	Gastropoda	Undetermined	Undetermined	1
	Other	Mollusca	Gastropoda	Undetermined	Undetermined	1
	GRCA	Mollusca	Scaphopoda	Dentaliida	*Dentalium* sp.	22
	GRCA	Mollusca	Scaphopoda	Dentaliida	*Plagioglypta* sp.	12
	GRCA	Mollusca	Scaphopoda	Dentaliida	*Prodentalium canna*	10
	Other	Mollusca	Scaphopoda	Dentaliida	*Prodentalium canna*	1
	GRCA	Mollusca	Scaphopoda	Undetermined	Undetermined	28
	Other	Mollusca	Undetermined	Undetermined	Undetermined	1
	GRCA	Porifera	Demospongea	Lithistida	*Actinocoelia maeandrina*	1
	Other	Porifera	Demospongea	Lithistida	*Actinocoelia maeandrina*	1
	MNA	Porifera	Demospongea	Lithistida	*Actinocoelia* sp.	1
	Other	Porifera	Demospongea	Lithistida	*Actinocoelia* sp.	1
	GRCA	Porifera	Undetermined	Undetermined	Undetermined	29

***Appendix Table A-4**. Continued*

Unit	Source	Phylum	Class	Order	Species	#
Pk (continued)	MNA	Porifera	Undetermined	Undetermined	Undetermined	5
	Other	Porifera	Undetermined	Undetermined	Undetermined	1
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	477
Pu	MNA	Brachiopoda	Rhynchonellata	Spiriferida	*Squamularia* sp.	1
	USNM	Brachiopoda	Strophomenata	Orthotetida	*Meekella occidentalis*	1
	USNM	Brachiopoda	Strophomenata	Productida	*Rugatia paraindica*	1
	USNM	Bryozoa	Stenolaemata	Trepostomatida	*Rhombotrypella* sp.	1
	USNM	Mollusca	Bivalvia	Cardiida	*Wilkingia wyomingensis*	2
	USNM	Mollusca	Gastropoda	Euophalina	*Glyptospira cristulata*	8
	GRCA	Undetermined	Undetermined	Undetermined	Undetermined	27

Appendix B

Paleozoic Invertebrate Body Fossils From GRCA From the Literature

This appendix lists Paleozoic invertebrates which have been reported from the literature from GRCA localities with their stratigraphic occurrences and references (see the main “Literature Cited” of this article for full citations). The same taxonomic caveats discussed in appendix A apply here. As with the tables in appendix A, the tables have been split into four to improve navigation and readability: appendix table B-1, Cambrian; appendix table B-2, Devonian and Mississippian; appendix table B-3, Supai Group; and appendix table B-4, post-Supai Permian. Stratigraphic unit abbreviations are per appendix A.

Appendix Table B-1. *Cambrian invertebrate taxa reported from GRCA localities in the literature. For abbreviations see text. Continued on following page.*

Unit	Phylum	Class	Species	Reference
Ctu	Arthropoda	Ostracoda	Undetermined	Walcott, 1890
	Arthropoda	Trilobita	*Anoria* sp.	Walcott, 1890
	Arthropoda	Trilobita	*Athabaskia kanabensis*	Resser, 1945
	Arthropoda	Trilobita	*Elrathiella?* aff. *E. insueta*	Resser, 1945
	Arthropoda	Trilobita	*Glossopleura boccar*	Palmer E&R 1963/10/17; Bonde and others, 2018
	Arthropoda	Trilobita	*Glossopleura* sp.	Palmer E&R 1963/10/17; Bonde and others, 2018
	Arthropoda	Trilobita	*Glyphaspis kwaguntensis*	Resser, 1945
	Arthropoda	Trilobita	*Kochina angustata*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia mckeei*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia* sp.	Resser, 1945
	Arthropoda	Trilobita	*Olenoides* sp.	Walcott, 1890
	Arthropoda	Trilobita	*Parehmania kwaguntensis*	Bonde and others, 2018
	Arthropoda	Trilobita	*Parehmania nitida*	Resser, 1945
	Arthropoda	Trilobita	*Proehmaniella hebes*	Resser, 1945
	Arthropoda	Trilobita	*Ptarmigania* sp.	Resser, 1945
	Arthropoda	Trilobita	*Spencella diligens*	Resser, 1945
	Arthropoda	Trilobita	*Spencella* sp.	Resser, 1945
	Arthropoda	Trilobita	*Trachycheilus typicale*	Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia kanabensis*	Walcott, 1908, 1912a; Resser, 1945
	Brachiopoda	Lingulata	*Acrothele* sp.	Walcott, 1890
	Brachiopoda	Lingulata	*Lingulella* aff. *L. winona* subsp. *convexa*	Walcott, 1890; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella kanabensis*	Walcott, 1912a
	Brachiopoda	Lingulata	*Lingulella* sp.	Resser, 1945
	Brachiopoda	Lingulata	*Lingulella zetus*	Walcott, 1898, 1912a, 1916a; Resser, 1945
	Brachiopoda	Paterinata	*Iphidea ornatella*	Walcott, 1890
	Brachiopoda	Paterinata	*Micromitra (Paterina) crenistria*	Walcott, 1897, 1912a, 1916a; Resser, 1945
	Brachiopoda	Rhynchonellata	*Protorthis* sp.	Walcott, 1912a
	Problematica	Hyolitha	*Hyolithes* sp.	Walcott, 1890; Resser, 1945
Ctt	Arthropoda	Trilobita	*Olenellus* sp.	Resser, 1945

Appendix Table B-1. *Continued*

Unit	Phylum	Class	Species	Reference
Ctt	Brachiopoda	Obolellata	Undetermined	Schuchert, 1918a
Ctba	Arthropoda	Bradoriida clade	*Bradoria tontoensis*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Dielymella* aff. *D. recticardinalis* subsp. *angustata*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Dielymella appressa*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Dielymella dorsalis*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Dielymella nasuta*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Dielymella recticardinalis*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Indianites curtus*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Indianites faba*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Indianites impressus*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Indianites intermedius*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella apicalis*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella breviuscula*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella concentrica*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella leperditoides*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella limatula*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella longula*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella nitida*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella oblonga*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella obsoleta*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella pulchella*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella scitula*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella subtruncata*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Bradoriida clade	*Walcottella ventrosa*	Ulrich & Bassler, 1931; Resser, 1945
	Arthropoda	Trilobita	*Acrocephalops?* cf. *A. arizonaensis*	Resser, 1945
	Arthropoda	Trilobita	*Albertella schenki*	Resser, 1945
	Arthropoda	Trilobita	*Albertella* sp.	Schenk & Wheeler, 1942; Bonde and others, 2018
	Arthropoda	Trilobita	*Alokistocare lepida*	Schenk & Wheeler, 1942
	Arthropoda	Trilobita	*Alokistocare* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Alokistocare* sp. or *Ehmaniella* sp.	Bonde and others, 2018

Appendix Table B-1. *Continued*

Unit	**Phylum**	**Class**	**Species**	**Reference**
Ctba (continued)	Arthropoda	Trilobita	*Alokistocare?* sp.	Schenk & Wheeler, 1942
	Arthropoda	Trilobita	*Amecephalus althea*	Walcott, 1916a, 1916b; Schuchert, 1918a; Noble, 1922; Schenk & Wheeler, 1942; Resser, 1945; Foster, 2011
	Arthropoda	Trilobita	*Amecephalus* cf. *A. althea*	Schenk & Wheeler, 1942
	Arthropoda	Trilobita	*Amecephalus* cf. *A. packi*	Foster, 2011
	Arthropoda	Trilobita	*Anoria* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Anoria tontoensis*	Walcott, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1945; Foster, 2011
	Arthropoda	Trilobita	*Antagmus arizonaensis*	Resser, 1945; Bonde and others, 2018
	Arthropoda	Trilobita	*Athabaskia* sp.	Resser, 1945
	Arthropoda	Trilobita	*Ehmaniella* aff. "*E. arizonaensis*"	Resser, 1945
	Arthropoda	Trilobita	*Ehmaniella* sp.	Bonde and others, 2018
	Arthropoda	Trilobita	*Elrathia nitens*	Resser, 1945
	Arthropoda	Trilobita	*Elrathia* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Glossopleura* aff. *"G. walcotti"*	Foster, 2011
	Arthropoda	Trilobita	*Glossopleura boccar*	Walcott, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1935, 1945; Schenk & Wheeler, 1942; Palmer E&R 1963/10/17; Foster, 2011; Bonde and others, 2018
	Arthropoda	Trilobita	*Glossopleura* sp.	Resser, 1945; Elliott & Martin, 1987
	Arthropoda	Trilobita	*Glyphaspis* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Glyphaspis vulsa*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia simplex*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia* sp.	Foster, 2011
	Arthropoda	Trilobita	*Olenellus* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Olenoides* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Pachyaspis fonticola*	Resser, 1945
	Arthropoda	Trilobita	*Pachyaspis moorei*	Resser, 1945; Bonde and others, 2018
	Arthropoda	Trilobita	*Pachyaspis* sp.	Resser, 1945
	Arthropoda	Trilobita	*Parehmania kwaguntensis*	Bonde and others, 2018
	Arthropoda	Trilobita	*Parehmania* sp.	Resser, 1945
	Arthropoda	Trilobita	*Parehmania tontoensis*	Resser, 1945
	Arthropoda	Trilobita	*Proehmaniella basilica*	Bonde and others, 2018

Appendix Table B-1. Continued

Unit	Phylum	Class	Species	Reference
Ctba (continued)	Arthropoda	Trilobita	*Ptarmigania* sp.	Resser, 1945
	Arthropoda	Trilobita	*Spencia tontoensis*	Resser, 1945
	Arthropoda	Trilobita	Undetermined	Bonde and others, 2018
	Arthropoda	Trilobita	Undetermined (Olenellidae)	Palmer E&R 1963/10/17
	Arthropoda	Trilobita	*Zacanthoides* cf. *Z. walapai*	Resser, 1945
	Arthropoda	Trilobita	*Zacanthoides* sp.	Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia obscura*	Walcott, 1905, 1912a, 1916a; Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia* sp.	Schenk & Wheeler, 1942
	Brachiopoda	Kutorginata	*Nisusia?* sp.	Resser, 1945
	Brachiopoda	Lingulata	*Lingula* sp.	Strother & Beck, 2000
	Brachiopoda	Lingulata	*Lingulella acutangulus*	Walcott, 1912a; Noble, 1922
	Brachiopoda	Lingulata	*Lingulella chuarensis*	Walcott, 1898, 1912a, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1945; Foster, 2011
	Brachiopoda	Lingulata	*Lingulella euglypha*	Walcott, 1898, 1912a, 1916a; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella lineolata*	Walcott, 1898, 1912a, 1916a; Noble, 1922; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella mckeei*	Resser, 1945; Foster, 2011; Bonde and others, 2018
	Brachiopoda	Lingulata	*Lingulella* sp.	Walcott, 1890; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella spatula*	Walcott, 1902, 1912a; Noble, 1922; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella zetus*	Walcott, 1898, 1912a, 1916a; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella?* aff. *L. themis*	Walcott, 1905, 1912a; Noble, 1922; Resser, 1945
	Brachiopoda	Lingulata	*Lingulella?* cf. *L. monticula*	Frech, 1893
	Brachiopoda	Obolellata	*Obolella* aff. *O. polita*	Frech, 1893
	Brachiopoda	Obolellata	*Obolella* sp.	Frech, 1893
	Brachiopoda	Paterinata	*Dictyonina arizonaensis*	Walcott, 1912a; Noble, 1922; Resser, 1945; Bonde and others, 2018
	Brachiopoda	Paterinata	*Micromitra (Paterina) crenistria*	Walcott, 1897, 1912a, 1916a; Resser, 1945
	Brachiopoda	Paterinata	*Micromitra (Paterina) superba*	Walcott, 1897, 1912a, 1916a; Noble, 1922; Resser, 1945
	Brachiopoda	Paterinata	*Micromitra pealei*	Walcott, 1912a, 1916a
	Brachiopoda	Paterinata	*Paterina?* sp.	Resser, 1945
	Brachiopoda	Rhynchonellata	*Diraphora?* sp.	Resser, 1945
	Brachiopoda	Undetermined	Undetermined	McKee, 1945

Appendix Table B-1. *Continued*

Unit	Phylum	Class	Species	Reference
Ctba (continued)	Echinodermata	Eocrinoidea	*Eocystites* sp.	Walcott, 1916a; Noble, 1922
	Echinodermata	Eocrinoidea	*Gogia multibrachiatus*	Resser, 1945; Foster, 2011
	Echinodermata	Eocrinoidea	*Gogia?* aff. *G. longidactylus*	Foster, 2011
	Porifera	Archaeocyatha	Undetermined	Resser, 1945
	Problematica	Coeloscleritophora	*Chancelloria* sp.	Elliott & Martin, 1987
	Problematica	Hyolitha	*Hyolithes* sp.	Walcott, 1916a; Noble, 1922; Schenk & Wheeler, 1942; Resser, 1945; Foster, 2011; Bonde and others, 2018
	Problematica	Undetermined	*Margaretia?* sp.	Schenk & Wheeler, 1942
	Problematica	Undetermined	*Tontoia kwaguntensis*	Walcott, 1912b; Resser, 1945
Ctm	Arthropoda	Trilobita	*Alokistocare* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Anomocarella* sp.	Noble, 1922
	Arthropoda	Trilobita	*Anoria* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Athabaskia* sp.	Resser, 1945
	Arthropoda	Trilobita	*Bathyurus?* sp.	Noble, 1922
	Arthropoda	Trilobita	*Bolaspis aemula*	Resser, 1945
	Arthropoda	Trilobita	*Bolaspis*? sp.	Resser, 1945
	Arthropoda	Trilobita	*Dorypyge* sp.	Stoyanow, 1936
	Arthropoda	Trilobita	*Glossopleura* sp.	Schenk & Wheeler, 1942; Resser, 1945; Palmer E&R 1963/10/17; Bonde and others, 2018
	Arthropoda	Trilobita	*Glossopleura* sp. or *Anoria* sp.	Resser, 1945
	Arthropoda	Trilobita	*Glyphaspis* sp.	Schenk & Wheeler, 1942; Resser, 1945
	Arthropoda	Trilobita	*Glyphaspis tecta*	Resser, 1945
	Arthropoda	Trilobita	*Glyphaspis?* sp.	Resser, 1945
	Arthropoda	Trilobita	*Kootenia havasuensis*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia mckeei*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia schenki*	Schenk & Wheeler, 1942; Resser, 1945; Palmer E&R 1963/10/17; Bonde and others, 2018
	Arthropoda	Trilobita	*Kootenia simplex*	Resser, 1945
	Arthropoda	Trilobita	*Kootenia* sp.	Schenk & Wheeler, 1942; Resser, 1945; Palmer E&R 1963/10/17
	Arthropoda	Trilobita	*Kootenia?* sp.	Resser, 1945
	Arthropoda	Trilobita	*Neolenus* sp.	Noble, 1922

Appendix Table B-1. *Continued*

Unit	Phylum	Class	Species	Reference
Ctm (continued)	Arthropoda	Trilobita	*Pachyaspis moorei*	Resser, 1945; Bonde and others, 2018
	Arthropoda	Trilobita	*Pagodia?* sp.	Noble, 1922
	Arthropoda	Trilobita	*Ptychoparia* sp.	Walcott, 1883, 1890; Noble, 1922
	Arthropoda	Trilobita	*Ptychoparia?* sp.	Noble, 1922
	Arthropoda	Trilobita	*Saukia* sp.	Noble, 1922
	Arthropoda	Trilobita	*Spencella erosa*	Resser, 1945
	Arthropoda	Trilobita	*Spencella porcata*	Schenk & Wheeler, 1942; Resser, 1945; Palmer E&R 1963/10/17; Bonde and others, 2018
	Arthropoda	Trilobita	*Spencella* sp.	Resser, 1945
	Arthropoda	Trilobita	Undetermined	Stoyanow, 1936; Palmer E&R 1963/10/17
	Arthropoda	Trilobita	*Zacanthoides* sp.	Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia* aff. *N. noblei*	Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia noblei*	Walcott, 1924; Resser, 1945
	Brachiopoda	Kutorginata	*Nisusia* sp.	Palmer E&R 1963/10/17; Bonde and others, 2018
	Brachiopoda	Kutorginata	*Nisusia?* sp.	Palmer E&R 1963/10/17
	Brachiopoda	Lingulata	*Acrotreta?* sp.	Noble, 1922
	Brachiopoda	Lingulata	*Discina* sp.	Noble, 1922
	Brachiopoda	Lingulata	*Lingula* sp.	Noble, 1922
	Brachiopoda	Lingulata	*Lingulella (Lingulepis)* sp.	Walcott, 1883, 1890; Noble, 1922
	Brachiopoda	Lingulata	*Lingulepis prima*	Noble, 1922
	Brachiopoda	Lingulata	*Trematis* sp.	Noble, 1922
	Brachiopoda	Paterinata	*Dictyonina* sp.	Resser, 1945
	Brachiopoda	Rhynchonellata	*Finkelnburgia* sp.	Noble, 1922
	Brachiopoda	Rhynchonellata	*Syntrophia* sp.	Noble, 1922
	Brachiopoda	Strophomenata	*Clitambonites* sp.	Noble, 1922
	Brachiopoda	Undetermined	Undetermined	McKee, 1945
	Mollusca	Helcionelloida	*Helcionella* sp.	Palmer E&R 1963/10/17; Bonde and others, 2018
	Porifera	Archaeocyatha	Undetermined	Resser, 1945
	Problematica	Coeloscleritophora	*Chancelloria* cf. *C. eros*	Schenk & Wheeler, 1942
	Problematica	Coeloscleritophora	*Chancelloria?* sp.	Resser, 1945
	Problematica	Hyolitha	*Hyolithes* aff. *H. primordialis*	Noble, 1922

Appendix Table B-1. *Continued*

Unit	Phylum	Class	Species	Reference
Ctm (continued)	Problematica	Hyolitha	*Hyolithes* sp.	Noble, 1922; Schenk & Wheeler, 1942; Resser, 1945
	Problematica	Hyolitha	*Hyolithes?* sp.	Resser, 1945
	Problematica	Monoplacophora?	*Scenella hermitensis*	Resser, 1945

Appendix Table B-2. *Devonian and Mississippian invertebrate taxa reported from GRCA localities in the literature. For abbreviations see text.*

Unit	Phylum	Class	Species	Reference
Dtb	Brachiopoda	Undetermined	Undetermined	Walcott, 1883; Stoyanow, 1936
	Cnidaria	Anthozoa	*Streptelasma?* sp.	Schenk & Wheeler, 1942
	Cnidaria	Anthozoa	Undetermined ("cup corals")	Noble, 1922
	Cnidaria	Anthozoa	Undetermined ("cyathophylloids")	Walcott, 1883
	Mollusca	Gastropoda	Undetermined	Walcott, 1883
	Undetermined	Undetermined	Undetermined	McKee, 1969; McKee & Gutschick, 1969b, 1969e
Mr	Arthropoda	Trilobita	*Aprathia* sp.	McKee & Gutschick, 1969d, 1969f; Brezinski, 2017
	Arthropoda	Trilobita	*Breviphillipsia* sp.	Cisne, 1971
	Brachiopoda	Rhynchonellata	*Camarotoechia* sp.	Noble, 1922
	Brachiopoda	Rhynchonellata	*Camarotoechia?* sp.	Noble, 1922
	Brachiopoda	Rhynchonellata	*Composita?* sp.	Noble, 1922
	Brachiopoda	Rhynchonellata	*Dielasma* sp.	Carter and others, 2014
	Brachiopoda	Rhynchonellata	*Mirifusella* cf. *M. fortunata*	Carter and others, 2014
	Brachiopoda	Rhynchonellata	*Neospirifer striatus*	Frech, 1893
	Brachiopoda	Rhynchonellata	*Prospira* sp.	Carter and others, 2014
	Brachiopoda	Rhynchonellata	*Pugnoides* sp.	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Rhipidomella* sp.	Noble, 1922
	Brachiopoda	Rhynchonellata	*Spirifer* aff. *S. incertus*	Noble, 1922
	Brachiopoda	Rhynchonellata	*Spirifer centronatus*	Schuchert, 1918b; Noble, 1922
	Brachiopoda	Rhynchonellata	*Spirifer* cf. *Elivina occidentalis*	Grant E&R 1963/10/16; Bonde and others, 2018
	Brachiopoda	Rhynchonellata	*Spirifer redwallensis*	Carter and others, 2014
	Brachiopoda	Rhynchonellata	*Spirifer* sp.	Schuchert, 1918b; Grant E&R 1963/10/16; McKee & Gutschick, 1969d
	Brachiopoda	Rhynchonellata	*Spirifer* sp.	Grant E&R 1963/10/16
	Brachiopoda	Rhynchonellata	*Syringothyris?* sp.	Noble, 1922; Grant E&R 1963/10/16; Bonde and others, 2018
	Brachiopoda	Rhynchonellata	*Unispirifer minnewankensis*	Carter and others, 2014
	Brachiopoda	Rhynchonellata	Undetermined	McKee & Gutschick, 1969b, 1969d
	Brachiopoda	Strophomenata	*Floweria chemungensis*	Noble, 1922
	Brachiopoda	Strophomenata	*Leptagonia* sp.	McKee & Gutschick, 1969b
	Brachiopoda	Strophomenata	*Tomiproductus gallatinensis*	Carter and others, 2014

***Appendix Table B-2**. Continued*

Unit	Phylum	Class	Species	Reference
Mr (continued)	Brachiopoda	Strophomenata	Undetermined	McKee & Gutschick, 1969b, 1969d, 1969e
	Brachiopoda	Undetermined	Undetermined	McKee & Gutschick, 1969b, 1969d
	Bryozoa	Stenolaemata	*Cystodictya* sp.	McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Dichotrypa* sp.	Duncan, 1969; McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Fenestella* sp.	McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Fenestralia?* sp.	McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Penniretepora* sp.	McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Polypora* sp.	Schuchert, 1918b; McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	*Polypora*? sp.	McKee & Gutschick, 1969d
	Bryozoa	Stenolaemata	Undetermined	McKee & Gutschick, 1969d
	Bryozoa	Undetermined	Undetermined	McKee & Gutschick, 1969e
	Cnidaria	Anthozoa	*Amplexizaphrentis* sp.	Sando & Bamber, 1985
	Cnidaria	Anthozoa	*Cladochonus?* sp.	Noble, 1922
	Cnidaria	Anthozoa	*Clisiophyllum* sp.	Schuchert, 1918b
	Cnidaria	Anthozoa	*Diphyphyllum?* cf. *Lithostrotion* sp.	Noble, 1922
	Cnidaria	Anthozoa	*Diphyphyllum?* sp.	Noble, 1922
	Cnidaria	Anthozoa	*Dorlodotia* cf. *D. inconstans*	Easton & Gutschick, 1953
	Cnidaria	Anthozoa	*Dorlodotia inconstans*	Easton & Gutschick, 1953
	Cnidaria	Anthozoa	*Dorlodotia* sp.	Sando & Bamber, 1985
	Cnidaria	Anthozoa	*Homalophyllites paucicinctus*	Easton & Gutschick, 1953
	Cnidaria	Anthozoa	*Homalophyllites subcrassus*	McKee & Gutschick, 1969d; Sando, 1969
	Cnidaria	Anthozoa	*Menophyllum excavatum*	Schuchert, 1918b
	Cnidaria	Anthozoa	*Sychnoelasma* sp.	Sando & Bamber, 1985
	Cnidaria	Anthozoa	*Syringopora aculeata*	McKee & Gutschick, 1969d; Sando, 1969
	Cnidaria	Anthozoa	*Syringopora* aff. *S. surcularia*	Sando E&R 1963/10/14
	Cnidaria	Anthozoa	*Syringopora* cf. *S. surcularia*	Schuchert, 1918b
	Cnidaria	Anthozoa	*Syringopora* sp.	McKee & Gutschick, 1969d; Sando & Bamber, 1985
	Cnidaria	Anthozoa	*Syringopora surcularia*	Sando E&R 1963/10/14; Bonde and others, 2018
	Cnidaria	Anthozoa	Undetermined	McKee & Gutschick, 1969d, 1969e
	Cnidaria	Anthozoa	*Vesiculophyllum incrassatum*	Easton & Gutschick, 1953; Sando E&R 1963/10/14, 1969; McKee & Gutschick, 1969d; Bonde and others, 2018

Appendix Table B-2. *Continued*

Unit	Phylum	Class	Species	Reference
Mr (continued)	Cnidaria	Anthozoa	*Vesiculophyllum* sp.	Sando & Bamber, 1985
	Cnidaria	Anthozoa	*Zaphrentites persimilis*	Sando E&R 1963/10/14; Bonde and others, 2018
	Echinodermata	Blastoidea	*Pentremites* sp.	McKee & Gutschick, 1969d; Macurda, 1969
	Echinodermata	Crinoidea	Undetermined	Frech, 1893; Schuchert, 1918b; Noble, 1922; McKee & Gutschick, 1969b, 1969d, 1969e; Beus, 1987
	Foraminifera	Fusulinata	*Calcisphaera* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Earlandia* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra* aff. *E. gutschicki*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra* aff. *E. tantala*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra* aff. *E. trachida*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra kleina*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra tantula*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Endothyra trachida*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Eoendothyranopsis* aff. *E. spiroides*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Eoendothyranopsis spiroides*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Globoendothyra baileyi*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Globoendothyra baileyi* subsp*. poloumera*	McKee & Gutschick, 1969d; Skipp, 1969
	Foraminifera	Fusulinata	*Inflatoendothyra eospiroides*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Paracaligella?* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Paramillerella?* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Pohlia henbesti*	Skipp and others, 1966; McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Septabrunsiina* (*Spinobrunsiina*) *parakrainica*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Septabrunsiina* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Septaglomospiranella chernoussovensis*	Skipp and others, 1966; McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Septaglomospiranella rossi*	McKee & Gutschick, 1969d; Skipp, 1969
	Foraminifera	Fusulinata	*Septaglomospiranella* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Septatournayella*? sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Spinobrunsiina* aff. *S. torquida*	McKee & Gutschick, 1969d

Appendix Table B-2. *Continued*

Unit	Phylum	Class	Species	Reference
Mr (continued)	Foraminifera	Fusulinata	*Spinobrunsiina torquida*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Spinoendothyra* aff. *S. spinosa*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Spinoendothyra spinosa*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Spiroplectamminoides?* cf. *Spiroplectammina parva*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tournayella* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tournayella?* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tuberendothyra paratumula*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tuberendothyra* sp.	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tuberendothyra* sp.*?*	McKee & Gutschick, 1969d
	Foraminifera	Fusulinata	*Tuberendothyra tuberculata*	McKee & Gutschick, 1969d
	Mollusca	Cephalopoda	*Rayonnoceras* sp.	Breed, 1969
	Mollusca	Gastropoda	*Bellerophon* sp.	Noble, 1922
	Mollusca	Gastropoda	*Euconospira* aff. *"E. montezuma"*	Bonde and others, 2018
	Mollusca	Gastropoda	*Euomphalus?* sp.	Noble, 1922
	Mollusca	Gastropoda	*Euphemites?* sp.	Bonde and others, 2018
	Mollusca	Gastropoda	Undetermined	McKee & Gutschick, 1969d; Yochelson, 1969
	Undetermined	Undetermined	Undetermined	McKee, 1969; McKee & Gutschick, 1969b, 1969e
Msc	Arthropoda	Trilobita	*Paladin* cf. *P. chesterensis*	Beus, 1999
	Arthropoda	Trilobita	*Paladin* sp.	Gordon E&R 1979/1/23; Beus, 1999
	Brachiopoda	Rhynchonellata	*Anthracospirifer* aff. *A. curvilateralis*	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Anthracospirifer bifurcatus*	Gordon E&R 1973/1/3
	Brachiopoda	Rhynchonellata	*Anthracospirifer* cf. *A. curvilateralis*	Gordon E&R 1979/1/23
	Brachiopoda	Rhynchonellata	*Anthracospirifer curvilateralis*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Anthracospirifer* sp.	Gordon E&R 1979/1/23; Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Beecheria* cf. *B. arkansanum*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Beecheria* sp.	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Brachythyris (Spirifer) subcardiiformis*	Gordon E&R 1973/1/3
	Brachiopoda	Rhynchonellata	*Cleiothyridina* sp.	Beus, 1999
	Brachiopoda	Rhynchonellata	*Composita gibbosa*	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Composita laevis*	Beus, 1999

Appendix Table B-2. *Continued*

Unit	Phylum	Class	Species	Reference
Msc (continued)	Brachiopoda	Rhynchonellata	*Composita ovata*	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Composita* sp.	Gordon E&R 1979/1/23
	Brachiopoda	Rhynchonellata	*Composita subquadrata*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Cranaena* sp.	Gordon E&R 1979/1/23
	Brachiopoda	Rhynchonellata	*Eumetria* sp.	Beus, 1999
	Brachiopoda	Rhynchonellata	*Flexaria* sp.	Beus, 1999
	Brachiopoda	Rhynchonellata	*Leiorhynchoidea carbonifera*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Leiorhynchoidea* sp.	Gordon E&R 1979/1/23
	Brachiopoda	Rhynchonellata	*Macropotamorhynchus* cf. *M. purduei*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Pugnoides* sp.	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Rhipidomella nevadensis*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Rotaia neogenes*	Beus, 1999
	Brachiopoda	Rhynchonellata	*Schizophoria* sp.	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Torynifer* aff. *T. setiger*	Billingsley & McKee, 1982
	Brachiopoda	Rhynchonellata	*Torynifer* sp.	Beus, 1999
	Brachiopoda	Rhynchonellata	Undetermined	Billingsley & Beus, 1999a; Beus, 1999; Bonde and others, 2018
	Brachiopoda	Strophomenata	*Inflatia* aff. *I. clydensis*	Gordon E&R 1979/1/23; Billingsley & McKee, 1982
	Brachiopoda	Strophomenata	*Inflatia* sp.	Gordon E&R 1979/1/23
	Brachiopoda	Strophomenata	*Inflatia* sp. or *Sandia* sp.	Billingsley & McKee, 1982
	Brachiopoda	Strophomenata	*Inflatia?* sp.	Gordon E&R 1973/1/3
	Brachiopoda	Strophomenata	*Orthotetes* sp.	Beus, 1999
	Brachiopoda	Strophomenata	*Ovatia* sp.	Gordon E&R 1979/1/23; Billingsley & McKee, 1982
	Brachiopoda	Strophomenata	Undetermined	Billingsley & McKee, 1982; Beus, 1999; Billingsley & Beus, 1999a
	Brachiopoda	Undetermined	Undetermined	Billingsley & McKee, 1982; Billingsley & Beus, 1985, 1999a; Hodnett & Elliott, 2018
	Bryozoa	Fenestrida	*Archimedes* sp.	Beus, 1999
	Bryozoa	Undetermined	Undetermined	Billingsley & Beus, 1985, 1999a; Beus, 1999; Hodnett & Elliott, 2018
	Cnidaria	Anthozoa	*Amplexus* sp.	Beus, 1999
	Cnidaria	Anthozoa	*Barytichisma* sp.	Beus, 1999

Appendix Table B-2. *Continued*

Unit	Phylum	Class	Species	Reference
Msc (continued)	Cnidaria	Anthozoa	*Michelinia* sp.	Billingsley & McKee, 1982
	Cnidaria	Anthozoa	Undetermined	Billingsley & Beus, 1985; Hodnett & Elliott, 2018
	Cnidaria	Anthozoa	Undetermined (Rugosa)	Billingsley & Beus, 1999a
	Echinodermata	Asteroidea	Undetermined	Beus, 1999
	Echinodermata	Blastoidea	*Pentremites* sp.	Beus, 1999
	Echinodermata	Crinoidea	*Cymbiocrinus* sp.	Beus, 1999
	Echinodermata	Crinoidea	Undetermined	Beus, 1999; Billingsley and Beus, 1999a; Hodnett & Elliott, 2018
	Echinodermata	Echinoidea	Undetermined	Billingsley & Beus, 1999a
	Echinodermata	Undetermined	Undetermined	Billingsley & Beus, 1985, 1999a
	Echinodermata	Undetermined	Undetermined (Pelmatozoa)	Billingsley & McKee, 1982
	Foraminifera	Undetermined	Undetermined	Gordon E&R 1979/1/23
	Mollusca	Bivalvia	*Aviculopecten* sp.	Gordon E&R 1979/1/23
	Mollusca	Bivalvia	*Edmondia* sp.	Beus, 1999
	Mollusca	Bivalvia	*Schizodus* sp.	Billingsley & McKee, 1982
	Mollusca	Bivalvia	*Septimyalina* sp.	Beus, 1999
	Mollusca	Bivalvia	*Septimyalina*? sp.	Gordon E&R 1979/1/23
	Mollusca	Bivalvia	Undetermined	Billingsley & McKee, 1982
	Mollusca	Bivalvia	Undetermined	Billingsley & McKee, 1982
	Mollusca	Gastropoda	*Bellazona* sp.	Beus, 1999
	Mollusca	Gastropoda	*Bellerophon* (*Bellerophon*) sp.	Gordon E&R 1979/1/23; Billingsley & McKee, 1982
	Mollusca	Gastropoda	*Bellerophon* sp.	Beus, 1999
	Mollusca	Gastropoda	*Euomphalus* sp.	Gordon E&R 1979/1/23
	Mollusca	Gastropoda	*Glabrocingulum* sp.	Beus, 1999
	Mollusca	Gastropoda	*Loxonema* sp.	Beus, 1999
	Mollusca	Gastropoda	*Straparollus?* sp.	Billingsley & McKee, 1982
	Mollusca	Undetermined	Undetermined	Billingsley & Beus, 1985
	Undetermined	Undetermined	Undetermined	Billingsley & Beus, 1985; Beus, 1995

Appendix Table B-3. *Supai Group invertebrate taxa reported from GRCA localities in the literature. For abbreviations see text. Continued on following page.*

Unit	Phylum	Class	Species	Reference
IPswa	Arthropoda	Trilobita	*Paladin* sp.	Gordon, 1982; McKee, 1982a
	Arthropoda	Trilobita	*Paladin?* aff. librogenae	Gordon, 1982; McKee, 1982a
	Arthropoda	Trilobita	*Paladin?* sp.	Gordon, 1982
	Brachiopoda	Lingulata	*Lingula* sp.	Gordon, 1982; McKee, 1982a, 1982b
	Brachiopoda	Lingulata	*Orbiculoidea* aff. *O. meekana*	Gordon, 1982
	Brachiopoda	Lingulata	*Orbiculoidea meekana*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Lingulata	*Orbiculoidea* sp.	McKee, 1982b
	Brachiopoda	Rhynchonellata	*Anthracospirifer newberryi*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Anthracospirifer tanoensis*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Composita ovata*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Composita* sp.	Gordon, 1982; McKee, 1982a, 1982b
	Brachiopoda	Rhynchonellata	*Composita subtilita*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Cupularostrum?* sp.	Gordon, 1982
	Brachiopoda	Rhynchonellata	*Punctospirifer transversus*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Reticulariina gonionota*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Schizophoria* aff. S. *altirostris*	Gordon, 1982
	Brachiopoda	Rhynchonellata	*Schizophoria altirostris*	Gordon, 1982; McKee, 1982a
	Brachiopoda	Rhynchonellata	*Spirifer* sp.	McKee, 1982b
	Brachiopoda	Rhynchonellata	*Spiriferina?* sp.	McKee, 1982b
	Brachiopoda	Strophomenata	*Derbyia* aff. *D. robusta*	Gordon, 1982
	Brachiopoda	Strophomenata	*Derbyia* sp.	McKee, 1982a, 1982b
	Brachiopoda	Strophomenata	*Orthotetes* sp.	Gordon, 1982; McKee, 1982a
	Brachiopoda	Strophomenata	Undetermined	McKee, 1982a, 1982b
	Bryozoa	Stenolaemata	*Cystiodictya?* sp.	Gordon, 1982; McKee, 1982a
	Bryozoa	Stenolaemata	*Fenestella* sp.	Gordon, 1982; McKee, 1982a
	Bryozoa	Stenolaemata	Undetermined	Gordon, 1982; McKee, 1982a
	Bryozoa	Undetermined	Undetermined	McKee, 1982b
	Cnidaria	Anthozoa	*Michelinia* sp.	Gordon, 1982; McKee, 1982a
	Cnidaria	Anthozoa	Undetermined	McKee, 1982b
	Cnidaria	Staurozoa	Undetermined (Conularia)	Gordon, 1982; McKee, 1982a

Appendix Table B-3. *Continued*

Unit	Phylum	Class	Species	Reference
IPsw**a** (continued)	Echinodermata	Crinoidea	Undetermined	McKee, 1982b; Billingsley & Beus, 1999a
	Echinodermata	Undetermined	Undetermined	McKee, 1982a
	Foraminifera	Fusulinata	*Fusulinella* sp.	McKee, 1982a, 1982b
	Foraminifera	Fusulinata	*Pseudostaffella* sp.	McKee, 1982a, 1982b
	Mollusca	Bivalvia	*Aviculopecten* aff. *A. gravidus*	Gordon, 1982
	Mollusca	Bivalvia	*Aviculopecten gravidus*	Gordon, 1982; McKee, 1982a
	Mollusca	Bivalvia	*Aviculopecten* sp.	Gordon, 1982; McKee, 1982a
	Mollusca	Bivalvia	*Leptodesma* sp.	Gordon, 1982; McKee, 1982a
	Mollusca	Bivalvia	*Myalina* sp.	Gordon, 1982; McKee, 1982a
	Mollusca	Bivalvia	*Oriocrassatella* sp.	Gordon, 1982
	Mollusca	Bivalvia	*Permophorus* sp.	McKee, 1938
	Mollusca	Bivalvia	*Promytilus* sp.	Gordon, 1982; McKee, 1982a
	Mollusca	Bivalvia	*Schizodus* sp.	Gordon, 1982
	Mollusca	Bivalvia	Undetermined	Gordon, 1982; McKee, 1982a
	Mollusca	Gastropoda	*Euomphalus* sp.	Gordon, 1982
	Mollusca	Gastropoda	*Straparollus* sp.	McKee, 1982a
	Mollusca	Gastropoda	Undetermined	Gordon, 1982; McKee, 1982a, 1982b; Billingsley & Beus, 1999a
IPsm	Arthropoda	Ostracoda	Undetermined	McKee, 1982a
	Bryozoa	Undetermined	Undetermined	McKee, 1982b
	Echinodermata	Undetermined	Undetermined	McKee, 1982a
	Foraminifera	Fusulinata	*Endothyra media*	McKee, 1982a
	Foraminifera	Fusulinata	*Endothyra* sp.	McKee, 1982c
	Foraminifera	Fusulinata	*Endothyra teres*	McKee, 1982a
	Foraminifera	Fusulinata	*Eoschubertella* sp.	McKee, 1982a, 1982b
	Foraminifera	Fusulinata	*Fusulinella* sp.	McKee, 1982a, 1982b
	Foraminifera	Fusulinata	*Pseudostaffella* sp.	McKee, 1982a, 1982b
	Foraminifera	Fusulinata	*Schubertella* sp.	McKee, 1982a, 1982b
	Foraminifera	Fusulinata	Undetermined	McKee, 1982b, 1982c
	Foraminifera	Undetermined	Undetermined	McKee, 1982a
	Undetermined	Undetermined	Calcisphere bioclasts	McKee, 1982a
IPswe	Bryozoa	Undetermined	Undetermined	McKee, 1982b

Appendix Table B-3. *Continued*

Unit	Phylum	Class	Species	Reference
IPswe (continued)	Echinodermata	Undetermined	Undetermined	Gordon, 1982
	Foraminifera	Fusulinata	Undetermined	McKee, 1982b, 1982c
	Foraminifera	Undetermined	Undetermined	McKee, 1982a
Pse	Bryozoa	Undetermined	Undetermined	McKee, 1982b
	Cnidaria	Undetermined	Undetermined	McKee, 1982a
	Echinodermata	Undetermined	Undetermined	McKee, 1982a
	Foraminifera	Fusulinata	*Schubertella* sp.	McKee, 1982a
	Foraminifera	Undetermined	Undetermined	McKee, 1982a

Appendix Table B-4. *Post-Supai Group Permian invertebrate taxa reported from GRCA localities in the literature. For abbreviations see text. Continued on following page.*

Unit	Phylum	Class	Species	Reference
Ph	Arthropoda	Subphylum Chelicerata	*Hastimima?* sp.	White, 1929
	Arthropoda	Insecta	*Tupus gilmorei*	Carpenter, 1927; White, 1929
	Arthropoda	Insecta	*Tupus whitei*	Carpenter, 1928; White, 1929
	Arthropoda	Insecta	Undetermined (Blattodea)	Carpenter, 1928; Spamer, 1984
	Arthropoda	Insecta	Undetermined (Odonata)	Carpenter, 1928
Pt	Arthropoda	Ostracoda	Undetermined	McKee, 1938
	Brachiopoda	Rhynchonellata	*Composita* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Peniculauris ivesi*	McKee, 1938
	Bryozoa	Undetermined	Undetermined	McKee, 1938; Sorauf & Billingsley, 1991
	Echinodermata	Crinoidea	Undetermined	McKee, 1938; Sorauf & Billingsley, 1991
	Echinodermata	Echinoidea	*Archaeocidaris* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Mollusca	Bivalvia	*Allorisma* sp.	McKee, 1938
	Mollusca	Bivalvia	*Edmondia* sp.	McKee, 1938
	Mollusca	Bivalvia	*Nuculana?* sp.	McKee, 1938
	Mollusca	Bivalvia	*Permophorus* sp.	McKee, 1938
	Mollusca	Bivalvia	*Pteria* sp.	McKee, 1938
	Mollusca	Bivalvia	*Schizodus* sp.	McKee, 1938
	Mollusca	Bivalvia	*Solemya* sp.	McKee, 1938
	Mollusca	Bivalvia	Undetermined	McKee, 1938
	Mollusca	Cephalopoda	*Domatoceras?* sp.	McKee, 1938
	Mollusca	Gastropoda	*Aclisina* sp.	McKee, 1938
	Mollusca	Gastropoda	*Bellerophon* sp.	McKee, 1938
	Mollusca	Gastropoda	*Euomphalus* sp.	McKee, 1938
	Mollusca	Gastropoda	*Euphemites* sp.	McKee, 1938
	Mollusca	Gastropoda	*Goniospira* sp.	McKee, 1938
	Mollusca	Gastropoda	*Naticopsis* sp.	McKee, 1938
	Mollusca	Gastropoda	Undetermined	McKee, 1938
	Mollusca	Undetermined	Undetermined	McKee, 1938
Pk	Arthropoda	Trilobita	*Delaria sevilloidia*	Cisne, 1971

Appendix Table B-4. *Continued*

Unit	Phylum	Class	Species	Reference
Pk (continued)	Arthropoda	Trilobita	*Delaria snowi*	Cisne, 1971
	Arthropoda	Trilobita	*Ditomopyge* sp.	McKee, 1938; Sorauf & Billingsley, 1991; Thayer, 2009
	Arthropoda	Trilobita	*Novoameura mckeei*	Cisne, 1971
	Arthropoda	Trilobita	Undetermined	Billingsley & Beus, 1999a
	Brachiopoda	Rhynchonellata	*Composita arizonica*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Composita* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Rhynchonellata	*Composita subtilita*	McKee, 1938; Gordon, 1982
	Brachiopoda	Rhynchonellata	*Composita?* sp.	McKee, 1938
	Brachiopoda	Rhynchonellata	*Dielasma phosphoriense*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Hustedia* aff. *H. meekana*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Hustedia* sp.	Thompson, 1995
	Brachiopoda	Rhynchonellata	*Neophricadothyris* sp.	Thompson, 1995
	Brachiopoda	Rhynchonellata	*Phrenophoria pinguis*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Phricodothyris guadalupensis*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Pugnoides* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Rhynchonellata	*Punctospirifer?* sp.	McKee, 1938
	Brachiopoda	Rhynchonellata	*Rhipidomella hessensis*	Condra & Elias, 1944
	Brachiopoda	Rhynchonellata	*Rhipidomella transversa*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Spiriferellina hilli*	McKee, 1938
	Brachiopoda	Rhynchonellata	*Spiriferina?* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Rhynchonellata	*Squamularia* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Avonia* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Bathymyonia nevadensis*	McKee, 1938
	Brachiopoda	Strophomenata	*Chonetes* sp.	McKee, 1938
	Brachiopoda	Strophomenata	*Derbyia arizonensis*	McKee, 1938, 1941
	Brachiopoda	Strophomenata	*Derbyia nasuta*	McKee, 1938
	Brachiopoda	Strophomenata	*Derbyia* sp.	McKee, 1938; Sorauf & Billingsley, 1991; Thayer, 2009
	Brachiopoda	Strophomenata	*Dyoros* (*Tetragonetes*) *tetragonus*	King, 1931; Cooper and Grant, 1975
	Brachiopoda	Strophomenata	*Dyoros kaibabensis*	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Dyoros subliratus*	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Echinauris dorsoconcava*	McKee, 1938

Appendix Table B-4. *Continued*

Unit	Phylum	Class	Species	Reference
Pk (continued)	Brachiopoda	Strophomenata	*Echinauris newberryi*	McKee, 1938
	Brachiopoda	Strophomenata	*Echinauris* sp.	Thompson, 1995
	Brachiopoda	Strophomenata	*Kozlowskia* sp.	Thompson, 1995
	Brachiopoda	Strophomenata	*Kutorginella meridionalis*	McKee, 1938
	Brachiopoda	Strophomenata	*Liosotella popei*	McKee, 1938
	Brachiopoda	Strophomenata	*Marginifera* sp.	McKee, 1938
	Brachiopoda	Strophomenata	*Meekella pyramidalis*	Schuchert, 1918b; McKee, 1938
	Brachiopoda	Strophomenata	*Meekella* sp.	McKee, 1938; Sorauf & Billingsley, 1991; Thayer, 2009
	Brachiopoda	Strophomenata	*Peniculauris bassi*	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Peniculauris ivesi*	Schuchert, 1918b; McKee, 1938
	Brachiopoda	Strophomenata	*Peniculauris* sp.	Thayer, 2009
	Brachiopoda	Strophomenata	*Rugatia occidentalis*	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Strophomenata	*Rugatia paraindica*	McKee, 1938
	Brachiopoda	Strophomenata	*Rugatia* sp.	Thompson, 1995
	Brachiopoda	Strophomenata	*Waagenoconcha* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Brachiopoda	Undetermined	Undetermined	McKee, 1938
	Bryozoa	Stenolaemata	*Bascomella subsphaerica*	Condra & Elias, 1944
	Bryozoa	Stenolaemata	*Bicorbis arizonica*	Condra & Elias, 1945a, 1945b; McKinney, 1983
	Bryozoa	Stenolaemata	*Fistulipora* sp.	McKee, 1938; McKinney, 1983
	Bryozoa	Stenolaemata	*Girtypora maculata*	McKinney, 1983
	Bryozoa	Stenolaemata	*Meekopora parilis*	McKinney, 1983
	Bryozoa	Stenolaemata	*Meekopora* sp.	McKee, 1938
	Bryozoa	Stenolaemata	*Polypora spinulifera*	McKee, 1938
	Bryozoa	Stenolaemata	*Rhabdomeson* sp.	McKinney, 1983
	Bryozoa	Stenolaemata	*Rhombopora lepidodendroides*	McKee, 1938
	Bryozoa	Stenolaemata	*Septopora biserialis*	McKee, 1938
	Bryozoa	Stenolaemata	*Septopora* sp.	McKee, 1938
	Bryozoa	Stenolaemata	*Stenodiscus* sp.	McKinney, 1983
	Bryozoa	Stenolaemata	*Stenopora* sp.	McKee, 1938
	Bryozoa	Stenolaemata	*Streblotrypa sp.*	McKinney, 1983
	Bryozoa	Stenolaemata	Undetermined	McKinney, 1983

Appendix Table B-4. *Continued*

Unit	Phylum	Class	Species	Reference
Pk (continued)	Bryozoa	Undetermined	Undetermined	McKee, 1938; McKinney, 1983; Sorauf & Billingsley, 1991; Thompson, 1995
	Cnidaria	Anthozoa	*Lophophyllum* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Cnidaria	Anthozoa	Undetermined	McKee, 1938
	Cnidaria	Staurozoa?	*Conularia kaibabensis*	McKee, 1935; Sinclair, 1948; Spamer, 1984
	Echinodermata	Crinoidea	Undetermined	Shimer, 1919; McKee, 1938; Sorauf & Billingsley, 1991; Thayer, 2009
	Echinodermata	Echinoidea	*Archaeocidaris* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Mollusca	Bivalvia	*Acanthopecten coloradoensis*	Newell, 1937
	Mollusca	Bivalvia	*Astartella gurleyi*	Shimer, 1919; McKee, 1938
	Mollusca	Bivalvia	*Aviculopecten* sp.	McKee, 1938; Sorauf & Billingsley, 1991
	Mollusca	Bivalvia	*Bakewellia parva*	Shimer, 1919; McKee, 1938
	Mollusca	Bivalvia	*Nuculana?* sp.	McKee, 1938
	Mollusca	Bivalvia	*Permophorus* sp.	McKee, 1938
	Mollusca	Bivalvia	*Pteria* sp.	McKee, 1938
	Mollusca	Bivalvia	*Schizodus* sp.	McKee, 1938
	Mollusca	Bivalvia	*Solemya* sp.	McKee, 1938
	Mollusca	Bivalvia	Undetermined	McKee, 1938
	Mollusca	Cephalopoda	*Domatoceras bradyi*	Miller & Unklesbay, 1942; Miller & Youngquist, 1949
	Mollusca	Cephalopoda	*Domatoceras simplex*	McKee, 1938
	Mollusca	Cephalopoda	*Orthoceras* sp.	McKee, 1938
	Mollusca	Cephalopoda	*Stearoceras rotundatum*	Miller & Unklesbay, 1942; Miller & Youngquist, 1949
	Mollusca	Cephalopoda	*Stearoceras sanandreasense*	Miller & Unklesbay, 1942; Miller & Youngquist, 1949
	Mollusca	Gastropoda	*Bellerophon majusculus*	McKee, 1938
	Mollusca	Gastropoda	*Euomphalus* sp.	McKee, 1938
	Mollusca	Gastropoda	*Euphemites* cf. *E. carbonarius*	Shimer, 1919; McKee, 1938
	Mollusca	Gastropoda	*Euphemites* sp.	McKee, 1938
	Mollusca	Gastropoda	*Goniospira* sp.	McKee, 1938
	Mollusca	Gastropoda	*Murchisonia?* cf. *M. terebra*	Shimer, 1919; McKee, 1938
	Mollusca	Gastropoda	*Naticopsis* sp.	McKee, 1938
	Mollusca	Gastropoda	*Pleurotomaria* sp.	McKee, 1938

Appendix Table B-4. *Continued*

Unit	Phylum	Class	Species	Reference
Pk (continued)	Mollusca	Gastropoda	Undetermined	McKee, 1938
	Mollusca	Scaphopoda	*Prodentalium canna*	Shimer, 1919; McKee, 1938
	Mollusca	Undetermined	Undetermined	McKee, 1938
	Porifera	Demospongiae	*Actinocoelia maeandrina*	Griffin, 1966
	Porifera	Demospongiae	*Actinocoelia* sp.	Thayer, 2009
	Porifera	Undetermined	Undetermined	Schuchert, 1918b; McKee, 1938; Sorauf & Billingsley, 1991

Appendix C

Paleozoic Invertebrate Body Fossil Taxa Named From GRCA

Befitting a park with such a long history of paleontological investigations and diversity of fossiliferous rocks, GRCA has been the source for numerous type specimens. At least 80 species of fossil invertebrates have been named from specimens discovered within 2019 GRCA boundaries. They are listed in appendix table C-1 in alphabetical order within phyla, using the original species names. An additional 11 invertebrate species have been named from specimens possibly derived from GRCA locations (see the following appendix D). The great majority of these taxa were collected and named during the National Park era (1919–present), although not all of the discovery localities were within GRCA at the time of discovery due to park boundary changes. For example, some type specimens recovered from what is now far western GRCA were in Lake Mead National Recreation Area (LAKE) during the 1930s. Pre-1919 taxa are primarily Walcott's Cambrian invertebrates and a few species from the very early era of exploration. Some land once part of southern GRCA was transferred to the Havasupai Indian Reservation in 1975. Although there are some fossil sites described in the pre-1975 literature as within GRCA that are now outside the park boundaries, no type specimen locations were affected by the change in ownership. Stratigraphic unit abbreviations are per appendix A. Dashes in the notes column indicate no information to relate.

Appendix Table C-1. *Fossil invertebrate taxa named from specimens collected from GRCA. Species are listed with stratigraphic unit, taxonomic group, original name, source citation, specimen accession identifiers, and notes. Continued on following page.*

Unit	Phylum	Original Name	Citation	Type Specimen	Notes
Ctba	Arthropoda	*Acrocephalops*? *arizonaensis*	Resser, 1945	USNM 108624	Trilobite
Ctba	Arthropoda	*Albertella schenki*	Resser, 1945	USNM 108583	Trilobite
Ctba	Arthropoda	*Alokistocare althea*	Walcott, 1916a	Lectotype USNM 61574	Trilobite
Ctm	Arthropoda	*Bolaspis aemula*	Resser, 1945	USNM 108602a	Trilobite
Ctu	Arthropoda	*Bradoria tontoensis*	Ulrich & Bassler, 1931	USNM 81377	Bradoriid
Ctba or Ctm	Arthropoda	*Clavaspidella kanabensis*	Resser, 1945	USNM 108578a	Trilobite
Pk	Arthropoda	*Delaria macclintocki*	Cisne, 1971	GCNPM 3949	Trilobite
Ctba	Arthropoda	*Dielymella appressa*	Ulrich & Bassler, 1931	USNM 56506	Bradoriid
Ctba	Arthropoda	*Dielymella dorsalis*	Ulrich & Bassler, 1931	USNM 56505	Bradoriid
Ctba	Arthropoda	*Dielymella nasuta*	Ulrich & Bassler, 1931	Cotypes USNM 56508, 56509	Bradoriid
Ctba	Arthropoda	*Dielymella recticardinalis*	Ulrich & Bassler, 1931	USNM 56510	Bradoriid
Ctba	Arthropoda	*Dielymella recticardinalis angustata*	Ulrich & Bassler, 1931	USNM 56511	Bradoriid
Ctba	Arthropoda	*Dolichometopus tontoensis*	Walcott, 1916b	Lectotype USNM 62685	Trilobite, *Anoria tontoensis*
Ctba	Arthropoda	*Ehmaniella arizonaensis*	Resser, 1945	USNM 108603a	Trilobite
Ctba or Ctm	Arthropoda	*Ehmaniella hebes*	Resser, 1945	USNM 108612a	Trilobite
Ctba	Arthropoda	*Elrathia nitens*	Resser, 1945	USNM 108625	Trilobite
Ctba or Ctm	Arthropoda	*Elrathiella*? *insueta*	Resser, 1945	USNM 108621a	Trilobite
Ctba	Arthropoda	*Glossopleura mckeei*	Resser, 1935	USNM 62714	Trilobite
Ctba or Ctm	Arthropoda	*Glyphaspis kwanguntensis*	Resser, 1945	USNM 108618a	Trilobite
Ctm	Arthropoda	*Glyphaspis tecta*	Resser, 1945	USNM 108596a	Trilobite
Ctba	Arthropoda	*Glyphaspis vulsa*	Resser, 1945	USNM 108595a	Trilobite
Ctba	Arthropoda	*Indiana curta*	Ulrich & Bassler, 1931	USNM 56466	Bradoriid
Ctba?	Arthropoda	*Indiana faba*	Ulrich & Bassler, 1931	USNM 56458	Bradoriid
Ctba?	Arthropoda	*Indiana faba intermedia*	Ulrich & Bassler, 1931	USNM 56462	Bradoriid
Ctba	Arthropoda	*Indiana impressa*	Ulrich & Bassler, 1931	USNM 56463	Bradoriid
Ctba or Ctm	Arthropoda	*Kochina? angustata*	Resser, 1945	USNM 108610	Trilobite

Appendix Table C-1. *Continued*

Unit	Phylum	Original Name	Citation	Type Specimen	Notes
Ctba or Ctm	Arthropoda	*Kootenia mckeei*	Resser, 1945	USNM 108588a	Trilobite
Ctm	Arthropoda	*Kootenia schenki*	Resser, 1945	USNM 108586a	Trilobite
Ctba	Arthropoda	*Kootenia simplex*	Resser, 1945	USNM 108591a	Trilobite
Ctba	Arthropoda	*Pachyaspis fonticola*	Resser, 1945	USNM 108608	Trilobite
Ctba or Ctm	Arthropoda	*Parehmania kwaguntensis*	Resser, 1945	USNM 108620a	Trilobite
Ctba or Ctm	Arthropoda	*Parehmania nitida*	Resser, 1945	USNM 108613a	Trilobite
Ctba	Arthropoda	*Parehmania tontoensis*	Resser, 1945	USNM 108614	Trilobite
Ctba or Ctm	Arthropoda	*Solenopleurella diligens*	Resser, 1945	USNM 108627a	Trilobite
Ctm	Arthropoda	*Solenopleurella erosa*	Resser, 1945	USNM 108616a	Trilobite
Ctm	Arthropoda	*Solenopleurella porcata*	Resser, 1945	USNM 108626a	Trilobite
Ctba	Arthropoda	*Spencia tontoensis*	Resser, 1945	USNM 108611a	Trilobite
Ctba or Ctm	Arthropoda	*Trachycheilus typicale*	Resser, 1945	USNM 108619	Trilobite
Ph	Arthropoda	*Typus gilmorei*	Carpenter, 1927	USNM 71279	Insect, *Tupus gilmorei*
Ph	Arthropoda	*Typus whitei*	Carpenter, 1928	USNM 71713	Insect, *Tupus whitei*
Ctba?	Arthropoda	*Walcottella apicalis*	Ulrich & Bassler, 1931	Cotypes USNM 56477, 56478	Bradoriid
Ctba	Arthropoda	*Walcottella breviuscula*	Ulrich & Bassler, 1931	USNM 56481	Bradoriid
Ctba?	Arthropoda	*Walcottella concentrica*	Ulrich & Bassler, 1931	Cotypes USNM 56479, 56480	Bradoriid
Ctba	Arthropoda	*Walcottella leperditoides*	Ulrich & Bassler, 1931	USNM 56484	Bradoriid
Ctba	Arthropoda	*Walcottella limatula*	Ulrich & Bassler, 1931	USNM 56488	Bradoriid
Ctba	Arthropoda	*Walcottella longula*	Ulrich & Bassler, 1931	USNM 56491	Bradoriid
Ctba	Arthropoda	*Walcottella nitida*	Ulrich & Bassler, 1931	USNM 56485	Bradoriid
Ctba	Arthropoda	*Walcottella oblonga*	Ulrich & Bassler, 1931	USNM 56486	Bradoriid
Ctba	Arthropoda	*Walcottella obsoleta*	Ulrich & Bassler, 1931	USNM 56487	Bradoriid
Ctba	Arthropoda	*Walcottella pulchella*	Ulrich & Bassler, 1931	USNM 56483	Bradoriid
Ctba	Arthropoda	*Walcottella scitula*	Ulrich & Bassler, 1931	USNM 56482	Bradoriid
Ctba	Arthropoda	*Walcottella subtruncata*	Ulrich & Bassler, 1931	USNM 56490	Bradoriid
Ctba	Arthropoda	*Walcottella ventrosa*	Ulrich & Bassler, 1931	USNM 56489	Bradoriid

Appendix Table C-1. *Continued*

Unit	Phylum	Original Name	Citation	Type Specimen	Notes
Pk	Brachiopoda	*Avonia subhorrida newberryi*	McKee, 1938	USNM 102301	*Echinauris newberryi*
Ctba	Brachiopoda	*Billingsella obscura*	Walcott, 1905	USNM 52258a	*Nisusia obscura*
Pk	Brachiopoda	*Chonetes quadratus*	King, 1931	YPM 10830a	*Dyoros* (*Tetragonetes*) *tetragonus*
Pk	Brachiopoda	*Composita arizonica*	McKee, 1938	Syntypes USNM 102303, 102304, 102305	–
Pk	Brachiopoda	*Derbyia regularis*	McKee, 1938	Syntypes USNM 102290, 102291	*Derbyia arizonensis*
Ctba?	Brachiopoda	*Dictyonina arizonaensis*	Resser, 1945	USNM 108557	–
Ctm	Brachiopoda	*Finkelnburgia noblei*	Walcott, 1924	USNM 69750–69752	*Nisusia noblei*
Ctba	Brachiopoda	*Iphidea crenistria*	Walcott, 1897	USNM 26431a	*Micromitra* (*Paterina*) *crenistria*
Ctba?	Brachiopoda	*Iphidea superba*	Walcott, 1897	USNM 26429a	*Micromitra* (*Paterina*) *superba*
Ctba or Ctm	Brachiopoda	*Lingulella kanabensis*	Resser, 1945	USNM 33829a	–
Ctba	Brachiopoda	*Lingulella mckeei*	Resser, 1945	USNM 108561a	–
Ctba or Ctm	Brachiopoda	*Nisusia* (*Jamesella*) *kanabensis*	Walcott, 1908	USNM 52300	–
Ctba?	Brachiopoda	*Obolus* (*Lingulella*) *chuarensis*	Walcott, 1898	USNM 57020a	*Lingulella chuarensis*
Ctba	Brachiopoda	*Obolus* (*Lingulella*) *euglyphus*	Walcott, 1898	USNM 27316a	*Lingulella euglypha*
Ctba?	Brachiopoda	*Obolus* (*Lingulella*) *lineolatus*	Walcott, 1898	USNM 27325a	*Lingulella lineolata*
Ctba	Brachiopoda	*Obolus* (*Lingulella*) *spatulus*	Walcott, 1902	USNM 35290a	*Lingulella spatula*
Ctba	Brachiopoda	*Obolus* (*Lingulella*) *zetus*	Walcott, 1898	USNM 27347b	*Lingulella zetus*
Ctba	Brachiopoda	*Obolus* (*Westonia*) *themis*	Walcott, 1905	USNM 51732a	*Lingulella themis*
Pk	Bryozoa	*Bascomella subsphaerica*	Condra & Elias, 1944	NGS 449	–
Pk	Bryozoa	*Bicorbula arizonica*	Condra & Elias, 1945a	NGS 264	*Bicorbis arizonica*
Pk	Bryozoa	*Girtypora maculata*	McKinney, 1983	FMNH PE 24301	–
Pk	Cnidaria	*Conularia kaibabensis*	McKee, 1935	USNM 102289 (was GCNPM FK211)	Conulariid, also *Paraconularia kaibabensis*
Ctba	Echinodermata	*Eocrinus multibrachiatus*	Kirk (in Resser, 1945)	USNM 108556a	*Gogia multibrachiatus*
Mr	Foraminifera	*Endothyra baileyi poloumera*	Skipp, 1969	USNM 641727	*Globoendothyra baileyi poloumera*
Mr	Foraminifera	*Septaglomospiranella rossi*	Skipp, 1969	USNM 641578	–
Ctm	Problematica	*Scenella hermitensis*	Resser, 1945	USNM 108568a	*Incertae sedis*
Ctba?	Problematica	*Tontoia kwaguntensis*	Walcott, 1912b	USNM 57660	*Incertae sedis*

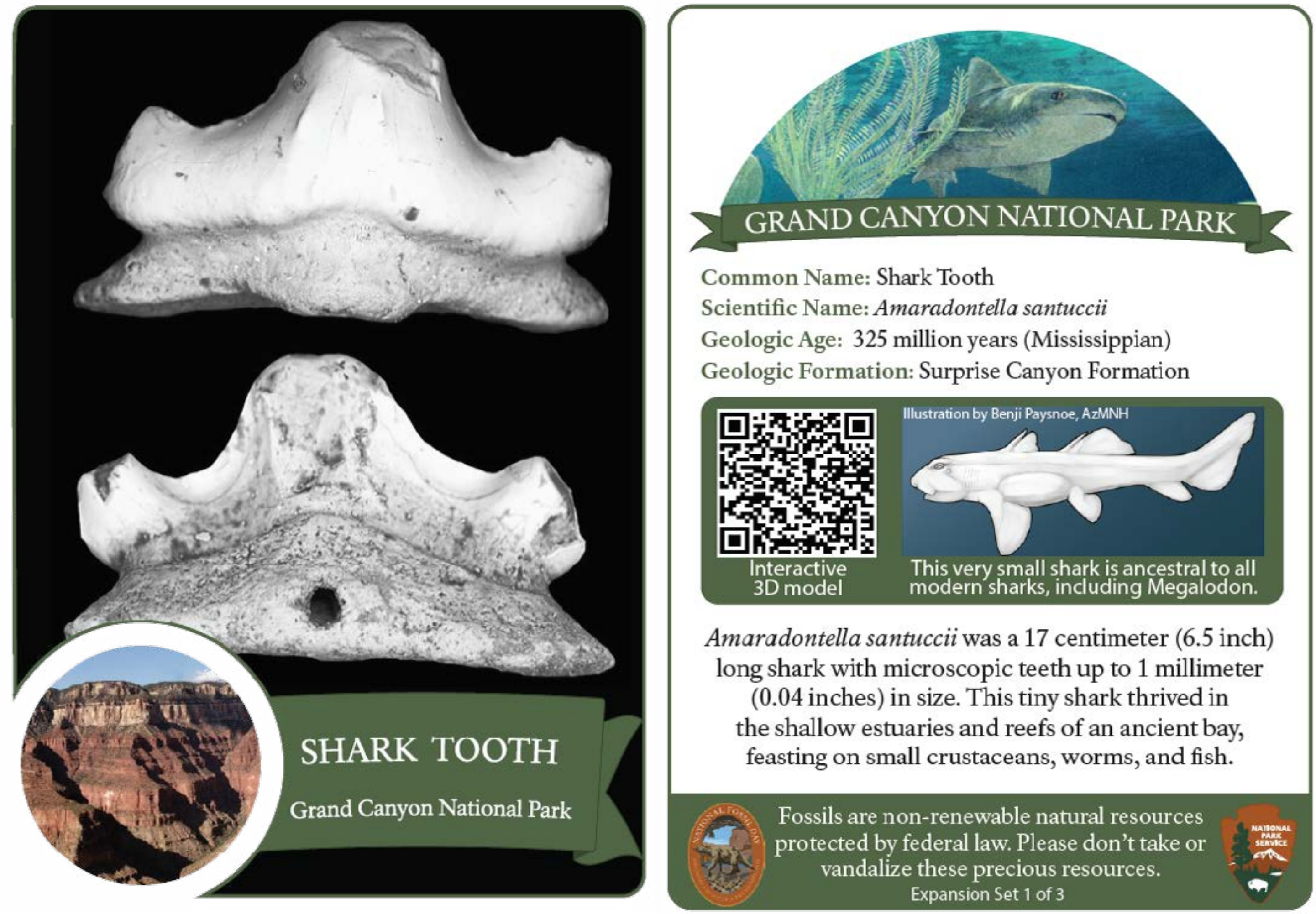
Appendix D

Paleozoic Invertebrate Body Fossil Taxa Potentially Named From GRCA

A small number of taxa have been named from fossils discovered somewhere in the Grand Canyon area, but with insufficient provenance information to determine the exact location. Some, all, or none of the type specimens may have come from GRCA. Names are listed as first defined. Some names may be revised in other sources. However, not all changes are reflected in the inventory at this time. Stratigraphic unit abbreviations are per appendix A. Dashes in the notes column indicate no information to relate.

Appendix Table D-1. *Fossil taxa named from specimens possibly found within GRCA. Species are listed with stratigraphic unit, taxonomic group, original name, source citation, specimen accession identifiers, and notes.*

Unit	Phylum	Original Name	Citation	Type Specimen	Notes
Ctm	Arthropoda	*Kootenia havasuensis*	Resser, 1945	USNM 108601a	Trilobite
Ctm	Arthropoda	*Pachyaspis moorei*	Resser, 1945	USNM 108606a	Trilobite
Pk	Brachiopoda	*Avonia dorsoconcava*	McKee, 1938	GCNPM 9993	*Echinauris dorsoconcava*
Pk	Brachiopoda	*Chonetes kaibabensis*	McKee, 1938	Syntypes USNM 102292, 102293, 102294	*Dyoros kaibabensis*
Pk	Brachiopoda	*Marginifera meridionalis*	McKee, 1938	Syntype USNM 102302	*Kutorginella meridionalis*
Pk	Brachiopoda	*Productus (Dictyoclostus) bassi*	McKee, 1938	Lectotype USNM 102295a	*Peniculauris bassi*
Pk	Brachiopoda	*Productus (Dictyoclostus) paraindicus*	McKee, 1938	Lectotype USNM 102297	*Rugatia paraindica*
Pt	Brachiopoda	*Productus ivesi*	Newberry, 1861	Syntypes USNM 5356a–c	*Peniculauris ivesi*
Pt or Pk	Echinodermata	*Archaeocidaris gracilis*	Newberry, 1861	Syntypes CU 604, USNM 5412	–
Pt or Pk	Echinodermata	*Archaeocidaris longispinus*	Newberry, 1861	CU 6419G	–
Pt or Pk	Echinodermata	*Archaeocidaris ornatus*	Newberry, 1861	Syntypes CU 6000G	*Archaeocidaris coloradensis*



SHARK TOOTH

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Shark Tooth
Scientific Name: *Amaradontella santuccii*
Geologic Age: 325 million years (Mississippian)
Geologic Formation: Surprise Canyon Formation

Illustration by Benji Paysnoe, AzMNH

Interactive 3D model

This very small shark is ancestral to all modern sharks, including Megalodon.

Amaradontella santuccii was a 17 centimeter (6.5 inch) long shark with microscopic teeth up to 1 millimeter (0.04 inches) in size. This tiny shark thrived in the shallow estuaries and reefs of an ancient bay, feasting on small crustaceans, worms, and fish.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

Expansion Set 1 of 3

Grand Canyon National Park Fossil Trading Card featuring the fossil shark tooth Amaradontella santucci *from the Mississippian Surprise Canyon Formation (NPS).*

PALEOZOIC VERTEBRATE PALEONTOLOGY OF GRAND CANYON NATIONAL PARK: RESEARCH HISTORY, RESOURCES, AND POTENTIAL

John-Paul Michael Hodnett[1] and David Kenneth Elliott[2]

ABSTRACT

A hundred years of field work and research on the Paleozoic vertebrate body fossil record at the Grand Canyon National Park (GRCA) is reviewed and updated. Vertebrate body fossil remains have been found through much of the stratigraphic section of GRCA; most of these consist of fish fossils. The oldest of these fish fossils comes from the Temple Butte Limestone where there is a record of antiarch placoderms and a possible sarcopterygian. The Early to Middle Mississippian Redwall Limestone has two records of holocephalan chondrichthyans coming from GRCA. A diverse record of chondrichthyans fishes (approximately 31 taxa) was recently reported from the Late Mississippian Surprise Canyon Formation, as well as a number of undescribed actinopterygian fish and small tetrapods. The Pennsylvanian Supai Group has vertebrate body fossil records in the Watahomigi Formation and the Wescogame Formation. The Watahomigi Formation has records of a marine xenacanth shark, a holocephalan chondrichthyan, and a bony fish. The Wescogame has holocephalan chondrichthyan records, though currently none are conserved in museum collections. The early Permian Pakoon Limestone from the western Grand Canyon has a few reports of chondrichthyan fossils. The early to middle Permian Kaibab Formation has a rich record of chondrichthyans and actinopterygians including the type specimen of *Megactenopetalus kaibabanus*, a very large petalodont chondrichthyan fish. All geologic horizons mentioned above have high potential to yield new important specimens and information, making GRCA an important resource for understanding vertebrate life during the Paleozoic.

INTRODUCTION

The Grand Canyon is an awe-inspiring place and is a physical testament of deep time. More than 150 years' worth of geologic research has yielded a rich paleontological record, documenting approximately a half billion years of life on this planet. Much of the Grand Canyon is composed of Paleozoic rocks, with the oldest going back to the Cambrian. The fossil record of these Paleozoic rocks is dominated by a rich invertebrate heritage. The vertebrate record, however, is typically portrayed as unusually sparse. The Paleozoic vertebrate record at the Grand Canyon is best known for the varied trace fossils of tetrapods from the Pennsylvanian–early Permian Supai Group and the Permian Coconino Sandstone, where multiple different ichnotaxa have been described (e. g., McKee, 1982; Spamer, 1984; Elliott and Blakey, 2005; Hunt and others, 2005). However, no tetrapod body fossils have been identified from these beds. Much of the research and literature on the body fossil record of vertebrates from the Grand Canyon has been focused on Pleistocene vertebrates from cave sites along the length of the canyon (e. g., Lucas and Morgan, 2005; Mead, 2005).

Nevertheless, Paleozoic vertebrate body fossils have been reported from the Grand Canyon. Walcott (1880) made the first report of vertebrate fossils from the Devonian Temple Butte Limestone during the initial surveys made by the United States Geological Survey (USGS). McKee (1938) reported and described the first Permian vertebrate body fossil, a chondrichthyan tooth plate,

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from the Kaibab Formation. In 1944, the chondrichthyan *Megactenopetalus kaibabanus* was described from a large tooth collected from the North Rim at Point Sublime, and this is the first designated holotype of a Paleozoic vertebrate fossil from the Grand Canyon (David, 1944). Other reports of vertebrate body fossils are from the Mississippian Redwall Limestone (McKee and Gutschick, 1969) and the Pennsylvanian–Permian Supai Group (McKee, 1982). Reviews of these vertebrate body fossils from the Paleozoic of the Grand Canyon have been made in the past (Spamer, 1984; Elliott and Blakey, 2005; Hunt and others, 2005). Recently, a rich assemblage of chondrichthyans was described from the Upper Mississippian Surprise Canyon Formation from the western Grand Canyon (Hodnett and Elliott, 2018).

The purpose of the report presented here is to both collate previous documentation of Paleozoic vertebrate body fossils from the Grand Canyon and present the current physical record of specimens that have been collected from Grand Canyon National Park (GRCA). We have identified the presence of Paleozoic body fossils from seven geologic horizons within the Grand Canyon, which includes records outside of GRCA boundaries. We have included these records as part of our review as a "total record" approach to understanding the taxonomic richness of these seven geologic horizons. This additional information should assist in fossil resource planning, management, and priority assessment for further Paleozoic vertebrate research at GRCA.

Institutional Abbreviations—GRCA, Grand Canyon National Park Museum, Grand Canyon, Arizona; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **USNM**, National Museum of Natural History Paleobiology Collections, Washington, D.C.

DEVONIAN

Temple Butte Limestone

The Temple Butte Limestone is the only Devonian formation exposed at GRCA, and it also extends into southeast Nevada. The Temple Butte Limestone consists of thin, discontinuous lenses no more than 30 m (100 ft) thick deposited in paleo-valleys cut into the underlying Muav Limestone within the eastern Grand Canyon (Beus, 2003a). The central and western sections of the Temple Butte Limestone are more continuous (Beus, 2003a). The Temple Butte Limestone consists of a westward thickening wedge of interbedded dolomite, sandy dolomite, sandstones, mudstones, and limestones, ranging from purple, reddish-purple, and dark to light gray (Beus, 2003a). The eastern paleo-valleys of the Temple Butte strata consist of interbedded mudstones, sandstones, dolomite, and conglomerates (Beus, 2003a). The upper and lower contacts of the Temple Butte Limestone represent major unconformities with the underlying middle Cambrian Muav Limestone and the overlying Lower Mississippian Redwall Limestone (Beus, 2003a). The model for deposition of the Temple Butte Limestone is similar to that of the younger Surprise Canyon Formation (Beus, 2003a). The Temple Butte Limestone is a contemporaneous equivalent to the Martin Formation found in central and southern Arizona, which is known for a diverse vertebrate assemblage (Elliott and Blakey, 2005). Both the Temple Butte Limestone and the Martin Formation are considered to be early Late Devonian (Frasnian) in age (Elliott and Blakey, 2005).

History

The first report of a vertebrate fossil from the Grand Canyon was by Charles Doolittle Walcott (1880), who reported: "The purple sandstones deposited in the hollows of the Silurian limestones are characterized by the presence of Placoganoid fishes of a Devonian type," which he identified during a field excursion in 1879. Schuchert (1918) communicated with L. Noble on a series of scales and plates of fish collected from the Temple Butte Limestone in 1916. These fish fossils were identified by J. W. Gidley of the Smithsonian Institution as the plates of the antiarch placoderm fish *Bothriolepis nitidens* and the scales of the sarcopterygian *Holoptychius* (Schuchert, 1918; Noble, 1922). Noble (1922) made no report of *Holoptychius* scales in the summary he published from Gidley's analysis. Denison (1951) accepted the occurrence of *Holoptychius* and revised the Temple Butte placoderm to *Bothriolepis coloradensis* based on similar outer dermal plate ornamentation morphology.

GRCA Resources

At present there are only two specimens identified in the National Museum of Natural History Paleobiology collections that come from the Temple Butte Limestone of the Grand Canyon (figure 1). USNM PAL 328639 consists of part and counterpart of the proximal part of a pectoral appendage (figures 1A and 1B) and fragments and impressions of indeterminate plates of *Bothriolepis* cf. *B. coloradensis* that were collected by C. D. Walcott on January 17, 1883 as part of the United States Geological Survey study. This specimen is here considered to be the first discovered and oldest fossil vertebrate to be catalogued from the Grand Canyon. In addition, USNM PAL 328643 (figures 1C–E) is a collection of approximately 30+ elements consisting of pectoral appendage, dorsal and ventral shield, and cephalic plates of *Bothriolepis coloradensis* collected by L. F. Noble in April 1916 and later mentioned by Denison (1951). At present, no specimens of *Holoptychius* from the Temple Butte Limestone have been identified in a museum collection.

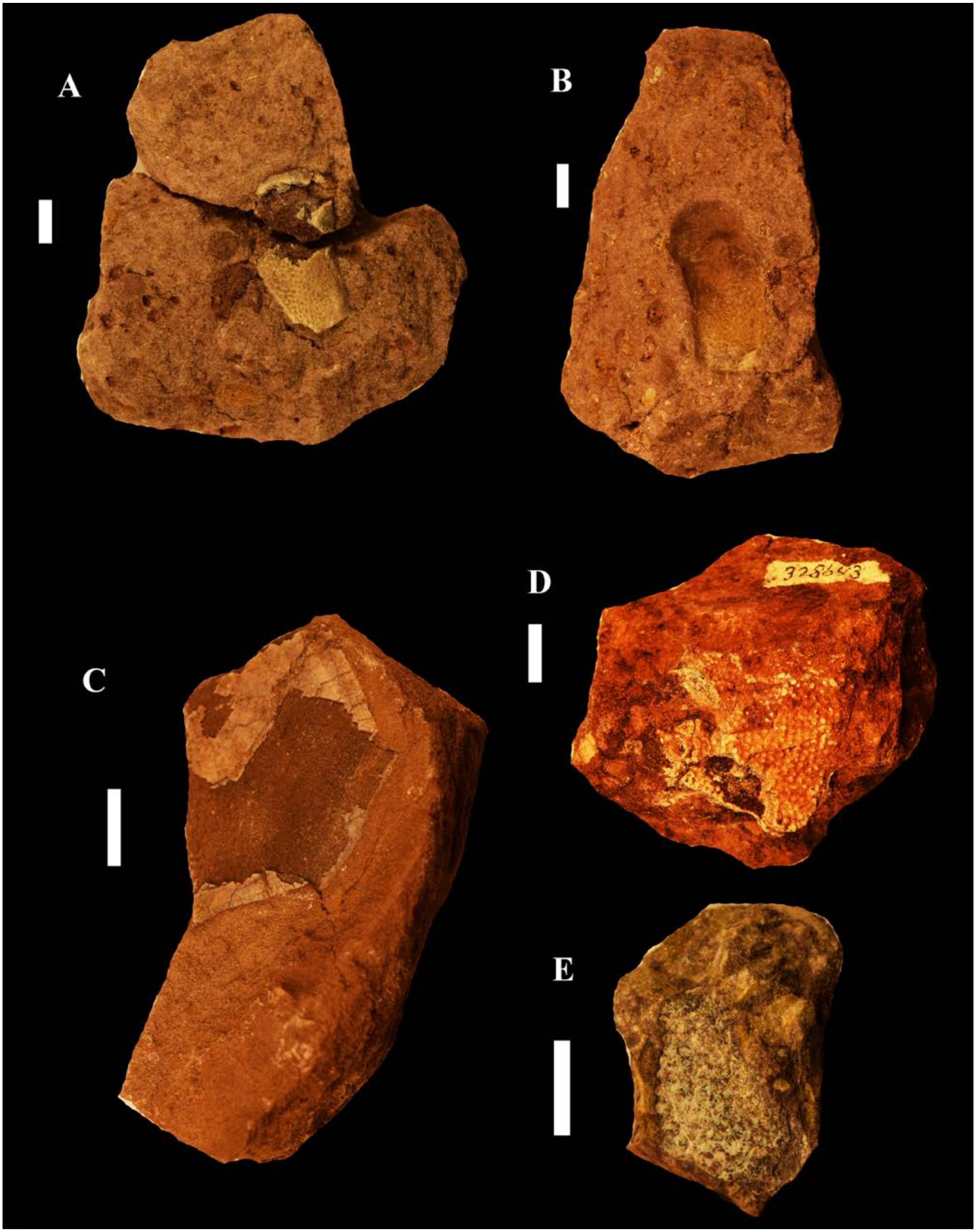

Figure 1. *Antiarch placoderm,* Bothriolepis*, fossils from the Temple Butte Limestone, Grand Canyon (JOHN-PAUL HODNETT).* ***A–B****. USNM PAL 328639,* Bothriolepis *cf.* B. coloradensis*, the proximal part of a pectoral appendage collected by C. D. Walcott.* ***C–E****. USNM PAL 328643,* Bothriolepis coloradensis*, a selection of plates collected by L. F. Noble. Scale equals 1 cm (0.4 in).*

Potential

Notes by Noble (1922) suggest that vertebrate remains from the Temple Butte are common but fragmentary approximately 1 m (3 ft) above the base of the Temple Butte Limestone and its contact with the Muav Limestone, in an impure dolomitic limestone. Noble (1922) speculated that other deposits within the Temple Butte Limestone could similarly be rich in vertebrate material.

MISSISSIPPIAN

Redwall Limestone

The Redwall Limestone is a cliff-forming unit of early to middle Mississippian age sedimentary rocks (Beus, 2003b). It consists primarily of light-olive-gray to light gray, thin- to thick bedded cherty limestones, interbedded crystalline dolomites, and limestone layers with chert lenses (Beus, 2003b). The Redwall Limestone is divided into four lithologic units starting with the Whitmore Wash Member at the base, and ascending up to the Thunder Springs Member, Mooney Falls Member, and Horseshoe Mesa Member, respectively (McKee and Gutschick, 1969). The Redwall Limestone was formed through two marine transgression and regression events from a seaway to the west (McKee and Gutschick, 1969). The Whitmore Wash Member represents the first transgression event, and the Thunder Springs Member represents the first regression event, followed by the second transgression event of the Mooney Falls Member, and the final regression of the Horseshoe Mesa Member (McKee and Gutschick, 1969). The Redwall Limestone has an upper unconformable contact with the Surprise Canyon Formation, which represents a time of uplift and karstic paleo-valleys cutting into the Redwall Limestone (Beus, 2003). The Redwall Limestone has a rich invertebrate record. Regional variation of fossil faunas are noted within it, particularly of the corals and foraminifers (McKee and Gutschick, 1969).

History

McKee and Gutschick (1969) reported a number of durophagous holocephalan chondrichthyan tooth plates and a spine from multiple localities within the Redwall Limestone in northern and central Arizona. The fossils were submitted to D. H. Dunkle, then at the National Museum of Natural History, for identification. Dunkle identified from the Mooney Falls Member the euchondrocephalan *Orodus major* and the holocephalans *Psephodus* sp., *Deltodus*, sp., *Helodus* sp., and *Psammodus* sp., as well as a few unidentified fish teeth (McKee and Gutschick, 1969). A single dorsal spine of *Physonemus* was also identified (McKee and Gutschick, 1969). An indeterminate fish tooth is reported from the Horseshoe Member at Bright Angel Trail (McKee and Gutschick, 1969). D. H. Dunkle noted that much of the Redwall fish fauna was similar to taxa found in the Early Mississippian Burlington Limestone of Iowa (St. John and Worthen, 1875; McKee and Gutschick, 1969). Elliott and Blakey (2005) noted that the Redwall Limestone is approximately contemporaneous with the Escabrosa Limestone in southern Arizona, which has a rich but poorly studied fish assemblage (Gass, 1963). Outside of the Grand Canyon, a dolostone nodule from the Redwall preserved the external mold and some bony debris of a large gyracanthid acanthodian pectoral spine (USNM 409810; Babcock and Feldmann, 1986). Babcock and Feldmann (1986) identified this specimen as *Oracanthus* sp., and it was collected from the top of a mesa between Rock and Blye canyons south of Peach Springs Arizona. This is the first record of a gyracanthid fish from the state of Arizona.

GRCA Resources

Unfortunately, none of the fish taxa reported in McKee and Gutschick (1969) is represented by specimens in a museum collection with the exception of GRCA 20037 (figure 2A), a tooth of *Helodus* sp. from Kaibab Trail, “Member C [Mooney Falls Member] of Redwall Limestone.” This specimen was collected by E. D. McKee on March 4, 1959. An uncataloged specimen collected by George Billingsley from the Mooney Falls Member of the Redwall Limestone at Surprise Canyon, was given to us (DKE) for identification (figure 2B). The specimen consists of a partial tooth whorl of two teeth that are similar to *Helodus* (*Psephodus*) *didymus* of the Mississippian (Visean) of Ireland (Stahl, 1999). This specimen is currently under study by the authors.

Potential

There seems to be high potential for more vertebrate materials to be collected from the Redwall Limestone at GRCA.

Surprise Canyon Formation

The Surprise Canyon Formation is the name given to a series of channel fills and karstic cave deposits of Late Mississippian (Serpukhovian) age in Grand Canyon (Billingsley and Beus, 1985). These represent a considerable hiatus between the Redwall Limestone and the overlying Supai Group, and were originally recognized by McKee and Gutschick (1969), who gave several examples and descriptions of these deposits, although at that time considering them to be part of the basal Supai Group. The channels were originally described by Billingsley (1978) and later interpreted as paleo-valleys by Billingsley and McKee (1982). The formation is nowhere continuous and consists of isolated, lens-shaped outcrops scattered over Grand Canyon and Marble Canyon to the east, representing deposits in del-

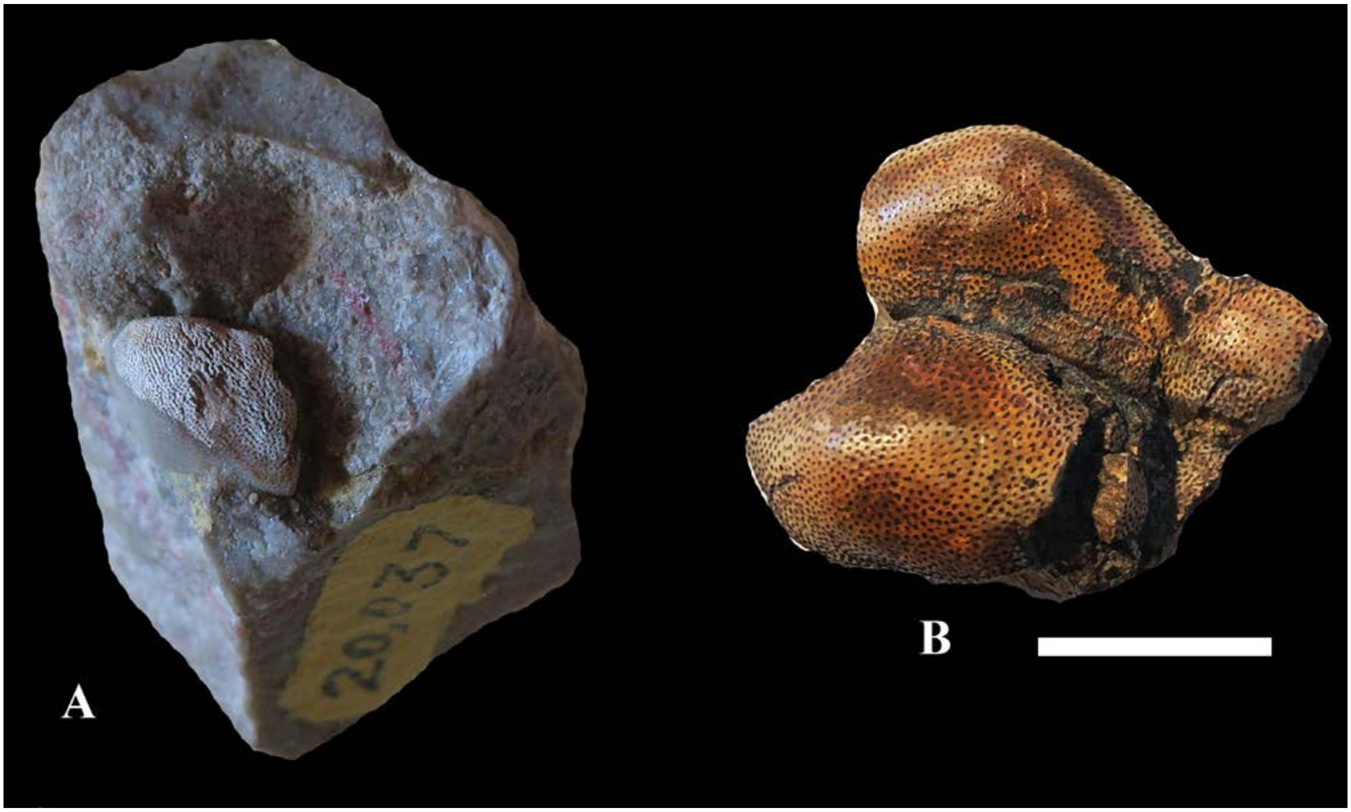

Figure 2. *Chondrichthyan fossils from the Mooney Fall Member, Redwall Limestone (JOHN-PAUL HODNETT).* ***A.*** *GRCA 20037,* Helodus *sp. from Kaibab Trail.* ***B.*** *Uncatalogued specimen, cf.* Helodus *(*Psephodus*)* didymus*, from Surprise Canyon. Scale equals 1 cm (0.4 in).*

taic and tidal channels that drained into an estuary to the east. Outcrops are generally up to 45 m (150 ft) thick in central Grand Canyon close to the presumed headwaters of the paleochannels but reach 122 m (400 ft) in the west in proximity to the estuary (Billingsley and Beus, 1985). Description of the extensive fossil invertebrate assemblages was carried out by Beus (1985, 1986, 1999), who showed that the lower beds are fluvial, whereas the upper part of the succession is marine.

The Surprise Canyon Formation was originally divided into a lower unit consisting of fluvial clastics and an upper marine unit composed of siltstones and limestones (Billingsley and Beus, 1985). Subsequent studies indicated the presence of three units: a lower fluvial chert pebble conglomerate interbedded with coarse- to fine grained red-brown sandstone and siltstone mainly of terrestrial origin; a middle marine unit of grey-yellow or reddish-brown, coarsely crystalline, thin-bedded limestone separated from the lower unit by an erosional unconformity; and an upper marine unit of reddish-brown, calcareous siltstone, with minor limestone. Some of the lower fluvial rocks in western Grand Canyon include interbedded limestone and shale suggesting brief marine incursions into paleoriver drainages (Billingsley and Beus, 1999).

The sequence in the paleo-valley fills is interpreted as representing deposition in channels developed in the Redwall Limestone. These were shallow deltaic and tidal drainage channels formed during the westward retreat of the sea in which the Redwall Limestone had accumulated. Development of karst and entrenchment of the channels probably occurred in the early Serpukhovian (Billingsley and Beus, 1999) and led to the development of a network of drainages. Highlands to the east became a source area for detrital material that was incorporated into deposits of the Surprise Canyon Formation. In the late Chesterian/Serpukhovian a period of subsidence allowed marine waters to gradually flood the eroded valleys forming local estuaries (Billingsley and Beus, 1999). As the sea transgressed the estuaries also moved eastwards, their deposits forming the marine Middle and Upper members of the Surprise Canyon Formation. A minor unconformity between the Surprise Canyon Formation and the overlying Watahomigi Formation (the basal formation of the Supai Group) suggests a regional interval of uplift and erosion (Billingsley and Beus, 1999).

History

McKee (1982) reported “a shark dentition” from the middle unit of the then-undefined Surprise Canyon Formation, which was below the contact of the Watahomigi Formation. This shark dentition was not identified. Billingsley and Beus (1999) reported the occurrence of vertebrate remains from the lower basal conglomerate member and from the Middle and Upper limestone members. These large vertebrate fossils (macro-teeth and spines) were sent to Richard Lund of Adelphi University for identification and later deposited at the National Museum of Natural History (R. Lund, pers comm., 2016). Martin (1992) and Martin and Barrick (1999) recorded the occurrence of micro-vertebrate remains from conodont residues from multiple localities in the Lower and Middle members of the Surprise Canyon Formation, but they did not identify these vertebrate taxa.

Hodnett and Elliott (2018) reviewed both the macro and micro chondrichthyan teeth and spines from the Surprise Canyon Formation and identified 31 taxa from the Lower, Middle, and Upper members at seven localities within the Grand Canyon, some from GRCA and others from Hualapai Nation land. Of the 31 taxa from the Surprise Canyon Formation, four new taxa were named: *Novaculodus billingsleyi*, *Microklomax carrieae*, *Cooleyella platera*, and *Amaradontus santuccii*. The chondrichthyans of the Lower Member include the taxa *Microklomax carrieae*, *Cooleyella platera*, *Amaradontus santuccii*, *Heteropetalus* sp., orodontid indet., *Deltodus* cf. *D. angularis*, *Deltodus* cf. *D. cingulatus*, *Amelacanthus* sp., and *Acondylacanthus* sp. The chondrichthyans of the Middle Member include the taxa *Thrinacodus gracia*, *Bransonella nebraskensis*, Stethacanthid indet., falcatid indet. 1, falcatid indet. 2, *Denaea williamsi*, cf. "*Ctenacanthus*" *costellatus*, ctenacanthid indet., *Clairina* sp., *Microklomax carrieae*, *Novaculodus billingsleyi*, cf. *Mesodmodus* sp., *Hamiltonichthys* sp., *Cooleyella fordi*, *Cooleyella platera*, *Amaradontus santuccii*, *Srianta* cf. *S. srianta*, eugenodontid indet., petalodontid indet., *Cochliodus* cf. *C. contortus*, and *Deltodus* sp. The chondrichthyans from the Upper Member include the taxa *Cladodus* cf. *C. marginatus*, *Srianta* cf. *S. srianta*, *Helodus*? sp., and *Deltodus* cf. *D. angularis*.

Aside from the chondrichthyans, there were also a number of isolated teeth, scales, and bones of actinopterygian fishes from the Lower and Middle member samples collected by Martin (1992). From Blue Mountain Canyon small tetrapods are represented by a few jaws with closely spaced teeth, which are the first record of Paleozoic tetrapods from the Grand Canyon. The actinopterygians and tetrapods are currently under study by the authors of this report.

GRCA Resources

The collection of vertebrates described from the Surprise Canyon Formation is housed in the National Museum of Natural History Paleobiology collections and the Museum of Northern Arizona Geology Department. It should be noted that the type specimens of *Novaculodus billingsleyi*, *Microklomax carrieae*, *Cooleyella platera*, and *Amaradontus santuccii* were collected from Hualapai Nation land in the Grand Canyon. The following list contains all the material collected from GRCA:

USNM: *Cladodus* cf. *C. marginatus*, USNM PAL 412169 (figure 3A); *Helodus*? sp., USNM PAL 603799; *Cochliodus* cf. *C. contortus* (figure 3C), USNM PAL 412147; *Deltodus* cf. *D. angularis*, USNM PAL 412170, 603798 (figure 3B), 412168; *Deltodus* cf. *D. cingulatus*; *Deltodus* sp., USNM PAL 412173, 412174. *Amelacanthus* sp., USNM PAL 412150; *Acondylacanthus* sp., USNM PAL 412149. Specimens not used in Hodnett and Elliott (2018), indeterminate cladodont-grade tooth, USNM PAL 603801; indeterminate bone, USNM PAL 412172, 412171.

MNA: *Microklomax carrieae*, MNA V11301 (figure 3G); *Cooleyella platera*, MNA V11308, V11309 (figure 3F); *Amaradontus santuccii*, MNA V11314, V11315 (figure 3E); *Heteropetalus* sp., MNA V11320 (figure 3D), V 11321; orodontid indet. MNA V11322.

Potential

It is evident from the extensive chondrichthyan fauna (Hodnett and Elliott, 2018) and the number of undescribed micro-remains of bony fish and tetrapods (Hodnett and Elliott pers. obs.) that the Surprise Canyon Formation has a relatively rich assemblage of vertebrates. However, we still have a relatively poor understanding of the species richness between the three members of the Surprise Canyon Formation. It is recommended that more extensive fieldwork in the Surprise Canyon Formation be conducted, particularly in the canyons north of the Colorado River, to collect additional specimens for study.

PENNSYLVANIAN

Supai Group

The Supai Group is a slope-forming unit composed of Pennsylvanian to early Permian red bed deposits found throughout the Grand Canyon. The Supai Group is made up of four geologic formations, which are, in ascending order, the Watahomigi Formation, Manakacha Formation, Wescogame Formation, and Esplanade Sandstone/ Pakoon Limestone. Presently, only the Pennsylvanian Watahomigi and Wescogame formations and the early Permian Pakoon Limestone have records of vertebrates.

Watahomigi Formation

The Watahomigi Formation is the lowest formation in the Supai Group. This geologic unit began as an eastwards transgression during the Late Mississippian (Surprise Canyon Formation) (McKee, 1982). This marine transgression event spread over the relatively flat Redwall Limestone and the filled Surprise Canyon Formation paleo-valleys (McKee, 1982). The Watahomigi Formation averages 91 m (300 ft) thick in the western portion of the Grand Canyon, 61 m (200 ft) thick in the

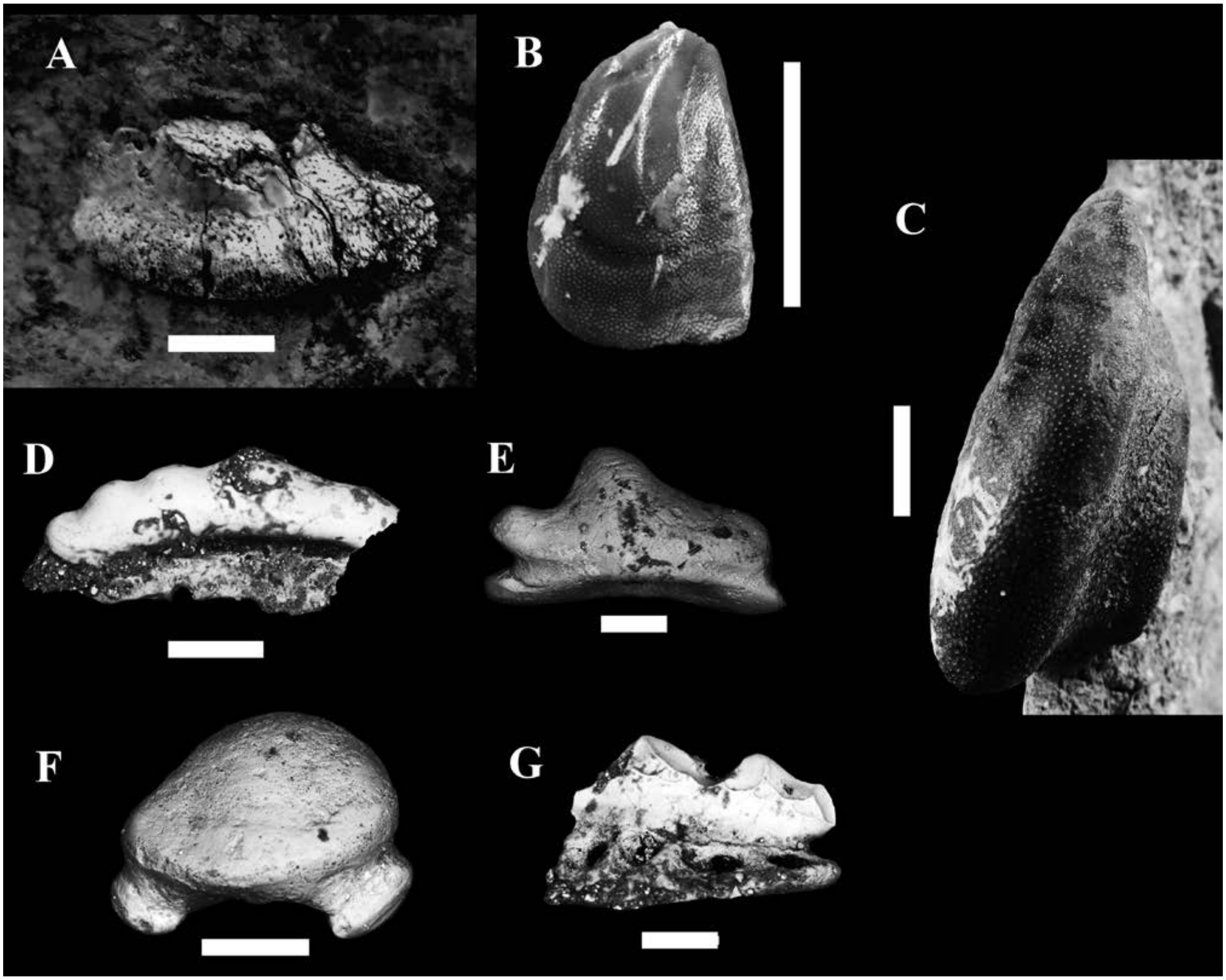

*Figure 3. Chondrichthyans from the Surprise Canyon Formation collected from Grand Canyon National Park (JOHN-PAUL HODNETT). **A.*** Cladodus *cf.* C. marginatus*, USNM PAL 412169. **B.*** Deltodus *cf.* D. angularis*, USNM PAL 603798. **C.*** Cochliodus *cf.* C. contortus*, USNM PAL 412147. **D.*** Heteropetalus *sp., MNA V11320. **E.*** Amaradontus santuccii*, MNA V11315. **F.*** Cooleyella platera*, MNA V11309. **G.*** Microklomax carrieae*, MNA V11301. Scale for **A–C** equals 1 cm (0.4 in), scale for **D–G** equals 500 µm (0.02 in).*

central area, and about 30 m (100 ft) thick in the eastern sections of the canyon (McKee, 1982). The lower section of the Watahomigi is made up of thin gravel sheets, followed by layers of mud, silt, and eventually carbonate deposits (McKee, 1982).

The initial age determination of the Redwall and Watahomigi formations was based on calcareous foraminiferans (Skipp, 1969) and corals (Sando, 1969). Based on these studies the youngest Redwall strata were thought to be Osagean or early Meramecian and the lowest Watahomigi beds were thought to be middle Pennsylvanian. This meant that the erosional unconformity between them represented the Late Mississippian and the early Pennsylvanian. The subsequent discovery of an erosional remnant of Redwall containing late Meramecian or early Chesterian foraminifera and corals (Skipp, 1969; Sando, 1969) reduced the gap between the Redwall and the Watahomigi formations to the Chesterian and part of the Morrowan. This gap was further narrowed by the determination of a mid-Morrowan (Bashkirian) age for the lowermost units of the Watahomigi Formation based on brachiopods (Gordon, 1982).

History

McKee (1982) noted the occurrence of tooth plates of the holocephalan *Deltodus* and an indeterminate fish spine from the Grand Canyon. Hodnett and Elliott (2018) described a tooth plate of *Deltodus* sp. Martin (1992) and Martin and Barrick (1999) noted chondrichthyan remains from their conodont residues. Hodnett and Elliott (2018) reviewed this material, which contained a new xenacanth shark taxon *Hokomata parva* (figure 4A–C). Not included in the study by Hodnett and Elliott (2018) were a few chondrichthyan dermal denticles and the jaw of a small actinopterygian fish (figure 4D–E).

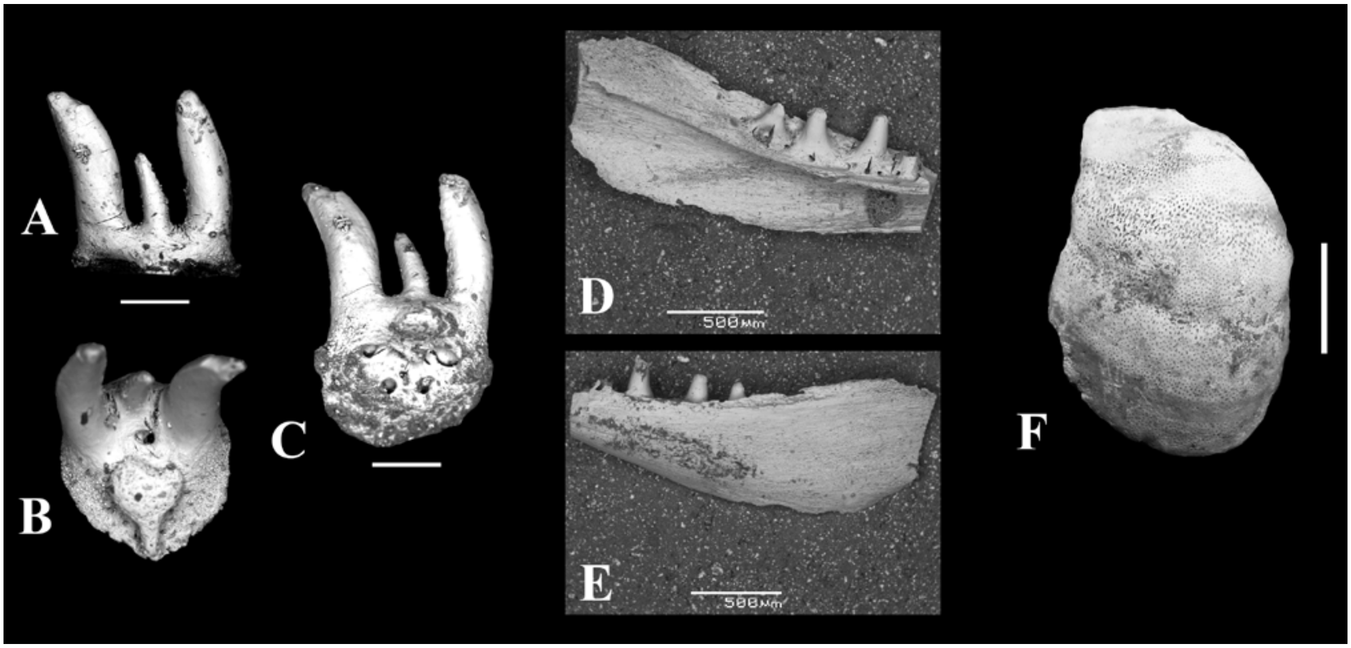

Figure 4. Fish fossils from the Watahomigi Formation (JOHN-PAUL HODNETT). A–C. Holotype (MNA V11264) of the xenacanth shark Hokomata parva*: A. Labial view; B. Oral view; C. Aboral view. D–E. Uncatalogued actinopterygian fish jaw: D. Medial view; E. Lateral view. F.* Deltodus *sp., USNM PAL 412145. A–E, scale equals 500 µm (0.02 in); F, scale equals 1 cm (0.4 in).*

GRCA Resources

The *Deltodus* teeth mentioned by McKee have not been located in any museum collection. The *Deltodus* sp. tooth described by Hodnett and Elliott (2018) is in the National Museum of Natural History Paleobiology Collections (USNM PAL 412145) (figure 4F). The microvertebrate fossils from Martin (1992), Martin and Barrick (1999), and Hodnett and Elliott (2018) come from the Hualapai Reservation and are held in the collections of the Museum of Northern Arizona Geology Department along with the type specimen of *Hokomata parva* (MNA V11264). The other microvertebrate fossils are currently under study by the authors.

Potential

The Watahomigi Formation has a high potential for other vertebrate remains to be discovered, in the form of both macro- and micro-remains.

Wescogame Formation

The Wescogame Formation represents another large marine transgression event after an unconformity with the underlying Manakacha Formation (McKee, 1982). The lower beds of the Wescogame Formation are marked by numerous channel beds made up of gravels of siltstone, limestone and conglomerate. The upper beds consist of carbonates, marine clays and sandstones (McKee, 1982). The age of the Wescogame is considered to be Virgilian based on the invertebrate assemblages (McKee, 1982).

History

McKee (1982) reported the tooth plates of *Deltodus* sp., identified by D. H. Dunkle, from Grand Canyon and the adjacent Lake Mead National Recreation Area.

GRCA Resources

The *Deltodus* tooth plates mentioned in McKee (1982) have not been located in any museum collection.

Potential

There is good potential for additional vertebrate fossils to be collected from this area.

PERMIAN

Pakoon Limestone

The Pakoon Limestone is the western lateral marine equivalent to the Esplanade Sandstone in the Grand Canyon and consists of thin- to thick-bedded dolomitic limestones, which inter-tongue with the Esplanade Sandstone (McKee, 1982). These beds mark the last member of the deposition of the Supai Group, which is followed by the Hermit Formation. The Pakoon Limestone extends from the western Grand Canyon and north into southwestern Utah and is Wolfcampian (early Permian) in age (McKee, 1982). An abundance of marine fossils, which include corals, pelmatozoans, and bivalves, are known from the western margins of the Pakoon Limestone, whereas the Esplanade Sandstone only has a fragmentary invertebrate fossil record (McKee, 1982).

History

McKee (1982) recorded the presence of two chondrichthyan tooth types from the Pakoon Limestone, *Cladodus* sp. and *Deltodus* sp., from the westernmost end of the Grand Canyon. Both taxa were identified by David Dunkle. The *Cladodus* sp. identification is most likely another cladodont shark taxon as *Cladodus* historically served as a "waste bin" for Paleozoic cladodont-grade chondrichthyan teeth. *Cladodus sensu strictu* is a genus of ctenacanth shark found only in the Mississippian (Duffin and Ginter, 2006). Hunt and others (2005) erroneously referred these specimens from the Pakoon Formation to the younger Kaibab Formation.

GRCA Resources

At present, no specimens of *Cladodus* or *Deltodus* from the Pakoon Limestone of the Grand Canyon have been transferred to any museum collection and are considered here to be missing.

Potential

The fossiliferous nature of the Pakoon Formation with its high abundance of marine invertebrates (McKee, 1982) and the record of at least two possible chondrichthyan taxa indicates a strong potential for more vertebrate material to be recovered where the Pakoon Formation is exposed.

Kaibab Formation

The marine limestones, dolomitic limestones, and sandstones of the Kaibab Formation are extensive throughout northern Arizona, southern Utah, east-central Nevada and southeast California. At the Grand Canyon, the Kaibab Formation forms the upper rim, which many park visitors stand upon while looking out over the canyon. The age of the Kaibab Formation is late early Permian (Leonardian/Kungurian) to early middle Permian (Guadalupian/Roadian) based on conodont analysis and the invertebrate assemblages (Thompson, 1995; Hopkins and Thompson, 2003). The depositional environment of the Kaibab represents a broad continental shelf exceeding approximately 125 km (200 mi) in width (Hopkins and Thompson, 2003). Frequent periods of sea level changes led to major lateral shifts of supratidal, subtidal, and shallow-marine environments that led to complex interlayering of different types of carbonate and clastic sediments (Hopkins and Thompson, 2003). McKee (1938) proposed the division of the Kaibab Formation into three members, from oldest to youngest, the gamma, beta, and alpha. Sorauf (1962) combined the beta and gamma members into a single unit, the Fossil Mountain Member, and renamed the alpha member as the Harrisburg Member.

Previously, vertebrate fossils have been considered rare within the Kaibab Formation (David, 1944). However, vertebrate fossils from the Kaibab are now known from multiple locations within GRCA and southward towards the Flagstaff metropolitan area (Hodnett and others, 2011a, 2011b, 2012; Elliott and Hodnett, 2013). Between GRCA collections and those from the Flagstaff localities the Kaibab Formation has one of the most extensive marine vertebrate assemblages for the global Permian, with an estimated 40+ chondrichthyan taxa and a large number of indeterminate osteichthyans including actinopterygians and coelacanths (Hodnett and others, 2011a, 2011b, 2012; Elliott and Hodnett, 2013). This high number of taxa comes from both macro and micro vertebrate remains.

History

The earliest account of a vertebrate fossil from the Kaibab of the Grand Canyon came from an anonymous note in 1926 that reported fish remains consisting of "imprint of ribs and backbone" coming from the Kaibab Formation and collected by A. L. Brown from Bright Angel Ranger Station on the North Rim. Spamer (1984) later relayed a personal communication with E. D. McKee that this fish specimen was in fact the scyphozoan *Conularia kaibabensis*. McKee (1938) reported the first definitive fish remains from the Grand Canyon. He examined three teeth in the USGS paleontology collection that had been collected by C. D. Walcott in 1882, which he indicated came from the Alpha Member (now Harrisburg Member) of the Kaibab Formation. McKee gave no taxonomic identification for the three teeth Walcott collected. McKee collected and figured (1938: Plate 15, Figure 4) a mandibular tooth plate of *Deltodus mercurii* (figure 6B) from an undisclosed locality in the Beta Member (Fossil Mountain Member) at the Grand Canyon.

Hussakoff (1943) described a number of fish teeth and a fin spine from a site known locally as the "Bottomless Pits," northwest of Walnut Canyon National Monument and on the east side of Flagstaff, Arizona. The taxa identified by Hussakoff (1943) include the teeth of the chondrichthyans *Deltodus mercurii*, *Psephodus* sp., and *Janassa* sp., a euselachian shark spine fragment referred to "*Hybodus* sp.," and isolated actinopterygian teeth. A year later, David (1944) described the type specimen of *Megactenopetalus kaibabanus*, which consisted of an upper symphysial tooth of a large species of petalodontimorph chondrichthyan from the North Rim of GRCA (figure 5A–B). Additional specimens of *Megactenopetalus* have been collected from the Kaibab Formation near Sedona, Arizona, and juvenile teeth have recently been identified from Flagstaff, Arizona (Ossian, 1976; Hodnett and others, 2011b). Outside of the Kaibab Formation, *Megactenopetalus* has been found in the

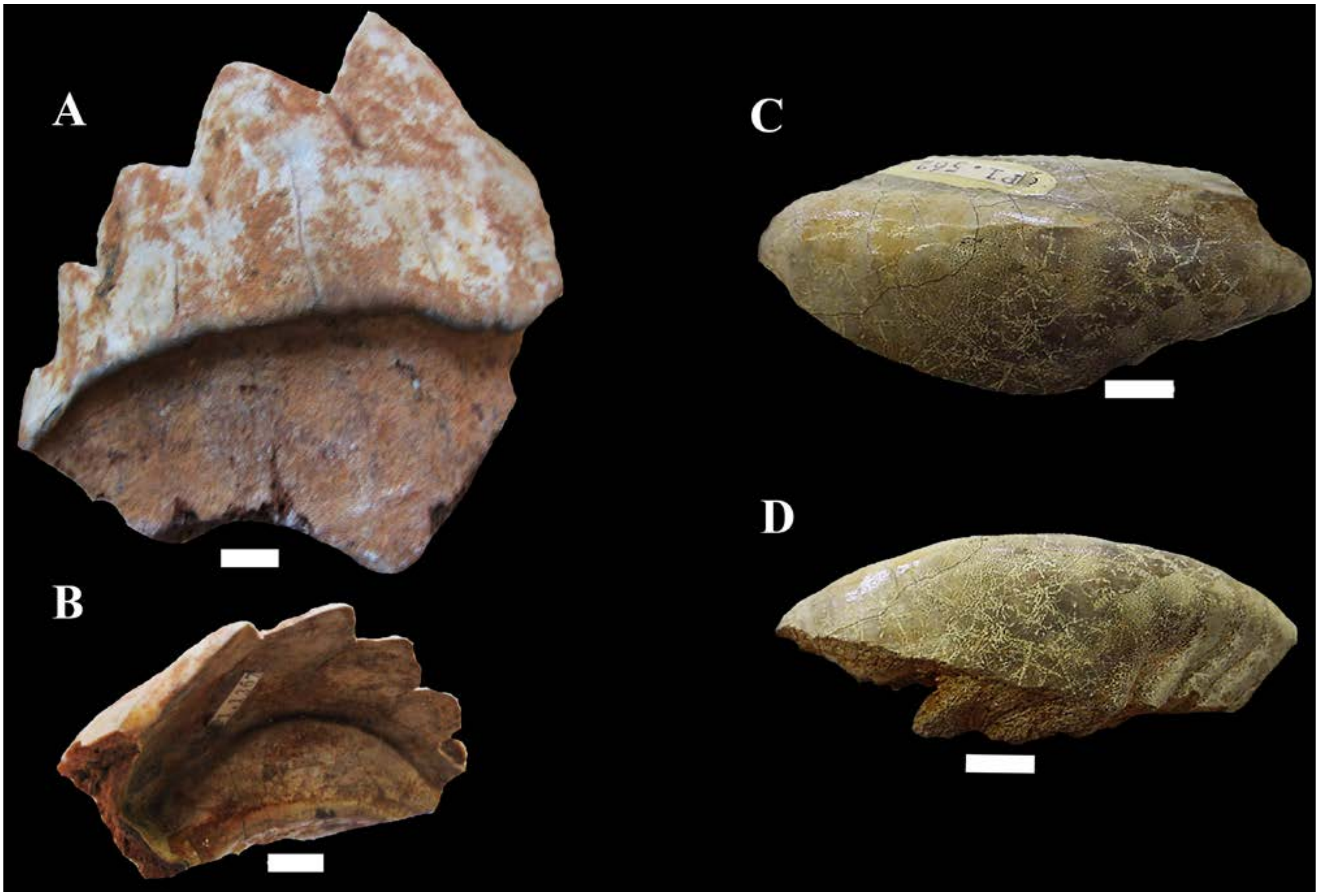

*Figure 5. Chondrichthyan fossils collected from the Kaibab Formation on the North Rim of Grand Canyon National Park (JOHN-PAUL HODNETT). **A–B**. MNA V. 1367, holotype of* Megactenopetalus kaibabanus*: **A.** Labial view; **B.** Orolingual view. **C–D**, MNA Pl. 562,* Psephodus *sp.: **C.** Oral view; **D**. Distal view. Scale equals 1 cm (0.4 in).*

approximately contemporaneous Permian sediments of the Concha Limestone in southeastern Arizona (Hansen, 1978) and New Mexico (Ossian, 1978; Hunt and Lucas, 2005), the Glass Mountain region of Texas (Ossian, 1976; Hunt and Lucas, 2005), China (Young, 1950), and Iran (Golshani and Janvier, 1974).

Gass (1963) briefly described a large tooth plate he referred to *Psephodus* sp. that was also collected on the North Rim of GRCA. The genus *Psephodus* is known primarily from the early Carboniferous (Mississippian) of Europe and North America, but there are records of Permian *Psephodus* from Pakistan and Russia (Stahl, 1999). The GRCA *Psephodus* would be the first Permian record of this taxon in North America. Johnson and Zidek (1981) reported on the dental palatal plates of platysomid fishes from the GRCA Bright Angel Trail (figure 6C) and a locality within the Kaibab National Forest. Additional Kaibab platysomid tooth plates and isolated teeth were collected within the Flagstaff vicinity and in central Arizona (Johnson and Zidek, 1981). Recently the mold of a large platysomid tooth plate was found in situ in a block of Kaibab Formation along the Hermit Trail by S.G. Lucas (New Mexico Museum of Natural History and Science, Albuquerque) in 2018 but not collected. Platysomid fishes are deep-bodied actinopterygians and are known from the Pennsylvanian to the Permian of Europe and North America (Johnson and Zidek, 1981; Zidek, 1992; Mickle and Bader, 2009).

Thompson (1995) briefly described a number of vertebrate micro-remains from the Fossil Mountain type section within GRCA. Vertebrate fossils include the teeth of an indeterminate hybodont (identified as *Polyacrodus* cf. *P. witchitaensis* in Hodnett and others, 2011a) and the early neoselachian *Cooleyella peculiaris*, a taxon related to *Cooleyella platera* from the Upper Mississippian Surprise Canyon Formation (Hodnett and Elliott, 2018). Thompson also reported a tooth of *Symmorium* cf. *S. reniforme*, a symmoriid chondrichthyan from the Upper Pennsylvanian of the Black Shales (Ginter and others, 2010). We reviewed these specimens and they appear to be worn teeth of *Heslerodus divergen*s, a taxon known from the Kaibab Formation near Flagstaff (Hodnett and others, 2012) and a new record of a jalododont chondrichthyan. Thompson (1995) also identified a number of isolated dermal and buccal membrane denticles of chondrichthyians such as *Cooperella striatulata*, *Sturgenonella quinqueloba*, *Moreyella typicalis*, *Kirkella typicalis*, and a *Petrodus*-like taxon. These

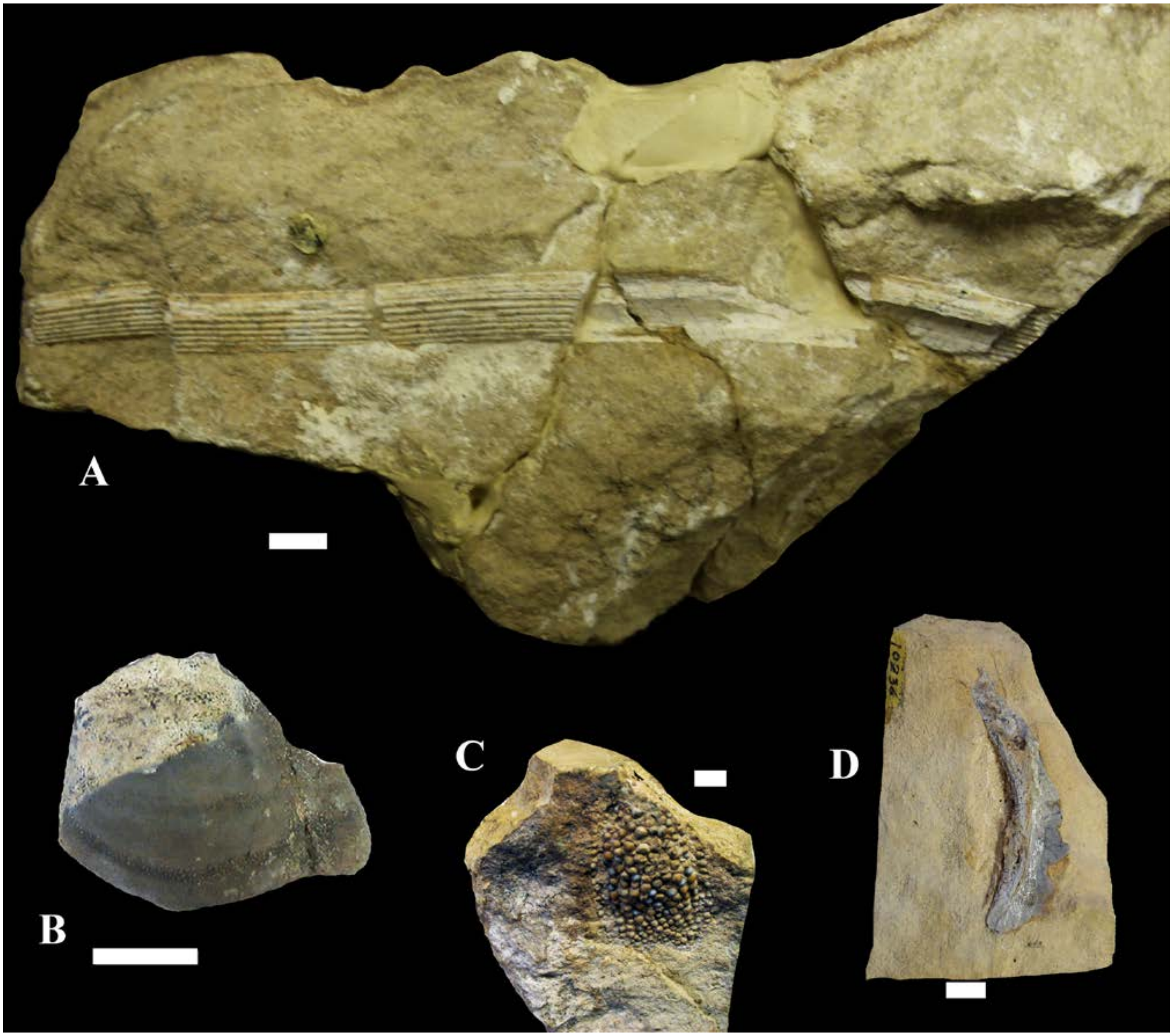

***Figure 6.** Kaibab vertebrate fossils in GRCA collections (JOHN-PAUL HODNETT). **A.** GRCA 10030, euselachii indeterminate dorsal fin spine. **B.** GRCA 9368,* Deltodus mercurii *mandibular tooth plate. **C.** Platysomid indeterminate fish tooth plate. **D.** GRCA 10326, indeterminate actinopterygian cleithrum. Scale equals 1 cm (0.4 in).*

denticles are often associated with multiple different family groups of chondrichthyans including hybodonts, petalodonts, symoriids, and holocephalans. A number of isolated indeterminate actinopterygian teeth have also been identified from the Fossil Mountain locality (Thompson, 1995). Hodnett and others (2011a, 2011b, 2012, 2013) and Elliott and Hodnett (2013) reported on a number of new chondrichthyan taxa from the Kaibab Formation. These include at least seven taxa of ctenacanthiform sharks, a xencanthimorph, seven hybodontiform sharks, and six petalodontimorph chondrichthyans; most of which were collected from the vicinity of Flagstaff, Arizona. Stable and radiogenic isotope analyses of the Flagstaff Kaibab chondrichthyan teeth showed depleted δ18OP values giving a signature of extreme salinity and warm waters for the Kaibab assemblage (Fisher and others, 2014). However, it was determined that the Kaibab tooth samples used had gone through a diagenetic alteration that skewed the results, making accurate interpretation not possible (Fisher and others, 2014).

GRCA Resources

At present, the teeth collected by C. D. Walcott in 1882 reported in McKee (1938) have not been relocated in the USGS Collections.

MNA: The two teeth collected from the North Rim of GRCA are housed at the Museum of Northern Arizona, Flagstaff. The type of *Megactenopetalus kaibabanus* (MNA V. 1367) is on permanent display in the Geology Hall of the museum gallery, while the *Psephodus* sp. (MNA Pl. 562) tooth plate is in the paleontology collections (figures 5C and 5D). The vertebrate samples reported in Thompson (1995) are all housed at the Museum of Northern Arizona. The platysomid tooth plates reported in Johnson and Zidek (1981) are a cast (MNA PL. 556) and a tooth plate (MNA PL. 43).

GRCA: Specimens (excluding casts) collected from the Kaibab at Grand Canyon National Park include: GRCA 9368, *Deltodus mercurii* mandibular tooth plate (from McKee, 1938: 166, Plate 15, Figure 14); GRCA 10030, euselachian indeterminate dorsal fin spine (figure 6A); GRCA 10229, platysomid tooth plate (may be the same specimen listed as a cast in Johnson and Zidek, 1981 under MNA PL. 556); GRCA 10326, indetermi-nate actinopterygian cleithrum (figure 6D).

Potential

Based on previous reports and new work conducted at fossil sites in the Flagstaff vicinity, there is an extremely high potential for the Kaibab exposed at GRCA to yield a significant amount of vertebrate fossils.

CONCLUSIONS

As demonstrated above, the Grand Canyon has a surprisingly rich Paleozoic body fossil record, although the majority of these records are of the teeth and dermal spines of chondrichthyan fishes. This is not surprising as much of the geologic history of the Paleozoic at the Grand Canyon is the record of multiple marine transgression and regression events. Unfortunately, even though the literature lists multiple records of vertebrate body fossil remains, many of those records are not supported by physical specimens in museum collections for verification or further research. As such, it our opinion that a need to return to these sites to look for and collect additional vertebrate material is warranted.

The Devonian through Permian rocks of Grand Canyon National Park have a high potential to reveal a further wealth of information to understand the dynamics of a constantly changing physical world and its impact on the organisms that lived during those times. In terms of an advance in our knowledge of paleoichthyology, the geographical position and the amount of time covered at Grand Canyon could give us a large dataset of how fishes evolved during the Paleozoic, as there are few localities in the American southwest that expose such an extensive geological sequence of time for marine and near-marine sedimentary rocks. There is good potential for the occurrence of early tetrapods in the Devonian Temple Butte Formation, as well as collecting additional tetrapod remains from the Upper Mississippian Surprise Canyon Formation.

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PALEOZOIC PALEOBOTANY OF GRAND CANYON NATIONAL PARK

Cassi Knight[1]

ABSTRACT

A review of known Paleozoic plant macrofossil resources in Grand Canyon National Park was completed, detailing previously published plant fossil occurrences from the Surprise Canyon Formation, the Supai Group, and the Hermit Formation. No new paleobotanical sites are added to the fossil record in this report, but an effort was made to update the taxonomy for plant fossils included in this chapter. These updates are based on previously published literature, and include the following: *Callipteris conferta* to *Autunia conferta*, *Callipteris raymondii* to *Gracilopteris raymondii*, *Callipteris arizonae* to *Rhachiphyllum* sp., *Callipteris* sp. to *Rhachiphyllum* sp., *Walchia dawsoni* to *Hermitia dawsoni*, *Walchia gracillima* to *Hermitia* sp., *Walchia hypnoides* to *Otovicia hypnoides*, and *Ullmannia frumentaria* to *Feysia* sp. Many of the taxonomic names used by David White in his 1929 monograph on the plant fossils of the Hermit Shale need to be reviewed in light of more recent publications—however, no formal analysis of these fossils was undertaken here, due to lack of preserved epidermal information and reproductive structures.

INTRODUCTION

Grand Canyon National Park (GRCA) is certainly one of the most awe-inspiring natural sculptures on Earth. From the rich black Vishnu Schist lining the depths of the canyon, to the shining white cliffs of the Kaibab Formation perched on the canyon rim, the exposed rocks display approximately one-third of all of Earth's history in a well-exposed geologic section. Each of the rock layers that form the intricacies of Grand Canyon's walls represents a different environment that existed in this place as the Colorado Plateau changed over hundreds of millions of years. Many of the sediments deposited in these different environments preserve fossils that provide an immense wealth of information about the evolution of life on earth.

Grand Canyon exposes rocks that were formed starting in the Precambrian through the middle Permian in the Paleozoic and are ~1800–270 million years (Ma) old. The most visible rocks in the canyon—the flat-lying layers that dominate many vistas from the rim—are the Paleozoic portion of Grand Canyon's stratigraphy. During the early and middle Paleozoic, the Colorado Plateau was largely inundated by shallow seas and the marine sediments deposited during this time (~545–335 Ma) reflect these conditions. Local sea level started falling during the Mississippian, and the resulting deposits of the Surprise Canyon Formation, Supai Group, Hermit Formation, and Coconino Sandstone represent a range from nearshore to estuarine to terrestrial environments. The fossil plants reported from Grand Canyon National Park are found in the Surprise Canyon Formation, members of the Supai Group, and the Hermit Formation.

The Hermit Formation preserves the most diverse and well-preserved flora from Grand Canyon, with 42 different species reported, and 25 type specimens known from the associated collections **(appendix A)**. There are seven identified plant taxa reported from the Supai Group and 12 from the Surprise Canyon Formation, many of which are fragmentary and more poorly preserved. Whereas plant fossils are not overly abundant in Grand Canyon, they are certainly significant because they add to the limited record of Mississippian, Pennsylvanian, and Permian age paleofloras from the western margin of the Pangean supercontinent, a region subject to considerably different climatic conditions than contemporaneous areas in the more central Euramerican regions.

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HISTORY OF RESEARCH

The first paleobotanical remains from the Grand Canyon were discovered by Charles Schuchert in 1915 in the Hermit Formation along the Hermit Trail in the Waldron Basin at a locality called Red Top. Schuchert sent a small collection of these specimens to U.S. Geological Survey (USGS) paleobotanist David White for identification. White noted *Walchia*, "*Gigantopteris*" (likely *Supaia*), *Sphenophyllum*, and *Callipteris* in this initial sampling, and these findings were published in 1918 (Schuchert, 1918; White, 1929b). A few more plant fossils were found and reported to White by Levi F. Noble and Charles Gilmore between White's 1918 publication and his Carnegie Institution funded collecting trips during the summers of 1926–1928. White's systematic collecting during these field trips yielded the specimens that he would publish in his 1929 monograph on the Hermit Formation paleoflora. Most of his plant collection came from a quarry he made along the Yaki Trail (now called the South Kaibab Trail) and is marked today by the "fossil fern exhibit" constructed by the Civilian Conservation Corps (CCC) in 1937 just to the west of the trail on Cedar Ridge (figure 1).

David White also spent time searching the Supai Group for plant fossils, particularly during the summer of 1928, and published a mention of his findings in his 1929 Hermit Formation monograph (White, 1929a). White reported the conifer *Walchia* and algal trace fossil *Rivularites* from multiple horizons in the lower and middle Supai, and an assemblage of *Walchia*, *Taeniopteris*, *Neuropteris* (*incertae sedis*), *Cordaites* (conifer), and *Calamites* (horsetails) from 7.6 m (25 ft) above the base of the Watahomigi Formation near the South Kaibab Trail (McKee, 1982). Plant fossils were next reported from the Supai Group by Edwin D. McKee in a large USGS report, having been found during field work supporting this publication. From many measured sections throughout the Supai, occurrences of *Walchia*, stems, ferns, *Rivularites*, stromatolites, miscellaneous algae, and bioclasts are noted (McKee, 1982).

The Surprise Canyon Formation is the most recently recognized sediment package in GRCA. USGS geologist George Billingsley first noticed the large dark red-brown channel fills sitting on top of the Redwall Limestone during mapping reconnaissance flights in the 1970s (Beus, 1986). Between 1975 and 1983, Billingsley and Beus measured sections for many of the larger Surprise Canyon outcrops and observed a fairly consistent assemblage of plant fossils in the terrestrial deposits at the base of these channels. They repeatedly reported tree impressions, wood fragments, and leaves, and spores attributable to ferns and lycopods like *Lepidodendron* (Beus, 1986). A brief description of this flora was published in Billingsley and McKee (1982), with USGS paleobotanist Serge Mamay identifying two ferns and five sphenophytes. Other unidentified plant fragments and 22 spore and pollen taxa were described in this report as well, but none of the plant or palynological specimens were figured (Tidwell and others, 1992). Beus later collected 40 additional plant specimens, and these contributed to a closer review of the Surprise Canyon flora by Tidwell and others (1992) who identified a total of 12 plant taxa.

STRATIGRAPHIC DISTRIBUTION OF FOSSILS

The Paleozoic rocks of Grand Canyon include, from oldest to youngest, the Tapeats Sandstone, Bright Angel Shale, Muav Limestone, Temple Butte Formation, Redwall Limestone, Surprise Canyon Formation, the Supai Group, Hermit Formation, Coconino Sandstone, Toroweap Formation, and Kaibab Formation (McKee,

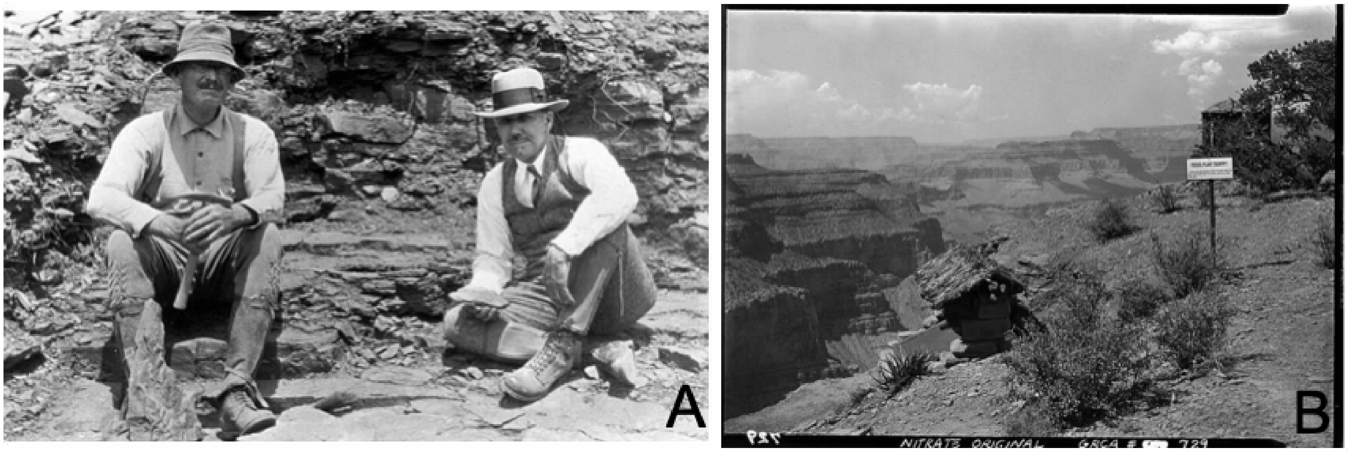

Figure 1. A. *Paleobotanist David White (left) and John C. Merriam working in the Cedar Ridge fossil quarry during field work in the summer of 1927 (NPS).* ***B.*** *Fossil Fern Exhibit constructed by the Civilian Conservation Corps (CCC) at the site of White's quarry on Cedar Ridge, South Kaibab Trail (NPS).*

1982). Some portions of the Surprise Canyon Formation, the Supai Group, and all of the Hermit Formation were deposited under terrestrial and/or estuarine conditions and account for the Paleozoic floras reported from GRCA. The Surprise Canyon Formation represents ancient coastal plain and estuarine environments and records a sparse assemblage of fossil plants. The Supai Group preserves sporadic plants in some of its members, in the sandy and silty terrestrial deposits left by intervals of low sea level. The Hermit Formation was deposited in a seasonally dry (Cecil, 2003; Gastaldo and Demko, 2011) lowland environment, an interpretation based on the composition of the paleoflora, and preserves the most robust fossil plant assemblage in the canyon.

Plant fossils from the Hermit Formation and the Supai Group are mostly known from eastern portions of GRCA, especially from outcrops near the South Kaibab, Bright Angel, and Hermit Trails. This is somewhat unsurprising, given the difficulty and exposure of the general terrain—prospecting for new fossil sites can be rather challenging. Conversely, the Surprise Canyon flora is mostly reported from sites in western GRCA, where the isolated channels of this formation are largest. Most of the access to these sections was helicopter supported through a USGS project, so the fossil sites reflect a larger spatial distribution and are largely inaccessible by foot.

Surprise Canyon Formation

The Surprise Canyon Formation is latest Mississippian in age (~325 Ma) and is exposed throughout Grand Canyon as isolated lenses filling old erosional valleys, caves, and karst collapse structures in the top of the Redwall Limestone (Billingsley and Beus, 1985; Beus, 1986). The conglomerate and mudstone beds that make up the channel fills were originally considered to be part of the Watahomigi Formation, the basal unit of the Supai Group. The rocks that form the Surprise Canyon Formation were only identified as a unique sediment package in 1979 by George Billingsley (Billingsley, 1979), and formally described by Billingsley and Beus (1985). The Surprise Canyon Formation occurs throughout Grand Canyon and in parts of Marble Canyon, and is rather difficult to identify because of its discontinuous nature and because its larger, more visible outcrops occur in remote areas of western Grand Canyon (Tidwell and others, 1992).

In the western Grand Canyon, the Surprise Canyon Formation occurs as thicker sections in western Grand Canyon with channels typically 45 to 60 m (150 to 200 ft) wide, and as thick as 120 m (400 ft) (Tidwell, 1992). It is divided into three major units: 1) terrestrial conglomerate and sandstone; 2) marine skeletal limestone; and 3) marine siltstone and silty to sandy limestone (Tidwell, 1992). Most channels, however, only contain the basal terrestrial and the upper fine-grained clastic and carbonate rocks. Plant fossils are found only in the sandstone, siltstone, and shale beds of the lower unit, particularly in western GRCA, and include tree impressions, wood fragments, and plant compressions (Billingsley and Beus, 1985).

Identified taxa include the horsetails *Calamites cistiiformis* and *Calamites* sp., the lycopods *Lepidodendron aculeatum*, *L. mannabachanese, L. volkmannianum*, *Lepidostrobus* sp. cf. *L. ornatus*, *Lepidostrobophyllum* sp. and *Stigmaria ficoides*, the fern *Pecopteris* cf. *P. aspera*, the pteridosperm seed *Wardia* sp., and *Cyperites* sp. and *Knorria* sp. (*incertae sedis*) (Beus, 1990, 1995; Tidwell and others, 1992; Hodnett and Elliot, 2018). There are also poorly preserved plants that Billingsley and McKee (1982) reported, based on personal communication with Mamay, as two ferns (one described as "a very delicate, small-pinnuled sphenopterid or pecopterid"), five sphenopsids ("the sphenopsid fragments are parts of the fruiting organs of a phyllothecoid plant"), and other unidentifiable plant fragments. A brief mention of stromatolites at the top of the Surprise Canyon sequence at the Quartermaster Canyon section was made by Beus (1990). While this flora is neither well-preserved, abundant, or diverse, it is significant because Mississippian and early Permian age floras are rare in the western US, and this is the first flora of this age reported from Arizona (Tidwell and others, 1992).

In addition to the megaflora, an assemblage of 22 pollen and spore taxa was recovered from the Surprise Canyon Formation (see list below) and suggests that this plant community was more diverse than its megafossil record implies (Billingsley and McKee, 1982; Tidwell and others, 1992). The palynological samples were collected from the basal terrestrial sand and conglomerate unit at the Granite Park section locality (Billingsley and McKee, 1982).

Per Billingsley and McKee (1982), pollen and spore taxa known from the Surprise Canyon Formation include the following:

- *Anapiculatisporites concinnus*
- *Anaplanisporites globulus*
- *Auroraspora solisortus*
- *Calamospora* sp.
- *Convolutispora florida*
- *Convolutispora* sp.
- *Dictyotriletes* cf. *D. clatriformis*
- *Granulatisporites granulatus*
- *Granulatisporites* sp.
- *Hadrohercos stereo*

- *Knoxisporites triradiatus*
- *Lycospora* spp.
- *Punctatisporites* cf. *P. heterofiliferous*
- *Punctatisporites* cf. *P. nitidus*
- *Punctatisporites pseudolevatus*
- *Punctatisporites solidus*
- *Punctatisporites validus*
- *Punctatisporites* spp.
- *Reticulatisporites* sp.
- *Schulzospora rara*
- *Triquitrites* sp.
- Monosaccates indet.
- Unassigned (? algal)

Lepidodendrales

Several fossils from the Surprise Canyon flora represent different organ or tissue types of arborescent lycopsid, an extinct plant group commonly known as scale trees or giant clubmosses. The trunk impressions that preserve different leaf cushion patterns belong to three species of the genus *Lepidodendron*, the spore-producing lycopsid cones are assigned to *Lepidostrobus* sp. *cf. L. ornatus*, isolated sporophyll impressions to *Lepidostrobophyllum* sp., and the root structures to *Stigmaria ficoides* (Tidwell and others, 1992). Based on the leaf cushion patterns on the trunks' exterior, three different types of lycopsid bark were identified: *Lepidodendron aculeatum*, *L. mannabachanese*, and *L. volkmannianum* (Tidwell and others, 1992).

Filicales and Pteridosperms

Fragmentary remains of the marattialean tree fern frond *Pecopteris* sp. were reported by Tidwell and others (1992), who mentioned it closely resembles *P. aspera*, but there is not sufficient evidence to conclusively make this identification. Seeds that have been recovered from limestone beds were reported as *Wardia* sp.—platyspermic winged seeds: bilaterally flattened, spherical bodies with small wing-like projections along their lateral flanks. Based on other floras from North America, *Wardia* sp. is associated with the compound, pinnate (fern-like) foliage of the pteridosperm *Aneimites* (Tidwell and others, 1992).

Incertae Sedis

Several impressions of what appear to be the subsurface bark layer of lycopsid trunks are tentatively reported from the Surprise Canyon flora, and have been listed as *Knorria* sp. (Tidwell and others, 1992). These fossils show the pattern of leaf vasculature where it connects from the lycopsid trunk to its leaves, and the best preserved specimen shows helically arranged leaf bases, but lacking features allowing more detailed classification. Arborescent lycopsids belong to the still-extant order Isoetales, commonly known as the quillworts, one of three extant orders in the class Lycopsida, the earliest still-extant group of vascular plants (Taylor and others, 2009). Additionally, isolated, fragmentary leaves of *Cyperites* sp. are poorly preserved in the Surprise Canyon Formation and their taxonomic relationships to particular lycopsid stem taxa is indeterminate (most of the stem forms produced very similar, grass-like leaves that are difficult to differentiate in compression preservation).

Supai Group

The Supai Group spans the Early Pennsylvanian to the middle early Permian (315–285 Ma), and crops out prominently as a red, stair-stepped slope throughout the Grand Canyon (McKee, 1982). The erosion-resistant Esplanade Sandstone at its top creates the iconic Esplanade Platform in the western reaches of GRCA. Sediments of the Supai Group were deposited during the late Paleozoic Ice Age. The sediment packages range from terrestrial to fully marine deposits (with intermediate environments also represented), reflecting a time of great sea-level fluctuation caused by global glacial-interglacial cycles (Fielding and others, 2008; Montañez and Poulsen, 2013). The Supai Group records four separate marine transgressions, and each distinct event corresponds to one of the four formations in the Supai Group: the Watahomigi Formation, Manakacha Formation, Wescogame Formation, and the Esplanade Sandstone (McKee, 1982). With each transgression, the sea level rose progressively higher and flooded increasingly large portions of Arizona and the San Juan Basin (New Mexico, Utah, and Colorado) (McKee, 1982).

Each of the four members of the Supai Group have some portion of terrestrial deposits that contain plant fossils belonging to the horsetails, seed ferns, conifers, and plant remains of undetermined affiliation (White, 1929a; McKee, 1982). These terrestrial sediments largely consist of siltstones and mudstones, and somewhat commonly preserve mud crack and raindrop surfaces (White, 1929a; McKee, 1982). From the marine limestones of the Supai, fossils identified as algae or algal structures, and several types of bioclasts have also been reported (McKee, 1982).

Watahomigi Formation

This marine deposit is composed mostly of limestone that grades into sandstone and siltstone beds that are thicker in the eastern part of the Grand Canyon. The environment of deposition is interpreted to be a relatively shallow, low energy embayment. Plants reported from the Watahomigi Formation include the horsetail relative *Calamites* sp., the seed fern *Neuropteris* sp., the conifer relative *Cordaites* sp., the conifer *Walchia* sp., *Taeniopteris* sp. (*incertae sedis*), and other unidentified plant fragments. These are found in the siltstone and sandstone beds in the eastern Grand Canyon near the base of the Watahomigi. These beds also preserve mud crack and rain drop surfaces, and their equivalent facies to the west are limestone (White, 1929a; McKee, 1982). Miscellaneous algal structures are also reported from the Watahomigi Formation, but without much accompanying information (White, 1929a; McKee, 1982).

Manakacha Formation

The Manakacha Formation was deposited during a second, larger transgression that flooded further inland to the northeast. Hence, it is mostly marine sandstone with some carbonate rock. The only identifiable plant foliage reported from the Manakacha Formation are ultimate branches of the conifer *Walchia* sp., and an undetermined fern (Filicopsida), which are found in shaly mudstone beds. Other reported plant fossils include algal limestone nodules, *Girvanella* bioclasts and calcisphere bioclasts (White, 1929a; McKee, 1982). The *Girvanella* and calcisphere bioclasts occur as bioclastic debris in carbonate facies in central and eastern Grand Canyon.

Wescogame Formation

The base of the Wescogame Formation lies on an unconformable surface marked by large (up to 24 m/80 ft deep) channel cuts (McKee, 1982). The channel cuts are filled with conglomerate, and the overlying Wescogame Formation above consists largely of sand and mud in eastern Grand Canyon, that grades into limestone to the west. The Wescogame Formation, having been deposited in a higher energy marine environment, does not include well-preserved plant remains. Plants found in this formation are miscellaneous algae, including *Rivularites* (Spamer, 1992), and possible algal and organic features (White, 1927; McKee, 1982). Additionally, some occurrences of *Walchia* sp. have been noted in the Grand Canyon area by Spamer (1992). "Fern or cycadofilice" fragments are reported from shaly beds with many mud crack and rain pit surfaces, but these may be from the overlying Esplanade Sandstone (Schuchert, 1918; McKee, 1982).

Esplanade Formation

The Esplanade is the thickest and most extensive member of the Supai Group. Its base is mostly mudstone and siltstone, coarsening upwards to cross bedded sandstone, which is especially prominent in central and eastern Grand Canyon (McKee, 1982). The Esplanade Sandstone preserves rare shoots of *Walchia* sp., some undetermined plants, and plant fragments (White, 1929a; McKee, 1982).

Hermit Formation

The Hermit Formation, often referred to as the Hermit Shale, is early Permian in age (~280 Ma), and forms a soft, deep red slope near the top of Grand Canyon. It is composed of interbedded mudstones, shale, and fine sandstones, and represents sediments accumulating on a broad coastal plain in an environment that experienced strong seasonal drought (White, 1929a). The Hermit Formation is one of very few fully terrestrial deposits in Grand Canyon and preserves by far the most detailed and diverse paleoflora from the park. The Permian represents a time of dramatic fluctuation in climate, in response to global cyclic glaciation (Fielding and others, 2008; Montañez and Poulsen, 2013). In addition to these overall global-scale cycles, a more seasonal drought regime is interpreted for equatorial Pangea, in which dry periods became increasingly drier (Fielding and others, 2008; Montañez and Poulsen, 2013). The Hermit Formation provides unique insight into less-often preserved plant communities that inhabited the continental basins during drier times.

The Hermit Formation flora is significant in that it is distinct from all other North American Permian floras, being a mix of cosmopolitan Permian species, and species with greater affinities to Gondwanan taxa than to North American taxa. Additionally, David White named 25 species from this formation (**see appendix A**).

The Hermit Formation lies directly above the Supai Group, filling erosional channels cut into the top of the Esplanade Sandstone, and forming an extensive deep red slope throughout the canyon. It was at one time included as part of the Supai Group, and was officially named a separate unit in 1922 by L. F. Noble, who removed the upper red shaley beds from the Supai Formation and named them the Hermit Formation (Noble, 1922). The Supai Formation was later subdivided into the four current members of the Supai Group by McKee (1982). The Hermit Formation is composed mostly of thinly bedded silts and sandy silts, with thin discontinuous sandstone beds occurring in the basal and top portions of the formation, and represents deposition in a broad fluvial environment. The Hermit Formation thickens to the west, measured as ~68.6 m (225 ft) thick at the South Kaibab trail and ~83.8 m (275 ft) thick in the Hermit Basin (near the Hermit Trail) (White, 1929a).

This fossil flora is described only in a 1929 monograph by David White, but the record of known Permian floras extends to other localities in Arizona, Utah, Colorado, New Mexico, and Texas in the western United States, and also from China, France, Spain, and the Czech Republic (White, 1929a; Gand and others, 1997; Wang, 1997; DiMichele and others, 2005, 2006, 2007, 2012, 2013; Galtier and Broutin, 2008; Opluštil and others, 2017). Of the 32 fully named plant fossil species listed by White (1929a) (with 10 additional species only identified to genus level, or of uncertain identification), about half of them were newly described species at the time he published them (see appendix A). However, it is likely that there are truly about half that many species in the Hermit Flora because many were poorly preserved and doubtfully described (Read and Mamay, 1964). The major groups represented include Spermatopsida (seed plants, including seed ferns), conifers, horsetails, Ginkgoopsida, and algae (White, 1929a).

Spermatopsida

The seed ferns (Spermatopsida) are a group of plants that were abundant in the Paleozoic and Mesozoic (Taylor and others, 2009), and they are an informal grouping of seed plants that otherwise cannot be firmly attributed to the seed plant lineages, conifers, cycadophytes, gnetaleans, or ginkgoes (Hilton and Bateman, 2006). Their foliage superficially resembles that of ferns, but they produced seeds instead of spores as true ferns do. White listed 18 different species of seed fern (and five additional unidentified species) belonging to six different genera. The genera include *Autunia* or *Rhachiphyllum* (formerly *Callipteris* [Kerp and Haubold, 1988]); *Supaia*, *Brongniartites*, *Yakia*, and *Neuropteridium* (Supaiaceae); and *Taeniopteris* (*incertae sedis*; *Taeniopteris* is included under seed ferns in White [1929a] but is truly a vast form genus that includes species of seed ferns and ferns) (table 1).

The genus *Supaia* was established by White (1929a) to describe fern-like foliage dominant in the Hermit Formation flora (figure 2). A key character of this genus is a single bifurcation in the lower frond that splits into two simply pinnate sections. The angle of the split is acute. White interpreted *Supaia* to be closely related to *Autunia* or *Rhachiphyllum* (what White referred to as *Callipteris*) (Kerp and Haubold, 1988). DiMichele and others (2018) commented specifically on *Supaia anomala*, and moved it into the genus *Auritifolia* Chaney, as *Auritifolia anomala*. The authors Kerp and Haubold (1988) commented specifically on the species *Callipteris conferta*, designating it *Autunia conferta*, and on the species *Callipteris raymondii*, designating it to the morphogenus *Sphenocallipteris raymondii*, as they argued that the name *Callipteris* should be abandoned. Kerp and others (1991) then renamed *Sphenocallipteris* as *Gracilopteris*, meaning the most current name for *Callipteris raymondii* is *Gracilopteris raymondii*. The other species of *Callipteris* mentioned by White (1929) likely belong to the morphogenus *Rhachiphyllum* (Kerp and Haubold, 1988), but no formal evaluation is presented here.

White reported several seeds potentially attached to different specimens of *Supaia* in both his 1929 monograph and in another article published in 1934 (which did not include any figures or references to specimens). Evidence for physical attachment of these seeds to foliage was unclear at best, was reviewed by Mamay and Watt (1971), and is currently interpreted to be some type of insect damage (William DiMichele and colleagues, pers. comm.).

Yakia was another genus newly established by White (1929a) and is defined by "closely spaced, relatively even and parallel ultimate divisions, and by the rather distant, narrow, crooked leaves, which have the appearance of being irregularly lobed…" (figure 3). White also tentatively assigned a fructification that appears as five oblong bodies packed together in what White called "clusters of sporangia or (possibly seeds)", located at the bases of the pinnules (White, 1929a: plate 40, figures 1 and 2). The distinction between *Supaia* and the other genera included by White in Supaiaceae (*Brogniartites* and *Yakia*) is the size and overall shape (proportion) of the foliage—the bifurcated fronds, pinnules, and venation are all otherwise very similar (it may be that they represent different leaf sizes produced by the same parent taxon).

Coniferophyta

The conifers found in the Hermit Formation number ten different species (and two undetermined species) belonging to seven different families (table 2). These include *Walchia*, *Ullmannia*, and *Voltzia* (Araucariaceae); *Paleotaxites* and *Taxites* (Paleotaxaceae); and *Brachyphyllum* and *Pagiophyllum* (Pinales?).

Walchia is a morphogenus that describes leafy coniferous foliage, ultimate shoots and penultimate branch systems, that are all visually similar and typically too poorly preserved to allow certain identification (and with no preserved epidermal structure) (Visscher and others, 1986). There are several species of *Walchia* reported in White (1929a), and the author recognized the fact that there are multiple different species of conifer included under each name, noting that sometimes different cones are attached to branches of the same morphological form. *Walchia* is restricted to Euramerica during the Permian, and the species reported in the 1929 monograph were described based on their similarities to species of *Walchia* described from Europe by European authors. Visscher and others (1986) established a new morphogenus (*Hermitia* Kerp and Clement-Westerhof) "to accommodate coniferous foliage without preserved epidermal structure; uncertain affinity at the family level" and commented on its relevance to some of the *Walchia* specimens described by White (1929a). Visscher and others (1986) considered *Walchia piniformis* Sternberg sufficiently well known for the name to stand, and placed *Walchia dawsoni* in *Hermitia* as *H. dawsoni* (White, 1929a) Kerp and Clement-Westerhof. Kerp and others (1990) transferred *Walchia hypnoides* to a new

Table 1. *List of all pteridosperm species reported in White (1929a), including locality information. Taxa marked with an asterisk are new species described by White (1929a). (Note:* Callipteris *is no longer a valid name, and these species likely belong to* Autunia *or* Rhachiphyllum *[Kerp and Haubold, 1988]).*

Fossil Plant Species	Family	Localities
Autunia conferta (*Callipteris conferta*)	*Incertae sedis*	Bright Angel Trail and South Kaibab Trail
*Callipteris arizonae**	*Incertae sedis*	Hermit Basin
Gracilopteris raymondii (*Callipteris raymondii*)	*Incertae sedis*	Bright Angel Trail and Hermit Trail
Callipteris ? sp.	*Incertae sedis*	Hermit Basin
*Supaia thinnfeldioides**	Supaiaceae	Hermit Basin
*Supaia rigida**	Supaiaceae	Hermit Basin
*Supai sturdevantii**	Supaiaceae	Bright Angel Trail
*Supaia merriami**	Supaiaceae	Hermit Trail
Supai compacta	Supaiaceae	Hermit Trail
Auritifolia anomala (*Supaia anomala**)	Supaiaceae	Hermit Basin and Bright Angel Trail
*Supaia linearifolia**	Supaiaceae	Bright Angel Trail
*Supaia breviloba**	Supaiaceae	Bright Angel Trail
*Supaia subgoepperti**	Supaiaceae	South Kaibab Trail
Supaia sp.	Supaiaceae	Hermit Basin
Supaia sp. indet	Supaiaceae	Hermit Basin
Supaia ? sp.	Supaiaceae	South Kaibab Trail
Brogniartites ? *yakiensis**	Supaiaceae	South Kaibab Trail and Hermit Trail
Brogniartites ? *aliena**	Supaiaceae	South Kaibab Trail
*Yakia heterophylla**	Supaiaceae	Hermit Basin and Bright Angel Trail
Neuropteridium sp.	Supaiaceae	Bright Angel Trail
Taeniopteris cf. *eckhardti*	*Incertae sedis*	Bright Angel Trail and Hermit Trail
*Taeniopteris angelica**	*Incertae sedis*	Bright Angel Trail
Taeniopteris coriacea	*Incertae sedis*	Bright Angel Trail, Hermit Basin

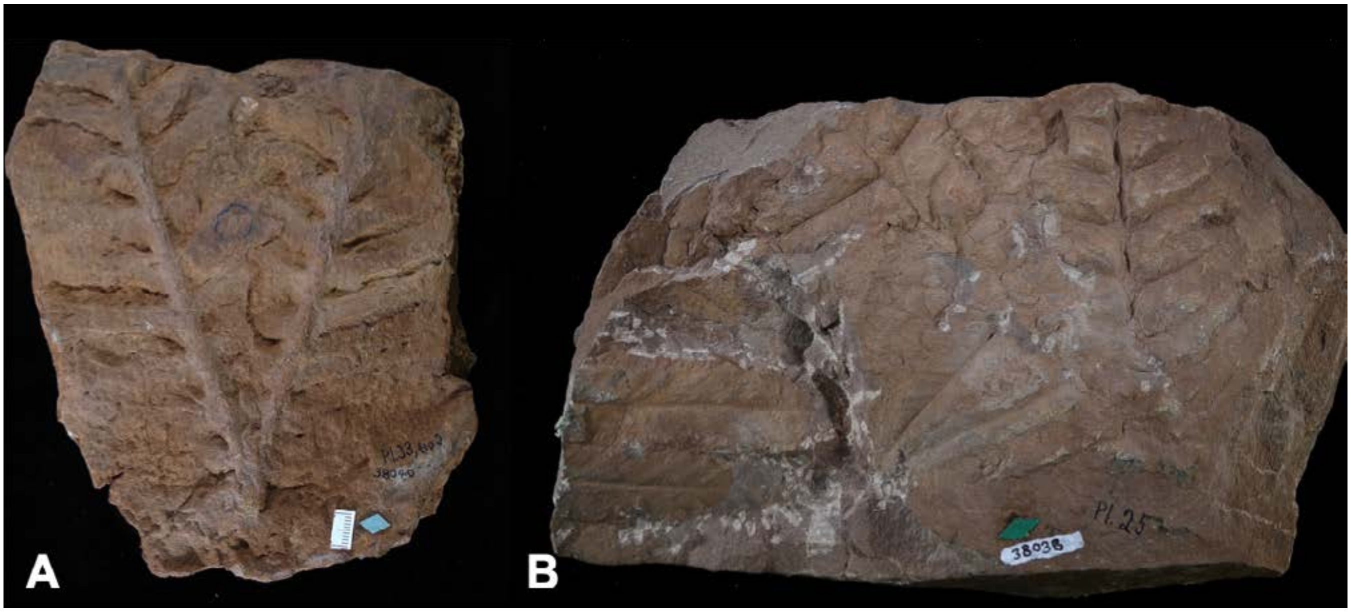

Figure 2. Supaia *specimens (CASSI KNIGHT).* ***A.*** Supaia *sp. specimen USNM 38040;* ***B.*** Supaia subgoepperti *specimen USNM 38038.*

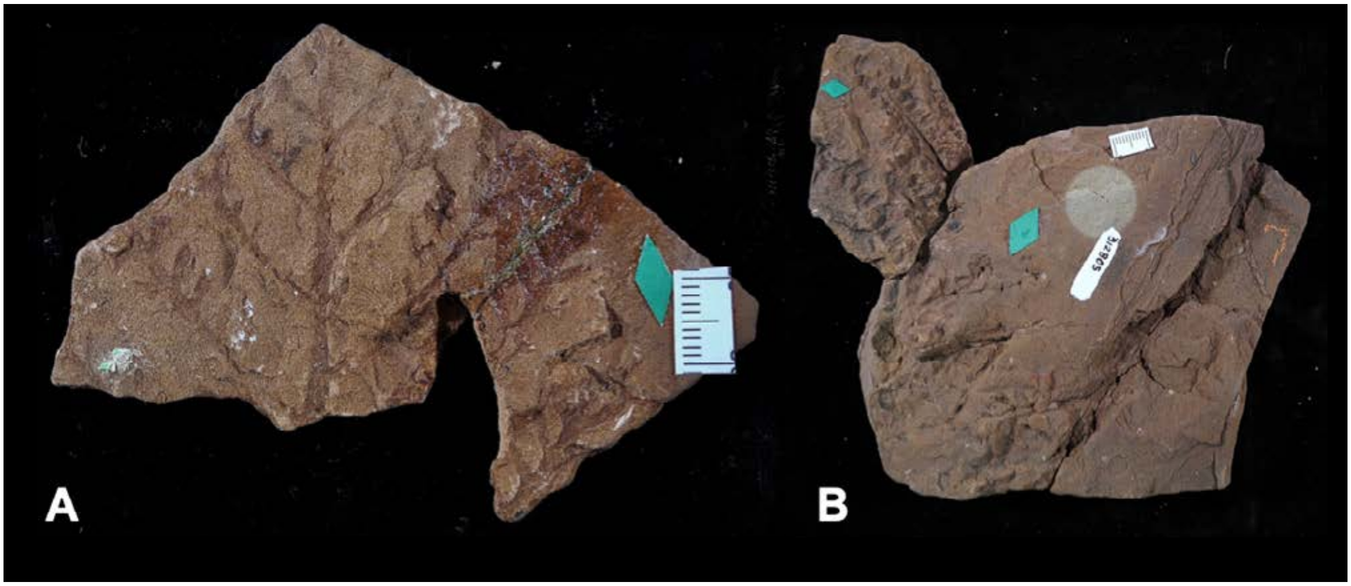

Figure 3. Yakia heterophylla *(CASSI KNIGHT)* ***A.*** *USNM 312802* ***B.*** *USNM 312805. The "clusters of sporangia or possibly seeds" mentioned by White (1929a) can be seen in the upper left corner of the specimen.*

Table 2. *List of all conifer species reported in White (1929a), including locality information. Taxa marked with an asterisk are new species described by White (1929a).*

Fossil Plant Species	**Family**	**Locality**
Brachyphyllum arizonicum	?	Hermit Basin
Brachyphyllum tenue	?	Hermit Basin and Bright Angel Trail
Feysia sp. ? (*Ullmannia frumentaria*)	?	Hermit Trail and Bright Angel Trail
Hermitia dawsoni (*Walchia dawsoni**)	?	Hermit Basin
Hermitia sp. ? (*Walchia gracillima**)	?	South Kaibab Trail
Otovicia hypnoides ? (*Walchia hypnoides*)	?	South Kaibab Trail
Pagiophyllum dubium	?	Hermit Basin
Paleotaxites precursor	Paleotaxaceae	Hermit Basin and South Kaibab Trail
Taxites ? sp.	Paleotaxaceae	Hermit Basin
Voltzia dentiloba	?	Hermit Basin
Voltzia sp.	?	No locality given
Walchia piniformis	?	Hermit Basin, South Kaibab Trail, and Bright Angel Trail

genus *Otovicia hypnoides*. *Walchia gracillima* fits the description of *Hermitia* (leafy shoots with needle-like leaves that lack preserved epidermal structures) and likely belongs to this morphogenus (Visscher and others, 1986; Broutin and Kerp, 1994), but without preserved epidermal features or reproductive structures, no formal analysis will be presented here.

White reported some specimens of *Ullmannia frumentaria* with small, oval seeds or cones associated with foliage, and compared *U. frumentaria* to *Buriadica*, a genus found in India. His comparison is based on leaves that fork near their apex, but the description for *Ullmannia* does not include bifurcated leaves; this is common for penultimate leaves and cone bracts of Walchian conifers (Schweitzer, 1986). Furthermore, Broutin and Kerp (1994) designated a new morphogenus *Feysia* (which accommodates broad-leaved conifers), and strongly suggested that many specimens of *Ullmannia* likely could be referred to a species of *Feysia* (Broutin and Kerp, 1994).

There are several conifer taxa that are only known from very few specimens or are particularly rare in the Hermit Formation flora. *Voltzia dentiloba* is known from the Hermit only by two moderately well-preserved cone bracts, and *Voltzia* sp. is known only from a single cone bract. *Paleotaxites* is a new morphogenus established by White (1929) of conifer with short, compact needles that are densely packed and spirally arranged. Some branches have cones closely associated, which are leathery in texture and have small scales at their base. The single species of *Paleotaxites* reported from the Hermit Formation, *P. precursor*, is rather rare.

White (1929a) also created a new species, *Pagiophyllum dubium*, to include fragmentary twigs and leaves that are not detailed enough to allow certain description, but all distinctly belong to a single species. These plants are loosely assigned to the genus *Pagiophyllum*, but more evidence is needed to confirm this assignment (White, 1929a).

Equisetopsida

A single species of horsetail, *Sphenophyllum gilmorei* (figure 4A), is reported from the Hermit Formation paleoflora, and is yet another new species established by White (1929a). The genus *Sphenophyllum* was originally assigned to Arthrophyta by White, but this division is an old name that is no longer used, and the genus *Sphenophyllum* is now attributed to Equisetopsida, which is the class commonly known as horsetails. *S. gilmorei* is similar to only one other species from this genus, *S. stoukenbergi* from the Ural Mountains, but has much larger, more elongate leaves.

Sphenophyllum gilmorei is most commonly found in thin sandstone beds deposited within the channel cuts in the Esplanade Sandstone. It reportedly becomes much rarer outside the Hermit Basin, and a few specimens have been found near the Bright Angel and South Kaibab Trails. It can be found preserved in association with small vertebrate tracks on “slime mud” surfaces. Some specimens are preserved perpendicular to bedding, suggesting that *S. gilmorei* grew in shallow pools of water and were buried in situ. White interpreted the ecology of the plant to be one that grew in dense stands in sandy bottomed, intermittent pools, reaching a height of up to 1 m (3 ft) (White, 1929a).

Ginkgoopsida

White reported one species of ginkgo in his 1929 monograph, and a second species of ginkgo is known from specimens in the Grand Canyon Museum collections. These plants are *Psygmophyllum* ? sp. and *Rhipidopsis* sp.?, respectively. *Psygmophyllum* ? sp. is known only from a single, poorly preserved leaf fragment found in the lower part of the Hermit Formation in the Hermit Basin (figure 4B). The leaf fragment appears to be covered in a veil of silt and “slime”, obscuring many of the detailed features. White also compared this specimen to the ginkgo *Rhipidopsis ginkgoides*. Both ginkgoes are known from the Asian portion of Gondwana (White, 1929a).

Algae

One species of algae, *Rivularites permiensis* (figure 4C), is found in the Hermit Formation. White described this as a new species in his 1929 monograph, and attributed *R. permiensis* to Thallophyta, which as a now abandoned term for algae. *R. permiensis* was identified based on its similarity to fossil *Rivularites* from France and living *Rivularites* from the French coast, but described as a new species because of some notable round protuberances that occurred in the Arizona specimens, but not those from Europe. There is, however, no firm evidence to suggest a direct relation between the fossil and modern blue-green algae.

Rivularites is common in the lower portion of the Hermit Formation, but has only been found in the channels that are cut into the underlying Esplanade Sandstone in the Hermit Basin. Colonies of the algae are found often on large ripple surfaces and may reach 0.5 m (nearly 2 ft) in diameter, but most tend to be smaller in size. White proposed that the algae grew in mats in moving water,

Figure 4. *Various taxa (CASSI KNIGHT).* ***A.*** Sphenophyllum gilmorei *specimen USNM 38025.* ***B.*** Psygmophyllum *sp. specimen USNM 38050.* ***C.*** Rivularites permiensis *specimen USNM 38024.*

based on the presence of associated ripple marks and the observation that all the protuberances were consistently pointed or pulled in a single direction (White, 1929a).

Other Plants

A category for "fruits of uncertain affinities" includes three genera of different seed types, *Cyclocarpon*, *Carpolithus*, and *Eltovaria*, and gymnospermous ament. (table 3). The different seed types are reportedly very rare in the Hermit Formation, and not many specimens have been found. The seeds *Cyclocarpon angelicum*, C. sp., and *Carpolithus* sp. both are small, round forms that are associated with pteridosperms, meaning they came from plants belonging to *Autunia*, *Rhachiphyllum*, or *Supaia*. There is only one known specimen of *Carpolithus* sp., and it is not particularly well-preserved.

What is likely some type of fruitification formed by a modified leaf that is apparently folded longitudinally to create a type of pod is identified as *Eltovaria bursiformis*, *Eltovaria* being a new genus established by White for this form (White, 1929a). The modified leaf most closely resembles *Taeniopteris* or *Supaia*, and White interpreted this structure as belonging to *Taeniopteris*. A small, single fragment of poorly preserved material is tentatively described as an ament (catkin-like structure) from a gymnosperm and, in this case, is likely some type of female pollen cone.

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Table 3. *Fruits of uncertain affinities reported by David White (1929a) with locality information. Taxa marked with an asterisk are new species described by White (1929a).*

Fossil Species	Locality
*Cyclocarpon angelicum**	Bright Angel Trail below El Tovar
Cyclocarpon sp.	No locality given
Carpolithus sp.	Hermit Basin
Eltovaria bursiformis	Bright Angel Trail and Hermit Basin

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Appendix A

Paleobotanical Type Specimens

Appendix Table A-1. *Table of all known paleobotanical type specimens from GRCA, including name and specimen numbers. All of the newly created plant species were described by David White in his 1929 monograph (White, 1929a), and were originally discovered in the Hermit Formation flora.*

Species	Age	Unity	Reference	Plant Group	Syntype Specimens
Brachyphyllum arizonicum	Permian	Hermit	White, 1929a	Conifer	USNM 38060
Brachyphyllum tenue	Permian	Hermit	White, 1929a	Conifer	USNM 38061, 312783, 312784
Brongniartites? *yakiensis*	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38042, 312807–312812, 324554–324559
Brongniartites? *aliena*	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38043, 312785–312789
Rhachiphyllum sp. (*Callipteris arizonae*)	Permian	Hermit	White, 1929a	Pteridophyte?	USNM 38027
Cyclocarpon angelicum	Permian	Hermit	White, 1929a	Seed/Fruit	USNM 38063
Eltovaria bursiformis	Permian	Hermit	White, 1929a	Seed/Fruit	USNM 38066
Pagiophyllum dubium	Permian	Hermit	White, 1929a	Conifer	USNM 38062, 312790–312792
Palaeotaxites praecursor	Permian	Hermit	White, 1929a	Conifer	USNM 38058, 38060, 324560–324564
Sphenophyllum gilmorei	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38025, 324567–324575
Supaia anomala	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38035, 324581–324588
Supaia breviloba	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38037
Supaia compacta	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38034, 324590–324593
Supaia linearifolia	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38036 and 324594
Supaia merriami	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38033
Supaia rigida	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38031, 324595, 324596
Supaia sturdevantii	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38032, 38038, 324597
Supaia subgoepperti	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38038
Supaia thinnfeldioides	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38030, 324598–324603
Taeniopteris angelica	Permian	Hermit	White, 1929a	Pteridophyte or Gingko	USNM 38048, 324565, 324566, 342587
Voltzia dentiloba	Permian	Hermit	White, 1929a	Conifer	USNM 38056
Hermitia dawsoni (*Walchia dawsonI*)	Permian	Hermit	White, 1929a	Conifer	USNM 38052, 312796–312798
Hermitia sp. (*Walchia gracillima*)	Permian	Hermit	White, 1929a	Conifer	USNM 38053, 312793–312795
Yakia heterophylla	Permian	Hermit	White, 1929a	Pteridophyte	USNM 38044, 312799–312804
Rivularites permiensis	Permian	Hermit	White, 1929a	Cyanobacteria colonies	USNM 38024

SEED FERN

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Seed Fern
Scientific Name: *Pteridospermaphyta*
Geologic Age: 285 million years ago (Permian)
Geologic Formation: Hermit Formation

Interactive 3D model

The red shale of the Hermit Formation preserves the most plants.

Abundant plants on Earth during the early Permian released lots of oxygen into the atmosphere. Today, the atmosphere is 21% oxygen, much less than 35% during the Permian. Besides seed ferns, other early Permian plants include horsetails, ginkgos, conifers, and algae.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

6 of 9

Grand Canyon National Park Fossil Trading Card featuring fossil seed fern foliage from the Permian Hermit Formation (NPS).

PALEOZOIC INVERTEBRATE ICHNOLOGY OF GRAND CANYON NATIONAL PARK

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ABSTRACT

Grand Canyon National Park (GRCA) contains an extraordinary record of invertebrate trace fossils that provide valuable information on paleoecology throughout the Paleozoic Era. Trace fossils are a reflection of organism behavior (ethology) in relation to the substrate (toponomy) and are classified by their morphology. Ichnodisparity, the evaluation of structural complexity of ichnoassociations by the number of architectural designs, is used to understand the variability of morphology among trace fossils and to classify groupings of similar morphologies into 79 different architectural designs. Because organisms were often transported away from their original habitat prior to fossilization, their trace fossil counterparts can provide environmental information that those body fossils lack. Therefore, trace fossils can occur in otherwise unfossiliferous units and may be the only available source of information on ancient life. Trace fossils indicate varying organism responses to changing environmental conditions over time and space, and give insight into their paleoenvironments as represented by ichnofacies, or recurrent associations of trace morphologies. This highlights the importance of ichnology in the Grand Canyon, where almost every Paleozoic geological unit contains trace fossils. The majority of reported ichnofossils include worm burrows, arthropod tracks and trails, and dwelling or feeding structures. The Cambrian Tonto Group holds the most extensively reported invertebrate trace fossil record in Grand Canyon, particularly the Bright Angel Shale, where 21 ichnogenera have been reported and classified into 15 architectural designs. Other formations with relatively high ichnodisparity and high diversity of ichnogenera include the Tapeats Sandstone, the Hermit Formation, and the Coconino Sandstone, all of which contain a minimal to non-existent body fossil record. Invertebrate trace fossils are regarded as significant, non-renewable resources that must be protected. New specimens and ichnotaxa are likely to be discovered in Grand Canyon as scientific research continues.

INTRODUCTION

Grand Canyon National Park (GRCA) encompasses an extensive stratigraphic record that typifies the evolution of diverse ecosystems and their inhabitants throughout the Paleozoic. The occurrence of invertebrate traces (ichnofossils) is not uncommon in these strata and represents direct evidence of interactions between the organisms and the substrates on which and/or in which they lived. During the Paleozoic, a diverse array of invertebrate groups were capable of producing trace fossils on or within the substrates where they lived, including arthropods (such as crustaceans, insects, arachnids, trilobites, and xiphosurans), mollusks (especially bivalves and mobile benthonic groups), brachiopods, cnidarians, echinoderms, various worm taxa (such as annelids and priapulids), and other rare taxa.

Some ichnogenera are specific to ichnofacies that reflect the bathymetry and/or the depositional features of marine or terrestrial depositional environments (Seilacher, 1964; Hunt and Lucas, 1998, 2007; MacEachern and others, 2010). Certain ichnofacies encompass many different types of ichnogenera, depending on the depositional context of the formation. These groupings of ichnogenera model the organisms' interaction with the sediment based on recurring behaviors and provide further interpretation of their depositional environments (MacEachern and others, 2010). They are reflected in most of the Grand Canyon's Paleozoic strata and provide valuable information on the paleoecology of invertebrate organisms. Thus, protection of such trace

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fossils is crucial to advancing the field of ichnology and to enabling interpretation of the ancient environments represented by the strata exposed in the Grand Canyon.

TRACE FOSSIL CLASSIFICATIONS

Trace fossils differ from body fossils in that they are classified by an organism's behavior, rather than the organism's anatomy (morphology). They are, quite literally, the record of interaction between an organism and its substrate. Thus, they are classified primarily by their trace morphology that reflects specific behavior, which can be related to the anatomy of the producer, especially for trackways (e.g., Bertling and others, 2006; Minter and others, 2007; Marchetti and others, 2019a).

The morphology of a trace fossil is not only a reflection of the behavior of an organism and the nature of preservation, but it also variably reflects the anatomy of the producer (e.g., Minter and others, 2007). In particular, trackways record the foot structure and some other aspects of producer anatomy, whereas burrows do so less, in part because different organisms with very different anatomy can more readily produce the same burrow structure than they can produce the same kinds of trackways. This is why vertebrate ichnology, which mostly focuses on trackways, often treats the morphology consistent with the anatomy of the producer, but not the taxonomy of the producer, as a key element in ichnotaxonomy (e.g., Marchetti and others, 2019a). In invertebrate taxonomy, what can be called the problem of homeomorphy—same trace fossil structure, different producers—is more prevalent, so the emphasis in ichnotaxonomy is on morphological features indicative of behavior, rather than of producer anatomy.

Invertebrate trace fossils are classified independent of the identity of their producer (and its taxonomy) using a binomial nomenclature (i.e., the ichnogeneric plus the ichnospecific epithets) analogous, but parallel to, the taxonomic classification of zootaxa (ICZN, 1999). This is why the classification of trace fossils, or ichnotaxonomy, can be considered a parataxonomy. Ichnofamilies may be used to group ichnogenera into larger ichnotaxonomic groups, but they are generally less extensively studied and discussed than in the phylogenetic taxonomy of body fossils (Pemberton and Frey, 1982). This is because ichnotaxonomy is separated from the taxonomic classification of zootaxa and has an ethological component (Pemberton and Frey, 1982), therefore it is more difficult to group morphologies and assign categories that are a complex result of different behaviors and different anatomies.

The list of valid ichnotaxa in a defined unit and/or locality is named an ichnoassociation, and the composition of an ichnoassociation can be used to define ichnodiversity. A further informal approach to trace fossil classification evaluates ichnodisparity (e.g., Buatois and others, 2017), which is the evaluation of the structural complexity of the ichnoassociations based on the number of architectural designs that are present. For such analysis, 79 architectural designs have been introduced that encompass 523 invertebrate-produced ichnogenera (Buatois and others, 2017).

Seilacher (1964) created a broad ethological classification consisting of five major behavioral (ethological) categories for invertebrate traces that has since been expanded into 13 categories, plus some subordinate subcategories (MacEachern and others, 2010; Vallon and others, 2016). Seilacher's (1964) original five comprise: Domichnia (dwelling), Fodinichnia (feeding), Pascichnia (grazing), Repichnia (locomotion), and Cubichnia (resting). The subsequently proposed additional groups comprise: Agrichnia (farming), Calichnia (brooding), Chemichnia (chemosymbiotic traces), Digestichnia (digestion), Ecdysichnia (molting), Fixichnia (attachment), Fugichnia (escaping), and Praedichnia (predation) (MacEachern and others, 2010; Vallon and others, 2016). These behaviors seen in the trace fossil record reveal the way in which organisms respond to environmental changes such as climate, food resources, lithology, soil moisture, turbidity, water table fluctuations, and the energy of deposition (MacEachern and others, 2010). The dynamics of the depositional environment can be inferred based on the range of behavior present. However, the use of these ethological terms is rare among ichnologists, and behavior is more often described in simple descriptive terms (e.g., "feeding trace", "dwelling trace", etc.).

One can also informally classify trace fossils on a toponomic basis (relationship to the sediment) in order to understand their orientation and preservation within the sediment. Seilacher (1964) differentiated full-relief trace fossils, occurring within the sediment, from semi-relief traces, which are preserved along bedding surfaces. He grouped the semi-relief traces as epirelief (top surface of a bed) and hyporelief (bottom surface of a bed), in which they each can be concave (mold) or convex (cast). Martinsson (1970) went further and created four general groups of toponomic classification: endichnia, epichnia, exichnia, and hypichnia. Endichnia refers to traces within the medium, similar to Seilacher's (1964) full-relief traces. Epichnia refers to ridges or grooves on the top surface of a bed. The opposite is hypichnia, referring to ridges or grooves on the bottom surface of a bed. Exichnia refers to traces that have been filled in with sediment different from the surrounding medium.

Trace fossils reflect behavioral adaptations to specific environmental conditions. Some ichnotaxa are restricted to environmental settings or even to particular lithofacies. Therefore, ichnoassociations will be recurrent over geologic time whenever the respective environmental conditions recur. These ideas were used by Seilacher (1964) as the foundation for the concept of ichnofacies. Ichnofacies are distinct and recurrent (in space and time) associations of fossil traces (ichnoassociations) that reflect specific combinations of the organisms' responses to particular environmental conditions (MacEachern and others, 2007). In his seminal work, Seilacher (1964) recognized six archetypical ichnofacies, based on associations of invertebrate traces: *Skolithos* Ichnofacies, *Cruziana* Ichnofacies, *Zoophycos* Ichnofacies, *Nereites* Ichnofacies, *Glossifungites* Ichnofacies, and *Scoyenia* Ichnofacies. Among them, only the last one is present in continental settings. This framework was consequently expanded so that nine other invertebrate ichnofacies were proposed: *Celliforma* Ichnofacies, *Coprinisphaera* Ichnofacies, *Cubiculum* Ichnofacies, *Octopodichnus–Entradichnus* Ichnofacies, *Palaeoscolytus* Ichnofacies, *Psilonichnus* Ichnofacies, *Teredolites* Ichnofacies, *Termitchnus* Ichnofacies, and *Trypanites* Ichnofacies (MacEachern and others, 2007; Hunt and Lucas, 2007; Lucas, 2016). These new ichnofacies recognize greater ichnofaciological diversity in continental settings than was known to Seilacher (1964), and thus represent a more diverse array of environmental settings (paleosols, eolian dunes, supratidal deposits, etc.). The following will discuss the ichnological record of some units from the Grand Canyon in the light of the ichnofacies paradigm, but more complete and updated information on ichnofacies in general can be found in MacEachern and others (2012).

Ichnology is essential in providing missing paleoecological information for those organisms whose fossilized bodies are frequently studied and even those that are never discovered, but it poses a challenge in associating trace fossils with their producers. For example, trace fossils are often found in strata that lack body fossils, and thus provide the only available biogenic information for paleoenvironmental reconstructions. This phenomenon is very common in continental desert deposits, such as the Permian Coconino Sandstone, where invertebrate traces and tetrapod tracks comprise the only evidence of the occupation of that paleoenvironment by organisms (see discussion below). Fortunately, there is a relatively long history of Grand Canyon trace fossil research, so that this linkage has been achieved with some success (e.g., Elliott and Martin, 1987; Lane and others, 2003). Currently, a project by one of the authors (AEM, pers. obs.) is addressing these challenges by studying the ichnology of the Bright Angel Shale, which holds the most diverse and well-preserved invertebrate trace fossils from Grand Canyon's Paleozoic strata. This study is intended to not only link potential producers to their traces, but also determine ichnofacies and ichnoassociations to better understand Cambrian paleoecology. The work should advance the field of invertebrate ichnology of the Cambrian, but it will also pose more questions and suggest important future work. Therefore, it is imperative that the significant trace fossil specimens in GRCA are preserved and protected because they provide opportunities for advancing our understanding of the history of life recorded in the Park.

STRATIGRAPHIC DISTRIBUTION OF TRACE FOSSILS

Trace fossils have been reported from almost every Paleozoic geological unit of the Grand Canyon. Some of these reports lack comprehensive ichnotaxonomic lists, and this may be attributed to the poorly studied trace fossil record of some of the Paleozoic formations. The most extensively reported trace fossil record from Grand Canyon is from the Cambrian strata of the Tonto Group. Out of the five formations that comprise the Tonto Group, the Bright Angel Shale has yielded the majority of these reports. This is due to the sheer number and diversity of trace fossils preserved in the Bright Angel Shale relative to other units. Although the Coconino Sandstone is famous for its vertebrate trackways, it contains the second most reported invertebrate traces next to the Tonto Group. The Hermit Formation has also been the source of a few reports on invertebrate trace fossils, some of which have been considered to be of plant origin. These units represent completely different time periods and depositional environments and therefore contribute to a diverse invertebrate ichnological record for Grand Canyon. The Toroweap Formation has little to no published information on invertebrate trace fossils, so it is not included in this article, though trace fossils likely are present in that stratigraphic unit.

The following text is organized by geologic age and formation, including a list of collected museum specimens from GRCA (table 3 for the Bright Angel Shale). The specimens only documented in the field and not collected were not numbered. For each formation, the ichnotaxa are listed by different architectural designs (according to Buatois and others, 2017), citing the relevant literature in chronologic order. For the most relevant ichnoassociations, a paragraph discussing ichnodiversity, ichnodisparity and ichnofacies of that specific unit was added. A list of valid ichnotaxa from GRCA is provided in table 1. A list of invalid ichnotaxa from unpublished theses is also provided (table 2).

Institutional Abbreviations—GRCA, Grand Canyon National Park Museum, Arizona, USA; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MSP**, Museo di Serrapetrona, Macerata, Italy; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; **SMM**, Science Museum of Minnesota, Saint Paul, Minnesota, USA; **UCMP**, University of California, Berkeley, California, USA; **USNM**, Smithso-

Table 1. *List of valid ichnogenera and their respective architectural designs (sensu Buatois and others, 2017), ordered by geological unit (from lower to upper). (continued on following page)*

Unit	Valid ichnogenera	Architectural designs
Tapeats Sandstone	*Cruziana*	5: Bilobate trails and paired grooves
	Diplichnites	6: Trackways and scratch imprints
	Monomorphichnus	6: Trackways and scratch imprints
	Rusophycus	8: Bilaterally symmetrical short, scratched impressions and burrows
	Planolites	11: Simple actively filled (massive) horizontal to oblique structures
	Palaeophycus	10: Passively filled horizontal burrows
	Treptichnus	17: Horizontal burrows with horizontal to vertical branches
	Teichichnus	22: Horizontal burrows with simple vertically oriented spreiten
	Rhizocorallium	26: Burrows with horizontal spreiten
	Skolithos	35: Vertical unbranched burrows
	Arenicolites	36: Vertical single U- and Y-shaped burrows
	Diplocraterion	36: Vertical single U- and Y-shaped burrows
Bright Angel Shale	*Cochlichnus*	1: Simple horizontal trails
	Cruziana	5: Bilobate trails and paired grooves
	Angulichnus	6: Trackways and scratch imprints
	Diplichnites	6: Trackways and scratch imprints
	Dimorphichnus	6: Trackways and scratch imprints
	Monomorphichnus	6: Trackways and scratch imprints
	Rusophycus	8: Bilaterally symmetrical short, scratched impressions and burrows
	Palaeophycus	10: Passively filled horizontal burrows
	Planolites	11: Simple actively filled (massive) horizontal to oblique structures
	Nereites	14: Complex actively filled horizontal structures
	Scolicia	14: Complex actively filled horizontal structures
	Phycodes	17: Horizontal burrows with horizontal to vertical branches
	Treptichnus	17: Horizontal burrows with horizontal to vertical branches
	Monocraterion	19: Radial to rosetted structures
	Teichichnus	22: Horizontal burrows with simple vertically oriented spreiten
	Spirophycus	23: Horizontal helicoidal burrows
	Bergaueria	34: Vertical plug-shaped burrows
	Skolithos	35: Vertical unbranched burrows
	Arenicolites	36: Vertical single U- and Y-shaped burrows
	Diplocraterion	36: Vertical single U- and Y-shaped burrows
	Belorhaphe	46: Uniramous meandering graphoglyptids
Muav Limestone	*Phycodes*	17: Horizontal burrows with horizontal to vertical branches
Temple Butte Formation	*Palaeophycus*	10: Passively filled horizontal burrows
Surprise Canyon Formation	*Conostichus*	34: Vertical plug-shaped burrows
Wescogame Formation	*Helminthopsis*	1: Simple horizontal trails
	Diplichnites	6: Trackways and scratch imprints
Hermit Formation	*Lithographus*	6: Trackways and scratch imprints

Table 1. *Continued.*

Unit	Valid ichnogenera	Architectural designs
Hermit Formation	*Stiaria*	6: Trackways and scratch imprints
	Scoyenia	12: Simple actively filled (meniscate) horizontal to oblique structures
	Sphaerapus	13: Simple actively filled (pelletoidal) horizontal to oblique structures
Coconino Sandstone	*Diplopodichnus*	5: Bilobate trails and paired grooves
	Diplichnites	6: Trackways and scratch imprints
	Lithographus	6: Trackways and scratch imprints
	Paleohelcura	6: Trackways and scratch imprints
	Stiaria	6: Trackways and scratch imprints
	Octopodichnus	6: Trackways and scratch imprints
	Taenidium serpentinum	14: Complex, actively filled horizontal structures

Table 2. *List of invalid ichnotaxa, ordered by geological unit (from lower to upper).*

Unit	Invalid ichnotaxa	Current interpretation
Tapeats Sandstone	*Isopodichnus*	Junior synonym of *Cruziana*
	Corophioides	Junior synonym of *Diplocraterion*
	Stipsellus	Junior synonym of *Skolithos*
Bright Angel Shale	*Cruziana grandcanyonensis*	*Nomen nudum*
	Cruziana rusiformis	*Nomen nudum*
	Isopodichnus problematicus	Junior synonym of *Cruziana problematica*
	Scalarituba	Junior synonym of *Nereites*
	Scalarituba alternolobus	*Nomen nudum*
	Scalarituba novum	*Nomen nudum*
	Flectostriatus imporcatus	*Nomen nudum*
	Fodichnites bitumulus	*Nomen nudum*
	Phycodes pedum	Synonym of *Treptichnus pedum*
	Frondichnus vespirolatus	*Nomen nudum*
	Bicavichnites lophoseparatus	*Nomen nudum*
	Bicavichnites martini	*Nomen nudum*
	Corophioides	Junior synonym of *Diplocraterion*
Hermit Formation	*Walpia hermitensis*	Junior synonym of *Sphaerapus larvalis*
Coconino Sandstone	*Triavestigia niningeri*	Junior synonym of *Paleohelcura tridactyla*
	Paleohelcura dunbari	Junior synonym of *Paleohelcura tridactyla*
	Mesichnum	Junior synonym of *Paleohelcura*
	Octopodichnus minor	Junior synonym of *Octopodichnus didactylus*
	Octopodichnus raymondi	Regarded as *Paleohelcura* isp.
	Isopodichnus filiciformis	Regarded as *Diplichnites* isp.
	Unisulcus sinuosus	Probable junior synonym of *Diplopodichnus biformis*
	Scolecocoprus cameronensis	Junior synonym of *Taenidium serpentinum*
	Scolecocoprus arizonensis	Probable junior synonym of *Taenidium serpentinum*

nian, National Museum of Natural History, Washington, D.C., USA.

The museum collections of Grand Canyon National Park contain a robust record of invertebrate trace fossil specimens from several formations throughout GRCA's history. However, many have been deaccessioned or contain limited ichnotaxonomic, locality, and reference information because they were collected so long ago.

CAMBRIAN

Tonto Group

The Tonto Group sits upon the Precambrian basement and forms a gradual slope onto what is known as the Tonto Platform in Grand Canyon. These rocks can be traced from the west along the Colorado River to the east midway down the canyon. The Tonto Group has recently been expanded to comprise five formations, in ascending order the Sixtymile Formation, Tapeats Sandstone, Bright Angel Shale, Muav Limestone, and Frenchman Mountain Dolostone (Karlstrom and others, 2020). The Tapeats Sandstone, Bright Angel Shale, and Muav Limestone are the historic core of the Tonto Group and form a typical transgressive sequence. The Frenchman Mountain Dolostone, previously known as the undifferentiated dolomites first mentioned by McKee and Resser (1945), is cut into by the paleochannels of the Devonian Temple Butte Formation.

The Tonto Group represents a time of global sea level rise with minor transgressive and regressive events, creating an ideal habitat for Cambrian invertebrate organisms. Approximately 500 million years ago, Cambrian strata were deposited along the western coast of Laurentia near the palaeoequator. Tonto Group sediment accumulated on a shallow marine shelf with various tidal channels, embayments, intertidal flats, and monadnocks from the underlying Precambrian surface (McKee and Resser, 1945; Hereford, 1977; Middleton, 1989). The reaction between carbonate build-ups and the eroding, siliceous bedrock may have created nutrition for microbial mats, invertebrate grazers, and benthic feeders (Rose, 2003). Although the remains of invertebrates are relatively sparse in the Tonto Group, the preserved behavior of these organisms is extremely abundant. In fact, the Tonto Group contains the majority of invertebrate ichnogenera and ichnospecies reported from Grand Canyon. These trace fossils mainly consist of varied burrows, arthropod trackways, resting and feeding traces, dwelling structures, and other locomotive tracks (Martin, 1985; Lane and others, 2003; Middleton and Elliott, 2003).

Tapeats Sandstone

The Tapeats Sandstone, historically the basal-most unit of the Tonto Group, is known for its lower contact with the underlying Precambrian surface called "The Great Unconformity". Due to the uneven underlying surface, the Tapeats Sandstone varies in thickness from 30 to 120 m (98 to 394 ft) (Noble, 1922; Middleton and Elliott, 2003). The basal portion of the Tapeats Sandstone is composed of conglomeratic quartz and feldspar and commonly reflects the mineralogy of the Precambrian basement rocks. It typically forms a cliff of stacked, 1-m-thick (3 ft), cross-stratified sandstone beds. The upper unit consists of interbedded mudstone and fine- to medium-grained sandstone and grades into the upper Bright Angel Shale, via what is often referred to as the "transition zone" (McKee and Resser, 1945; Middleton and Elliott, 2003).

The Tapeats Sandstone was deposited on a shallow-marine shelf within intertidal areas of deposition seen in the older deposits toward the west, and fluvial regions of deposition seen in the younger deposits toward the east (Hereford, 1977). The maximum depositional ages obtained by U/Pb dating from detrital zircons are 505.4 ± 8 Ma to 501.4 ± 3.8 Ma (Karlstrom and others, 2018), indicating that the Tapeats Sandstone represents a gradual advancement of the sea during the Cambrian Series 3. An evolving, braided delta plain emptied into a high-energy shoreface environment in which sediment was constantly reworked (Schuchert, 1918; Rose, 2003). Due to the high-energy environment in the basal portion of the Tapeats Sandstone, trace fossils are more common in the upper transition zone where the energy waned and the sea advanced inland. These traces commonly consist of vertical burrows and a variety of horizontal tracks and trails (Middleton and Elliott, 2003) and were most likely created by gastropods and annelid worms (Spamer, 1992) as well as arthropods (trilobites and crustaceans).

Trace Fossils

Worm burrows and trilobite trails have been reported from the Tapeats Sandstone (e.g., Noble, 1922; Schenk and Wheeler, 1942; McKee and Resser, 1945), but detailed reports on the ichnotaxa are somewhat lacking. Many authors in the past used generalized identifications, such as annelid burrows or "fucoidal casts" (Schuchert, 1918). The word "fucoid" (from the Greek *fýkos*, seaweed) originally referred to algae, because many paleontologists from the 1800s thought that trace fossils were algal structures (Osgood, 1975). Thus, this word is only used here if it was the only identification in the literature or from collections in the past.

Passively Filled Horizontal Burrows: Schuchert (1918) first noted the presence of *Palaeophycus* in the Tapeats Sandstone and identified them as "seaweeds". *Palaeophycus* is now understood to be horizontally oriented, passively infilled burrows that record the dwelling behavior of predatorial or suspension-feeding organisms (Buatois and others, 2017).

Simple Actively Filled (Massive) Horizontal to Oblique Structures: Hagadorn and others (2011) reported a few occurrences of *Planolites* in the Tapeats Sandstone. *Planolites* is often confused with *Palaeophycus* due to their similar morphology, but *Planolites* shows an actively infilled burrow of sediment different from its matrix that indicates it was made by a deposit feeder (Pemberton and Frey, 1982).

Horizontal Burrows with Horizontal to Vertical Branches: *Treptichnus* was reported in eastern GRCA by Hagadorn and others (2011). *Treptichnus* is a horizontal to oblique, zig-zag burrow sometimes branching or overlapping. This ichnogenus encompasses various morphology types and therefore contains several ichnospecies, one of which is discussed further in the Bright Angel Shale section.

Horizontal Burrows with Vertically Oriented Spreiten (Sedimentary Laminae Caused by a Moving Organism): Hagadorn and others (2011) noted an abundance of *Teichichnus* in the shale interbeds of the Tapeats Sandstone. *Teichichnus* is a straight to slightly curved, horizontal burrow with tapered ends and vertically stacked spreiten (or laminae) that record vertical shifting in the sediment (Knaust, 2018).

Trackways and Scratch Imprints: A specimen collected by McKee in 1937 was assigned to *Diplichnites*, a well-known ichnogenus of arthropod trackway consisting of two parallel rows of closely spaced small tracks. Hagadorn and others (2011) reported the occurrence of *Diplichnites* in eastern GRCA and central Arizona. *Monomorphichnus* was also reported in the Tapeats Sandstone (Hagadorn and others, 2011) and consists of parallel sets of ridges or grooves indicating dragging or swimming behavior, usually of arthropods.

Bilobate Trails and Paired Grooves: A specimen collected by McKee and Wheeler in 1937 has been assigned to *Isopodichnus*, which is a synonym of the more commonly used ichnogenus name *Cruziana*. *Cruziana* is a near-surface, horizontal burrow consisting of lobed furrows covered by striations and was most commonly made by trilobites or other arthropods. *Cruziana* typically represents feeding behavior within a shallow-marine, fluvial, or lacustrine environment. Seilacher (1970) reported *Cruziana arizonensis* from the upper portion of the Tapeats Sandstone. *C. arizonensis* mainly consists of shorter tracks with a 2.5 to 5.5 cm (0.98 to 2.2 in) width. *Cruziana* was also reported in the Tapeats Sandstone by Hagadorn and others (2011).

Bilaterally Symmetrical, Short, Scratched Impressions and Burrows: Two specimens collected by McKee and Wheeler in 1937 at Grand Wash Cliffs have been assigned to *Rusophycus didymus* and *Rusophycus* isp. A specimen collected by Seilacher in 1955 from Indian Gardens is also assigned to *R. didymus*. *Rusophycus* is generally considered to be the resting trace made by the producer of *Cruziana* and thus has a similar morphology without the continuation of a trail. *Rusophycus* was reported in the Tapeats Sandstone by Hagadorn and others (2011) and observed by one of the authors (AEM) in central GRCA (figure 1).

Burrows with Horizontal Spreiten: A specimen collected by Seilacher in 1955 shows a U-shaped feeding burrow, assigned to *Rhizocorallium* or *Corophioides* (the latter is considered to be a junior synonym of *Diplocraterion*; see below). *Rhizocorallium* is a burrow with U-shaped spreiten parallel or oblique to the bedding plane and likely records dwelling or feeding behavior (Knaust, 2013).

Vertical Unbranched Burrows: *Skolithos* is common in the Tapeats Sandstone (Frech, 1893; McKee and Resser, 1945; Middleton and Elliott, 2003; Hagadorn and others, 2011). It consists of straight, vertical, unornamented cylindrical burrows made by a variety of invertebrates for dwelling, suspension feeding, and predation, and is found in almost every type of depositional environment throughout geologic history. Howell (1957) named *S. annulatus* for the *Skolithos* specimen collected by McKee and Resser (1945; plate 8, figure c). A specimen collected by Seilacher in 1955 has been assigned to *Skolithos* cf. *S. linearis*.

Figure 1. Rusophycus *in convex hyporelief within the Tapeats Sandstone in central Grand Canyon (NPS/ANNE MILLER).*

Howell (1957) applied the name *Stipsellus annulatus* to vertical, cylindrical burrows approximately 12 mm (0.47 in) in diameter with evenly spaced menisci (backfilled, annulate structures). These were found in the upper Tapeats Sandstone. Häntzschel (1975) considered *Stipsellus* a problematic ichnotaxon, and the illustration of it in Häntzschel (1975: figure 132.2) suggests that it may even be the cast of part of an eocrinoid column. Alpert (1974) considered *Stipsellus* a junior synonym of *Skolithos*.

Vertical Single U- and Y-Shaped Burrows: Schuchert (1918) mentioned the abundance of *Arenicolites*, which are vertically oriented, U- or J-shaped, cylindrical burrows that record feeding and dwelling behaviors made by a variety of invertebrate organisms, including polychaete worms and crustaceans. Hagadorn and others (2011) also reported the abundance of *Arenicolites* in the Tapeats Sandstone creating highly bioturbated beds at outcrops within eastern and western GRCA. *Diplocraterion* (formerly *Corophioides*) is another vertical, U-shaped burrow common in the Tapeats Sandstone (Hereford, 1977; Middleton and Elliott, 2003). However, *Diplocraterion* differs from *Arenicolites* in that it contains spreiten, which indicates adjusting behavior to maintain a connection with the changing sediment-water interface. *Diplocraterion* is primarily a dwelling burrow of crustaceans and is usually found in shallow-water environments.

Discussion

A total of 12 valid ichnogenera (*Arenicolites*, *Cruziana*, *Diplichnites*, *Diplocraterion*, *Monomorphichnus*, *Palaeophycus*, *Planolites*, *Rhizocorallium*, *Rusophycus*, *Skolithos*, *Teichichnus*, and *Treptichnus*) have been reported from the Tapeats Sandstone, but only a few of them were classified to the ichnospecies level (*C. arizonensis*, *R. didymus*, and *S. annulatus*) (table 1). The identification of *S. linearis* is still tentative, and its presence in the Tapeats Sandstone requires further evaluation. Other ichnotaxa proposed for this unit include *Isopodichnus* and *Corophioides*, which are currently interpreted as synonyms of *Cruziana* and *Diplocraterion*, respectively. Seven architectural designs can be recognized among the Tapeats Sandstone ichnological record. The ichnoassociation of the Tapeats Sandstone belongs to the transition between the *Cruziana* ichnofacies and the *Skolithos* ichnofacies of shallow marine settings; this should mean a more proximal, high-energy environment compared to the typical *Cruziana* ichnofacies (e.g., Buatois and Mángano, 2011).

GRCA Museum Collections

A "fucoid" specimen from the Tapeats Sandstone was collected along Bright Angel Trail in 1928 by Glen Sturdevant (GRCA 2088). In October 1929, Edwin McKee collected specimens of trilobite tracks and trails from the upper Tapeats Sandstone (or basal Bright Angel Shale) on the Tonto Platform (GRCA 2059, GRCA 2062, GRCA 2063, GRCA 2069, and GRCA 2071). That same year, he also collected "fucoids" from the upper Tapeats Sandstone (or basal Bright Angel Shale), also on the Tonto Platform (GRCA 8640). Trilobite tracks originally identified as *Isopodichnus* (currently *Cruziana*) were found in the Tapeats Sandstone and collected by McKee and Wheeler in January 1937 (GRCA 2137). In that same month at Grand Wash Cliffs, they also collected an indeterminate *Rusophycus* ichnospecies (GRCA 2138) and *R. didymus* (GRCA 2143) from the upper Tapeats Sandstone. In November 1937, McKee collected *Diplichnites* from a Tapeats Sandstone cast in Fern Glen Canyon (GRCA 2146). In March 1939, McKee collected two fossil trails near the top of the Tapeats Sandstone (GRCA 8603 and GRCA 8604, both deaccessioned) and one from Plateau Point (GRCA 8605—deaccessioned), all of which he attributed to worms. On September 9, 1955, Adolf Seilacher collected the vertical tubes of *Skolithos* cf. *S. linearis* (GRCA 8677), the resting traces of *Rusophycus didymus* (GRCA 8678), and the U-shaped feeding burrow *Rhizocorallium* or *Diplocraterion* (formerly *Corophioides*) (GRCA 8679) within the transition zone of the Tapeats Sandstone. On October 17, 1955, he also collected the U-shaped burrows of *Arenicolites* from the Tapeats Sandstone west of Plateau Point (GRCA 8700). In 1969, George Beck collected a Tapeats Sandstone specimen with "worm trails" (GRCA 21235—deaccessioned). A specimen with borings and numerous cylindrical structures was collected on August 2, 1963 (GRCA 17435—deaccessioned). *Skolithos annulatus* (formerly *Stipsellus annulatus*) was collected by Howell (1957) near Rampart Cave (GRCA 8538).

Bright Angel Shale

The Bright Angel Shale is a unit placed in the middle of the Tonto Group, forming the iconic light green slopes that grade onto the Tonto Platform. It is exposed throughout Grand Canyon, ranging from 99 m (325 ft) thick in the east and 82 m (269 ft) thick in central GRCA to more than 137 m (449 ft) thick in western GRCA (Middleton and Elliott, 2003). The wide range of thicknesses is due to the transitional nature of the upper and lower contacts, which are often interpreted differently by researchers. This is because the Bright Angel Shale gradationally overlies the Tapeats Sandstone and has an intertonguing relationship with the overlying Muav Limestone. The Bright Angel Shale consists of interbedded siliciclastic sandstone, siltstone, and shale. These rocks are mostly composed of quartz with some amount of potassium feldspar and muscovite, as well as glauconite that imbues the characteristic green color seen in the deposits. McKee and Resser (1945) recognized one formal member in the Bright Angel Shale, the Flour Sack Member, which comprises the uppermost strata of the unit in western GRCA. This member appears as a massive bed and contains sandstone, siltstone, and shale, as well as limestone tongues towards the top. Many of the massive sandstones in the Bright Angel Shale contain cross-stratification, and the interbedded strata often contain wavy or lenticular heterolithic bedding, all of which indicate a changing tidal environment.

The heterogeneous lithology and stratigraphy of the Bright Angel Shale represent strandline migration of a shallow-marine shelf that provided a habitat for many invertebrates. This environment was generally within subtidal to intertidal areas in which fair-weather suspension settling and storm influence was frequent (Martin, 1985; Middleton, 1989). Estuaries may have also existed in certain areas (Rose, 2006). Invertebrates such as trilobites, brachiopods, and gastropods flourished in this environment (see Lassiter and others in this volume).

McKee and Resser (1945) used trilobite fossil assemblages to constrain the age of the Bright Angel Shale. The basal portion in western GRCA contains the *Olenellus–Antagmus* horizon, which dates the bottom as late Cambrian Series 2. The upper portion of the Bright Angel in the east contains the *Alokistocare–Glossopleura* horizon, which dates the upper contact as Cambrian Series 3. However, Karlstrom and others (2018) noted that the Tapeats Sandstone is younger than previously thought and does not get younger to the east, as seen via recent U/Pb detrital zircon data from the basal portion matching correlative formations throughout the west. These detrital zircons from the basal Tapeats Sandstone were dated as 505–501 million years old. This means that the whole of the Bright Angel Shale is most likely Cambrian Series 3 in age, but more work is necessary to solidify the age constraints of the Tonto Group.

Trace Fossils

Body fossils are relatively rare in the Bright Angel Shale, but an astounding record of their behavior is common. Most invertebrate trace fossil reports include arthropod tracks and trails, worm burrows, and dwelling structures identified at the ichnogenus and ichnospecies level. Other reports only briefly mention traces with very limited ichnotaxonomic identifications. Noble (1922) mentioned the presence of "worm markings" and "fucoidal casts" within the green, glauconitic laminations of the Bright Angel Shale. McKee and Resser (1945) reported circular trails, worm borings, and "trilobite trails in hematitic sandstone". Strother and Beck (2000) found wrinkle structures in the Sumner Butte area similar to the "interference tadpole ripples" that McKee and Resser (1945) identified and compared them to modern microbial mats from supratidal regions. Baldwin and others (2004) used the same comparison and identified these structures as "wrinkle marks" formed when microbial mats bind with the sediment. Davies and others (2016) addressed the enigma of wrinkle structures and classified them as "microbially induced sedimentary structures" (MISS).

For the following list of ichnotaxa, it is important to note that any new ichnotaxonomic names proposed by Martin (1985) or Rose (2003) must be considered as *nomina nuda* according to the International Code of Zoological Nomenclature (1999) because they were only introduced in an unpublished thesis.

Simple Horizontal Trails: Martin (1985) identified *Cochlichnus*, which is a sinuous, locomotive, surface burrow in hypichnial preservation most likely made by annelid worms and often found in association with *Belorhaphe*, *Palaeophycus*, *Cruziana*, *Rusophycus*, and *Teichichnus*. *Belorhaphe* and *Cochlichnus* were both found in eastern GRCA.

Bilobate Trails and Paired Grooves: White (1874) identified *Cruziana linnarssoni* and *C. rustica* from the "Tonto Shale" (currently interpreted as part of the Bright Angel Shale) in Grand Canyon. *C. linnarssoni* has slightly pointed ends with a distinct, median furrow and contains little to no rugae (ridges) on the surface. *C. rustica* has blunt ends with a shallow, median furrow and contains many distinct rugae on the surface. "*Cruziana grandcanyonensis*" *nomen nudum* (proposed holotype MNA N3857) was found in sandstone throughout the Bright Angel Shale in eastern GRCA (Martin, 1985). This ichnospecies consists of horizontally oriented, elongated, ridged furrows in hypichnial preservation with medial grooves. It represents the crawling or feeding behavior of an arthropod and typically is associated with *Rusophycus*, which indicates that these traces were most likely made by the same organism. According to Rose (2003), "*Cruziana rusiformis*" *nom. nud.* (GRCA 76909) is his *nomen substitutum* for Martin's (1985) "*C. grandcanyonensis*" *nom. nud.*, but both are unpublished names, so they are *nomina nuda*. "*C. rusiformis*" *nom. nud.* was found in association with *Palaeophycus*, sometimes more specifically with *P. striatus*, and potentially showed predatory behavior in central Grand Canyon as well as outside the park (GRCA 76928). "*C. rusiformis"* *nom. nud.* often transitions to *Rusophycus dispar*. *Isopodichnus problematicus* (specimen MNA N3716, currently *Cruziana problematica*) was identified near Grand Wash Cliffs in cross-stratified sandstone and consists of bilobate burrows with a medial groove oriented horizontally in hypichnial preservation (Martin, 1985).

Trackways and Scratch Imprints: Martin (1985) identified *Diplichnites* (MNA N3718), which represents the walking tracks of arthropods and consists of obliquely oriented, parallel sets of ridges or tracks, which suggests

Figure 2. Cruziana *isp. from the Bright Angel Shale preserved in convex hyporelief (NPS/GRCA).*

a possible trilobite producer. This specimen was found near Grand Wash Cliffs and is usually associated with *Cruziana*, *Rusophycus*, *Dimorphichnus*, and *Monomorphichnus*. *Monomorphichnus* (MNA N3861) and *Dimorphichnus* (MNA N3858) were found in hypichnial preservation and record the walking behavior of arthropods along bedding planes (Martin, 1985). They both consist of parallel sets of ridges, but differ in that *Monomorphichnus* typically has one set of ridges that is more prominent, indicating swimming or dragging behavior along the sediment. They are both usually associated with similar arthropod traces, such as *Cruziana*, *Rusophycus*, and *Diplichnites*, as well as *Palaeophycus*, and are often found throughout the heterolithic facies of the Bright Angel Shale. In western GRCA, in situ *Monomorphichnus lineatus* var. *giganticus* preserved in convex hyporelief was identified by one of the authors (AEM, pers. obs.) (figure 3). It occurred within a green, micaceous shale layer beneath a fine sandstone in Martin's (1985) heterolithic facies. The specimen contains one 25-cm-long (9.8 in) row of laterally repeating, obliquely parallel striations and is distinguished from *M. lineatus* by its large size and is therefore a variation of the ichnospecies described by Crimes and others (1977). The specimen was found in association with *Teichichnus*, *Palaeophycus*, and *Rusophycus* and was most likely produced by a large trilobite approximately 26 cm (10 in) long.

Elliott and Martin (1987) identified *Angulichnus alternipes* from float material in the lower portion of the Bright Angel Shale in eastern GRCA (holotype MNA N3862) (figure 4). The trace consists of alternating tracks bordering a central zig-zag furrow in epichnial preservation and was most likely created by an arthropod walking across the sandy surface. The authors attributed the potential producer of *A. alternipes* to be the enigmatic arthropod *Habelia*, based on its body plan.

Bilaterally Symmetrical Short, Scratched Impressions and Burrows: "*Rusophycus biungis*" *nom. nud.* (proposed holotype MNA N3865) is similar to *Cruziana* in that it is a bilobate furrow, but *Rusophycus* is a resting trace and does not continue as a trail. Instead, it consists of a "coffee bean-shaped", horizontally oriented, hypichnial V-marking (figure 5). "*R. biungis*" was found in the heterolithic facies throughout the Bright Angel Shale in hypichnial preservation in close ichnoassociation with "*C. rusiformis/C. grandcanyonensis*", which most likely had the same producer (Martin, 1985). These invalid ichnospecies of *Cruziana* often transition to *R. dispar* (GRCA 76915). In some cases, *R. dispar* was found with superposed *Palaeophycus* and other scratch marks in western Grand Canyon (GRCA 76919). *R. dispar* was also found in association with *Teichichnus*,

Figure 3. *In situ* Monomorphichnus *aff.* lineatus *var.* giganticus *preserved in convex hyporelief from the lower Bright Angel Shale (NPS/ANNE MILLER).*

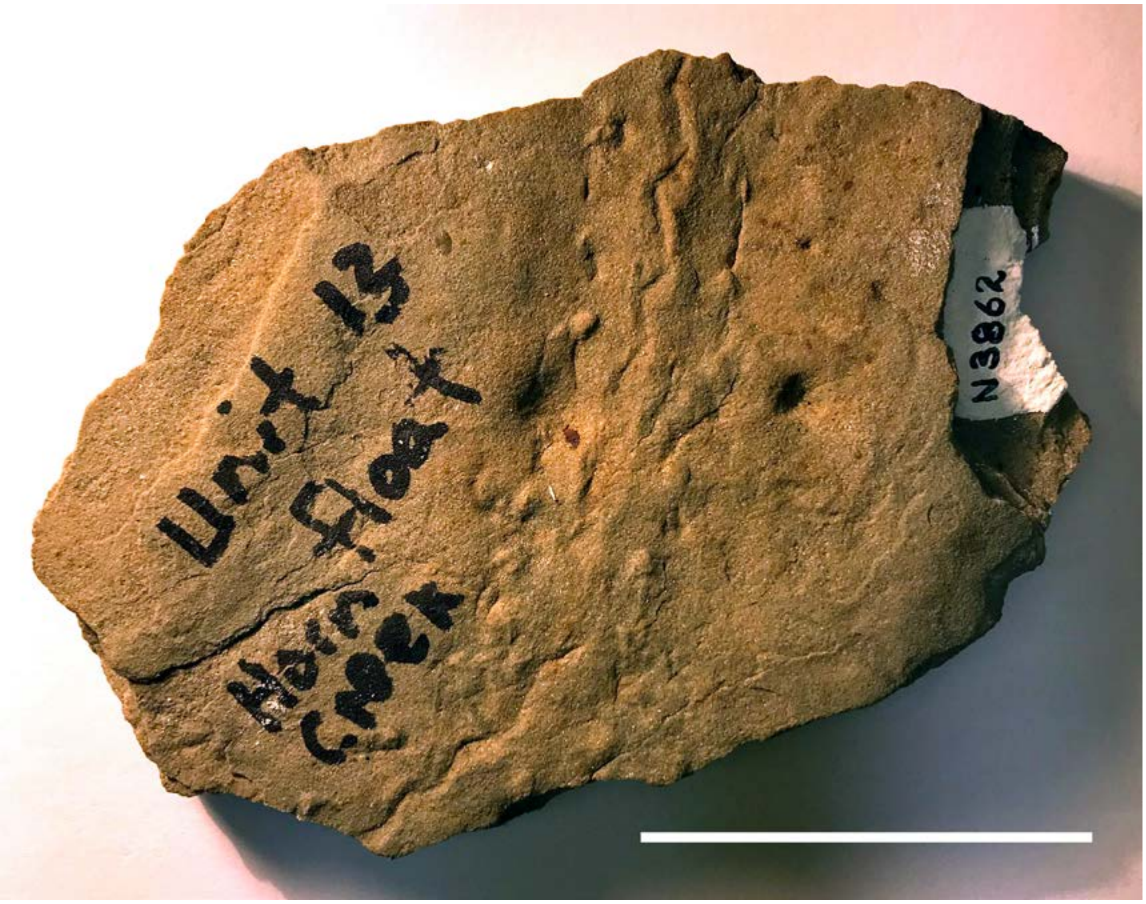

Figure 4. Angulichnus alternipes *from the Bright Angel Shale (holotype MNA N3862), showing trackway. Scale bar is 5 cm (2 in) (MUSEUM OF NORTHERN ARIZONA/DAVID GILLETTE).*

Figure 5. Rusophycus *isp. from the Bright Angel Shale preserved in convex hyporelief (NPS/ANNE MILLER).*

another example of predatory behavior from eastern Grand Canyon (GRCA76903).

Passively Filled Horizontal Burrows: In the heterolithic facies, *Palaeophycus* aff. *P. striatus* was identified as straight or curved, hypichnial, cylindrical burrows oriented horizontally and somewhat obliquely to the bedding plane (figure 6) (Martin, 1985; Baldwin and others, 2004). In marine settings, *Palaeophycus* is likely produced by predaceous polychaetes or other suspension-feeding organisms (Díez-Canseco and others, 2016) and is a common trace fossil in the Bright Angel Shale.

Simple, Actively Filled (Massive) Horizontal to Oblique Structures: Baldwin and others (2004) reported the presence of *Planolites* in the heterolithic beds (F2B facies) of the middle Bright Angel Shale. *Planolites* is a trace similar to *Palaeophycus*, but it has a burrow fill different from the host rock, whereas the fill of *Palaeophycus* is the same as the host rock. Thus, *Planolites* was an actively filled burrow, whereas *Palaeophycus* was passively filled (Pemberton and Frey, 1982).

Complex, Actively Filled Horizontal Structures: Martin (1985) identified *Scolicia* (MNA N3867), which was found in a cliff-forming sandstone and consists of horizontally oriented, sinuous crawling or grazing trails of gastropods in epichnial preservation. In the Bright Angel Shale, *Scolicia* tends to be associated with *Diplocraterion* within the *Cruziana* ichnofacies, even though it is more commonly associated with the *Nereites* ichnofacies elsewhere. Another ichnotaxon described from the Bright Angel Shale by Martin (1985) is *Scalarituba*, which is currently regarded as a junior synonym of *Nereites* (see ichnotaxonomic discussion in Uchman, 1995 and Mángano and others, 2000). It originally included two ichnospecies ("*S. alternolobus*" and "*S. novum*" *nom. nuda*), but both are considered *nomina nuda*.

"*Flectostriatus imporcatus*" *nom. nud.* (proposed holotype MNA N3860) was identified as a horizontally oriented, meandering burrow with lateral and medial ridges in epichnial preservation (Martin, 1985). It was found in cross-stratified sandstone and often has an ichnoassociation with "*Scalarituba alternolobus*" *nom. nud.*, which has a similar morphology. "*S. alternolobus*" (proposed holotype MNA N3866) differs from "*F. imporcatus*" *nom. nud.* in that it has biserially opposed lobes and medial chevrons in epichnial preservation (Martin, 1985). "*S. alternolobus*" *nom. nud.* was also found in cross-stratified sandstone and is interpreted as a backfilled feeding burrow made by worm-like organisms.

Rose (2003) identified "*Scalarituba novum*" in association with *Diplocraterion* in the central Grand Canyon (GRCA 76901; figure 7). In addition, *Scalarituba* was associated with *P. striatus* and *Diplocraterion* outside of Grand Canyon (GRCA 76930). "*Scalarituba novum*" exhibits plowing activity of the producer with a step-like morphology similar to Martin's (1985) "*Scalarituba alternolobus*" *nom. nud.* and "*Fodichnites bitumulus*" *nom. nud.*, which could be transitional forms. Rose (2003) also identified *Taphrhelminthopsis* (a preservational variant of *Scolicia*), which is a ribbon-like, spiral trail similar to *Scalarituba*, and was found to be associated with *Cruziana*, *Planolites*, and *Rusophycus*.

Horizontal Burrows with Horizontal to Vertical Branches: *Phycodes* aff. *P. circinnatum* (MNA N3709) was found in hypichnial preservation and appears as branched, cylindrical burrows oriented horizontally along one plane (Martin, 1985). *Phycodes* is generally thought to have been produced by annelid worms moving along the sand-mud interface. Martin (1985) also reported *Phycodes pedum* (MNA N3864) from the lenticular heterolithic facies at several locations. Recently, Buatois (2018) discussed the ichnotaxonomy of *Phycodes pedum*, arguing that this ichnospecies belongs to the ichnogenus *Treptichnus*. Buatois (2018) also noted the presence of *T. pedum* (formerly *P. pedum*) in the lower part of the Bright Angel Shale, where it seems to occur in association with *Cruziana*, *Diplichnites*, *Monomorphichnus*, *Palaeophycus striatus* (besides other forms of *Palaeophycus*), *Rusophycus*, and *Teichichnus*. *T. pedum* (formerly *P. pedum*) is a curved, horizontal burrow with oblique branches and represents a feeding trace produced by priapulids (figure 8) (Buatois, 2018).

Figure 6. Palaeophycus *isp. from the Bright Angel Shale preserved in convex hyporelief (NPS/ANNE MILLER).*

Figure 7. *"*Scalarituba novum*" (GRCA 76901) collected by Eben Rose in September 1998. Note the paired, funnel-shaped depressions of* Diplocraterion *in the lower left (Rose, 2003). Scale bar is 10 cm (4 in) (NPS/KLARA WIDRIG).*

Another ichnotaxon currently considered as a synonym of *T. pedum* (formerly *P. pedum*) is *Bicavichnites* (Lane and others, 2003; Seilacher and others, 2005). The proposed holotype (MNA N3242) of "*B. lophoseparatus*" *nom. nud*. was found in the dolomitic Meriwitica Tongue of the Bright Angel Shale near Grand Wash Cliffs (Martin, 1985). The type material of a second ichnospecies (*B. martini*; MNA N9500) (figure 9) also came from the same stratigraphic level (Lane and others, 2003). It consists of two parallel sets of circular impressions in epichnial preservation. Initially, it was interpreted as crawling or walking behavior of arthropods and is often associated with "*Frondichnus*" *nom. nud*. The putative producer of *Bicavichnites* has been interpreted as the lobopod *Aysheaia*. It is important to note that this interpretation was not considered for the synonymous ichnogenus, *Treptichnus*.

Horizontal Burrows with Simple, Vertically Oriented Spreiten: *Teichichnus rectus* (MNA N3869) is a common ichnospecies found in the Bright Angel Shale, occurring as hypichnial, epichnial, and exichnial preservation in the heterolithic facies (Martin, 1985). It consists of horizontally oriented burrows, probably produced by annelids, which are slightly curved and contain spreiten, exhibiting a stacked appearance (figure 10). Ichnoassociations for *T. rectus* include *Bergaueria*, *Cruziana*, *Palaeophycus*, *Phycodes*, and *Rusophycus* (Martin, 1985). According to Rose (2003), *Teichichnus* was found in association with *Palaeophycus* in central GRCA (GRCA 76925).

Two different potential morphotypes of *Teichichnus* were identified by one of the authors (AEM, pers. obs.) (figure 11). Figures 11A and 11B represent horizontally oriented, slightly curved burrows with vertically stacked spreiten preserved in both convex hyporelief and epirelief of very fine sandstone and are found in situ, protruding into platy, green, micaceous shale layers. *Teichichnus* in figures 11C and 11D have a similar morphology and occurrence, but is much smaller in size. The burrows in figures 11A and 11B have 18 cm lengths (7 in) with 12 mm diameters (0.5 in), and the burrows in figures 11C and 11D have 3 to 4 cm lengths (1 to 1.6 in) with 4 mm diameters (0.2 in). In addition, the larger burrows were found within a shale-dominated unit, and the smaller burrows were found within a rippled sandstone-dominated unit. Knaust (2018) interpreted *Teichichnus* as potentially produced by polychaetes, holothurians, bivalves, or crustaceans. However, more work is needed to narrow down the producers of *Teichichnus* and further resolve the ichnotaxonomy of different forms.

Figure 8. Treptichnus pedum *(formerly* Phycodes pedum*) from the Bright Angel Shale preserved in convex hyporelief (NPS/ ANNE MILLER).*

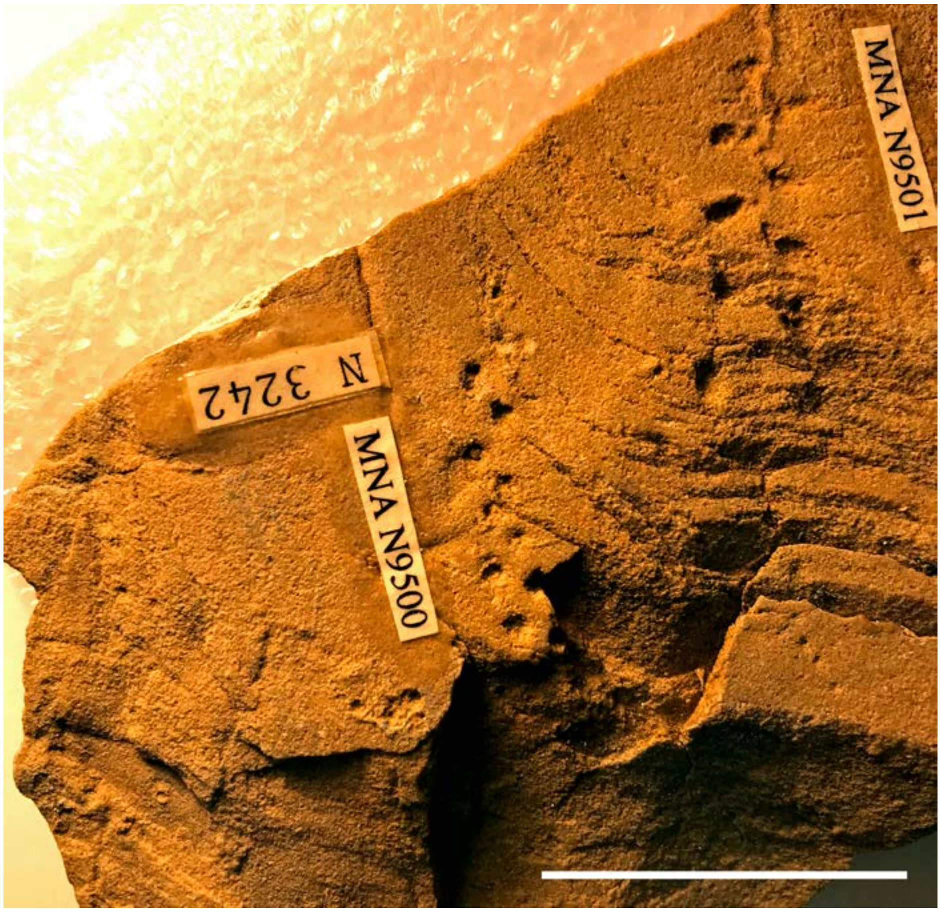

Figure 9. Bicavichnites martini *trackways (holotype MNA N9500 and second specimen MNA N5901) (MUSEUM OF NORTHERN ARIZONA/DAVID GILLETTE).*

Figure 10. Teichichnus isp. *from the Bright Angel Shale showing horizontal spreiten and tapering at one end (NPS/ANNE MILLER).*

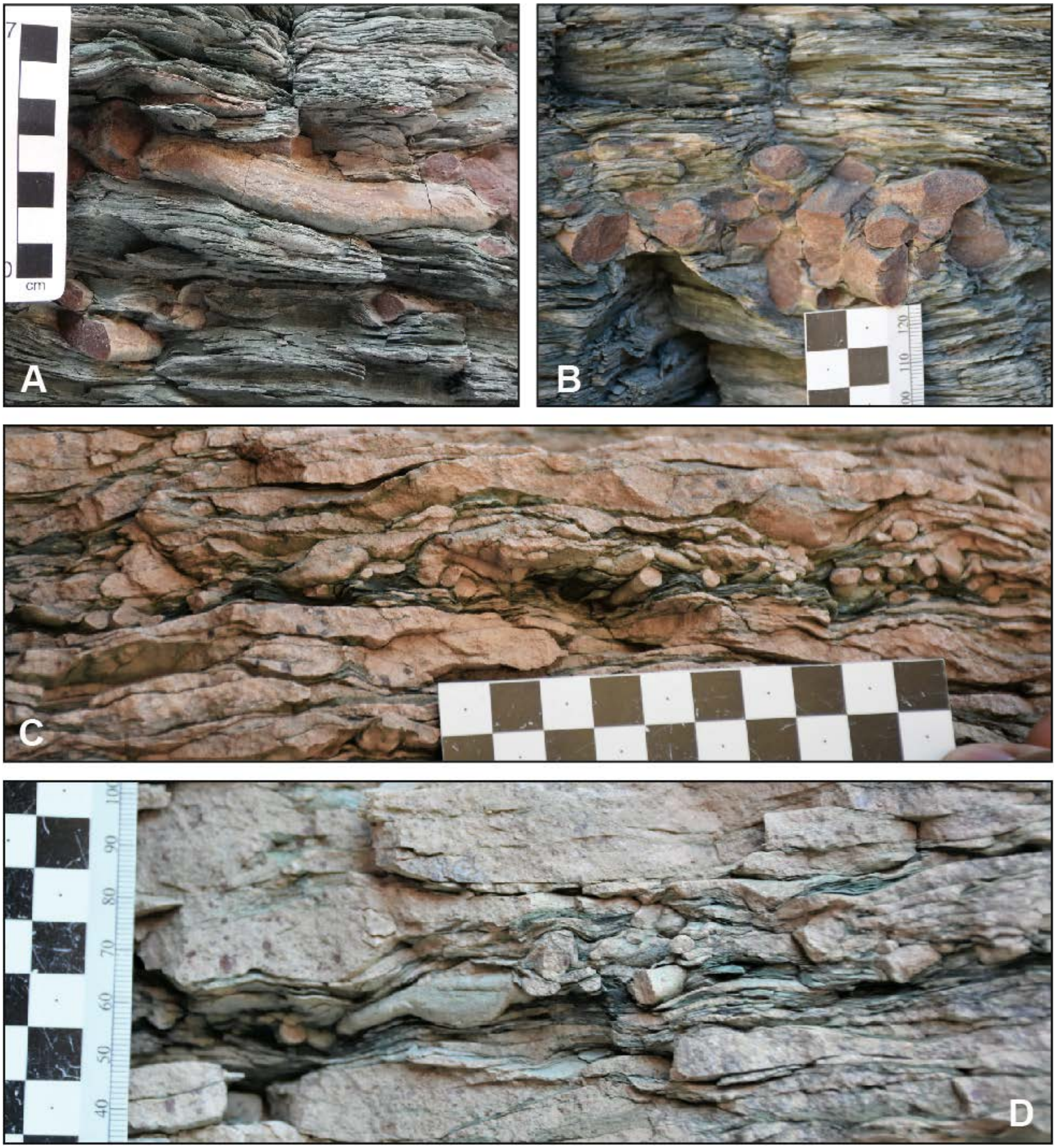

Figure 11. *In situ* Teichichnus *from the lower Bright Angel Shale (NPS/ANNE MILLER).* ***A*** *and* ***B.*** *Large form of* Teichichnus *in shale-dominated facies. Scale is 7 cm (3 in).* ***C*** *and* ***D****. Small form of* Teichichnus *in sandstone-dominated facies. Scale is 10 cm (4 in).*

Radial to Rosette Structures: Baldwin and others (2004) reported *Monocraterion* in the heterolithic facies, where it occurs in association with *Diplocraterion*.

Horizontal Spiral Burrows: Martin (1985) identified *Spirophycus* (MNA N3868) in hypichnial preservation. *Spirophycus* consists of an asymmetrical, horizontally oriented, coiled, grazing burrow within medium-grained sandstone.

Vertical Plug-Shaped Burrows: Martin (1985) identified *Bergaueria* aff. *B. perata*, which consists of vertically oriented cylinders with radial grooves surrounding its smooth walls in hypichnial preservation (figure 12). The specimen was found in the heterolithic facies and is often associated with *Teichichnus*, *Palaeophycus*, and *Cruziana*. *Bergaueria* is commonly thought to have been produced by actinarian, cerianthid, or pennatulacean cnidarians (Buatois and Mángano, 2011).

Vertical Unbranched Burrows: *Skolithos linearis* is composed of simple, cylindrical, vertical burrows and is found in cross-stratified sandstone at Tanner Canyon (Martin, 1985).

Vertical Single U- and Y-Shaped Burrows: Martin (1985) identified *Diplocraterion yoyo* (MNA N3859), which is a vertically oriented, U-shaped burrow containing spreiten, often with paired funnels on the surfaces of beds that connect to the burrow (figure 13). *D. yoyo* is found in thickly bedded sandstone throughout the Bright Angel Shale and is associated with unspecified, epichnial burrows. *Diplocraterion* is interpreted to be a dwelling burrow of suspension feeders such as crustaceans. Rose (2003) described the presence of *Corophioides* (GRCA 76924; a junior subjective synonym of *Diplocraterion*) in the lower Bright Angel Shale from the eastern Grand Canyon, where it occurs in association with *Bergaueria*. Baldwin and others (2004) reported the presence of *Arenicolites*.

Uniramous Meandering Graphoglyptids (Network of Dwelling Burrows): Martin (1985) identified *Belorhaphe*, a zig-zag, horizontal burrow in hypichnial

Figure 12. Bergaueria *isp. from the Bright Angel Shale (NPS/ANNE MILLER).* ***A.*** *and* ***B.*** *In situ specimens preserved in convex hyporelief.* ***C***. *Float specimens of small burrows (black arrow) and large burrows with central, linear depression (white arrow). Tick marks and boxes on scale bars equal 1 cm.*

Figure 13. Diplocraterion *isp. from the Bright Angel Shale showing vertical spreiten between limbs indicating downward shifting in the sediment by the tracemaker (NPS/ANNE MILLER).*

preservation, in association with *Cruziana*, *Palaeophycus*, *Rusophycus*, and *Teichichnus*. They tend to be found in Martin's (1985) lenticular heterolithic facies that represents a subtidal environment influenced by fair-weather suspension settling of mud, silt, and sand from periodic storm events.

Other Ichnotaxa Regarded as Nomina Nuda: "*Frondichnus versiprolatus*" *nom. nud*. (proposed holotype MNA N3856) is an epichnial trace composed of alternating, oblique furrows made by arthropods, but the behavior is unknown. It was also found in the dolomitic Meriwitica Tongue near Grand Wash Cliffs (Martin, 1985). "*Pholetichnus circinatus*" *nom. nud*. (proposed holotype MNA N3863) occurs in the heterolithic facies. This specimen is an epichnial trace exhibiting crawling behavior and consists of circular depressions on the bedding plane oriented in a spiral pattern. This trace was most likely produced by an organism with a proboscis that probed the sediment for food (Martin, 1985). The complete list of invalid ichnotaxa found in the Bright Angel Shale can be found in table 2.

Discussion

The ichnological record of the Bright Angel Shale is very diverse, including many valid ichnotaxa such as: *Angulichnus alternipes*, *Arenicolites* isp., *Belorhaphe* isp., *Bergaueria* aff. *B. perata*, *Cochlichnus* isp., *Cruziana linnarssoni*, *C. problematica*, *C. rusiformis*, *C. rustica*, *Dimorphichnus* isp., *Diplichnites* isp., *Diplocraterion yoyo*, *Monocraterion* isp., *Monomorphichnus lineatus* var. *giganticus, Nereites* isp., *Palaeophycus* aff. *Pa. striatus*, *Phycodes* aff. *Ph. circinnatum*, *Planolites* isp., *Rusophycus dispar*, *Scolicia* isp., *Spirophycus* isp., *Skolithos linearis*, *Teichichnus rectus*, and *Treptichnus pedum*. Other ichnotaxa ("*Bicavichnites lophosepara-*

tus" *nom. nud*., *B. martini*, "*Cruziana grandcanyonensis*" *nom. nud*., "*Isopodichnus problematicus*, "*Scalarituba alternolobus*" *nom. nud*., and *S. novum*) were formerly proposed for this unit, but recent works have reinterpreted them. The ichnodisparity of this record is also considered high, with 15 different architectural designs.

Baldwin and others (2004) classified ichnogenera from the Bright Angel Shale into three groups (or ichnoguilds) based on feeding behavior: sediment feeding, filter and suspension feeding, and surface feeding. Sediment-feeding refers to burrowing and furrowing horizontally along bedding planes and includes ichnogenera such as *Cruziana*, *Palaeophycus*, *Phycodes*, *Rusophycus*, and *Teichichnus*. Filter and suspension-feeding behavior creates vertical and "U"-shaped burrows and includes *Arenicolites*, *Diplocraterion*, *Monocraterion*, and *Skolithos*. Surface-feeding refers to trail casts on bedding surfaces and includes *Palaeophycus* and *Planolites*. *Teichichnus* and *Phycodes* were typically found densely packed together on the underside of resistant sandstone beds within highly bioturbated, heterolithic facies. The predominance of ichnotaxa related to deposit-feeding behaviors (e.g., *Cruziana*, *Palaeophycus*, *Phycodes*, *Planolites*, *Scolicia*, and *Teichichnus*) characterizes the *Cruziana* Ichnofacies. This ichnofacies is typical of shallow-marine settings with moderate to low energy, ranging from the offshore to most distal shoreface. Low rates of sedimentation and erosion favor the preservation of locomotion traces of mobile carnivorous or scavenger invertebrates (e.g., *Angulichnus*, *Diplichnites*, *Dimorphichnus*, and *Monomorphichnus*). The high ichnodiversity and disparity of traces found in the Bright Angel Shale is typical of the *Cruziana* Ichnofacies.

GRCA Museum Collections

Muav Limestone

The Muav Limestone is mainly exposed as cliffs above the Tonto Platform and has an intertonguing relation-

Table 3. *List of collected trace fossil specimens from the Bright Angel Shale in Grand Canyon, housed in the GRCA Museum Collections. (continued on following page)*

Catalog #	Name	Collector	Collection Date
GRCA 2072	*Scolicia*	Edwin D. McKee	07/1930
GRCA 2078	"fucoid"	Edwin D. McKee	11/1930
GRCA 2079	*Rusophycus*	Unknown	Unknown
GRCA 2080	*Rusophycus*	Edwin D. McKee	07/1930
GRCA 2081	Worm trail	R. L. Nichols	08/1930
GRCA 2082	"fucoid"	Unknown	Unknown
GRCA 2083	*Bergaueria*	Edwin D. McKee	04/1930
GRCA 2084	"fucoid"	Unknown	Unknown
GRCA 2085	*Teichichnus*	Unknown	Unknown
GRCA 2086	"fucoid"	Edwin D. McKee	10/1929
GRCA 2087	"fucoid"	Edwin D. McKee	10/1929
GRCA 2090	*Rusophycus*	Edwin D. McKee	11/1930
GRCA 2091	*Teichichnus*	Edwin D. McKee	11/1930
GRCA 2092	*Teichichnus*	Edwin D. McKee	11/1930
GRCA 2093	*Teichichnus*	Edwin D. McKee	1930
GRCA 2097	"fucoid"	Barbara Hastings	1929
GRCA 2101	"fucoid"	Lloyd Davis	1931
GRCA 2102	"fucoid"	Lloyd Davis	1931
GRCA 2103	"fucoid"	Lloyd Davis	1931
GRCA 2104	"fucoid"	Lloyd Davis	1931
GRCA 2105	"fucoid"	Lloyd Davis	1931
GRCA 2106	"fucoid"	Edwin D. McKee	08/1928
GRCA 2107	"fucoid"	Barbara Hastings	05/1929
GRCA 2109	*Rusophycus*	Edwin D. McKee	08/1933

Table 3. *Continued.*

Catalog #	Name	Collector	Collection Date
GRCA 2110	“fucoid”	Edwin D. McKee	08/1935
GRCA 2111	“fucoid”	Edwin D. McKee	08/1936
GRCA 2116	*Teichichnus*	Edwin D. McKee	07/1928
GRCA 2117	Trilobite trail	Glen Sturdevant	Unknown
GRCA 2119	“fucoid”	Edwin D. McKee	05/1936
GRCA 2120	Spiracle fossil	Edwin D. McKee	05/1936
GRCA 2124	*Rusophycus didymus*	Edwin D. McKee	1936
GRCA 2126	Trilobite trail	Edwin D. McKee	05/1936
GRCA 2144	*Rusophycus*	Frank Richardson	05/1938
GRCA 2516	*Rusophycus*	Frank Richardson	05/1938
GRCA 2538	*Teichichnus*	Unknown	Unknown
GRCA 2563	Trilobite trail	Edwin D. McKee	05/1936
GRCA 2579	“fucoid”	Edwin D. McKee	02/1937
GRCA 2580	“fucoid”	Edwin D. McKee	02/1937
GRCA 2654	“fucoid”	Edwin D. McKee	05/1936
GRCA 2655	“fucoid”	Edwin D. McKee	05/1936
GRCA 2656	“fucoid”	Edwin D. McKee	05/1936
GRCA 2657	“fucoid”	Edwin D. McKee	05/1936
GRCA 2658	“fucoid”	Edwin D. McKee	05/1936
GRCA 2659	“fucoid”	Edwin D. McKee	05/1936
GRCA 2660	“fucoid”	Edwin D. McKee	05/1936
GRCA 2661	“fucoid”	Edwin D. McKee	05/1936
GRCA 2662	“fucoid”	Edwin D. McKee	05/1936
GRCA 2663	“fucoid”	Edwin D. McKee	05/1936
GRCA 5266	“fucoid”	Edwin D. McKee	02/1936
GRCA 5267	“fucoid”	Edwin D. McKee	02/1936
GRCA 5268	“fucoid”	Edwin D. McKee	02/1936
GRCA 6386	“fucoid”	Edwin D. McKee	02/1936
GRCA 8528	*Teichichnus*	Edwin D. McKee	07/1928
GRCA 8596	burrow	Edwin D. McKee	04/1939
GRCA 8643	burrow	Dorothy Gardner	05/09/1943
GRCA 8645	“fucoid”	Bill Meadows	01/1947
GRCA 8667	*Cruziana*	Adolf Seilacher	09/22/1955
GRCA 8674	burrow	Adolf Seilacher	10/1955
GRCA 8675	burrow	Adolf Seilacher	10/1955
GRCA 8683	*Rusophycus didymus*	Adolf Seilacher	09/22/1955
GRCA 8684	*Phycodes pedum*	Adolf Seilacher	09/25/1955
GRCA 8685	*Phycodes pedum*	Adolf Seilacher	09/25/1955
GRCA 8686	*Phycodes pedum*	Adolf Seilacher	09/1955
GRCA 8687	*Phycodes pedum*	Adolf Seilacher	09/1955
GRCA 8688	*Phycodes pedum*	Adolf Seilacher	09/1955

Table 3. *Continued.*

Catalog #	Name	Collector	Collection Date
GRCA 8689	*Phycodes pedum*	Adolf Seilacher	09/1955
GRCA 8691	Trilobite trail	Adolf Seilacher	10/1955
GRCA 8693	*Teichichnus*	Adolf Seilacher	09/25/1955
GRCA 8701	*Scolicia*	Adolf Seilacher	10/17/1955
GRCA 8702	*Corophioides*	Adolf Seilacher	10/17/1955
GRCA 8703	*Corophioides*	Adolf Seilacher	10/17/1955
GRCA 8704	*Bergaueria*	Adolf Seilacher	10/17/1955
GRCA 8706	*Sinusites*	Adolf Seilacher	10/17/1955
GRCA 8707	*Sinusites*	Adolf Seilacher	10/17/1955
GRCA 8708	*Sinusites*	Adolf Seilacher	10/17/1955
GRCA 8709	Ichthidian	Adolf Seilacher	10/17/1955
GRCA 11448	*Rusophycus*	Edwin D. McKee	07/1930
GRCA 11449	*Rusophycus*	Edwin D. McKee	07/1930
GRCA 11450	“fucoid”	Edwin D. McKee	04/1930
GRCA 11451	“fucoid”	Edwin D. McKee	04/1930
GRCA 11452	*Rusophycus*	Edwin D. McKee	11/1930
GRCA 14467	*Teichichnus*	Unknown	09/1966
GRCA 14468	*Teichichnus*	Unknown	09/1966
GRCA 14469	*Teichichnus*	Unknown	09/1966
GRCA 14471	“fucoid”	Unknown	09/1966
GRCA 15231	*Rusophycus*	Unknown	Unknown
GRCA 15232	*Rusophycus*	Unknown	Unknown
GRCA 17182	Trilobite trail	Unknown	Unknown
GRCA 17415	trail	Edwin D. McKee	02/1936
GRCA 21046	“fucoid”	Edwin Rothfuss	04/20/1963
GRCA 21047	“fucoid”	Edwin Rothfuss	04/20/1963
GRCA 21402	“fucoid”	Edwin D. McKee	10/1939
GRCA 39124	“fucoid”	Unknown	Unknown
GRCA 76901	*Scalarituba novum*	Eben C. Rose	09/1998
GRCA 76902	*Palaeophycus*	Eben C. Rose	05/1998
GRCA 76903	*Rusophycus dispar*	Eben C. Rose	09/1998
GRCA 76904	*Rusophycus dispar*	Eben C. Rose	09/1998
GRCA 76905	*Monomorphichnus*	Eben C. Rose	05/1999
GRCA 76909	*Cruziana rusiformis*	Eben C. Rose	05/1999
GRCA 76910	*Diplichnites*	Eben C. Rose	08/1999
GRCA 76911	*Teichichnus*	Eben C. Rose	09/1998
GRCA 76913	*Rusophycus dispar*	Eben C. Rose	08/1998
GRCA 76914	*Palaeophycus*	Eben C. Rose	09/1999
GRCA 76915	*Palaeophycus*	Eben C. Rose	09/1999
GRCA 76916	*Palaeophycus*	Eben C. Rose	09/1999
GRCA 76917	*Cruziana rusiformis*	Eben C. Rose	05/1999

Table 3. *Continued.*

Catalog #	Name	Collector	Collection Date
GRCA 76918	*Scalarituba novum*	Eben C. Rose	08/1999
GRCA 76919	*Rusophycus dispar*	Eben C. Rose	05/1998
GRCA 76920	*Palaeophycus*	Eben C. Rose	05/1999
GRCA 76921	*Cruziana rusiformis*	Eben C. Rose	05/1998
GRCA 76922	*Scalarituba novum*	Eben C. Rose	03/1998
GRCA 76924	*Corophioides*	Eben C. Rose	08/1998
GRCA 76925	*Teichichnus*	Eben C. Rose	09/1998
GRCA 76926	*Treptichnus pedum*	Eben C. Rose	05/1999
GRCA 76928	*Cruziana rusiformis*	Eben C. Rose	05/1999
GRCA 76929	*Treptichnus pedum*	Eben C. Rose	05/1999
GRCA 76930	*Scalarituba*	Eben C. Rose	05/1999
GRCA 76931	*Palaeophycus*	Eben C. Rose	09/1999
GRCA 76932	*Treptichnus pedum*	Eben C. Rose	05/1999
GRCA 85217	Eocrinoidea	Kate Watters	10/25/2005

ship with the underlying Bright Angel Shale. According to Schuchert (1918), faunal assemblages date the Muav Limestone as late Cambrian (Furongian). He also noted the potential for finding strata younger than Cambrian, below the Devonian contact with the Temple Butte Formation, although no research on this possibility has occurred. Seven members were designated by McKee and Resser (1945) based on invertebrate faunal assemblages and lithology. The top three members can be traced throughout Grand Canyon, and the lowest four members are only present in the western half. The Muav Limestone is generally composed of mottled mudstone and packstone, both calcareous and dolomitic in composition, as well as conglomeratic beds (Middleton and Elliott, 2003). Most of the Muav Limestone beds are structureless or horizontally laminated, although many localities do contain cross-stratified beds. The thickness of the formation ranges from 42 m (138 ft) in eastern exposures to 252 m (827 ft) in the western Grand Canyon (Middleton and Elliott, 2003). Beds are thicker in the west, but the siliciclastic content is higher in the east. These features are compatible with the overall perspective of eastward coastline advancement.

The Muav Limestone represents a series of transgressive and regressive events in an offshore marine environment, conducive to supporting a habitat for invertebrates. The transgressive events were recorded in five members of the Muav Limestone, namely (ascending): Rampart Cave, Sanup Plateau, Spencer Canyon, Peach Springs, and Kanab Canyon members. The intertonguing relationship with the underlying Bright Angel Shale reveals a step-like pattern in which the Muav Limestone diagonally crosses time planes. This is because the sea advanced in rapid, periodic stages, interrupted by at least four regressive events of a lesser extent. The regressive events are recorded in the various tongues of sediment that protrude into the limestone (McKee and Resser, 1945). Although body fossils are sparse in the Muav Limestone, bioturbation is extremely common within calcareous-dominated sediment and is responsible for the mottled appearance (Schuchert, 1918).

Trace Fossils

Trace fossils are common in the Muav Limestone, but there has never been a comprehensive ichnotaxonomic treatment. Schuchert (1918) stated, “The writer has not seen a Paleozoic marine deposit more bored into and consumed by mud eaters than this one”. Noble (1922) also noted that almost every carbonate bed in the Muav Limestone contains “fucoidal markings”. Clearly, this unit yields a substantial amount of traces, but those reported have not yet been placed within any particular ichnotaxon. Schuchert (1918) pointed out that, although most of the traces in the Muav Limestone are not easily recognizable, there is sufficient, observable evidence that annelids were very common. These annelid burrows were mostly preserved within the layers of shale as heaps or “circular sausage-like strings” (Schuchert, 1918). Nonspecific worm borings and trails were also reported in the Muav Limestone by Schuchert (1918), Noble (1922), and McKee and Resser (1945).

Horizontal Burrows with Horizontal to Vertical Branches: The only ichnotaxon reported from the Muav Limestone was a specimen collected by Schellbach in 1936 and assigned to *Phycodes* isp.

GRCA Museum Collections

Unspecified "fucoids" were found in the Muav Limestone and collected by Edwin McKee in October and November 1930 (GRCA 2089, GRCA 2095, and GRCA 2096). Louis Schellbach collected several, unspecified "fucoid" traces from the Muav Limestone in September 1936 (GRCA 2127, GRCA 2128, GRCA 2129, GRCA 2130, GRCA 2131, GRCA 2132, and GRCA 2133). He also collected *Phycodes* in September 1936 (GRCA 2134). Edwin McKee collected two "fucoid" specimens from the base of the Muav Limestone near Grand Wash Cliffs in the fall of 1936 that he identified as "worm tubes" (GRCA 8541 and GRCA 8542). Adolf Seilacher collected specimens with vertical tubes and branching "worm trails" from the upper Muav Limestone near Indian Gardens on September 20, 1955 (GRCA 8676 and GRCA 8682). Four reticulate burrow specimens were collected from the upper Muav Limestone along the Kaibab Trail by Adolf Seilacher on September 22, 1955 (GRCA 8668, GRCA 8669, GRCA 8670, and GRCA 8671). On the same day, Seilacher also collected a specimen identified as *Eophyton*, which are actually inorganic drag marks or tool marks found in the upper Muav Limestone along Kaibab Trail (GRCA 8672). "Fucoids" were also collected from the Muav Limestone from an unknown location by an unknown collector (GRCA 2098, GRCA 2108, and GRCA 17153).

Frenchman Mountain Dolostone

The Frenchman Mountain Dolostone is an interval of dolomite overlying the Muav Limestone, creating an unconformity that is distinguished by a high-relief, erosional surface. Historically known as the "undifferentiated dolomites", it was assigned to the Frenchman Mountain Dolostone by Karlstrom and others (2020), who made it the uppermost unit of the Tonto Group. It is mostly exposed in the western portion of Grand Canyon and extends from Kanab Creek to Nankoweap Canyon (Noble, 1922). This dolomitic sequence is up to 131 m (430 ft) thick and has its best exposure at Grand Wash Cliffs (Middleton and Elliott, 2003). Three lithofacies were identified by McKee and Resser (1945) and were described as a white, structureless dolomite, a yellow, bedded dolomite, and a gray, bedded dolomite. Some facies contain ripples and cross-stratification. Carbonates with oolitic grainstones and stromatolites were documented by Brathovde (1986), which indicates a shallow subtidal to intertidal environment.

Trace Fossils

The most common trace fossils present in this unit are invertebrate trackways and horizontal burrows (Middleton and Elliott, 2003). These burrows and trails were first reported by McKee (1945), but no comprehensive report has been completed.

DEVONIAN

Temple Butte Formation

The Temple Butte Formation is exposed as scattered, inconspicuous lenses cutting into the Tonto Group. The lenses are relatively thin at 30 m (98 ft) thick and discontinuous in the eastern portion of Grand Canyon and are more than 220 m (722 ft) thick and continuous towards the central and western regions, often merging with the overlying Redwall Limestone cliffs (Beus, 2003a). These lenses are considered to be paleochannels or paleo-valleys (up to 120 m or 394 ft wide) that had cut into the underlying, undifferentiated dolomites as well as the Muav Limestone. The Temple Butte Formation mainly consists of dolomite with some sandstone, limestone, and conglomerate.

The Temple Butte Formation is considered to be early Late Devonian in age, potentially in part as old as the Middle Devonian based on conodont assemblages, making this formation the only Devonian unit in Grand Canyon (Beus, 2003a). The discontinuous lenses in eastern GRCA are thought to represent tidal channels, and the fossils in the central and western portion of GRCA indicate a shallow, subtidal, open-marine environment. These conditions allowed for invertebrates to flourish.

Trace Fossils

Several reports have mentioned the occurrence of worm borings and trails in the Temple Butte Formation (Schuchert, 1918; Noble, 1922; Stoyanow, 1936; Bond and others, 2018), but very little was identified and described, most likely due to the nature of preservation and difficulty of access.

Passively Filled Horizontal Burrows: Beus (2003a) noted the presence of certain unidentified, cylindrical traces that look similar to the ichnogenus *Palaeophycus*, found in dolomitic beds within the lower Temple Butte Formation. Beus (2003a) mentioned that they are sub-horizontal and straight or gently curved with a micritized core and could potentially resemble some form of algal activity.

GRCA Museum Collections

In September 1938, Edwin McKee collected a Devonian limestone slab with "worm borings" outside of Grand Canyon National Park along Sycamore Creek near Verde Valley, Arizona (GRCA 5443).

MISSISSIPPIAN

Redwall Limestone

The prominent, red-stained cliffs that are exposed nearly mid-way vertically down the canyon are outcrops of the

Redwall Limestone. The unit sits horizontally on the Cambrian Tonto Group and the lenses of the Devonian Temple Butte Formation. Redwall Limestone cliffs are 150 to 250 m (492 to 820 ft) high, stained by the overlying, iron oxide-rich material drained down from the Supai Group (Beus, 2003b). The unweathered surface, however, is mainly light to dark gray in color. The Redwall Limestone can be traced throughout GRCA, from the east in Marble Canyon all the way to the west at Grand Wash Cliffs. Its thickness increases to the northwest, from about 120 m (394 ft) thick near Tanner Trail to about 245 m (804 ft) thick at Iceberg Ridge (McKee and Gutschick, 1969). The Redwall Limestone consists of four members, in ascending order the Whitmore Wash Member, Thunder Springs Member, Mooney Falls Member, and Horseshoe Mesa Member. The two oldest members consist of limestone that transitions to mostly dolomite towards the central and eastern portion of GRCA, both thickening to the west. The thickest member is the overlying Mooney Falls Member, which is mostly limestone. The Redwall Limestone is topped by the Horseshoe Mesa Member, consisting of alternating beds of dark chert and light carbonate. The Redwall Limestone represents a shallow sea that contained a diverse assemblage of organisms such as mollusks, echinoderms, arthropods, bryozoans, and fish. These fossilized organisms date the Redwall Limestone as Early Mississippian in age (Beus, 2003b).

Trace Fossils

Though trace fossils are scarce in the Redwall Limestone, Stoyanow (1936) noted "impressions of fucoids on bedding planes". Edwin McKee collected several invertebrate trace specimens in 1952–1962 that mainly consist of horizontal trails.

GRCA Museum Collections

Edwin McKee collected three limestone slabs that contain "worm trails" on the surface. The slabs were collected in 1952–1962 (GRCA 17937, GRCA 17938, and GRCA 17939). He also collected "worm trail" specimens near the top of the Redwall Limestone on October 13, 1958 (GRCA 20017, GRCA 20018, and potentially GRCA 20019, which is listed as by an unknown collector from the same locality). One "fucoid" specimen associated with "worm trails" was collected near the top of the Redwall Limestone by George Beck in August 1968 (GRCA 21226).

Surprise Canyon Formation

The Surprise Canyon Formation is exposed as lenses of clastic and carbonate sediment that filled in the karst topography of the Redwall Limestone during the Late Mississippian. The paleo-valleys thicken to the west from 45 to 60 m (148 to 197 ft) and can be up to 1 km wide (0.6 mi). They consist of a sandstone conglomerate at the base, skeletal limestone in the middle unit, and slope-forming siltstone and limestone at the top (Beus, 2003b). The Surprise Canyon Formation was deposited in a broad valley by dendritic streams that filled in collapsed sinkholes of the Redwall Limestone as the sea receded.

Trace Fossils

Although body fossils are more common in the Surprise Canyon Formation, there have been a few brief mentions of invertebrate trace fossils. Trace fossils typical of the *Skolithos* ichnofacies have been found in the basal sandstone/conglomerate. Trace fossils typical of the *Cruziana* ichnofacies were seen in the middle unit of Surprise Canyon Formation (Beus, 2003b). Bonde and others (2018) also noted the presence of unspecified trace fossils in the Surprise Canyon Formation.

Vertical Plug-Shaped Burrows: The basal sandstone/conglomerate unit contains vertical burrows and *Conostichus* (Beus, 2003b), which are cone-shaped burrows most likely produced by sea anemones. *Conostichus* is typical of the *Skolithos* ichnofacies.

PENNSYLVANIAN

Supai Group

The Supai Group is exposed as massive red beds and slopes forming a cliffy, stair-stepped profile that overlies the Redwall Limestone and the paleochannels of the Surprise Canyon Formation. The prominent red color comes from the ferritic pigment of shales washing through, while the unweathered surface is more of a light tan to pink color. The Supai Group mainly consists of sandstone, but some beds contain sandy shale and limestone (Noble, 1922). The group is divided into four formations including, from oldest to youngest, the Watahomigi Formation, Manakacha Formation, Wescogame Formation, and Esplanade Sandstone.

Trace Fossils

Burrows, most frequently smooth and cylindrical (parallel, perpendicular, and oblique to the bedding plane), occur mostly in carbonates and silty sandstones of the Supai Group. Invertebrate trackways and plant root bioturbation have also been observed (Blakey, 2003).

GRCA Museum Collections

Two limestone specimens with "fucoidal structures" were collected from indeterminate strata of the Supai Group by Edwin McKee near the Shivwits Plateau on an unknown date. The specimens were loaned to McKee on February 4, 1972 and never returned; thus, they were deaccessioned (GRCA 5669 and GRCA 6504). McKee also collected limestone slabs “covered with worm tubes” in 1952–1962 from the Supai Group near the Bright Angel Trail (GRCA 12753 and GRCA 12754).

Watahomigi Formation

The Watahomigi Formation is the oldest unit, thickening westward from 30 to 90 m (98 to 295 ft) and containing siltstone, mudstone, limestone, and dolomite (Blakey, 2003).

Trace Fossils

McKee (1982) mentioned the presence of “worm borings” in siltstone and limestone from two locations. Bonde and others (2018) also noted the presence of “worm tubes” and microbially induced sedimentary structures (MISS) in the Watahomigi Formation.

Manakacha Formation

The overlying Manakacha Formation is dominantly sandstone with a few mudstone beds and is thickest in the central portion of GRCA, averaging 90 m (295 ft) thick (Blakey, 2003).

Trace Fossils

“Horseshoe-crab-like invertebrate tracks” were observed by McKee (1982), as well as “worm borings and trails”.

Wescogame Formation

The Wescogame Formation ranges from 30 to 60 m (98 to 197 ft) in thickness and consists of lithologies similar to those of the underlying Manakacha Formation. The upper contact of the Wescogame Formation forms the boundary with the Permian rocks of the Esplanade Sandstone, the uppermost unit of the Supai Group (Blakey, 2003).

Trace Fossils

Gilmore (1928) described two arthropod trackways (USNM 11693 and 11740) from the same lithofacies where vertebrate tracks were found, i.e., cross-bedded sandstones of eolian origin (figure 14). McKee (1982) noted the presence of worm borings on a silty sandstone cliff unit from the lower portion of the Wescogame Formation. He also mentioned two different types of unknown invertebrate tracks were present.

Simple Horizontal Trails: On the holotype slab of the vertebrate ichnotaxon *Anomalopus sturdevanti* Gilmore, 1928 (USNM 11577; figure 14A), thin, shallow, horizontal, slightly meandering and unornamented burrows can be observed (width 2 mm or 0.08 in). They can be assigned to *Helminthopsis* isp.

Trackways and Scratch Imprints: The specimen USNM 11740B (figure 14B) shows an arthropod trackway with two parallel rows of closely spaced elongated tracks with a medial furrow, about 2 cm (0.8 in) wide. This is referable to *Diplichnites* isp.

PERMIAN

Esplanade Sandstone

The Esplanade Sandstone is the most sandstone-dominated unit of all of the Supai units, with cross-stratified sandstone beds. It begins the Permian strata of Grand Canyon and was mostly deposited in eolian settings (Blakey, 2003).

Trace Fossils

McKee (1982) mentioned the presence of “worm borings” in muddy films within siltstone and sandstone of the upper Esplanade Sandstone in several locations. He also noted that resistant sandstone from the basal part of the Esplanade Sandstone contains “worm borings”. A siltstone with these traces and mud pellets was found in 150-Mile Canyon (McKee, 1982). McKee (1982) measured vertical burrows that were 3.3 mm (0.13 in) in diameter, creating a resistant sandstone ledge in the Esplanade Sandstone. Some horseshoe-shaped tracks found in mudstone were also reported from the Esplanade Sandstone (McKee, 1982).

Hermit Formation

The Hermit Formation is a poorly exposed, slope-forming, siliciclastic unit that gradationally overlies the Supai Group. It is mainly composed of red-to-brown mudstone, siltstone, and very fine sandstone deposited in a low-energy coastal environment rich in flora and fauna. The siltstone and sandstone often contain ripple marks and cross-stratification associated with meandering streams. These rocks can also be observed in outcrops outside of GRCA near Sedona, Arizona. Structureless, 1-m-thick (3 ft) sandstone beds often form resistant ledges that may have been further lithified with calcitic concretions (Blakey, 2003). Siliciclastic mudstone forms slopes and is usually structureless with the occasional ripple mark. The thickness of the Hermit Formation ranges from 30 m (98 ft) in eastern Grand Canyon to over 270 m (886 ft) in western Grand Canyon (Blakey, 2003). It is sharply overlain by the Coconino Sandstone throughout Grand Canyon. The Hermit Formation is thought to be Leonardian in age (Cisuralian), which was first assigned by White (1929) and later repeated by McKee (1982) based on the plant fossil *Callipteris arizonae*.

Trace Fossils

The invertebrate trace fossil record of the Hermit Formation mainly consists of trackways, burrows, and

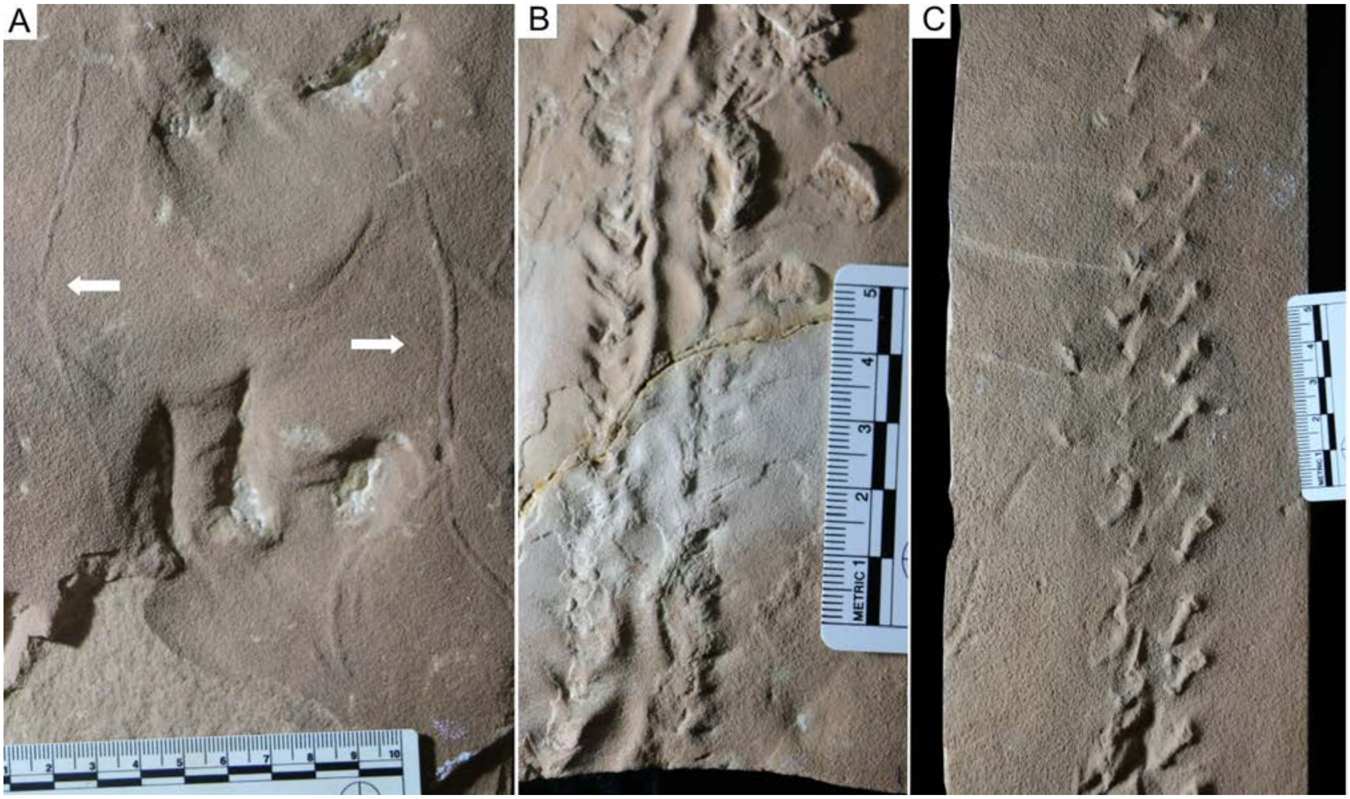

Figure 14. Invertebrate traces from the Wescogame Formation (LORENZO MARCHETTI). A. Helminthopsis *isp., indicated by arrows, convex hyporelief (USNM 11577). B.* Diplichnites *isp., concave epirelief (USNM 11740B). C. Partial arthropod trackway, undetermined, convex hyporelief (USNM 11740).*

resting and feeding traces, although root bioturbation and microbial structures are more common (White, 1929; Blakey, 2003). McKee (1982a) reported the presence of "worm burrows" and "worm tubes" in the Hermit Formation. Other invertebrate traces were reported by Spamer (1992). Unfortunately, many of these trace fossils are unidentifiable due to high levels of bioturbation. However, certain beds in the lower part of the formation reveal distinct traces that can be identified at the ichnogenus and ichnospecies level.

Trackways and Scratch Imprints: Two specimens from outside of GRCA in Gila County at Craddock Creek (UCMP-V 4012 and UCMP-V 4013) show arthropod trackways with two rows of regularly spaced sets of two to three elongated tracks perpendicular to each other, assignable to *Lithographus* isp. (figure 15B). The specimen UCMP-V 4013 also includes a possible arthropod resting trace. A specimen from Yavapai County (UMCP-V 75214; figure 15A) shows a trackway with two parallel rows of tracks arranged in series of three tracks with opposite symmetry; this is referable to *Stiaria* isp. These three specimens come from the Mogollon Rim area, from units correlated with the Hermit Formation of the Grand Canyon (Blakey, 1979).

Simple, Actively Filled (Meniscate) Horizontal to Oblique Structures: White (1929) identified the new ichnospecies *Scoyenia gracilis* (page 115, plate 4), found in the lower portion of the Hermit Formation (figure 16). *Scoyenia* is a deposit feeding or dwelling structure with straight, wrinkly, overlapping burrow structures and is thought to be made by either a larval or adult insect. White (1929) noted that *S. gracilis* was somewhat different than other possible forms of *Scoyenia* based on the fasciculate morphology and concluded that it was the mold of an animal boring into the substrate.

Simple, Actively Filled (Pelletoidal) Horizontal Burrows: The ichnospecies *Walpia hermitensis* (lectotype USNM 263675: figure 17A; paralectotype: USNM 263676; figure 17B) was proposed by White (1929: 117, plate 51) based on a specimen found in association with *Scoyenia gracilis*. White (1929) interpreted the nodules in *W. hermitensis* as possible fecal pellets produced by worms or crustaceans as they tunneled the substrate. Alternatively, Häntzschel (1975) interpreted the nodules to be sediment packets from arthropods excavating and backfilling as they burrowed along the surface. Lucas and others (2011) interpreted *Walpia* as an arthropod feeding or locomotion structure (most likely a shallow compaction burrow made by a hexapod) consisting of slightly curved to sinuous burrows or trails lined with small, rounded nodules. Recently, the ichnospecies *W. hermitensis* was regarded as a junior synonym of *Sphaerapus larvalis* (Lucas and others, 2013). Early

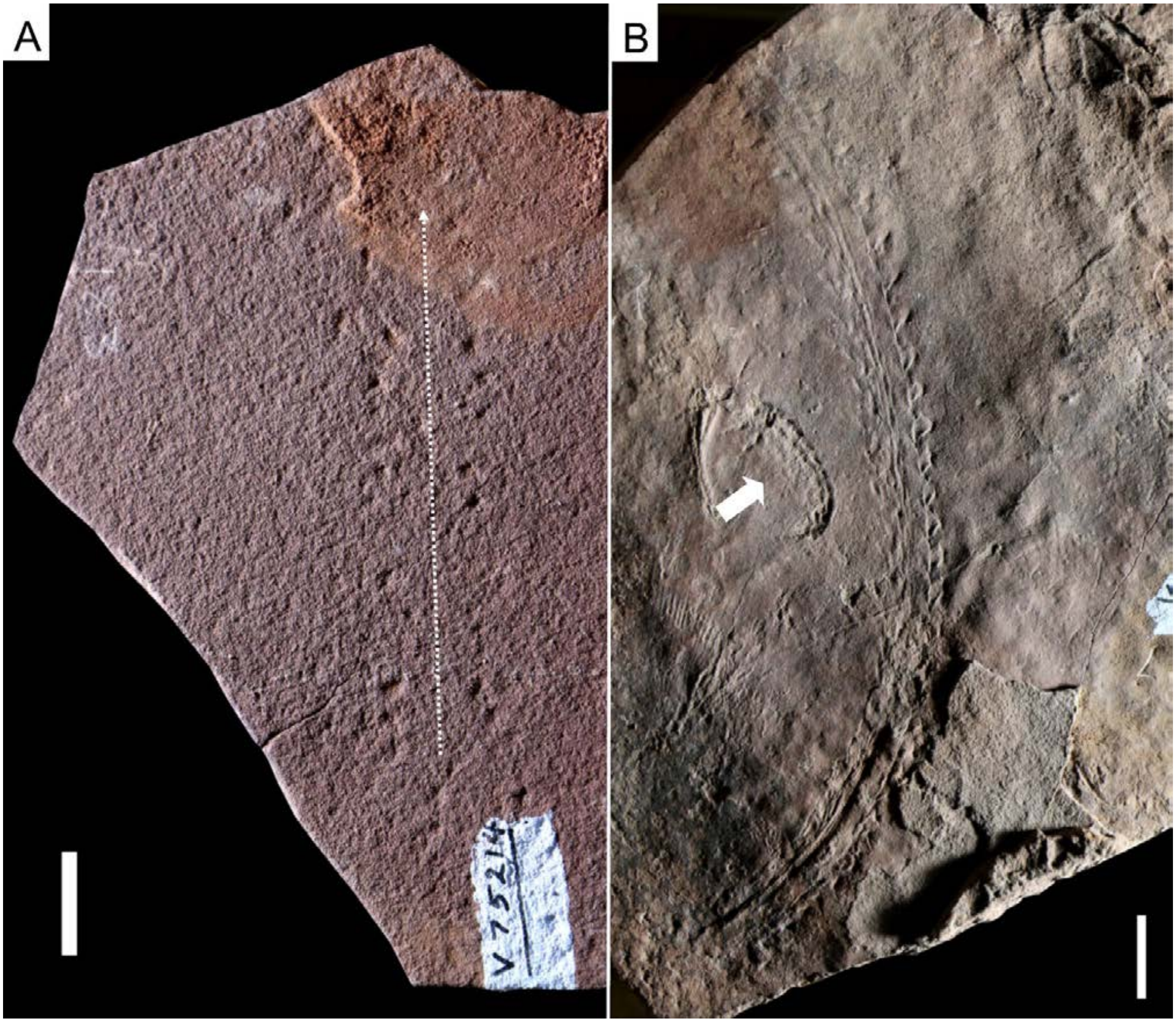

Figure 15. *Arthropod trackways from the Hermit Formation of the Mogollon Rim area (LORENZO MARCHETTI).* ***A.*** Stiaria *isp. (UMCP-V 75214).* ***B.*** Lithographus *isp. (UCMP-V 4012). Arrow indicates a possible arthropod resting trace. Scale bar is 1 cm (0.4 in).*

coleopterans could be the potential producers of *S. larvalis* due to the similarity to modern, beetle-produced burrows (Lucas and others, 2011, 2013).

GRCA Museum Collections

"Fucoid" specimens from the Hermit Formation with "worm trails and borings" were collected by Edwin McKee in 1929. One specimen was found along Yaki Trail (GRCA 3023) and the other was found in Hermit Basin and classified as "vermes" associated with *Scoyenia gracilis* (GRCA 3068; GRCA 8538, figure 16; White, 1929: 115, plate 4). McKee collected another "fucoid" specimen with worm trails from the Hermit Formation (GRCA 3200). A slab of shale with many "worm borings" from the Hermit Formation was collected in the adjacent Lake Mead National Recreation Area by Edwin McKee (GRCA 5793). McKee also collected a siltstone specimen containing worm trails from the Hermit Formation (GRCA 5815). Lawrence Goebels collected another worm trail specimen from the Hermit Formation (GRCA 3203).

Discussion

The Hermit Formation presents only four valid ichnotaxa (*Lithographus* isp., *Scoyenia gracilis*, *Sphaerapus larvalis*, and *Stiaria* isp.) classified among three architectural designs. Arthropod trackways and horizontal to oblique burrows produced in continental settings characterize the *Scoyenia* ichnofacies, which represents low energy, inundated (at least periodically) continental settings, such as riverine point bars, channel banks, and crevasse splays, and lake margins and floodplains

Figure 16. Scoyenia gracilis *(GRCA 8538) from the Hermit Formation (White, 1929). Scale bar is 1 cm (0.4 in) (NPS/KLARA WIDRIG).*

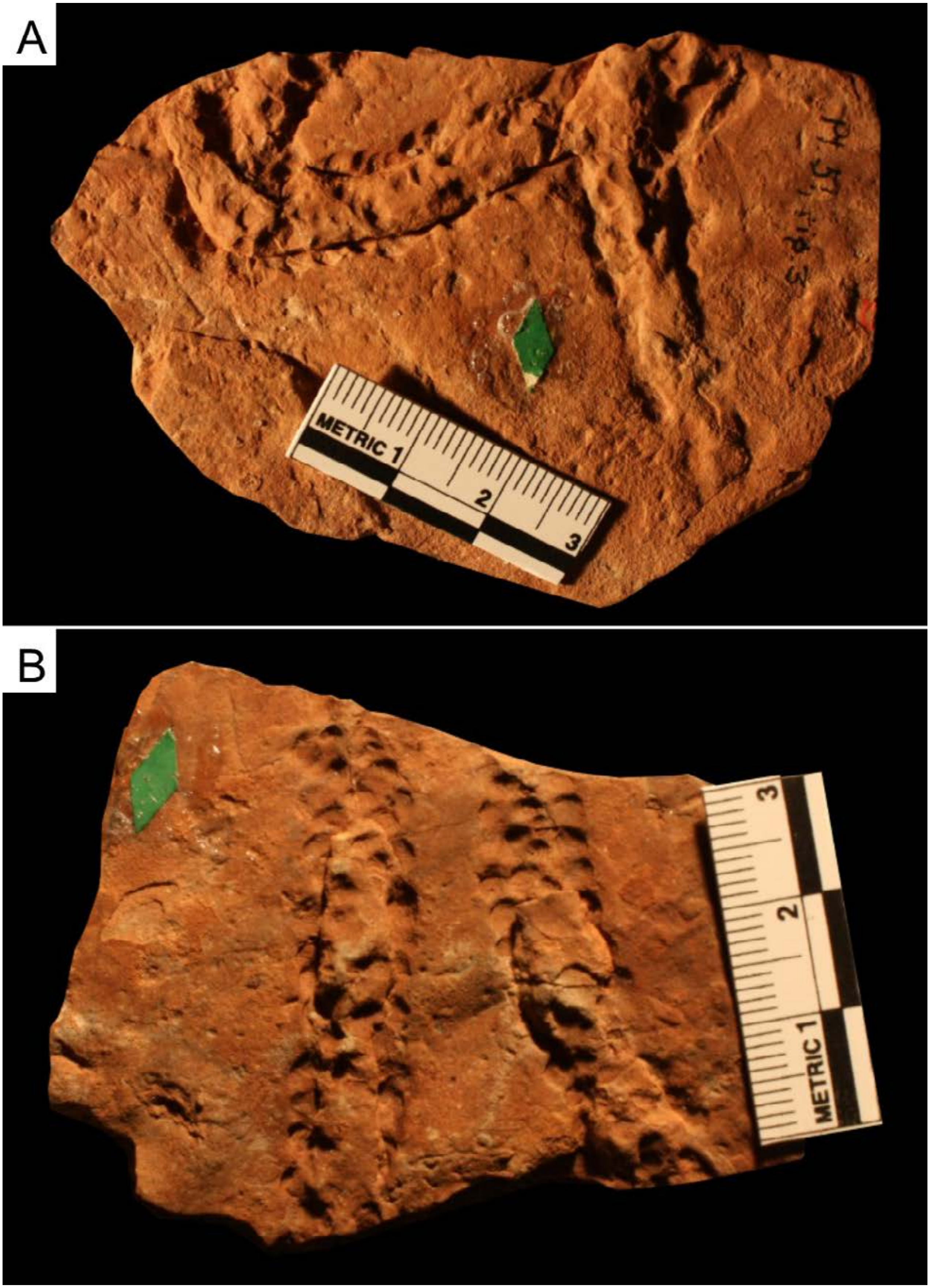

Figure 17. Walpia hermitensis *syntypes from the Hermit Formation (White, 1929) (SPENCER LUCAS).* ***A.*** *Lectotype in concave epirelief (USNM 263675).* ***B.*** *Paralectotype in concave epirelief (USNM 263676). Scale bar is 3 cm (1.2 in).*

(MacEachern and others, 2012). Tetrapod tracks (Gilmore, 1927; see Marchetti and others in this volume) that occur in association with invertebrate traces corroborate this interpretation.

Coconino Sandstone

The Coconino Sandstone is a relatively thick unit (up to 300 m or 984 ft) exposed in several areas of the southern Colorado Plateau (e.g., Blakey and Knepp, 1989), and especially in the GRCA and Mogollon Rim areas of Arizona. It is composed of large-scale cross-bedded sandstones of clear eolian origin (e.g., McKee, 1979). The foreset dune beds are usually inclined to about 15–30°. The sandstones are pale-buff and fine-grained. The grains are well rounded and quartz is predominant. Interdunal deposits are rare. This unit usually forms evident and recognizable cliffs due to its massive structure. In GRCA, this unit overlies the Hermit Formation, interfingers with and is overlain by the Toroweap Formation, and is overlain by the Kaibab Formation in areas where the Toroweap Formation is not present. Because of this stratigraphic position, it is considered to be early Permian (Kungurian/Leonardian) in age (Blakey and Knepp, 1989). This is consistent with the tetrapod footprint ichnoassociation, belonging to the *Erpetopus* footprint biochron (Marchetti and others, 2019b).

Trace Fossils

The only fossils known from the Coconino Sandstone are trace fossils (Spamer, 1984). Invertebrate traces are known from GRCA, including as possible producers, worms, millipedes, isopods, spiders, scorpions (e.g., Gilmore, 1926, 1927; Brady, 1947; Middleton and others, 1990), and insects (Spamer, 1992). The most common invertebrate ichnofossil is the possible scorpion track *Paleohelcura* (see Brady, 1939). Other arthropod tracks are also common (Gilmore, 1927; Brady, 1947; Sadler, 1993), and meniscate horizontal burrows (Brady, 1947) and conical pits have also been reported (Elliott and Bartlett, 2013). Invertebrate trace fossils from this unit have been the subject of numerous ichnotaxonomic studies (e.g., Gilmore, 1926, 1928; Brady, 1947, 1961; Alf, 1968; Sadler, 1993; Kramer and others, 1995; Minter and others, 2007; Davies and others, 2007). They are also an important reference for paleoecological studies through ichnofacies: the dune-low diversity *Octopodichnus–Entradichnus* ichnofacies is largely based on the Coconino invertebrate ichnoassociation (Ekdale and others, 2007; Hunt and Lucas, 2007; Buatois and Mángano, 2011). These traces usually come from the lower half of the unit and are commonly preserved on the foreset surfaces of the eolian dunes (e.g., Gilmore, 1926, 1927). The animal tracks in the Coconino Sandstone were probably made on dry sediments that were then moistened and covered by windblown dry sand before the sediments and tracks again dried out, or on dunes dampened by dew (Brady, 1939; McKee, 1944).

Trackways and Scratch Imprints: The ichnotaxon *Paleohelcura tridactyla* (figure 18) is common in the Coconino Sandstone. It was erected by Gilmore (1926) based on a long continuous trackway with sets of three tracks arranged in lines oblique to the midline and with a continuous medial impression (holotype USNM 11145; figure 18A). The ichnotaxon *Triavestigia niningeri* Gilmore, 1927 (holotype USNM 11510) is considered a junior subjective synonym of *Paleohelcura tridactyla* because it represents an incomplete specimen of *P. tridactyla* with only one row and a medial impression shifted laterally (Braddy, 1995). The ichnotaxon *Mesichnium benjamini* Gilmore, 1926 (holotype USNM 11155) was assigned to *Paleohelcura* (*P. benjamini*) and differentiated from *P. tridactyla* because of the peculiar discontinuous preservation of the medial impression (Kozur and others, 1994). The ichnospecies *P. dunbari* Brady, 1961 was erected based on the triangular arrangement of the three tracks preserved (holotype MNA-N 3694; figure 18B), distinguished from the linear arrangement of the *P. tridactyla* holotype. However, transitions between these two patterns are observed along the same trackway (Sadler, 1993), so this difference represents a minor extramorphological variant, and *P. dunbari* has to be considered a junior subjective synonym of *P. tridactyla* (e.g., Minter and Braddy, 2009). According to Minter and Braddy (2009), the ichnogenus *Paleohelcura* is similar in morphology and pattern to the ichnogenus *Stiaria* Smith, 1909. However, the ichnospecies *S. intermedia* can be distinguished by the maximum number of tracks (three) and the smaller maximum external width (18 mm or 0.71 in) (e.g., Minter and Braddy, 2009); the ichnospecies *S. quadripedia* can be distinguished by the linear arrangement of the four tracks (Walker, 1985), not observed in specimens of *Paleohelcura* showing four tracks per set (e.g., MNA-N 3669; figure 18C). Therefore, although the incomplete specimens can be very similar, we suggest continuing to distinguish these two ichnogenera. Due to the two sets of four tracks, the most likely producers were arachnids (Brady, 1947; Sadler, 1993). Experiments with present-day scorpions produced trackways with this specific pattern (e.g., Brady, 1947; Sadler, 1993).

The ichnotaxon *Octopodichnus didactylus* (figure 19) is common in the Coconino Sandstone. It was introduced by Gilmore (1927) based on a trackway with two parallel rows of alternating sets of four, anteriorly bifurcated tracks. The proximal track is in a medial position, and the three distal tracks are arranged on a line oblique to the midline, distally closer (holotype USNM 11501; figure 19A). This ichnotaxon was later amended by Sadler (1993). Based on a specimen from Seligman (holotype MNA-N 3654; figure 19B), Brady (1947) erected a sec-

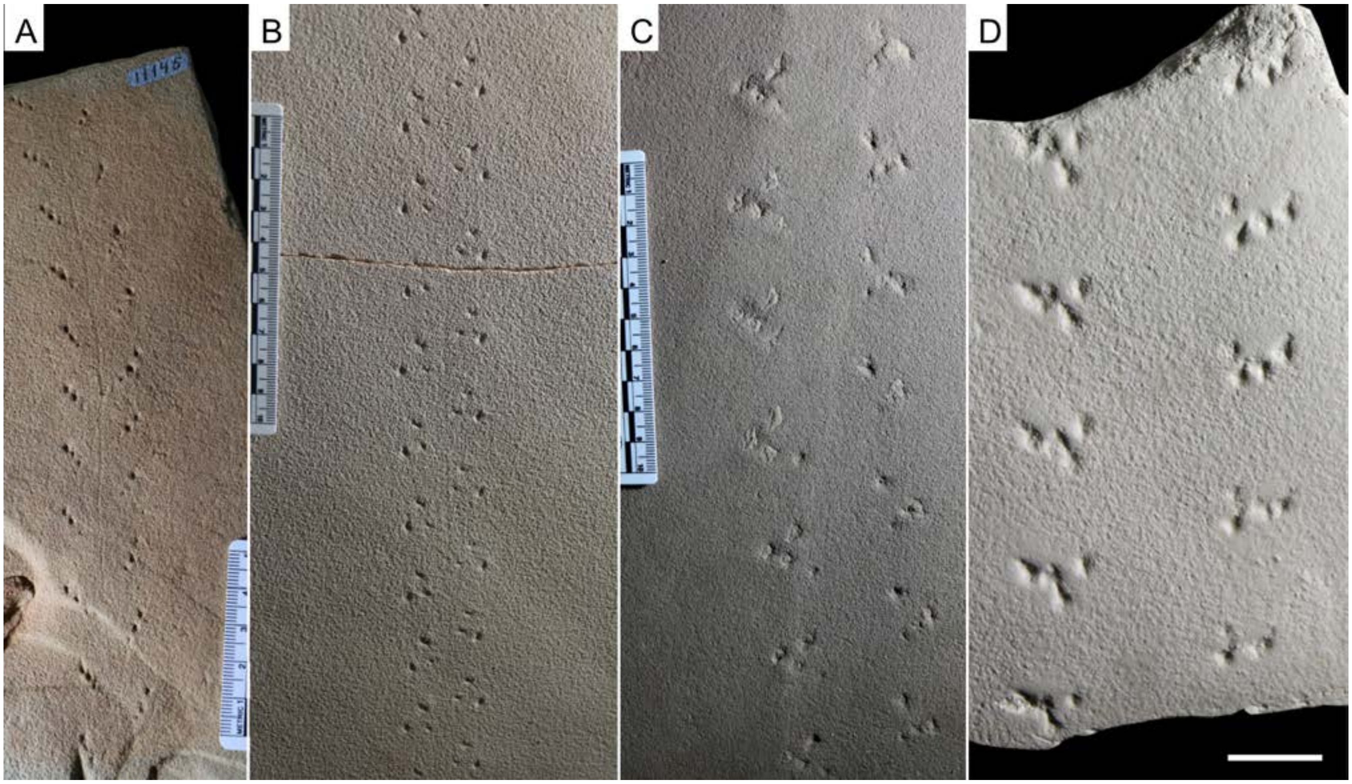

Figure 18. *Arthropod trackways from the Coconino Sandstone, attributed to* Paleohelcura tridactyla *(LORENZO MARCHETTI).* ***A.*** *Holotype of* P. tridactyla*, concave epirelief (USNM 11145).* ***B.*** *Holotype of* P. dunbari*, concave epirelief (MNA-N 3694).* ***C.*** *Trackways showing sets of four tracks, convex hyporelief (MNA-N 3669).* ***D.*** *Artificial cast of the holotype of* Octopodichnus raymondi*, concave epirelief (MNA-N 9391). Scale bar is 2 cm (0.4 in).*

ond ichnospecies, *O. minor*, characterized by smaller size and an opposite track arrangement in the series: the anterior track was medial and the three posterior tracks were oblique and progressively farther from the midline. However, the tracks can be oriented and bifurcated not only anteriorly, but also laterally and almost posteriorly due to the substrate inclination at the time of impression (similarly to the tetrapod tracks on foreset dune surfaces; Marchetti and others, 2019b). Therefore, the strong lateral bifurcation of the *O. minor* holotype probably caused an incorrect interpretation of the direction of progression, so that the pattern appeared to be the opposite of *O. didactylus*. As a consequence, *O. minor* may be a junior subjective synonym of *O. didactylus*.

A further ichnospecies was introduced by Sadler (1993) based on a specimen from Seligman (holotype RAM-JF 5905) first described by Alf (1968) as *O. raymondi*. However, the track arrangement and morphology of this trackway correspond to the diagnostic features of *Paleohelcura* from Gilmore (1926); therefore, this specimen is not considered to belong to *Octopodichnus*, but it is herein preliminarily assigned to *Paleohelcura tridactyla* (figure 19D). Due to the two sets of four tracks, the most likely producers were arachnids (Brady, 1947; Sadler, 1993). Although experiments with present-day animals have not thus far produced trackways with this specific pattern (e.g., Brady, 1947; Sadler, 1993), the lack of a telson (“tail”) impression and the slightly irregular pattern may indicate a spider as the producer.

Kramer and others (1995) erected the ichnospecies *Permichnium coconinensis* based on a specimen from Seligman, in the Mogollon Rim area (holotype SMM-P 92.3.1). This specimen shows a trackway composed of two parallel rows of sets of two tracks perpendicular to each other. These are diagnostic features typical of *Lithographus* isp. (figure 19C). The possible producers are insects such as blattoids (e.g., Kramer and others, 1995; Minter and Braddy, 2009). It is noteworthy that this trackway ends and changes its pattern in correspondence with a tetrapod trackway proceeding transverse to it with a quite high pace. This was interpreted as predation behavior of the tetrapod trackmaker on the insect trackmaker (Kramer and others, 1995), but Hunt and Lucas (1998) questioned that interpretation. The fast pace of the tetrapod trackway is actually due to downslope locomotion with a lateral component (Marchetti and others, 2019b), therefore the different appearance of the *Lithographus* trackway termination could be simply due to the deformation provided by the tetrapod passage, although predation cannot be excluded.

Based on a specimen from Seligman, in the Mogol-

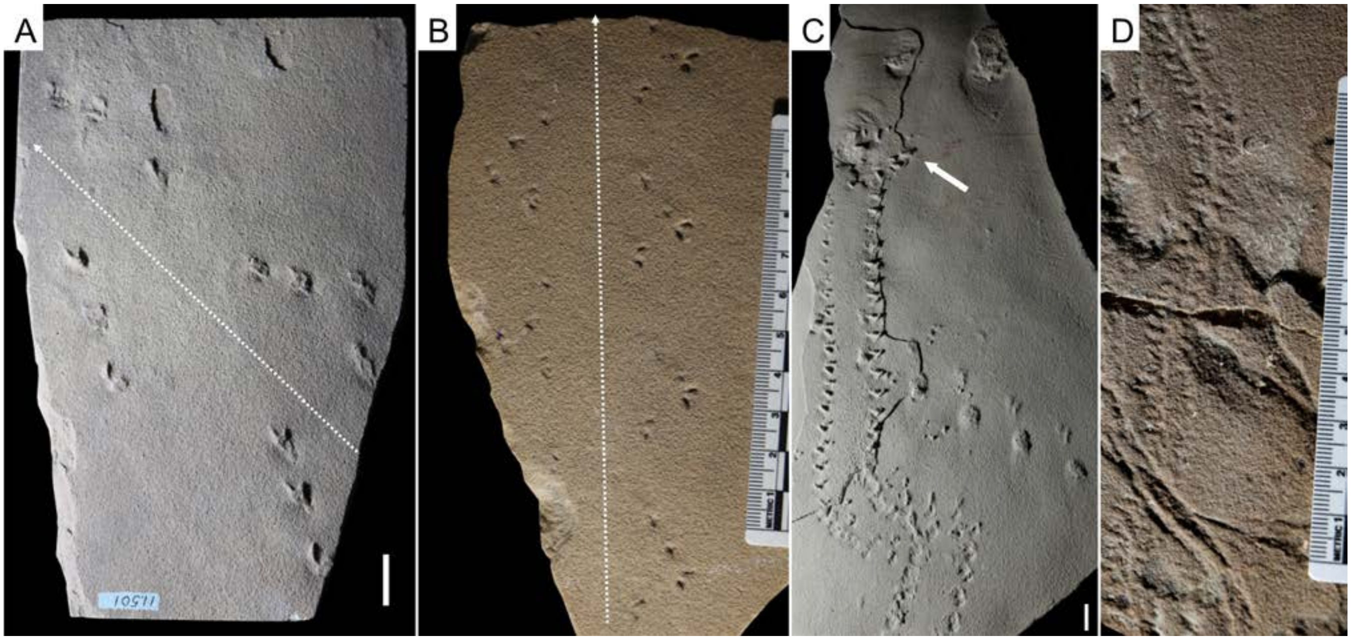

Figure 19.** Arthropod trackways from the Coconino Sandstone (LORENZO MARCHETTI). **A.** Holotype of* Octopodichnus didactylus*, convex hyporelief (USNM 11501). **B.** Holotype of* O. minor*, convex hyporelief (MNA-N 3654). **C. Lithographus *isp., holotype cast of* Permichnium coconinensis*. Trackway with change in direction and termination against a tetrapod trackway (arrow), convex hyporelief (MNA-N 9408). **D.*** Diplichnites *isp., holotype of* Isopodichnus filiciformis*, convex hyporelief. White scale bars in A and C are 2 cm (0.8 in).*

lon Rim area, Brady (1947) erected the ichnospecies *Isopodichnus filiciformis* (holotype MNA-N 3653). However, *Isopodichnus* is characterized by extremely closely spaced tracks, probably due to a feeding behavior on the substrate, while the described material shows less closely spaced tracks arranged in two parallel rows, probably due to locomotion behavior. The latter morphology is typical of the ichnogenus *Diplichnites*. Therefore, this material is probably assignable to *Diplichnites* (figure 19D). In addition, this form can be found in association with *Diplopodichnus*. Isopod crustaceans and millipedes are the most probable producers of *Diplichnites* (Brady, 1947; Davis and others, 2007; Minter and others, 2007).

Bilobate Trails and Paired Grooves: The ichnotaxon *Diplopodichnus biformis* (figure 20) is common in the Coconino Sandstone. It was introduced by Brady (1947) based on material from the Coconino Sandstone near Seligman in the Mogollon Rim area (holotype MNA-N 3657; figure 20A). It is characterized by two parallel grooves that may be separated by a continuous ridge. The trace course is continuous and slightly sinuous, and is about 4 to 10 mm (0.2 to 0.39 in) wide. Gilmore (1927) introduced a morphologically similar ichnotaxon, *Unisulcus sinuosus* (holotype USNM 11498; figure 20B). This is probably a poorly preserved *Diplopodichnus biformis*, because most of the trace is a single furrow, but occasionally two furrows and a ridge are recognizable. In some specimens and for small areas, it is possible to observe small, closely spaced tracks perpendicular to the medial ridge arranged in two parallel lines (GRCA 2882; figure 20C). This suggests a possible transition with *Diplichnites* or similar morphotypes (figure 20D). In three specimens, a possible transition to *Taenidium* cf. *T. serpentinum* has been observed (GRCA 2882, GRCA-NN 1 and MNA-N 3656). These compound traces suggest a single trackmaker capable of producing different morphologies and structures because of differing behavior. Brady (1947) considered this ichnotaxon as locomotion trails of myriapods, changing the morphology according to the trackway direction compared to the slope (the ridge seems to occur mostly in trackways with a downslope direction).

Complex, Actively Filled Horizontal Structures: Brady (1947) named *Scolecocoprus* (figure 21), thinking it was a string of coprolites, and two ichnospecies have been named: *Scolecocoprus cameronensis* (holotype MNA-N 3707; MNA P3.129; Locality 168; figure 21A) and *Scolecocoprus arizonensis* (holotype MNA-N 3655; figure 21B). DeCourten (1978) later re-interpreted *Scolecocoprus* as a burrow with the behavior of a suspension-feeding organism responding to rapid sedimentation in a shallow-marine environment, thus creating “vertical and lateral displacements” in the burrow, as did D’Alessandro and Bromley (1987), who considered it a junior synonym of *Taenidium*. Indeed, the similarity of *Scolecocoprus cameronensis* (the type ichnospecies) to *Taenidium serpentinum* is strong and supports the conclusion of D’Alessandro and Bromley (1987). Nevertheless, *S. arizonensis* was still retained

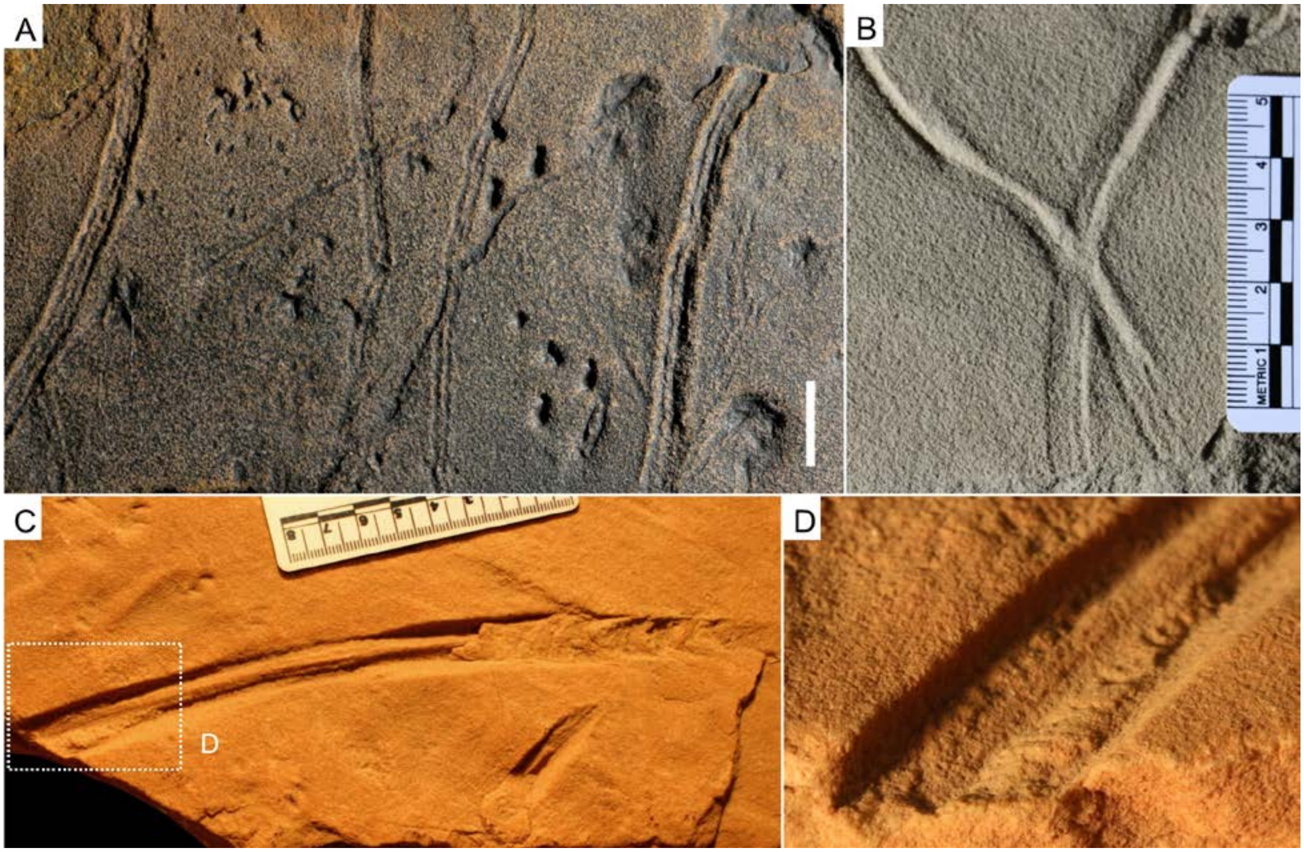

Figure 20. *Bilobate trails and paired grooves from the Coconino Sandstone.* ***A.*** *Holotype of* Diplopodichnus biformis *associated with* Paleohelcura *and* Octopodichnus*, concave epirelief (MNA-N 3657) (LORENZO MARCHETTI). Scale bar is 2 cm (0.8 in).* ***B.*** *Holotype of* Unisulcus sinuosus*, concave epirelief (USNM 11498) (LORENZO MARCHETTI).* ***C.*** *Possible transition of* Taenidium *with* Diplopodichnus*, convex hyporelief (GRCA 2882) (HEITOR FRANCISCHINI).* ***D.*** *Detail of the latter specimen, showing closely spaced imprints (HEITOR FRANCISCHINI).*

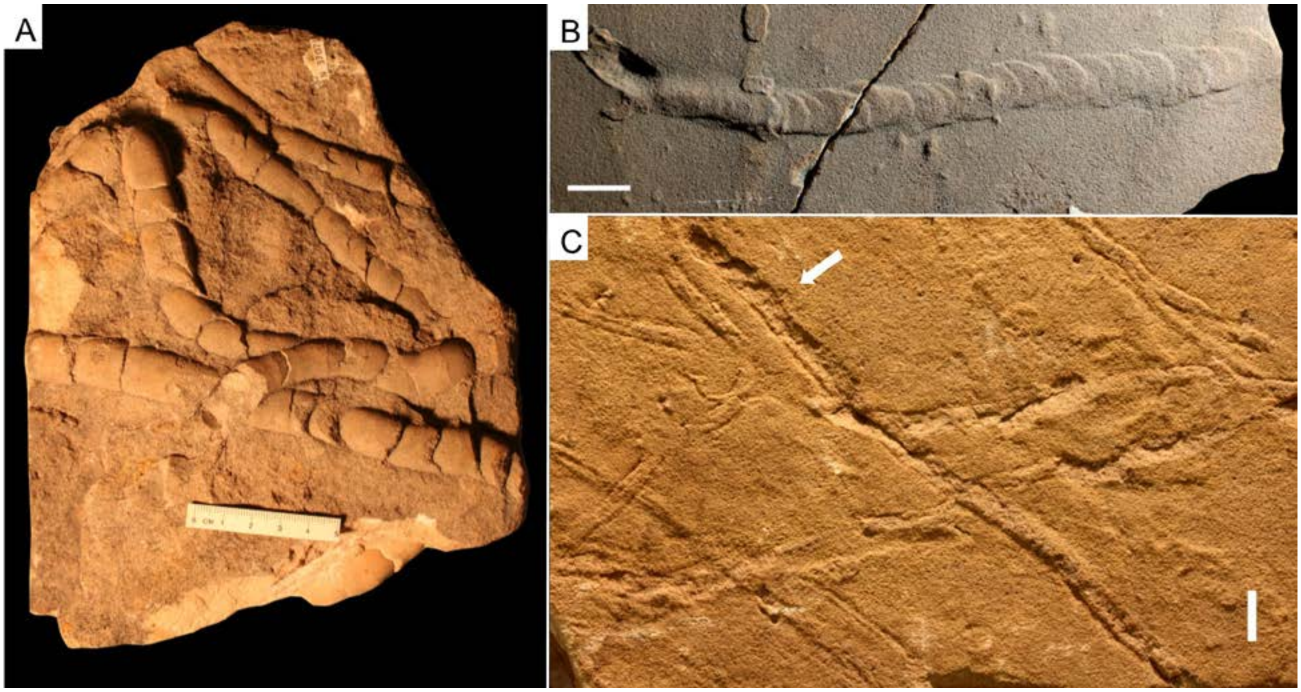

Figure 21. *Complex, actively filled horizontal structures from the Coconino Sandstone (LORENZO MARCHETTI).* ***A.*** Taenidium serpentinum*, holotype of* Scolecocoprus cameronensis*, convex hyporelief (MNA-N 3707).* ***B.*** Taenidium *cf. serpentinum, holotype of* Scolecocoprus *arizonensis, convex hyporelief (MNA-N 3655).* ***C.*** Scolecocoprus *isp. (arrow) in transition and associated with* Diplopodichnus*, convex hyporelief (GRCA-NN 1). White scale bar is 2 cm (0.8 in).*

and it was not reallocated to any *Taenidium* ichnospecies (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994). On the other hand, Buatois and others (2017) considered *Scolecocoprus* a distinct valid ichnogenus. More detailed research is necessary to provide reliable information regarding this peculiar meniscate ichnogenus, but here we follow D'Alessandro and Bromley (1987) and consider *Scolecocoprus* as a junior synonym of *Taenidium*. The two ichnospecies *S. cameronensis* and *S. arizonensis* are herein assigned to *Taenidium serpentinum* and *Taenidium* cf. *T. serpentinum,* respectively.

Discussion

A large number of invertebrate trace specimens, including long, complete, and beautifully preserved trackways and burrows, have been collected from the Coconino Sandstone. These specimens provide an ideal basis for ichnotaxonomy, because much extramorphological variation is registered. The effects of the trackmaker's locomotion on inclined planes and compound traces can also be recognized. Seven ichnogenera and 13 ichnospecies were erected based on Coconino Sandstone material. However, the number of valid ichnotaxa from this formation is relatively low, including six ichnogenera (*Diplichnites*, *Diplopodichnus*, *Lithographus*, *Octopodichnus*, *Palaeohelcura* and *Taenidium*). The number of architectural designs is even lower: only two types were recognized. This low-diversity ichnoassociation is less diverse and structurally complex than the typical continental ichnoassociations that are usually included in the *Scoyenia* ichnofacies. Because of this, a different ichnofacies based mostly on the Coconino ichnoassociation was proposed by Hunt and Lucas (2007), the *Octopodichnus* ichnofacies. Simultaneously, Ekdale and others (2007) proposed the *Entradichnus* ichnofacies based mostly on traces from the Jurassic Navajo Sandstone. Buatois and Mángano (2011) unified the two ichnofacies into the *Octopodichnus–Entradichnus* ichnofacies, which includes low-diversity dune ichnoassociations with arthropod tracks and non-diverse burrows. Note that Lucas and others (2010) and Lucas (2018) stated that the "*Entradichnus* ichnofacies" is supposedly characterized by an ichnofauna of *Arenicolites*, *Palaeophycus*, *Planolites*, *Skolithos*, and *Taenidium*, and ichnoassemblages that contain one or more of these ichnogenera are characteristic of interdunal facies in Permian–Jurassic eolianites of the American Southwest, although they can occur in what must have been moist dunal settings. Therefore, the "*Entradaichnus* ichnofacies" is not a distinctive ichnofacies, but simply a synonym of the *Scoyenia* ichnofacies in interdunal settings (Hunt and Lucas, 2016). The distinctive invertebrate ichnofacies of eolian paleoenvironments is the *Octopodichnus* ichnofacies, recognized by low diversity ichnofaunas of arthropod walking traces (*Octopodichnus*, *Paleohelcura*, etc.) and usually associated with footprints of the *Chelichnus* tetrapod ichnofacies.

GRCA Museum Collections

In July 1928, Edwin McKee collected a trackway specimen from the Coconino Sandstone within Hermit Basin that contained "worm trails" (GRCA 2883). In August 1928, a "fucoid" specimen from the base of the Coconino Sandstone with "worm trails showing body markings" was collected by McKee, but the specimen was never found (GRCA 2911; deaccessioned). In August 1931, McKee collected a trackway associated with "worm trails" from Marble Canyon (GRCA 2882). This specimen shows a transition between *Taenidium* and *Diplopodichnus*; the latter also includes transverse, closely spaced imprints. In November 1932, McKee collected invertebrate track specimens from the upper Coconino Sandstone outside of Grand Canyon in Apache County, Arizona at Kinlachee Creek (GRCA 2906 and GRCA 20652). An invertebrate track specimen, *Paleohelcura tridactyla*, was collected from the Coconino Sandstone in the Hermit Basin by an unknown collector at an unknown date; however, Gilmore (1926) named this specimen and may have been the collector (GRCA 2917). In October 1938, McKee collected a "worm trail" from the Coconino Sandstone (GRCA 2928). An invertebrate trackway identified as *Octopodichnus minor* (now regarded as *O. didactylus)*, was collected from the Coconino Sandstone outside of Grand Canyon National Park near Seligman, Arizona, and is associated with Brady's collections in his 1947 report (GRCA 2930). An un-numbered specimen (GRCA-NN 1) includes several *Diplopodichnus* trails and a *Taenidium* burrow, possibly in transition with *Diplopodichnus*.

Besides specimens collected and housed in museum collections, it is worth noting the presence of invertebrate trackways and trails in situ in the Coconino Sandstone. Among them, *Paleohelcura tridactyla* and *Diplopodichnus* isp. can be recognized at the same level in which tetrapod tracks occur. *Diplopodichnus* isp. also occurs in association with *Ichniotherium sphaerodactylum* tracks in the fallen boulder of Coconino Sandstone described by Francischini and others (2019). All these materials remain in situ.

Toroweap Formation

As noted earlier, we are not aware of any records of trace fossils from the Toroweap Formation, though we suspect that a careful search of that unit could reveal some.

Kaibab Formation

The youngest unit of Grand Canyon's Paleozoic stratigraphic section is the Kaibab Formation (Limestone). It forms the surface upon which visitors view the canyon from the rim at the top of the Kaibab and Coconino plateaus. The Kaibab Formation thickens westward from 90 to 120 m (295 to 394 ft) and sits upon the Woods

Ranch Member of the Toroweap Formation in Grand Canyon (Hopkins and Thompson, 2003). It consists of two conformable packages in GRCA: the Fossil Mountain Member and the overlying Harrisburg Member. The Fossil Mountain Member forms a cliff with hoodoo-like weathering that ranges from 75 to 105 m (246 to 344 ft) in thickness. It contains cherty, fossiliferous limestone in the west and becomes siliciclastic towards the east. The Harrisburg Member forms receding ledges and cliffs towards the rim of the Grand Canyon and ranges from 25 to 90 m (82 to 295 ft) thick westward. It is composed of dolomite, gypsum, chert, sandstone, and limestone. Fossiliferous carbonate beds appear increasingly toward the west (Hopkins and Thompson, 2003).

The Kaibab Formation was deposited in a subtidal, shallow-marine environment with mixed carbonates and siliciclastics affected by sea level changes. Invertebrate organisms such as brachiopods, bryozoans, mollusks, crinoids, sponges, and trilobites lived in this sea during the late Cisuralian. A diverse assemblage of selachian teeth is also known. Only a few invertebrate traces have been reported and collected.

Trace Fossils

"Fucoids, worm borings, and trilobite trails" have been reported from the Kaibab Formation (McKee, 1938; Spamer, 1992). McKee (1938) noted "small tubular structures which may represent worm borings" within inorganic chert layers. He also mentioned structures of algae within certain chert layers that may have made a soft substrate for worms to bore into.

GRCA Museum Collections

Specimens from the Kaibab Formation containing burrows and trails were collected by Louis Schellbach on October 7, 1941 east of Desert View (GRCA 2349, GRCA 2575, GRCA 2596, GRCA 10233, GRCA 11371, GRCA 14171, GRCA 14172). Invertebrate trackways were found in the Kaibab Formation and collected by Strickler in 1933 (GRCA 10043, GRCA 10045, and GRCA 14404). Cliff Carrol collected a marine "snail trail" from the Kaibab Formation near Yavapai Point (GRCA 10234 and GRCA 17336). In June 1936, a "worm trail" was collected by Everette Helman, found between Yaki and Grandview Points from near the top of the Kaibab Formation (GRCA 10044; figure 22). Edwin McKee collected sandstone slabs covered with "fucoids" from the Kaibab Formation at Desert View (GRCA 6026 and GRCA 6598).

CONCLUSIONS

The invertebrate trace fossil record of Grand Canyon is composed of trackways and traces produced in almost all geological units of this area, with the only exception being the Permian Toroweap Formation due to a lack of research. Although the records of some units (i.e., the Frenchman Mountain Dolostone, the Redwall Limestone, the Watahomigi Formation, the Manakacha Formation and the Esplanade Sandstone) only include indeterminate or informally described traces, up to 33 valid ichnogenera occur among the Tapeats Sandstone, the Bright Angel Shale, the Muav Limestone, the Temple Butte Formation, the Surprise Canyon Formation, the Wescogame Formation, the Hermit Formation, the Coconino Sandstone, and the Kaibab Formation. The Cambrian Bright Angel Shale presents the most prolific record. With 21 ichnogenera classified in 15 architectural designs, it represents a very diverse and disparate association of trace fossils from the *Cruziana* Ichnofacies. Other marine and continental units also present reasonably high ichnodiversity and ichnodisparity: the Tapeats Sandstone, the Hermit Formation, and the Coconino Sandstone. Trace fossils often serve as the only indicators of past life in a particular geologic time interval and paleoenvironment. In the Grand Canyon region, trace fossils add significant clues to the diversity of past life and behaviors, especially within those formations that are mostly devoid of body fossils. Invertebrate trace fossils continue to be discovered throughout GRCA's Paleozoic units and can be regarded as significant, non-renewable resources for the park. Research on such specimens also continues with the help of park managers as they play an important role in protecting such invaluable resources.

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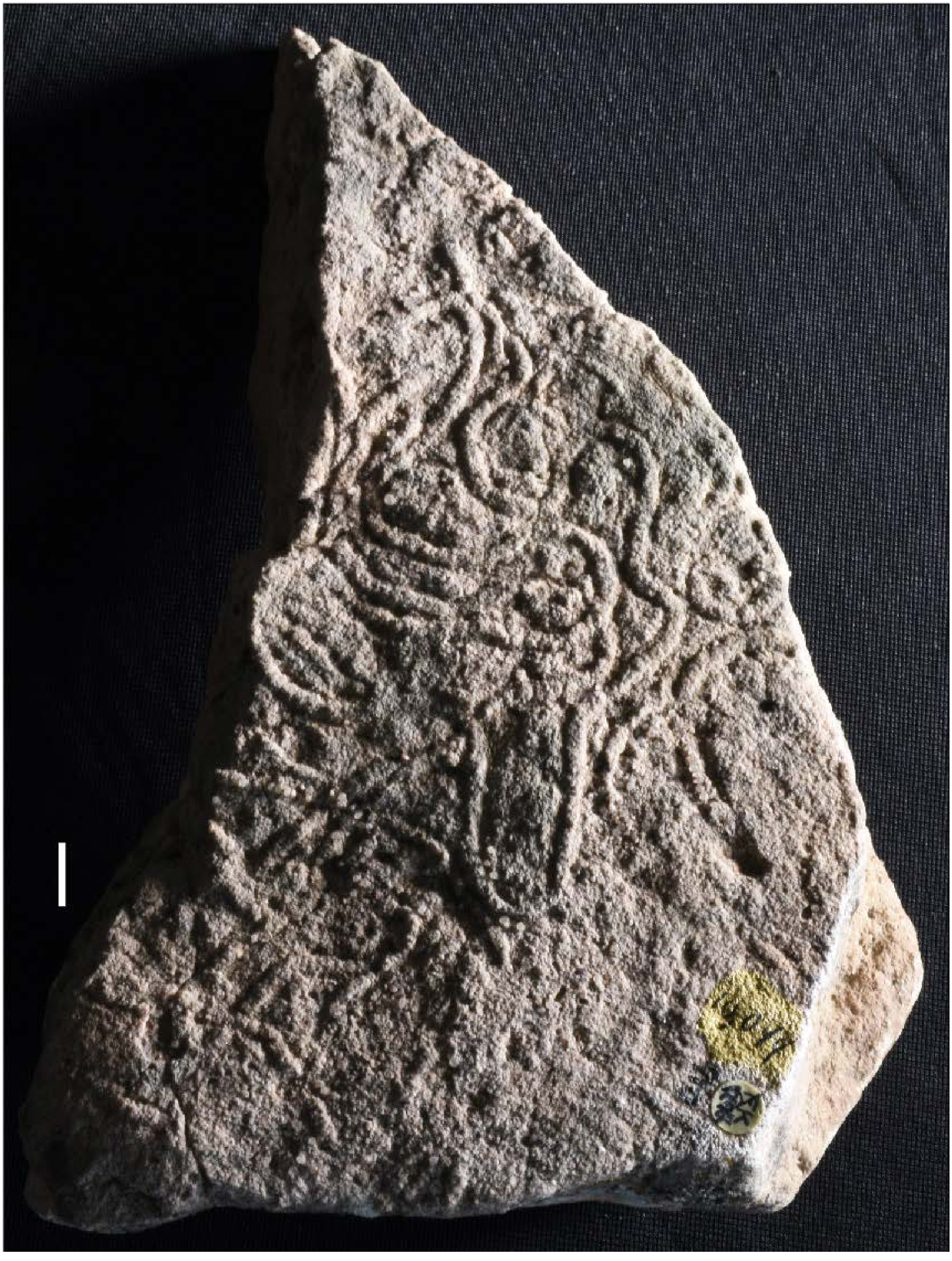

Figure 22. *Worm trail specimen in the upper Kaibab Formation collected by Everette Helman in June 1936 (GRCA 10044). Scale bar is 1 cm (0.4 in) (NPS/KLARA WIDRIG).*

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PALEOZOIC VERTEBRATE ICHNOLOGY OF GRAND CANYON NATIONAL PARK

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ABSTRACT

For more than a century, the Paleozoic units of Grand Canyon National Park (GRCA) and nearby areas have yielded a remarkable collection of terrestrial vertebrate trace fossils, which are studied by the discipline named vertebrate ichnology. These traces were registered in the sediment, rapidly covered but not eroded by other sediment and later fossilized in the process of rock diagenesis. Unlike bones, they were not transported before their burial and preservation. Moreover, they can occur in units completely devoid of vertebrate skeletal remains. This is the case for some of the Paleozoic units of GRCA, in which the only source of information on the extinct fauna is provided by vertebrate tracks. The GRCA vertebrate ichnofauna is composed of relatively small tracks of quadrupedal tetrapods, including eureptiles, parareptiles, synapsids and non-amniotes that lived in desert, fluvial and marginal marine paleoenvironments. In GRCA, the late Carboniferous Manakacha and Wescogame formations include the oldest evidence of vertebrate tracks from eolian paleoenvironments. The ichnoassociation of the early Permian Coconino and Hermit formations is dominated by reptile tracks, in agreement with a low-latitude and facies-crossing reptile radiation that started during the Artinskian. The Coconino Sandstone is crucial for the understanding of vertebrate locomotion and paleoecology in desert paleoenvironments and includes the first known evidence of non-amniotes in these settings. For all of these reasons, the vertebrate trace fossil collection from GRCA is of noteworthy scientific importance and needs to be protected and further investigated.

INTRODUCTION

Vertebrate tracks are the only fossils of terrestrial vertebrates known from Paleozoic strata of Grand Canyon National Park (GRCA), therefore they are of great importance for the reconstruction of the extinct faunas of this area. For more than 100 years, the upper Paleozoic strata of the Grand Canyon yielded a noteworthy vertebrate track collection, in terms of abundance, completeness and quality of preservation. These are key requirements for a classification of tracks through ichnotaxonomy. This article proposes a complete ichnotaxonomic revision of the track collections from GRCA and is also based on a large amount of new material. These Paleozoic tracks were produced by different tetrapod groups, such as eureptiles, parareptiles, synapsids and anamniotes, and their size ranges from 0.5 to 20 cm (0.2 to 7.9 in) footprint length. As the result of the irreversibility of the evolutionary process, they provide useful information about faunal composition, faunal events, paleobiogeographic distribution and biostratigraphy. Of note, these vertebrate trace fossils are always in situ (i.e., not transported before burial) and preserved in lithofacies representing different continental paleoenvironments (marginal marine, alluvial plain and desert), therefore they can provide useful paleoecological information. Also, the occurrence of surfaces with long trackways provides fundamental insights into the locomotion of the trackmakers on inclined planes, such as the paleosurfaces of dune foresets.

VERTEBRATE ICHNOLOGY

Vertebrate ichnology is the discipline that principally studies the traces left on the substrate by vertebrates during their lives. These traces can be produced by different behaviors, such as: walking, running, hopping, resting, swimming, etc. The main subject of vertebrate

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ichnology is thus the study of tracks left on the sediment during locomotion. The tracks can be preserved as concave epirelief (natural mold) and convex hyporelief (natural cast) and can be preserved on multiple layers, forming undertracks, underprints and overtracks. On the actual trampled surface, these ichnofossils sometimes preserve expulsion rims (i.e., a marginal rim of displaced sediment produced by the footfall; Allen, 1997). Their occurrence generally indicates subaerial exposure, the presence of a substrate adequate to record the footprint impression, and a non-erosive and rapid burial of the actual track surface. These conditions are common in intermittently wet environments such as lake margins, alluvial plains, tidal flats, fluvial channels, and/or in desert environments characterized by rapid sedimentary cover (dune foreset surfaces). In intermittently wet environments, they are often associated with mud cracks, rain drops, wave ripples, tool marks, and microbial structures, among other sedimentary structures, and with invertebrate tracks and burrows. In desert environments, they are often associated with sand avalanches, wind ripple crests and invertebrate tracks and burrows.

With regard to the Paleozoic, only footprints of quadrupedal vertebrates are known, which include front (manus) and hind (pes) foot imprints. Tail, body, and digit drag marks may be present, but are not relevant for footprint classification. These footprints are usually arranged in sequences of pes-manus couples, arranged in two parallel rows that form a trackway. From the footprint and trackway parameters, it is possible to infer the size, weight, gait and speed of the trackmakers (e.g., Leonardi, 1987). Generally, the Paleozoic terrestrial vertebrates were not fast moving, and most of them adopted a sprawling gait as seen in modern lizards and salamanders. Their size was also not very large, especially before the Guadalupian (maximum footprint length of about 20 cm or 7.9 in).

Tetrapod footprints are classified by their morphology, and especially by the anatomy-consistent morphology (e.g., Marchetti and others, 2019a). This is the morphology that reflects the actual lower side of the trackmaker foot, and thus it is strongly connected with the trackmaker's anatomical structure, which is subject to irreversible evolution. Tracks showing these anatomy-consistent features are regarded as well-preserved. This kind of preservation, named morphological preservation, can be evaluated through a numerical scale (Marchetti and others, 2019a). In the study of tetrapod tracks, it is necessary to exclude from the analysis those tracks that are not anatomy-consistent due to loss of information or deformation during (e.g., footprint wall collapse) and after track registration in the sediment (e.g., superimposition of other footprints and sedimentary structures and partial erosion). The footprints preserved on the dune foreset surfaces show a peculiar process that causes loss of information of the anatomy: the oblique direction of the gravity force due to the dune surface inclination (usually more than 30°). This causes the sliding of the trackmaker digits during locomotion, and asymmetrical trackway patterns and footprint preservation in trackways oblique to the slope (figure 1A–D). Also, the trackmaker speed was influenced, with very close pes-manus couples and secondary overstep in trackways directed upslope (slow gait) and well-spaced pes-manus couples and primary overstep (fast gait) in trackways directed downslope (figure 1A–D). Overstep is the preservation of the pes in front of the manus, different than what is usually seen (manus in front of the pes). This has been observed in trackways of the same track type (*Varanopus*), therefore these different gaits and morphologies are likely not due to different trackmakers (Marchetti and others, 2019b, 2019c).

After the selection of well-preserved material, the footprints and trackways are described and measured. The digit impressions are counted with Roman numbers, starting from the inner (medial) side of the trackway. Tracks with longer external digit impressions (commonly digit IV) are named ectaxonic. Common track measurements (figure 1E) include the foot length and width, and the sole/palm impression length and width; all compared to the digit III axis. Other measurements are the digit length and the interdigital angles. The distance between two consecutive tracks of the same kind (manus or pes) on the same trackway side is named stride length. The distance between two consecutive tracks of the same kind (manus or pes) on opposite trackway sides is termed (oblique) pace length, and the angle between two consecutive (oblique) pace lengths is termed pace angulation. The line equidistant from the manus-pes couples is the trackway midline. Other measurements are the trackway width, the manus-pes distance and the manus and pes divarication (i.e., its rotation), all compared to the trackway midline.

Ichnotaxonomy is the discipline that classifies tetrapod tracks and other traces. It is considered a parataxonomy because it is disentangled from the taxonomic classification of the producers. In fact, it is quite difficult to relate a track type directly to a trackmaker genus or species, with some exceptions (e.g., Voigt and others, 2007; Marchetti and others, 2017a). Tetrapod track ichnotaxa usually correspond to higher taxonomic levels than species and genera, because similar species and genera may produce very similar footprints (e.g., all of the "pelycosaur" synapsid genera, except for varanopids, may be attributed to a single ichnogenus, *Dimetropus*). The tetrapod tracks are classified with a binomial nomenclature (ichnogeneric epithet + ichnospecific epithet), following the procedures of the International Code of Zoological Nomenclature (1999). Ichnofamilies can be used as well, but are generally less extensively studied. The relevant criteria (ichnotaxobases) are the anatomy-consistent foot morphology and the trackway pattern, including

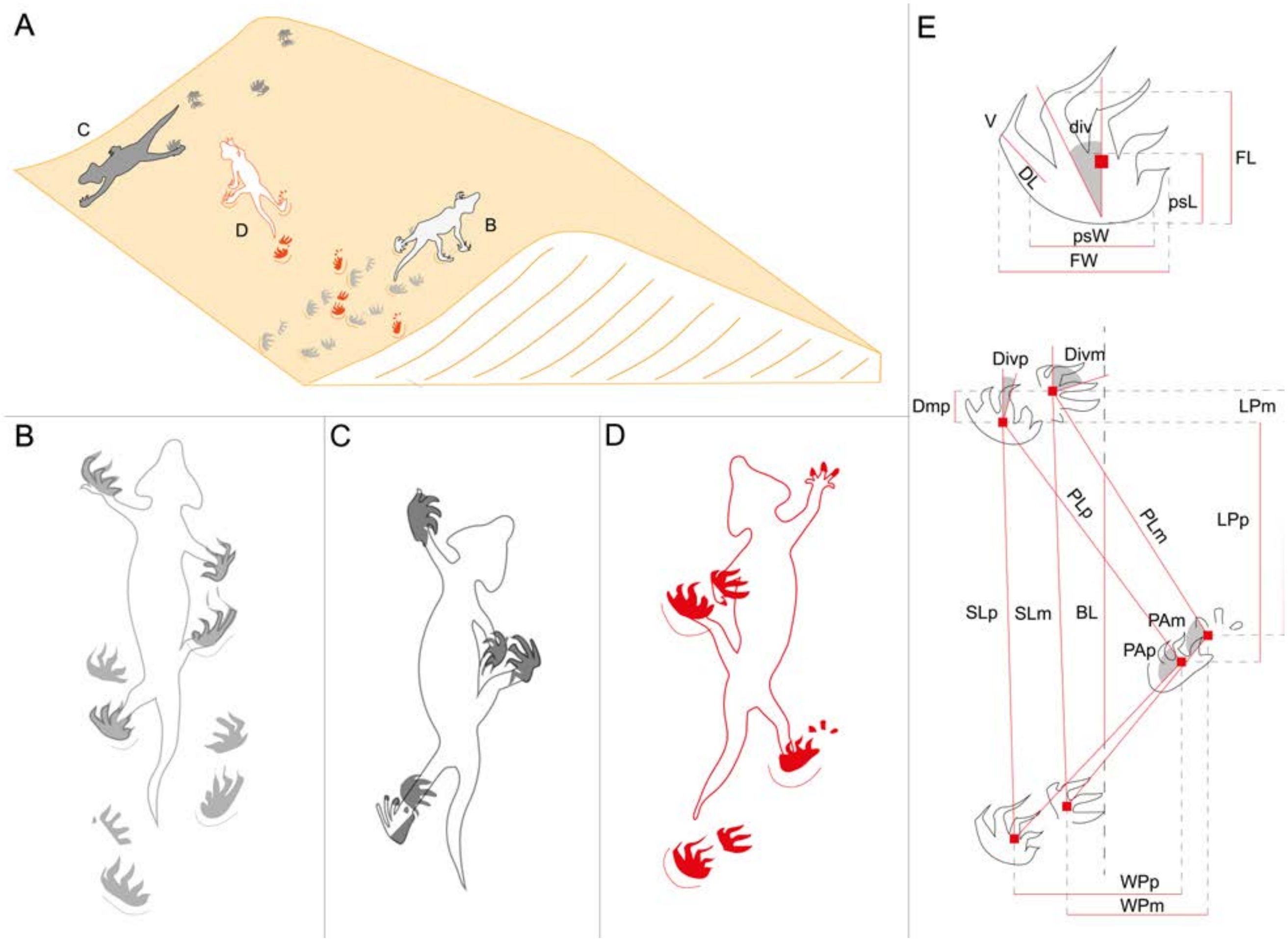

Figure 1. *Track formation and track measurements (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *Track formation on a dune foreset surface with different kind of progression:* ***B.*** *directly upslope,* ***C.*** *directly downslope and* ***D.*** *transversely upslope.* ***E.*** *Track and trackway measurements. FL=footprint length, FW=footprint width, psL=palm/sole length, psW=palm/sole width, DL=digit length, div=digit divergence, V=digit V, SLp=stride length of the pes, SLm=stride length of the manus, PLp=(oblique) pace length of the pes, PAp=pace angulation of the pes, PAm=pace angulation of the manus, PLm=(oblique) pace length of the manus, LPp=length of pace of the pes, LPm=length of pace of the manus, WPp=width of pace of the pes, WPm=width of pace of the manus, Divp=divarication from midline of the pes, Divm=divarication from midline of the manus, Dmp=manus-pes distance, BL=gleno-acetabular length.*

measurements. The list of ichnotaxa from a formation and/or area is referred to as an ichnoassociation and helps to define the ichnodiversity. The ichnoassociations can be time-constrained, because ichnotaxa have limited stratigraphic distributions. Also, being geographically widespread, they are useful to define a tetrapod footprint biostratigraphy (e.g., Lucas, 2007; Fillmore and others, 2012; Voigt and Lucas, 2018). Other useful information that can be inferred from ichnoassociations is paleobiogeography and paleoecology. Recurrent tetrapod ichnoassociations in space and time, related to specific paleoenvironments, are named tetrapod ichnofacies (Hunt and Lucas, 2006, 2007), similar to invertebrate ichnofacies. Although this approach has been criticized and must certainly be improved, the paleoecological signature of tetrapod ichnoassociations is evident from several studies (e.g., Voigt and Lucas, 2017; Marchetti and others, 2017b).

HISTORY OF TRACK COLLECTION IN GRAND CANYON AND MOGOLLON RIM AREAS

The first discoveries of Paleozoic tetrapod footprints in the Grand Canyon were by Charles Schuchert in 1915 along the Hermit Trail (Coconino Sandstone and Hermit Shale), with material being stored at Yale University and described by Lull (1918). The most important excavations were led by John C. Merriam in 1924 and Charles W. Gilmore in 1926 and 1927 along the Hermit and Yaki trails. This material comes from the Coconino Sandstone, the Hermit Shale and the Wescogame Formation and is stored at the Smithsonian Institution's National Museum of Natural History (Spamer, 1984). It was first described by Gilmore (1927, 1928) and later revised by several studies (e.g., Baird, 1952, Haubold, 1971; Haubold and others, 1995a, 1995b; Voigt, 2005; Francischini and others, 2019; Marchetti and others, 2019b).

Further finds from the Coconino Sandstone of the Grand Canyon were described by Brand (1979), Hunt and Santucci (2001), Francischini and others (2019) and Marchetti and others (2019b), including either specimens in the field and specimens stored in the GRCA, Smithsonian and Yale collections. Some historic photos of in situ specimens are also stored in the GRCA collection (figure 2). A slab bearing footprints, possibly coming from the Pennsylvanian Manakacha Formation (Supai Group), was reported by Rowland (2017). Other important finds come from the Coconino Sandstone of the Mogollon Rim area, and are stored at the University of California at Berkeley, the Museum of Northern Arizona and the Raymond Alf Museum of Paleontology (e.g., Brand and Tang, 1991; Lockley, 1992; Loope, 1992; Haubold and others, 1995b; Francischini and others, 2019; Marchetti and others, 2019b). A significant part of the GRCA park museum collection, including undescribed tracks from the Wescogame Formation, Hermit Shale and Coconino Sandstone, is described for the first time in this article. This also includes the first description of a specimen in the field found by Thomas Martens along the Bright Angel Trail, and of tetrapod tracks from the Hermit Shale of the Mogollon Rim area.

STRATIGRAPHIC DISTRIBUTION OF TRACKS

The tetrapod tracks from the Grand Canyon come from four different stratigraphic units, dated between the late Carboniferous (Pennsylvanian) and the early Permian (Cisuralian). These units are, from the oldest to the youngest: the Manakacha Formation, the Wescogame Formation, the Hermit Shale and the Coconino Sandstone (figures 3 and 4). The tetrapod ichnoassociations will be described and discussed separately for these four units, in stratigraphic order. Moreover, some specimens from the same units found in the Mogollon Rim area will be also described for completeness. All the ichnotaxa occurring in each unit will be described separately based on the material from that unit, and no diagnoses are provided. Lists with all the relevant specimens of the collections are also provided.

Institutional Abbreviations—GRCA, Grand Canyon National Park Museum, Grand Canyon, Arizona; **MNA,** Museum of Northern Arizona, Flagstaff, Arizona; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California; **UCMP**, University of California, Berkeley; **USNM**, Smithsonian, National Museum of Natural History, Washington, D.C.; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut.

Manakacha Formation

Geology

In the Grand Canyon, the Supai Group consists of five formations (in ascending order of oldest to youngest): Watahomigi, Manakacha, Wescogame, Pakoon

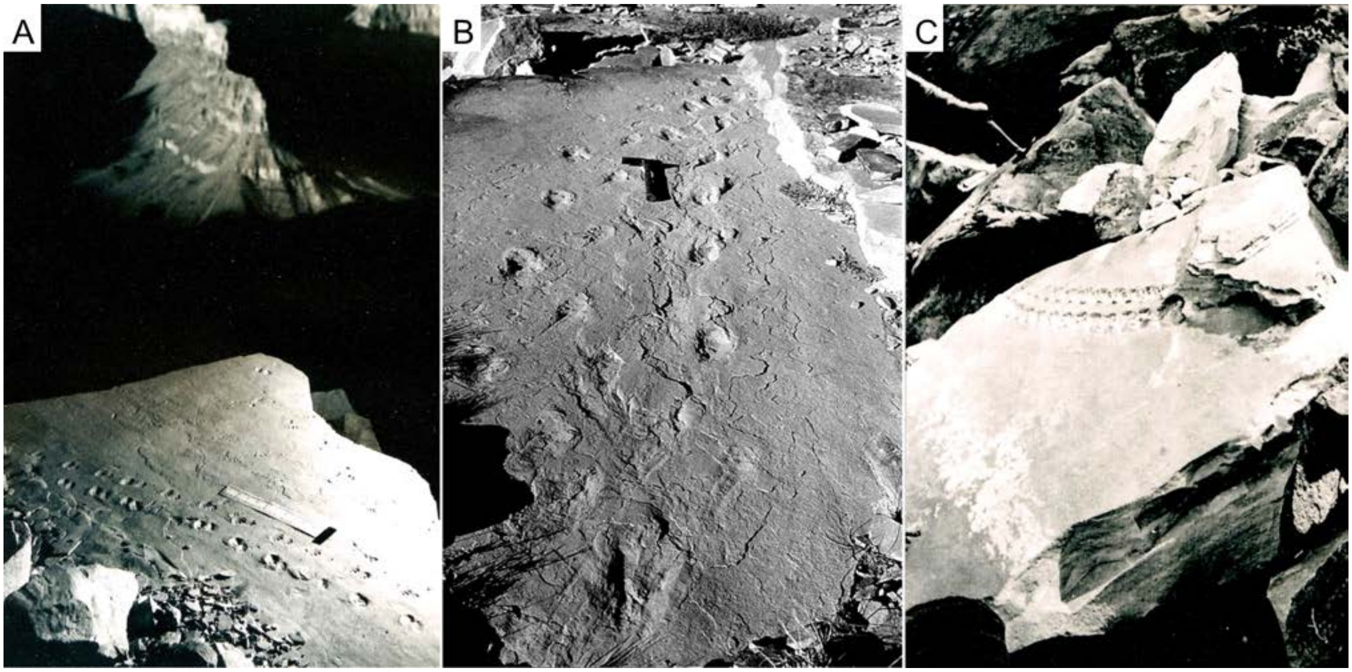

Figure 2. Historic photos of in situ vertebrate tracks from the Coconino Sandstone at GRCA. The original photos are in the collection of the GRCA museum. ***A.*** *Surface above a cliff showing a clear trackway.* ***B.*** *Surface with poorly preserved tracks, probably arranged in trackways. Hammer for scale.* ***C.*** *Surface on a fallen slab showing a clear trackway with a turn.*

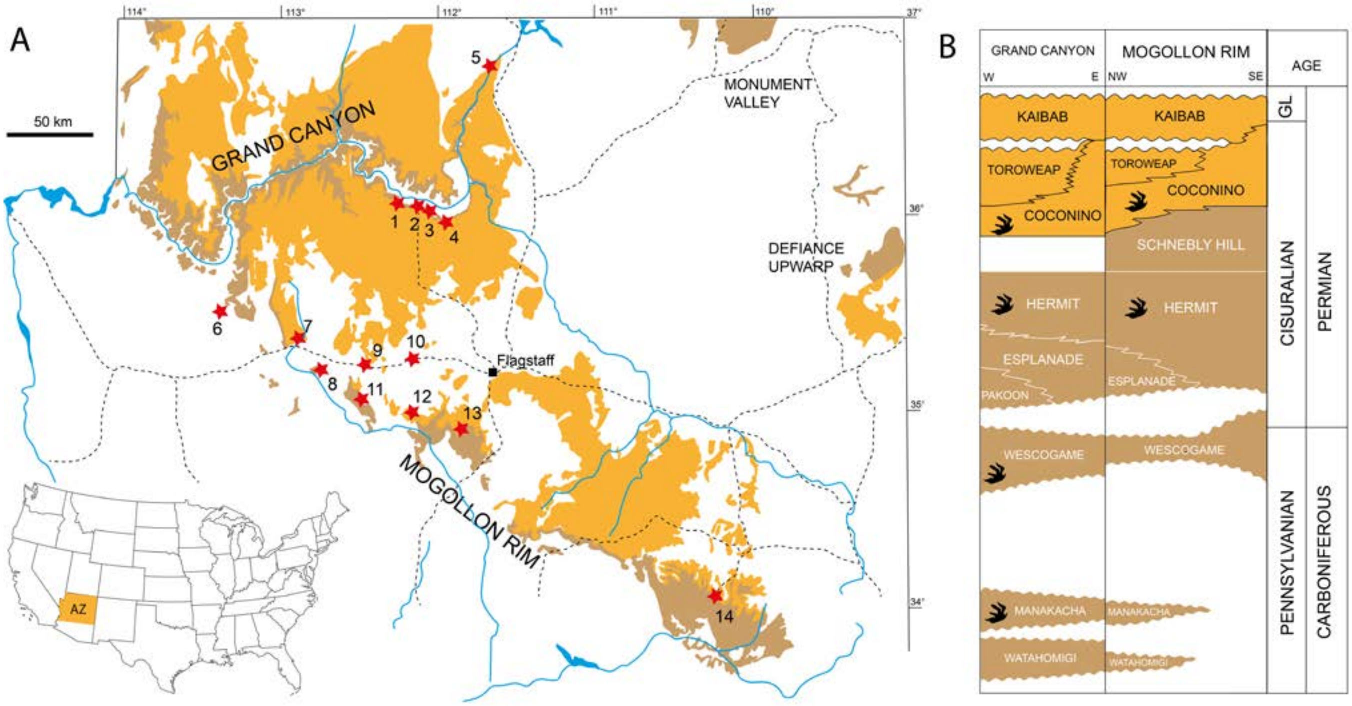

Figure 3. *Localities and geological setting (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *Simplified geologic map and localities. 1) Grand Canyon, Hermit Trail/Dripping Springs Trail. 2) Grand Canyon, Bright Angel Trail. 3) Grand Canyon, Yaki Trail/South Kaibab Trail. 4) Grand Canyon, Tanner Trail. 5) Soap Creek. 6) Peach Springs. 7) Seligman. 8) Picacho Butte. 9) Ash Fork. 10) Williams. 11) Limestone Canyon Mouth. 12) Perkinsville. 13) Sycamore Pass/Sedona. 14) Carrizo Creek.* ***B.*** *Chronostratigraphic scheme of the fossiliferous area (modified from Blakey and Knepp, 1989). GL=Guadalupian. Units including tetrapod footprints are indicated by a track outline.*

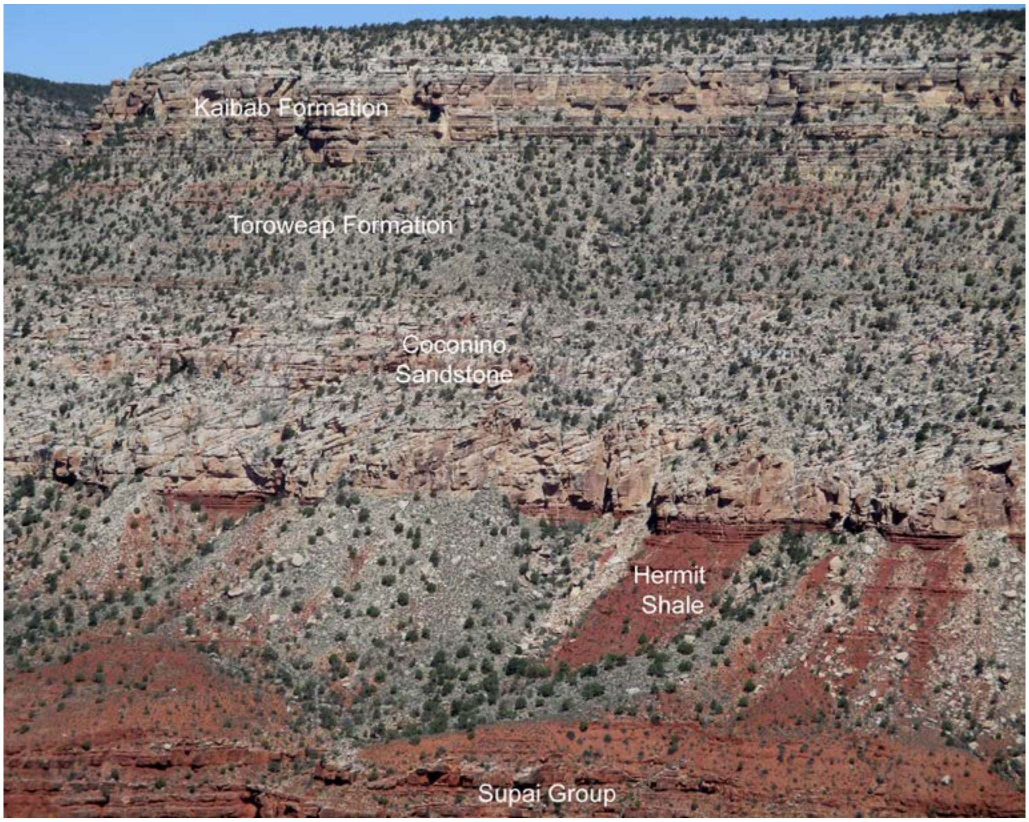

Figure 4. *Permian stratigraphy of the Grand Canyon. Panoramic view looking west at the wall of Hermit Canyon showing the track-bearing Permian units (LORENZO MARCHETTI & SPENCER LUCAS).*

and Esplanade Sandstone formations (e. g. McKee, 1982; Blakey and Knepp, 1989; Blakey, 1990). The unconformity-bounded Manakacha Formation is about 90 m (300 ft) thick and mostly interbedded quartzose sandstone and red-bed mudstone. Deposition was on a coastal plain, and Blakey (1990) has identified some of the cross-bedded sandstones of the Manakacha Formation as eolianites. Invertebrate fossils from the Supai Group (principally fusulinids and brachiopods) indicate it is mostly of Pennsylvanian age, and, based on these fossils, McKee (1982) assigned an Atokan (late Bashkirian–early Moscovian) age to the Manakacha Formation.

Previous Studies

The only mention of tetrapod footprints from the Manakacha Formation is the recent work of Rowland (2017) and Rowland and Caputo (2018), who reported a fallen slab along the Bright Angel Trail with a tetrapod trackway showing an unusual gait and assigned by them to *Chelichnus* isp. If the stratigraphic interpretation is correct, this is the oldest known tetrapod trackway from GRCA.

Trace Fossils

Undetermined Tracks: The slab reported by Rowland (2017) and Rowland and Caputo (2018) displays a trackway of a quadruped with closely spaced footprints showing all the characteristics of tetrapod locomotion on inclined planes (Marchetti and others, 2019b) (figure 5). The digit impressions are all elongated in the same direction, meaning a trackmaker sliding due to gravity. The tracks on the right side of the trackway are more deeply impressed than those on the left side. According to the slope direction inferred from the digit slide and expulsion rim directions, the trackmaker proceeded upslope with a transverse component, and this caused the evident asymmetry among the two trackway sides. The closely spaced tracks show a complete secondary overstep, which is typical of very slow locomotion. Due to the absence of clear and complete footprints showing all the digit impressions, this material is not classifiable (grade 1.0 of the preservation scale, Marchetti and others, 2019a) but it certainly represents a small-sized tetrapod walking upslope on an inclined plane such as a dune foreset surface.

Wescogame Formation

Geology

The Wescogame Formation, the middle unit of the Supai Group, is about 30 to 60 m (100 to 200 ft) thick in the Grand Canyon and is lithologically similar to the unconformably underlying Manakacha Formation—mostly quartzose sandstone and red-bed mudstone (McKee, 1982; Blakey and Knepp, 1989; Blakey, 1990). McKee (1982) assigned a Late Pennsylvanian (Virgilian/early Ghzelian) age to the Wescogame Formation (see above). Like the Manakacha Formation, it was deposited on a coastal plain by both fluvial and eolian processes (Blakey, 1990).

Previous Studies

A few tetrapod track occurrences have been reported from the middle part of the Supai Group (now known

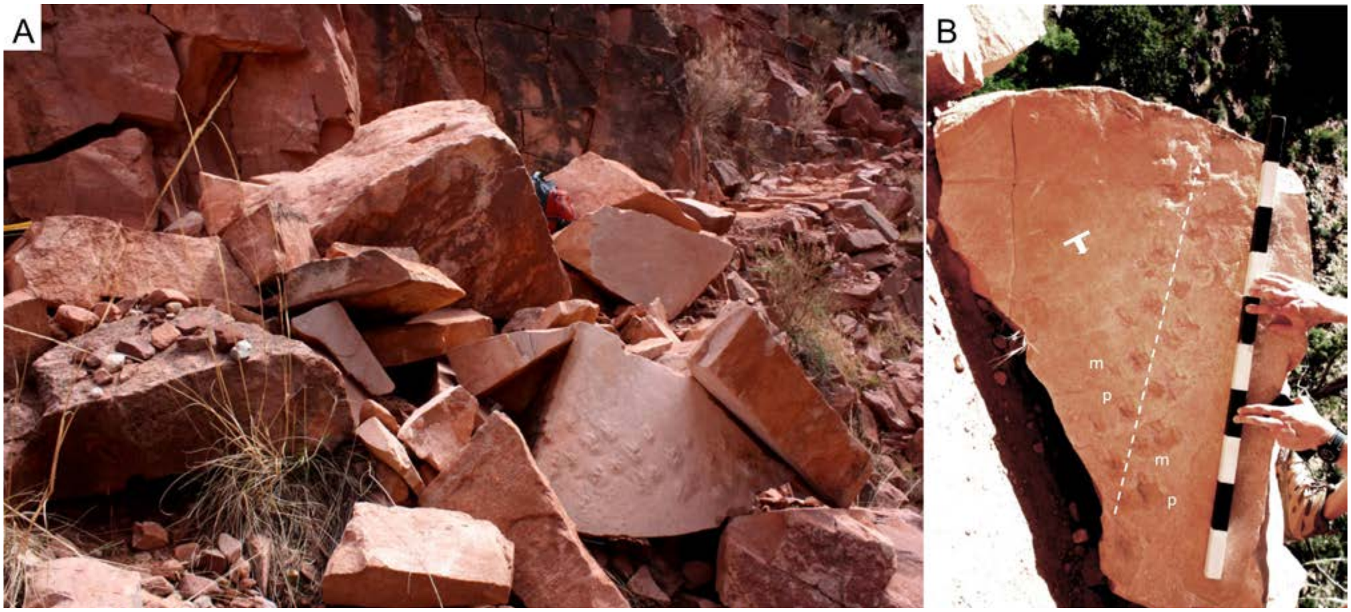

*Figure 5. Tetrapod footprints from the Manakacha Formation (STEPHEN ROWLAND). **A.** Fallen blocks including a natural cast of the trackway slab (convex hyporelief). **B.** The trackway slab preserved as a natural mold (concave epirelief). Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint. The scale bar in B is 1 m (3 ft) long.*

as the Wescogame Formation). Gilmore (1927) erected three new ichnotaxa basing on poorly preserved material (grade 1.0–1.5 of the preservation scale, Marchetti and others, 2019a): *Anomalopus sturdevanti*, *Stenichnus yakiensis* and *Tridentichnus supaiensis*. Haubold (1971) considered *Tridentichnus* a junior subjective synonym of *Anomalopus* and proposed the new combination *Anomalopus supaiensis*. Gilmore (1928) erected a further ichnotaxon for similarly preserved material: *Ammobatrachus turbatans*. Haubold (1971) considered *Ammobatrachus turbatans* as a junior subjective synonym of *Anomalopus supaiensis*. Marchetti and others (2019b) considered *Ammobatrachus turbatans* to be a *nomen dubium*.

Trace Fossils

Anamniote Tracks: The specimen USNM 11534 (figure 6A–B) shows a trackway composed of four consecutive pes-manus couples that can be tentatively assigned to cf. *Amphisauropus* isp. The pes and manus imprints are pentadactyl and ectaxonic with rounded digit terminations. The manus track is about half the size of the pes track (pes length 60 mm or 2.4 in). The sole imprint is elliptical in shape. The pace angulation is quite low (65–80°). The digit drag marks and trackway asymmetry indicate locomotion on an inclined paleosurface (dune foreset). Due to poor preservation caused by digit sliding, the assignment is only tentative. This specimen is the holotype of *Ammobatrachus turbatans* Gilmore, 1928, which is considered a *nomen dubium* (Marchetti and others, 2019b). *Amphisauropus* is generally regarded as the track of seymouriamorph anamniotes (Voigt, 2005; Marchetti and others, 2017a).

The specimen USNM 11691 (figure 6C–D) shows a trackway with 10 closely spaced consecutive pes-manus couples that can be tentatively assigned to cf. *Limnopus* isp. The tracks are plantigrade and ectaxonic. Only three digit impressions of the pentadactyl pes are clearly recognizable, and the manus imprint is apparently tetradactyl and smaller than the pes imprint (pes length is about 40 to 50 mm or 1.6 to 2.0 in). Digit impressions have rounded terminations. The pace angulation is very low (50–70°), and the trackway shows secondary overstep. These tracks are evidently deformed by digit sliding caused by upslope progression on an inclined paleosurface (dune foreset), so the assignment is tentative. This

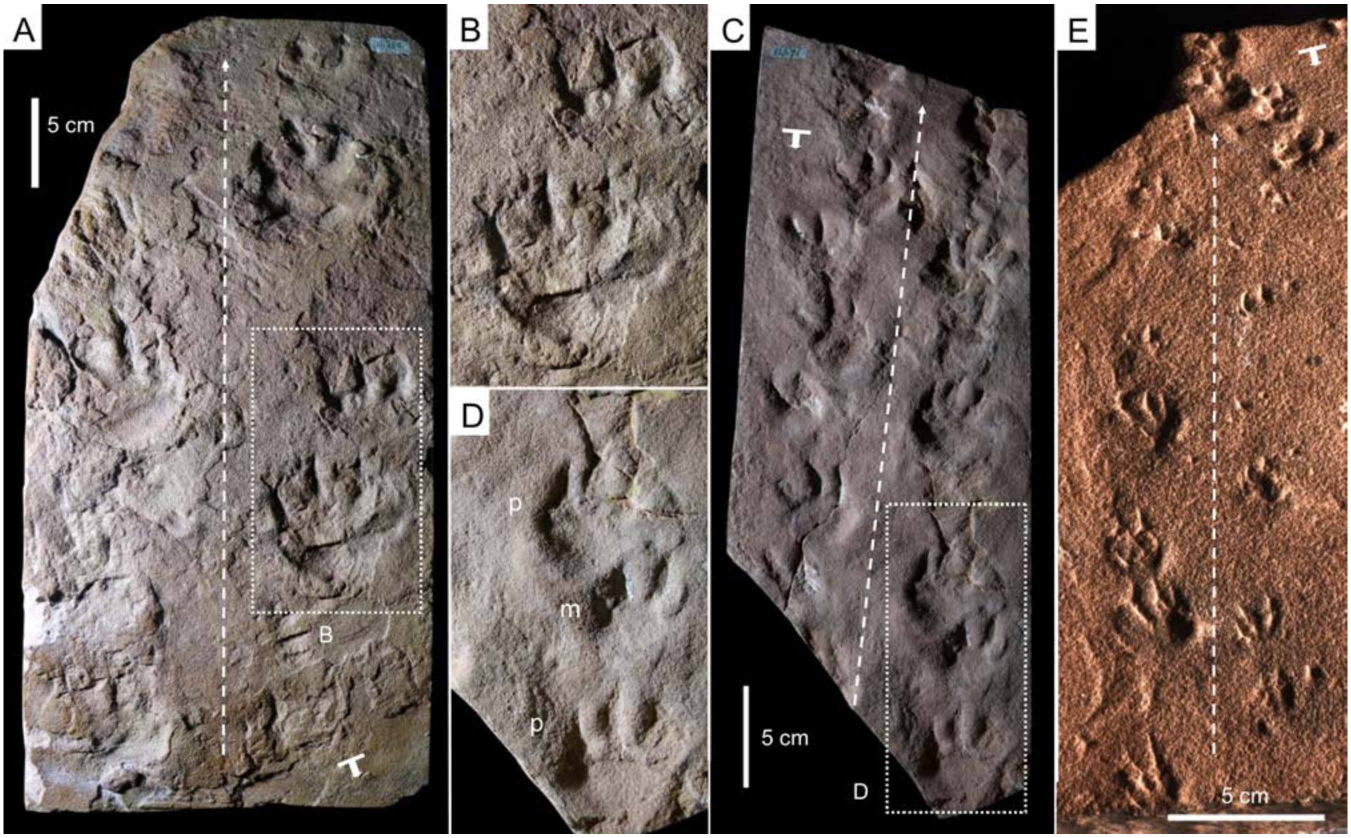

Figure 6. *Anamniote footprints from the Wescogame Formation (LORENZO MARCHETTI & SPENCER LUCAS).* ***A****. USNM 11534. cf.* Amphisauropus *isp., trackway, concave epirelief. Holotype of* Ammobatrachus turbatans *Gilmore, 1928,* nomen dubium*.* ***B.*** *Enlargement of A, right pes–manus couple.* ***C.*** *USNM 11691. cf.* Limnopus *isp., trackway, concave epirelief. Holotype of* Tridentichnus supaiensis *Gilmore, 1927,* nomen dubium*.* ***D.*** *Enlargement of C, three tracks.* ***E.*** *GRCA 4646.* Batrachichnus *isp., trackway, concave epirelief. Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint.*

is the holotype of the ichnotaxon *Tridentichnus supaiensis* Gilmore, 1927, which is herein considered a *nomen dubium* because of the poor preservation. *Limnopus* is generally regarded as the track of relatively large temnospondyls, such as eryopids (e.g., Voigt, 2005).

The specimen GRCA 4646 (figure 6E) displays a small-sized trackway (pes length 20 mm or 0.79 in) with tracks representing 10 consecutive pes-manus couples, that can be assigned to *Batrachichnus* isp. The tracks are ectaxonic, the pes imprint is pentadactyl and plantigrade, and the manus imprint is tetradactyl and semi-plantigrade; the manus imprint is about half the size of the pes imprint. The pace angulation is quite low (65–85°). The digit drag marks and trackway asymmetry indicate an inclined paleosurface (dune foreset). *Batrachichnus* is generally regarded as the track of small temnospondyl tetrapods (e.g., Voigt, 2005).

Reptile Tracks: The specimen GRCA 11288 (figure 7A) displays two consecutive pes-manus couples that can be assigned to *Varanopus* isp. These tracks are pentadactyl and ectaxonic, and the pes imprint is slightly larger than the manus imprint (pes length of about 40 mm or 1.6 in). Digit impressions are relatively long and thick and end in claw marks that can be bifurcated. The digit impression V of the pes is relatively long (about as long as the digit III impression) and straight. The footprints are semi-plantigrade, and the palm/sole imprint is relatively short. These tracks do not show typical features of locomotion on inclined paleosurfaces, therefore they were probably impressed in an interdune paleoenvironment.

The specimen USNM 11533 (figure 7B) shows a trackway with tracks belonging to 11 consecutive pes-manus couples assignable to cf. *Varanopus* isp. The tracks are ectaxonic, probably pentadactyl and show long and thin digit impressions. The pes imprint is larger than the manus imprint (pes length of about 40 mm or 1.6 in). The pace angulation is low (about 70°), and partial secondary overstep is observed. The digit drag marks and trackway asymmetry indicate locomotion on an inclined paleosurface (dune foreset). Due to poor preservation caused by digit sliding, the assignment is only tentative. This is the holotype of the ichnotaxon *Stenichnus yakiensis* Gilmore, 1927, which is herein considered a *nomen dubium* because of the poor preservation. *Varanopus* is generally regarded as a small captorhinomorph track (e.g., Voigt, 2005).

Undetermined Tracks: An additional relevant specimen is USNM 11577, the holotype of *Anomalopus sturdevanti* Gilmore, 1927, which is herein considered a

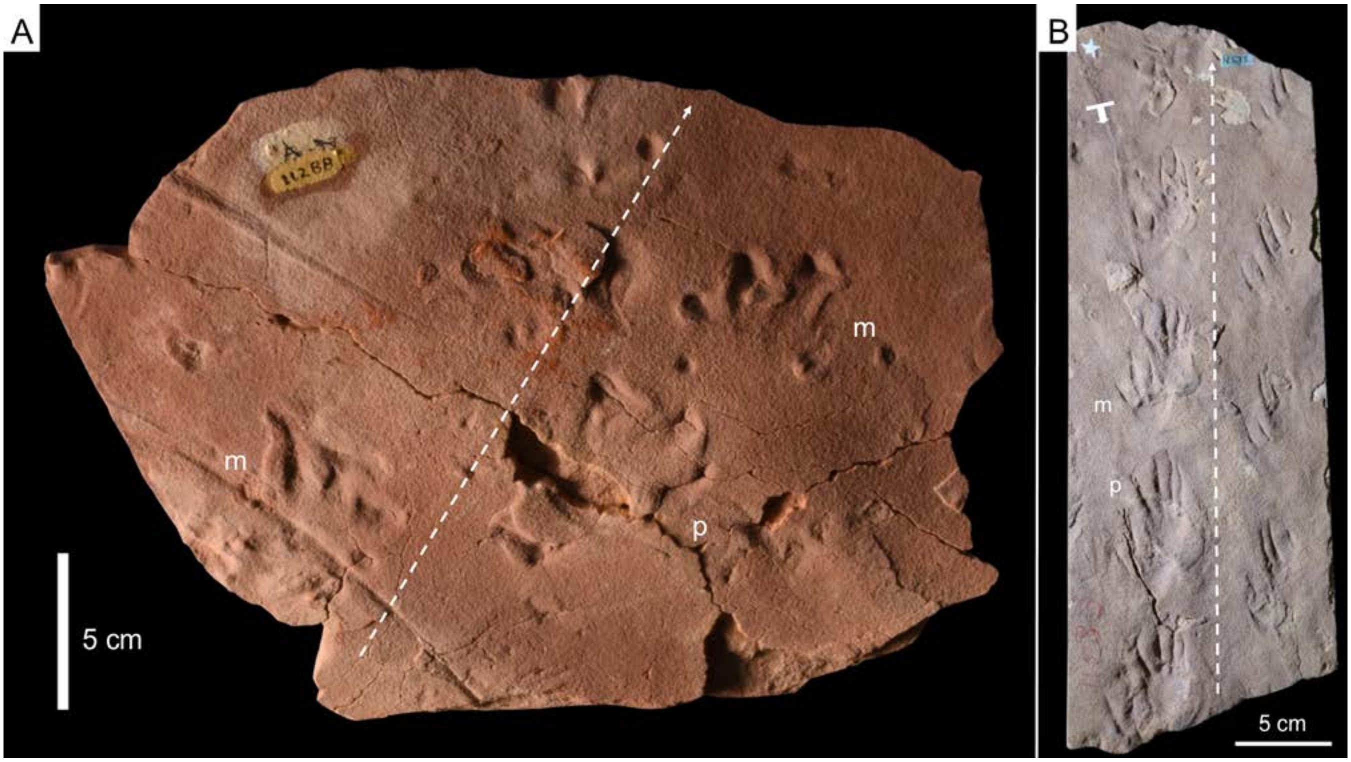

***Figure 7.** Reptile footprints from the Wescogame Formation (LORENZO MARCHETTI & SPENCER LUCAS). **A.** GRCA 11288.* Varanopus *isp., incomplete step cycle, concave epirelief. **B.** USNM 11533, cf.* Varanopus *isp., trackway, concave epirelief. Holotype of* Stenichnus yakiensis *Gilmore, 1927,* nomen dubium*. Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint.*

nomen dubium because of the poor preservation caused by digit sliding on an inclined plane (dune foreset).

Discussion

The revised tetrapod ichnoassociation from the Wescogame Formation is the oldest from GRCA (the Manakacha Formation has not so far yielded classifiable footprints), and also the oldest worldwide tetrapod ichnoassociation from eolian paleoenvironments. It includes (table 1): cf. *Amphisauropus* isp., *Batrachichnus* isp., cf. *Limnopus* isp., cf. *Varanopus* isp. from dune foreset paleoenvironments and *Varanopus* isp. from interdune paleoenvironments. All these ichnotaxa are described for the first time from this formation. The occurrence of *Amphisauropus* and *Varanopus* is consistent with the *Dromopus* footprint biochron, that began during the Late Pennsylvanian (Ghzelian) (e.g., Fillmore and others, 2012). This is in agreement with previous age interpretations of the Wescogame Formation.

It is noteworthy, as in the case of the Coconino and De Chelly sandstones (Marchetti and others, 2019b), that the tetrapod ichnoassociation is quite similar to flood-plain, lacustrine and coastal tetrapod ichnoassociations of the same age. This ichnoassociation includes quite diverse anamniote (seymouriamorphs and temnospondyls) tracks and fewer reptile tracks. This is an important datum that confirms the hypothesis of anamniote occurrence in eolian paleoenvironments (Francischini and others, 2019), in this case possibly including batrachomorphs as well. Moreover, the first occurrence of tracks in eolian paleoenvironments is significantly extended temporally (from the late early Permian to the late Carboniferous). Because few specimens are known and nevertheless encompass important data, further prospecting for footprints in the Wescogame Formation of GRCA is strongly recommended.

Hermit Shale

Geology

The Hermit Shale (Formation) is mostly slope-forming red beds of siltstone and very fine grained sandstone about 30 to 100 m (100 to 330 ft) thick in the Grand Canyon (Noble, 1922; Blakey, 1990) (figure 8). The fossil plants and footprints from the Hermit Shale have long been the basis for assigning it an early Permian (Leonardian; late Artinskian–Kungurian) age (e.g., White, 1929). Hermit Shale deposition was by fluvial processes on a seasonally arid coastal plain (Blakey, 1990).

Previous Studies

Abundant and well-preserved tetrapod tracks have been found in the Hermit Shale of GRCA. The first report is by Lull (1918), who erected the ichnotaxa *Exocampe*? *delicatula* and *Megapezia*? *coloradensis* based on specimens found by Charles Schuchert in 1915 along the Hermit Trail. These specimens come from the uppermost levels of what was then called the Supai Formation, now considered the Hermit Shale. This locality is stratigraphically placed in the basal part of the Hermit Shale (Gilmore, 1927), above an erosional surface on the underlying sandstones of the Esplanade Sandstone (figure 8). A new excavation at the same locality was led by Charles W. Gilmore in 1926, and the material was described in Gilmore (1927), who erected the ichnotaxa: *Batrachichnus obscurus, Collettosaurus pentadactylus, Dromillopus parvus, Hyloidichnus bifurcatus* and *Hylopus hermitanus*. He also proposed the new combination *Batrachichnus delicatulus* (Lull, 1918). After a further excavation in 1927, led by Charles W. Gilmore and David White along the Hermit and Yaki trails, Gilmore (1928) erected the ichnospecies *Hyloidichnus whitei* and described a large slab with several trackways of different forms (USNM 11707A, not relocated in Haubold and others, 1995a).

Although the preservation of these trace fossils is remarkable (commonly grade 2.0–3.0 of the preservation scale, Marchetti and others, 2019a), few additional finds and publications have appeared on the ichnology of the Hermit Shale. Haubold (1971) introduced the ichnogenus *Gilmoreichnus* with the new combination *Gilmoreichnus hermitanus* (Gilmore, 1927), adding to the type material some specimens from Germany. He

Table 1. *Museum collections, Wescogame Formation.*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
GRCA 4646	*Batrachichnus* isp.	N/A	N/A	N/A	concave epirelief	trackway	Thrasher, E.	1931	Grand Canyon, Yaki Trail
GRCA 11288	*Varanopus* isp.	N/A	N/A	N/A	concave epirelief	partial trackway	McKee, E. D.	1938	Grand Canyon, Tanner Trail
USNM 11533	cf. *Varanopus* isp.	holotype	*Stenichnus yakiensis* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Metzler, A.	1926	Grand Canyon, Yaki Trail
USNM 11534	cf. *Amphisauropus* isp.	holotype	*Ammobatrachus turbatans* Gilmore, 1928	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11577	Undetermined tracks	holotype	*Anomalopus sturdevanti* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Sturdevant, G. E.	1926	Grand Canyon, Yaki Trail
USNM 11691	cf. *Limnopus* isp.	holotype	*Tridentichnus supaiensis* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Sturdevant, G. E.	1927	Grand Canyon, Bright Angel Trail

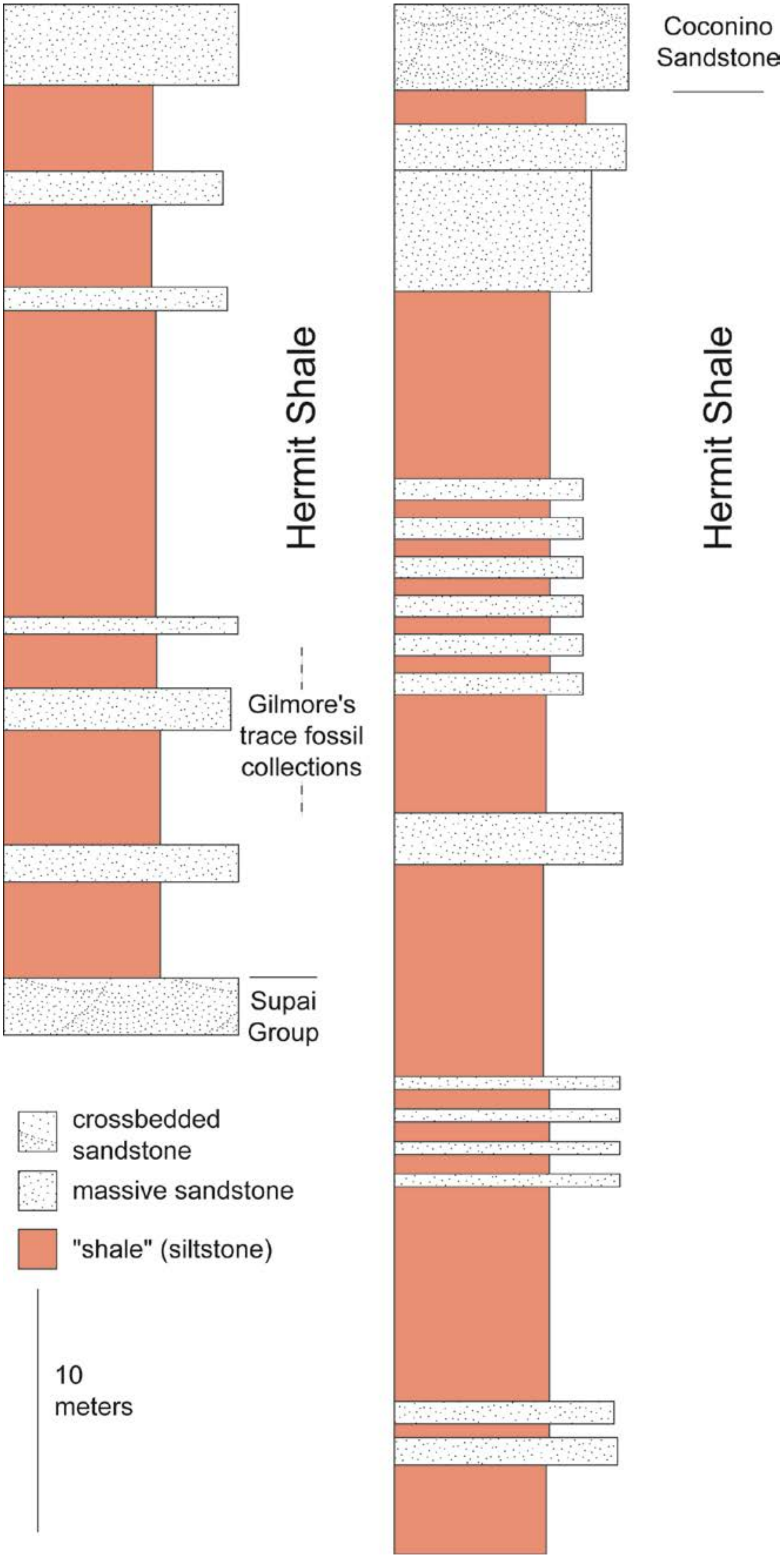

Figure 8. *Stratigraphic section of the Hermit Shale, measured by Noble (1922) near Bass Point in the Grand Canyon (LORENZO MARCHETTI & SPENCER LUCAS).*

also proposed the new combination *Batrachichnus parvus* (Gilmore, 1927). The only revision of the Hermit Shale material was proposed by Haubold and others (1995a), who recognized: *Batrachichnus delicatulus, Dimetropus* isp., *Hyloidichnus bifurcatus, Gilmoreichnus hermitanus and Parabaropus* isp. More recent studies proposed the invalidity of the ichnotaxon *Gilmoreichnus hermitanus*, because it was based on poorly preserved material actually assignable to different ichnotaxa (Voigt, 2005; Marchetti and others, 2019a).

Trace Fossils

Anamniote Tracks: The specimen USNM 11707A is a large slab showing more than 100 footprints and different ichnotaxa (figure 9). This slab includes a relatively long trackway (13 consecutive pes-manus couples) assignable to *Amphisauropus kablika*e (figure 10A–C). The footprints are well-preserved, pentadactyl and ectaxonic with straight digit impressions and round digit terminations on both the pes and the manus imprints, and the pes imprint is larger than the manus imprint (pes length about 70 mm or 2.8 in). The pes imprint is plantigrade and shows an elliptical sole impression, and the manus imprint is semi-plantigrade and distinctly wider than long. The trackway is broad, the pace angulation is about 70–110°, and the manus imprint is rotated towards the midline. Gilmore (1928) assigned this trackway to *Parabaropus coloradensis*, which was considered by Haubold and others (1995a) similar to *Amphisauropus latus*, later synonymized with *Amphisauropus kablikae* by Voigt (2005). However, the specimen USNM 11707A was not relocated. The type material of *Parabaropus coloradensis* (YPM 2145A-C) includes three syntype slabs from the Hermit Shale, showing: A) an isolated pes track, assignable to *Dimetropus* isp., B) an isolated pes track, assignable to cf. *Amphisauropus* isp., and C) several poorly preserved tracks, assignable to cf. *Amphisauropus* isp. Because this type material is incomplete and includes different morphotypes, we consider *Parabaropus* Gilmore, 1927 and *Parabaropus coloradensis* (Lull, 1918) to be *nomina dubia*. The specimen USNM 11707B includes a manus track and a partial pes track assigned to *Amphisauropus* isp. This ichnogenus is uncommon in the Hermit Shale and is generally regarded as the track of seymouriamorphs (Voigt, 2005; Marchetti and others, 2017a).

The ichnotaxon *Batrachichnus salamandroides* is a common track type in the Hermit Shale. This material is characterized by small ectaxonic tracks with pentadactyl, plantigrade pes imprints and tetradactyl, semi-plantigrade manus imprints; the pes imprint is larger than the manus imprint (foot length of about 10 to 20 mm or 0.39 to 0.79 in). The trackway pattern shows broad trackways in a simple alternating arrangement, with low pace angulation (usually lower than 100°). The ichnotaxa (1) *Exocampe*? *delicatula* Lull, 1918 (holotype YPM 3410), later assigned to *Batrachichnus* in the new combination *Batrachichnus delicatulus* by Gilmore (1927), and (2) *Dromillopus parvus* Gilmore, 1927 (holotype USNM 11537, figure 10D) are junior subjective synonyms of *Batrachichnus salamandroides* (Geinitz, 1861), following Haubold (2000) and Voigt (2005). Other significant material includes: USNM 11518, showing a trackway with slightly sinuous tail impression; USNM 11519 and USNM 11520, which are completely covered by tracks; GRCA 3051, showing tracks associated with groups of parallel scratches interpreted as swimming traces; and GRCA 3218, GRCA 19408 and UCMP-V 75209A, showing incomplete step cycles. Other materials assignable to *Batrachichnus salamandroide*s come from the Mogollon Rim area (figure 10E), including the specimens: UCMP-V 75216A-C and UCMP-V 4013A-B. Some other material from GRCA is of dubious attribution. The ichnotaxon *Batrachichnus obscurus* Gilmore, 1927 is assignable to cf. *Batrachichnus* isp. due to the poor preservation of the holotype trackway (USNM 11529), which shows a deep body/tail impression and unclear and incomplete tracks. The specimen USNM 11563 includes a rather poorly preserved trackway incorrectly assigned to *Gilmoreichnus hermitanus* by Haubold and others (1995a). This material is instead assignable to cf. *Batrachichnus* isp., according to Marchetti and others (2019b). *Batrachichnus* is generally regarded as the track of small temnospondyls (e.g., Voigt, 2005).

The ichnotaxon *Ichniotherium cottae* is known from a single specimen of the Hermit Shale (figure 10F), discovered along the Bright Angel Trail in 2005 and left in place. Available photographs show an incomplete step cycle composed of a left pes, a right pes-manus couple and another left pes preserved in convex hyporelief. There is no information on the manual imprint morphology as the only referred track has been lost by weathering except for the terminal impression of digit I. Nevertheless, ichnospecific assignation is unambiguous due to the characteristic pedal morphology. *Ichniotherium* is characterized by ectaxonic, pentadactyl and plantigrade pes imprints, straight digit impressions with enlarged and distally rounded tips, as well as an oval-shaped heel impression (Voigt, 2005). The ichnospecies *Ichniotherium cottae* is unique in its short impression of pedal digit V (about half of the length of pedal digit IV impression) and pedal tracks that are more or less parallel to the direction of the trackmaker's movement (Voigt, 2005; Buchwitz and Voigt, 2018). *Ichniotherium cottae* is most likely the track of advanced diadectid reptiliomorphs (Voigt and others, 2007; Buchwitz and Voigt, 2018).

Synapsid Tracks: The ichnotaxon *Dimetropus* is uncommon in the Hermit Shale. This material is characterized by relatively large, pentadactyl, plantigrade and ectaxonic tracks (pes length of 50 to 120 mm or

***Figure 9.** Tetrapod footprints from the Hermit Shale along Hermit Trail in USNM 11707A (LORENZO MARCHETTI & SPENCER LUCAS). This large slab shows more than 100 footprints and several different ichnotaxa (*Amphisauropus kablikae*, Hyloidichnus bifurcatus*, cf.* Batrachichnus *isp.) in concave epirelief.*

2.0 to 4.72 in). The pes imprint is much larger than the manus imprint and has a postero-laterally elongated sole impression. The digit impressions are short and terminate in claw impressions, when preserved. The digit impression base is arranged in a semi-circle. These tracks are often collapsed (e.g., USNM 11527, UCMP-V 4013B) or preserved as undertracks (e.g., USNM 11598). The incomplete step cycles show a probable slow gait, with relatively short stride and pace lengths.

The first mention of clear synapsid tracks from the Hermit Shale was by Haubold and others (1995a), who assigned to *Dimetropus* cf. *nicolasi* a single pes track (USNM 11528) and to *Dimetropus* isp., an incomplete step cycle previously assigned by Gilmore (1927) to *Parabaropus coloradensis* (USNM 11598). We assign USNM 11528 to *Dimetropus* isp. (figure 11B) and USNM 11598 to cf. *Dimetropus* isp., because of its poor preservation. Notably, USNM 11528 shows a collapsed track, and its undertrack is on the back of the slab. We also assign the single pes track of specimen YPM 2145A (syntype of *Parabaropus coloradensis, nomen dubium*) to *Dimetropus* isp. (figure 11A). Also, some of the material assigned to *Gilmoreichnus hermitanus* by Haubold and others (1995a), and notably the trackway of specimen USNM 11527, the holotype of *Collettosaurus pentadactylus* Gilmore, 1927 (*nomen dubium* after Marchetti and others, 2019a), is assigned to cf. *Dimetropus* isp. (figure 11D). Three specimens from the Mogollon Rim area (figure 11C), each an isolated track (UCMP-V 4010A-B, UCMP-V 4013B), are assigned to *Dimetropus* isp. This ichnotaxon is usually attributed to non-therapsid synapsids ("pelycosaurs"), with the exception of the family Varanopidae (e.g., Voigt, 2005).

Reptile Tracks: The ichnotaxon *Dromopus lacertoides* is uncommon in the Hermit Shale. This material is characterized by long, curved and tapering digit impressions ending in claw marks. Tracks are relatively small (pes length of 30 mm or 1.2 in), pentadactyl, semi-digitigrade and strongly ectaxonic. The impressions of digits I–IV are often superimposed and distally curved inwards, and the digit V impression is proximal and directed laterally. Often, only the digit III and IV impressions are preserved. Manus and pes tracks have the same morphology, but the manus imprint is smaller. The specimen GRCA 3171 (figure 12A) shows several tracks assignable to *Dromopus lacertoides*. Some specimens from the

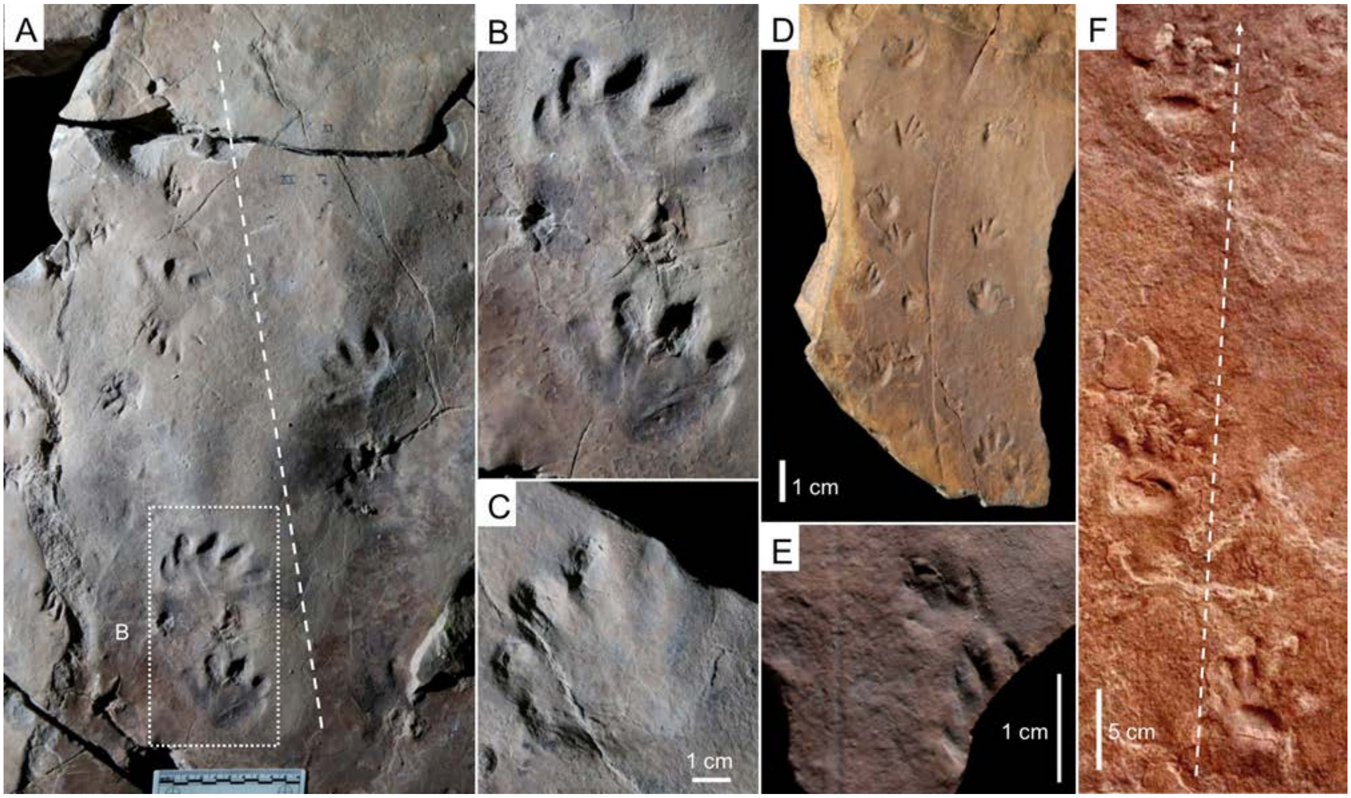

Figure 10. *Anamniote footprints from the Hermit Shale (LORENZO MARCHETTI & SPENCER LUCAS).* ***A–C.*** *USNM 11707A, Hermit Trail.* Amphisauropus kablikae*:* ***A.*** *trackway, concave epirelief;* ***B.*** *Enlargement of A, left pes–manus couple;* ***C.*** *Right pes.* ***D.*** *USNM 11537, Hermit Trail.* Batrachichnus salamandroides*, trackway with thin tail impression, concave epirelief. Holotype of* Dromillopus parvus *Gilmore, 1927.* ***E.*** *UCMP-V 4013A, Mogollon Rim.* Batrachichnus salamandroides*, right pes-manus couple and tail impression, concave epirelief.* ***F.*** Ichniotherium cottae*, incomplete step cycle. Specimen in situ in the Grand Canyon National Park, discovered by Thomas Martens. Dashed arrows indicate the direction of progression.*

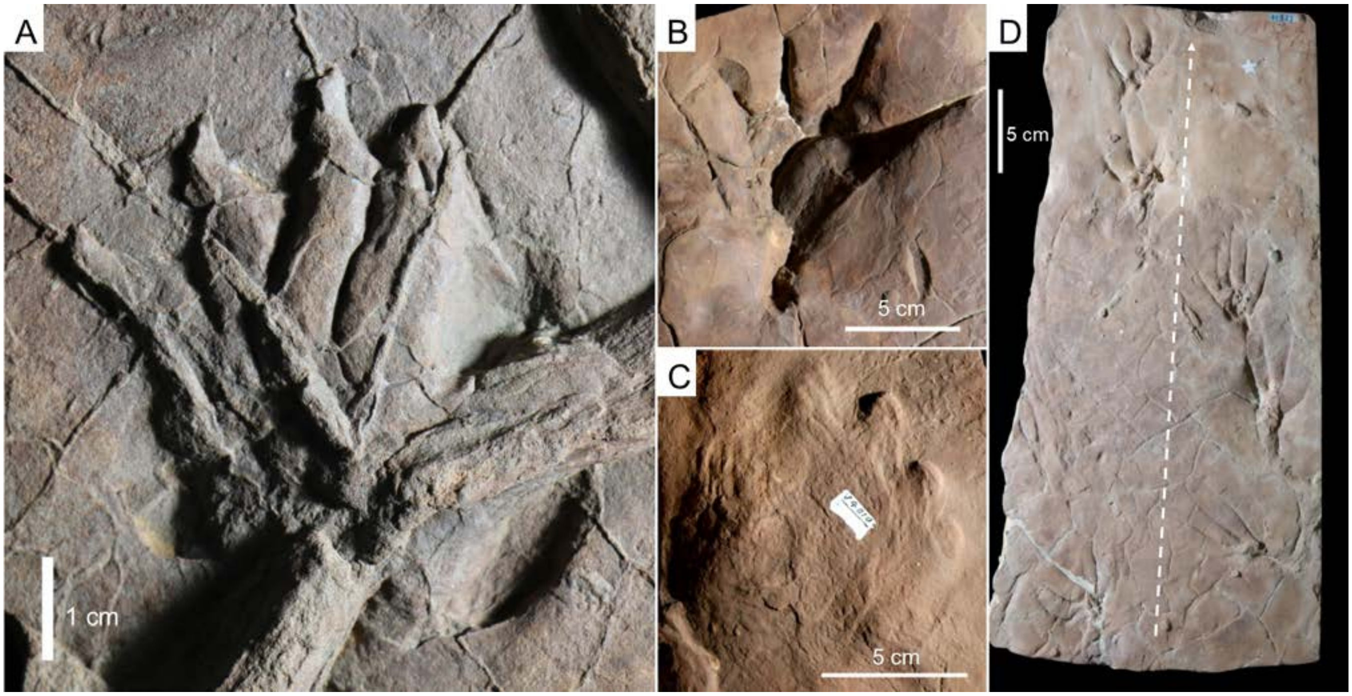

Figure 11. *Synapsid footprints from the Hermit Shale (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *YPM 2145A, Hermit Trail.* Dimetropus *isp., left pes cut by a mud crack, convex hyporelief. Syntype of* Parabaropus coloradensis *(Lull, 1918),* nomen dubium*.* ***B.*** *USNM 11528, Hermit Trail.* Dimetropus *isp., collapsed pes track, concave epirelief.* ***C.*** *UCMP-V 4010B, Mogollon Rim.* Dimetropus *isp., right pes, undertrack preservation, convex hyporelief.* ***D.*** *USNM 11527, Hermit Trail. cf.* Dimetropus *isp., trackway with collapsed tracks, concave epirelief. Holotype of* Collettosaurus pentadactylus *Gilmore, 1927,* nomen dubium*. Dashed arrows indicate the direction of progression.*

Mogollon Rim area (figure 12B) are also assignable to *Dromopus lacertoides* (UCMP-V 4010C and UCMP-V 4013C). This ichnotaxon is generally regarded as the track of araeoscelid diapsids or bolosaurid parareptiles (e.g., Voigt, 2005).

The ichnotaxon *Hyloidichnus bifurcatus* Gilmore, 1927 (figure 12C) is the most common track type in the Hermit Shale. This material is characterized by small to relatively large (pes length of 20 to 70 mm, or 0.79 to 2.7 in), pentadactyl, ectaxonic, and semi-plantigrade tracks. Digit impressions are long, straight and end in flat claw marks that are often bifurcated. The digit IV impression is the longest, digit III and IV impressions are of similar length, and the digit V impression is about as long as the digit I–II impressions. The palm/sole impression is very short and shows a convex to flat proximal margin. The pes imprint is slightly larger than the manus imprint. The trackways are broad, with a relatively low pace angulation and manus tracks rotated inward. The ichnogenus holotype (USNM 11518) (figure 12C) includes a trackway with five consecutive pes-manus couples.

The ichnospecies *Hyloidichnus whitei* Gilmore, 1928 (holotype USNM 11692) (figure 12D) is here considered a junior synonym of *Hyloidichnus bifurcatus*, in agreement with Haubold and others (1995a). We confirm the assignment to *Hyloidichnus bifurcatus* of a pes-manus couple on specimen USNM 11522 (Haubold and others, 1995a). The step cycle on USNM 11519 and the several trackways and isolated tracks on USNM 11707A (figure 9), assigned to *Hylopus hermitanus* by Gilmore (1927, 1928), and to *Gilmoreichnus hermitanus* by Haubold and others (1995a), are herein assigned to *Hyloidichnus bifurcatus*. The specimens YPM 304, showing differently impressed and superimposed trackways, and USNM 11711, showing a trackway, previously assigned to *Gilmoreichnus hermitanus* by Haubold and others (1995a), are herein assigned to *Hyloidichnus bifurcatus*. Other significant specimens assigned to this ichnotaxon are: UCMP-V 75209B, showing a large-sized pes-manus couple with evident digit impression bifurcation, and USNM 11529 and GRCA 3174, showing an incomplete step cycle. Some specimens assignable to *Hyloidichnus bifurcatus* come from the Mogollon Rim area (figure 12E): UCMP-V 75216F-G, showing an isolated pes and an isolated pes-manus couple, respectively. Because of the poor preservation, we consider the ichnogenus

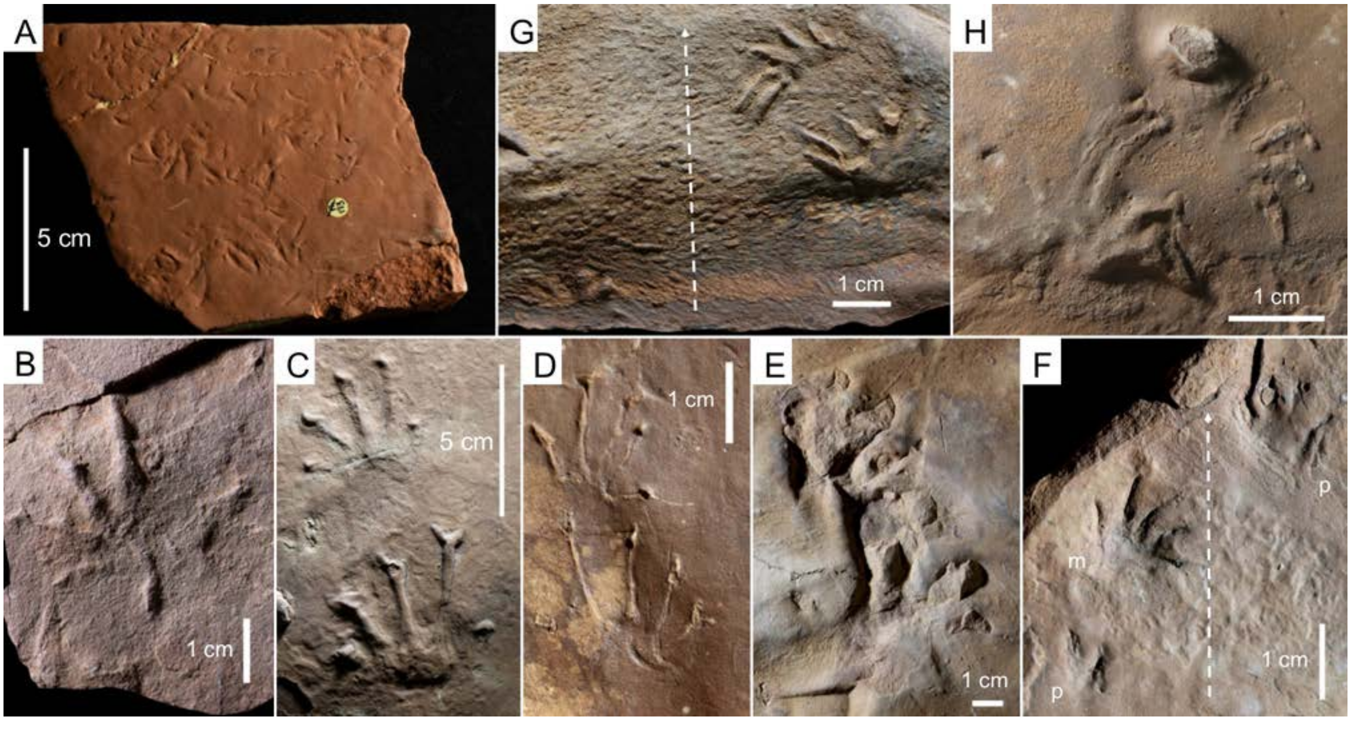

Figure 12. *Reptile footprints from the Hermit Shale (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *GRCA 3171, Yaki Trail.* Dromopus lacertoides*, several footprints, concave epirelief.* ***B.*** *UCMP-V 4010C, Mogollon Rim.* Dromopus lacertoides*, left footprint, convex hyporelief.* ***C.*** *USNM 11518, Hermit Trail. Holotype of* Hyloidichnus bifurcatus *Gilmore, 1927, left pes–manus couple, convex hyporelief.* ***D.*** *USNM 11692, Yaki/South Kaibab Trail.* Hyloidichnus bifurcatus*, left pes–manus couple, concave epirelief. Holotype of* Hyloidichnus whitei *Gilmore, 1928.* ***E.*** *UCMP-V 75216G, Mogollon Rim.* Hyloidichnus bifurcatus*, left pes–manus couple, concave epirelief.* ***F.*** *UCMP-V 75216D, Mogollon Rim.* Erpetopus *isp., partial trackway, convex hyporelief.* ***G.*** *UCMP-V 75216A, Mogollon Rim.* Erpetopus *isp., left pes–manus couple, convex hyporelief.* ***H.*** *UCMP-V 75209A, Hermit Trail.* Erpetopus *isp., partial trackway, convex hyporelief. Dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint.*

Gilmoreichnus Haubold, 1971, and the ichnospecies *Gilmoreichnus hermitanus* (Gilmore, 1927), based on the trackway holotype, USNM 11517, as *nomina dubia* and assign this material to cf. *Hyloidichnus* isp., in agreement with Marchetti and others (2019a). *Hyloidichnus* is generally related to captorhinid trackmakers, such as the Moradisaurinae (e.g., Voigt and others, 2010).

A single specimen from the Hermit Trail (UCMP-V 75209A) (figure 12F) and three specimens from the Mogollon Rim area (UCMP-V 75216A, D, E) (figures 12G and 12H), each showing an incomplete step cycle, are assignable to *Erpetopus* isp. A specimen from the Hermit Trail (USNM 11518) shows an incomplete step cycle with partial overstep of the pes on the manus and a possible body impression. Because of the lack of the pedal digit impression V, this material is assigned to cf. *Erpetopus* isp. These specimens are characterized by small (pes length of about 10 to 40 mm, or 0.39 to 1.6 in), pentadactyl, ectaxonic, semi-plantigrade footprints with relatively long and thin digit impressions ending in small claw impressions. The digit I–IV impressions are distally curved inwards, and the digit V impression is in a proximal position and distally curved backwards. The pedal digit III–IV impressions can be parallel. The digit IV impression is the longest, the digit III and IV impressions are of similar length, and the digit V impression is about as long as the digit I–II impressions. The palm/sole impression is very short and can show a concave proximal margin. The manus imprint is smaller than the pes imprint and rotated inward. The step cycles show a low pace length. This track type has been related to small captorhinomorph or parareptile producers (e.g., Haubold and Lucas, 2003; Marchetti, 2016).

Undetermined Tracks: A specimen from the Hermit Shale along the Yaki Trail (GRCA 3172–3173) (figure 13) displays a trackway with three small (pes length of about 30 mm or 1.2 in) pes-manus couples. These traces are pentadactyl and semi-plantigrade (although the pedal digit impression V is not impressed), with rounded digit terminations. The pes imprint is ectaxonic and more deeply impressed in its medial part, and the digit impressions are thick and straight; the imprint is about as long as wide. The manus imprint is wider than long and shows very short digit impressions. The impressions of digits III and IV are the longest and about equal in length, and the external digit impressions are reduced. The trackway is broad, with well-spaced pes-manus couples and a low pace angulation (70°). The pes imprint is somewhat similar to *Amphisauropus* and, to a lesser degree, *Limnopus*, but the manus imprint is different from these ichnotaxa. The manus imprint resembles some incomplete tracks of *Dimetropus*, but no claw marks were observed, and the pes imprint has a structure different from *Dimetropus*. In fact, the sole impression is shorter and not mediolaterally expanded, the digit impressions are relatively longer, and the footprints are more deeply impressed medially, whereas they are more deeply impressed laterally in *Dimetropus*. These features are instead typical of the Guadalupian track *Lunaepes* and the Lopingian track *Pachypes*. Further studies are needed in order

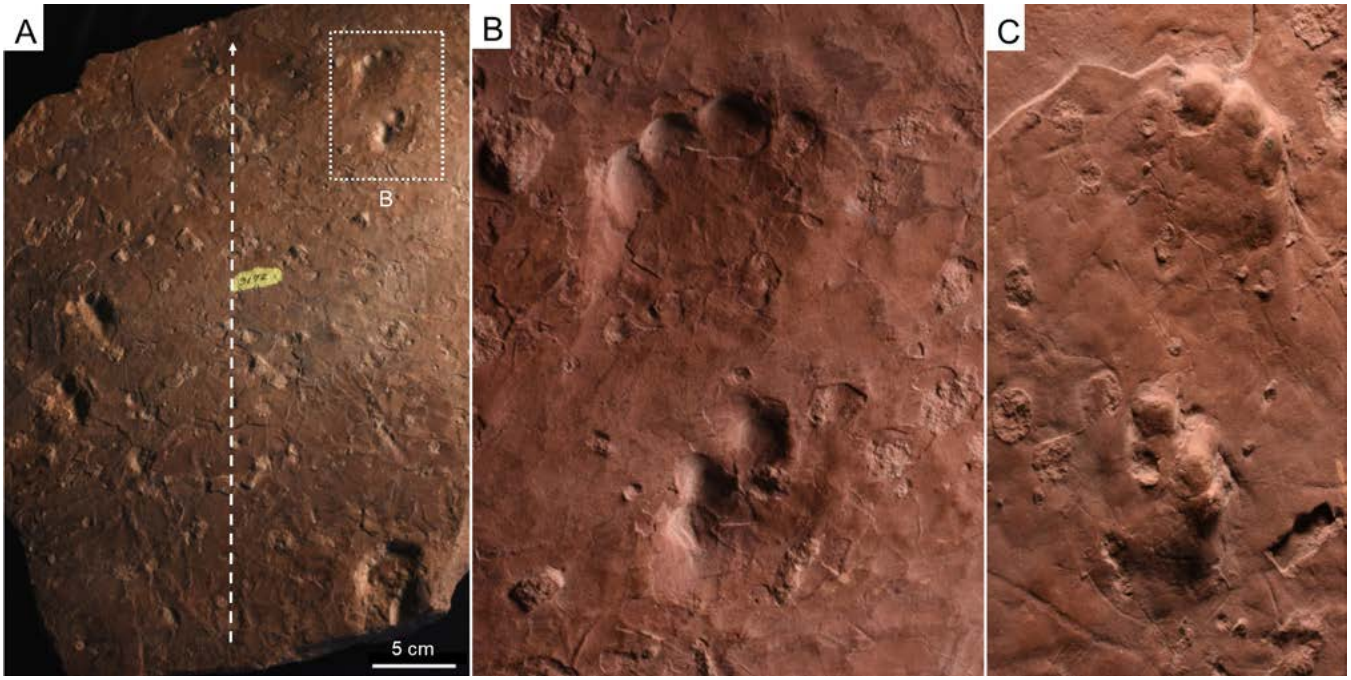

Figure 13. *Undetermined footprints from the Hermit Shale (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *GRCA 3172, Yaki/South Kaibab Trail. Trackway, concave epirelief.* ***B.*** *Enlargement of A, right pes–manus couple.* ***C.*** *GRCA 3173, counterpart of GRCA 3172. Right pes–manus couple, convex hyporelief. Dashed arrows indicate the direction of progression.*

to correctly assign this material, and the discovery of middle–late Permian (Guadalupian–Lopingian) track morphotypes in the early Permian (Cisuralian) would be noteworthy. This material cannot be attributed to therapsid trackmakers because the pes imprint is more deeply impressed medially (see Marchetti and others, 2019d). An attribution to small, heavily built parareptiles such as the nycteroleterids is more probable.

Discussion

The tetrapod ichnoassociation from the Hermit Shale is certainly the best-preserved and most diverse known from GRCA. It includes the following ichnotaxa (table 2): *Amphisauropus kablikae, Batrachichnus salamandroides, Dimetropus* isp., *Dromopus lacertoides, Erpetopus* isp., *Hyloidichnus bifurcatus*, and *Ichniotherium cottae*. The ichnogenera *Amphisauropus*, *Dromopus*, *Erpetopus* and *Ichniotherium* are here recognized for the first time from this formation, notably increasing the ichnodiversity. The occurrence of *Dimetropus* and *Ichniotherium* suggests a Kungurian minimum age, and the occurrence of *Erpetopus* suggests a late Artinskian maximum age. Therefore, this ichnoassociation belongs to the *Erpetopus* tetrapod footprint biochron and suggests a late Artinskian to Kungurian age for the Hermit Shale, probably late Artinskian–early Kungurian because the Hermit Shale is overlain by the late Kungurian Coconino Sandstone (Blakey and Knepp, 1989; Voigt and Lucas, 2018; Marchetti and others, 2019b). The ichnoassociation includes abundant and relatively diverse reptile and anamniote tracks and rarer synapsid tracks. This is consistent with the ichnofaunal composition of the late Artinskian–Kungurian ichnoassociations (e.g., Haubold and Lucas, 2003; Gand and Durand, 2006; Voigt and others, 2011; Marchetti and others, 2015a, 2015b; Voigt and Haubold, 2015; Mujal and others, 2016; Voigt and Lucas, 2017), characterized by an increased abundance and diversity of reptile tracks, therefore registering a low-latitude and possibly worldwide reptile radiation, whereas older ichnoassociations include more anamniote and synapsid tracks (Voigt and Lucas, 2018; Marchetti and others, 2019b).

Coconino Sandstone

Geology

In the Grand Canyon, the Coconino Sandstone forms bold cliffs characterized by large-scale crossbeds between red bed slopes of the Hermit Shale (below) and the Toroweap Formation (above). The contact of the Coconino Sandstone with the underlying Hermit Shale is an unconformity, whereas the overlying contact with the Toroweap Formation is gradational and intertonguing (Middleton and others, 1990). In the Grand Canyon, the Coconino Sandstone is 20 to over 183 m (66 to 600 ft) thick and consists entirely of quartz sandstone (figure 14). Deposition was in a large sand sea (erg) that covered much of northern Arizona and extended to the east to central New Mexico, where the equivalent lithosome is the Glorieta Sandstone (e.g., McKee, 1979; Blakey and Knepp, 1989; Middleton and others, 1990; Lucas and others, 2013). Coconino eolian deposits are primarily crossbedded sandstone that represent dunes, but there are some thin intervals of laminar and ripple laminar sandstone that are interdunal deposits (McKee, 1979). The Coconino has long been recognized as of early Permian (Leonardian) age because it is bracketed by units of that age, Hermit below and lower Kaibab Formation above (Middleton and others, 1990). The recently revised tetrapod ichnoassociation of the Coconino Sandstone is consistent with a Kungurian age (Marchetti and others, 2019b).

Previous Studies

The most famous track-bearing formation of the Grand Canyon is the Coconino Sandstone, which is a reference unit for describing tetrapod tracks in Paleozoic eolian environments, because of the noteworthy abundance of tracks and trackways preserved on dune foreset paleosurfaces (e.g., Lockley and others, 1994; Hunt and Lucas, 2006, 2007; Marchetti and others, 2019b). The first report of Coconino Sandstone tracks was by Lull (1918), who erected the ichnotaxa *Laoporus noblei* and *Laoporus schucherti* based on material collected by Charles Schuchert in 1915 along the Hermit Trail. The first large excavation along the Hermit Trail was led by John C. Merriam in 1924, and the material was described by Gilmore (1926). Based on this material, Gilmore erected the following ichnotaxa: *Agostopus matheri, Allopus*? *arizonae, Baropezia eakini, Barypodus palmatus, Dolichopodus tetradactylus, Nanopus merriami* and *Paleopus regularis*. The new combination *Baropezia arizonae* (Gilmore, 1926) was proposed by Baird (1952). At the same locality, a permanent exhibit with tracks exposed on the foreset paleosurfaces on the side of the Hermit Trail was prepared in 1924 by the director of the National Park Service, Stephen F. Mather, with the aid of Charles W. Gilmore. These surfaces are still exposed today (Marchetti and others, 2019b) (figure 15A). After a further excavation led by Charles W. Gilmore in 1926 at the same locality, he introduced the following ichnotaxa (in Gilmore, 1927): *Agostopus medius, Amblyopus pachypodus, Baropus coconinoensis, Barypodus metszeri, Barypodus tridactylus* and *Nanopus maximus*. All the material from the Hermit Trail came from the lower half of the Coconino Sandstone (Gilmore, 1926, 1927) (figure 14).

Subsequent studies of Coconino Sandstone footprints have focused on ichnotaxonomy, locomotion and paleoecology, with the study of new material from the

Table 2. *Museum collections, Hermit Shale. (continued on following page)*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
GRCA 3051	*Batrachichnus salamandroides*	N/A	N/A	N/A	convex hyporelief	several tracks, swimming traces	–	–	Grand Canyon
GRCA 3171	*Dromopus lacertoides*	N/A	N/A	N/A	concave epirelief	several tracks	–	–	Grand Canyon
GRCA 3172	Undetermined	N/A	N/A	N/A	concave epirelief	trackway	Goebels, L. A.	1937	Grand Canyon, Yaki Trail
GRCA 3173	Undetermined	N/A	N/A	N/A	convex hyporelief	counterpart of GRCA 3172	Goebels, L. A.	1937	Grand Canyon, Yaki Trail
GRCA 3174	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	partial trackway	Goebels, L. A.	1937	Grand Canyon, Yaki Trail
GRCA 3218	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	partial trackway	Richardson, F.	1960	Grand Canyon, Hermit Trail
GRCA 19408	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	partial trackway	Hill, W. H.	1968	Grand Canyon, Hermit Trail
UCMP-V 4010A	*Dimetropus* isp.	N/A	N/A	N/A	concave epirelief	pes imprint	Camp, C. L.	–	Yavapai County, Sedona
UCMP-V 4010B	*Dimetropus* isp.	N/A	N/A	N/A	convex hyporelief	pes imprint	Camp, C. L.	–	Yavapai County, Sedona
UCMP-V 4010C	*Dromopus lacertoides*	N/A	N/A	N/A	convex hyporelief	manus imprint	Camp, C. L.	–	Yavapai County, Sedona
UCMP-V 4013A	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	pes-manus couple	Camp, C. L.	1940	Gila County, Carrizo Cr.
UCMP-V 4013 B	*Batrachichnus salamandroides*, *Dimetropus* isp.	N/A	N/A	N/A	concave epirelief	trackway (Bs), pes imprint (D)	Camp, C. L.	1940	Gila County, Carrizo Cr.
UCMP-V 4013C	*Dromopus lacertoides*	N/A	N/A	N/A	convex hyporelief	pes-manus couple	Camp, C. L.	1941	Gila County, Carrizo Cr.
UCMP-V 75209A	*Batrachichnus salamandroides*, *Erpetopus* isp.	N/A	N/A	N/A	concave epirelief	partial trackway (Bs), partial trackway (E)	Richardson, F.	1938	Grand Canyon, Hermit Trail
UCMP-V 75209B	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	pes-manus couple	Richardson, F.	1938	Grand Canyon, Hermit Trail
UCMP-V 75216A	*Batrachichnus salamandroides*, *Erpetopus* isp.	N/A	N/A	N/A	concave epirelief	trackway and tail impression (Bs), partial trackway (E)	Camp, C. L.	1940	Navajo County, Limestone Canyon

Table 2. *Continued*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
UCMP-V 75216B	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	pes-manus couple	Camp, C. L.	1940	Navajo County, Limestone Canyon
UCMP-V 75216C	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	manus	Camp, C. L.	1940	Navajo County, Limestone Canyon
UCMP-V 75216D	*Erpetopus* isp.	N/A	N/A	N/A	convex hyporelief	incomplete step cycle	Camp, C. L.	1940	Navajo County, Limestone Canyon
UCMP-V 75216E	*Erpetopus* isp.	N/A	N/A	N/A	convex hyporelief	incomplete step cycle	Camp, C. L.	1940	Navajo County, Limestone Canyon
UCMP-V 75216F	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	convex hyporelief	pes imprint	Camp, C. L.	1940	Navajo County, Limestone Canyon
UCMP-V 75216G	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	pes-manus couple	Camp, C. L.	1940	Navajo County, Limestone Canyon
USNM 11517	cf. *Hyloidichnus* isp.	holotype	*Gilmoreichnus hermitanus* (Gilmore, 1927)	*nomen dubium*	concave epirelief and convex hyporelief	trackway	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail
USNM 11518	*Hyloidichnus bifurcatus*	holotype	*Hyloidichnus bifurcatus* Gilmore, 1927	valid	convex hyporelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11518	*Batrachichnus salamandroides,* cf. *Erpetopus* isp.	N/A	N/A	N/A	concave epirelief	trackway and tail impression (Bs), partial trackway (E)	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11519	*Batrachichnus salamandroides*, *Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	several tracks (Bs), partial trackway (Hb)	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11520	*Batrachichnus salamandroides*	N/A	N/A	N/A	concave epirelief	several tracks	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11522	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	pes-manus couple	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11527	cf. *Dimetropus* isp.	holotype	*Collettosaurus pentadactylus* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail
USNM 11528	*Dimetropus* isp.	N/A	N/A	N/A	concave epirelief	pes imprint	Sturdevant, G. E.	1926	Grand Canyon, Hermit Trail

Table 2. *Continued*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
USNM 11529	cf. *Batrachichnus* isp., *Hyloidichnus bifurcatus*	holotype	*Batrachichnus obscurus* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway and tail impression (B), partial trackway (Hb)	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail
USNM 11537	*Batrachichnus salamandroides*	holotype	*Dromillopus parvus* Gilmore, 1927	junior synonym	concave epirelief	trackway and tail impression	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11563	cf. *Batrachichnus* isp.	N/A	N/A	N/A	concave epirelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11598	cf. *Dimetropus* isp.	N/A	N/A	N/A	convex hyporelief	partial trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11692	*Hyloidichnus bifurcatus*	holotype	*Hyloidichnus whitei* Gilmore, 1928	junior synonym	concave epirelief	partial trackway	Gilmore, C. W., White, D.	1927	Grand Canyon, Yaki Trail
USNM 11707A	*Amphisauropus kablikae, Hyloidichnus bifurcatus*, cf. *Batrachichnus* isp.	N/A	N/A	N/A	concave epirelief	several trackways (Hb), trackway (Ak), trackway (B)	Gilmore, C. W., Metzler, A.	1927	Grand Canyon, Hermit Trail
USNM 11707B	*Amphisauropus kablikae*	N/A	N/A	N/A	concave epirelief	pes and manus imprints	Gilmore, C. W., Metzler, A.	1927	Grand Canyon, Hermit Trail
USNM 11711	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	trackway	Gilmore, C. W., Metzler, A.	1927	Grand Canyon, Hermit Trail
YPM 304	*Hyloidichnus bifurcatus*	N/A	N/A	N/A	concave epirelief	superimposed trackways	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
YPM 2145A	*Dimetropus* isp.	syntype	*Parabaropus coloradensis* (Lull, 1918)	*nomen dubium*	convex hyporelief	pes track	Schuchert, C.	1915	Grand Canyon, Hermit Trail
YPM 2145B	cf. *Amphisauropus* isp.	syntype	*Parabaropus coloradensis* (Lull, 1918)	*nomen dubium*	convex hyporelief	pes track	Schuchert, C.	1915	Grand Canyon, Hermit Trail
YPM 2145C	cf. *Amphisauropus* isp.	syntype	*Parabaropus coloradensis* (Lull, 1918)	*nomen dubium*	convex hyporelief	partial trackway	Schuchert, C.	1915	Grand Canyon, Hermit Trail
YPM 3410	*Batrachichnus salamandroides*	holotype	*Exocampe? delicatula* Lull, 1918	junior synonym	convex hyporelief	partial trackway	Schuchert, C.	1915	Grand Canyon, Hermit Trail

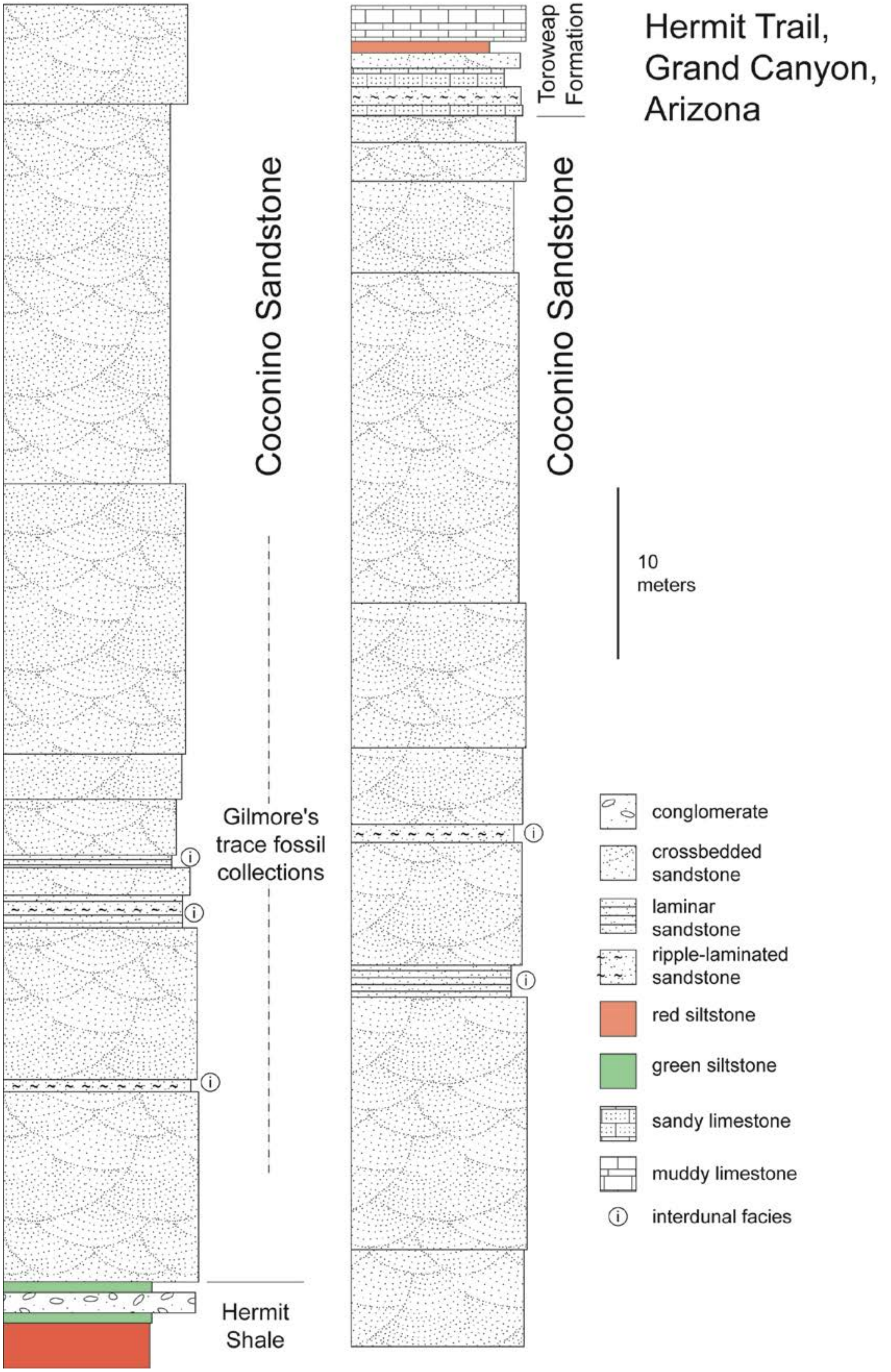

Figure 14. *Stratigraphic section of the Coconino Sandstone measured along the Hermit Trail (LORENZO MARCHETTI & SPENCER LUCAS).*

Mogollon Rim area and also through comparisons with modern equivalents (e.g., McKee, 1944, 1947; Baird, 1952; Brand, 1979; Brand and Tang, 1991; Lockley, 1992; Loope, 1992; McKeever and Haubold, 1996; Haubold, 2000; Hunt and Lucas, 2006, 2007; Citton and others, 2012; Francischini and others, 2019; Marchetti and others, 2019b). The material from Ash Fork in the Mogollon Rim area comes from the middle part of the Coconino Sandstone, showing a similar stratigraphic distribution compared to the GRCA tracks (e.g., Hunt and Lucas, 2005a). Some slabs coming from this locality show very long trackways, including the longest known trackway of the Paleozoic for number of tracks (figure 15B). Trackways with closely spaced tracks were interpreted as subaerial upslope progression by McKee (1944, 1947), and trackways with very asymmetric patterns were interpreted as subaqueous current-driven lateral progression (Brand and Tang, 1991). This latter hypothesis was rejected by Loope (1992), Lockley (1992) and Marchetti and others (2019b), also because of the clear eolian origin of the Coconino Sandstone lithofacies. Marchetti and others (2019b, 2019c) proposed a locomotion model in eolian paleoenvironments mostly based on Coconino Sandstone material, distinguishing trackways showing upslope and downslope progression, with a possible transverse component. In this context, the track morphology is strongly influenced by gravity and thus by sliding of the digits during the trackmaker's locomotion. So, most of the previous ichnotaxonomic assignments were incorrect because they interpreted digit drag marks as actual digit impressions. This caused: (1) an overestimation of footprint diversity in older works (e.g., Gilmore, 1926, 1927); and (2) an underestimation of footprint diversity in more recent works (McKeever and Haubold, 1996; Haubold, 2000). In fact, all the footprints from the Coconino Sandstone were assigned to the ichnogenus *Chelichnus* by McKeever and Haubold (1996) and Haubold (2000).

Based on this interpretation, Hunt and Lucas (2006, 2007) named the *Chelichnus* ichnofacies for low-diversity tetrapod ichnoassociations in eolian paleoenvironments, including the *Laoporus* ichnoassemblage of Lockley and others (1994). However, the material assigned to *Chelichnus* and *Laoporus* is characterized by short and parallel "digit impressions," which are actually digit drag marks of different ichnotaxa. After a comprehensive revision, Marchetti and others (2019b, 2019c) invalidated *Chelichnus*, *Laoporus* and several other ichnotaxa from the Coconino Sandstone and attributed the generally similar morphology of Paleozoic tetrapod footprints in desert paleoenvironments to the effects of locomotion on inclined planes. After excluding these effects, the Coconino Sandstone ichnoassociation is similar to the contemporary non-desert tetrapod ichnoassociations belonging to the *Erpetopus* footprint biochron, including: cf. *Amphisauropus* isp., cf. *Dromopus* isp., *Erpetopus* isp., *Ichniotherium sphaerodactylum*, cf. *Tambachichnium* isp. and *Varanopus curvidactylus.* Moreover, a possible facies-crossing, low-latitude and possibly worldwide reptile radiation was recognized in the tetrapod footprint record during the early Permian, and this is observable in the Coconino Sandstone as well (Marchetti and others, 2019b). Francischini and others (2019) described new noteworthy specimens of *Ichniotherium sphaerodactylum* from the Coconino Sandstone of GRCA and discussed the presence of diadectomorphs in desert paleoenvironments.

Trace fossils

Anamniote Tracks: The ichnogenus *Amphisauropus* is rare in the Coconino Sandstone, and only one specimen (USNM 11135) (figure 16A) showing an upslope-directed trackway has been tentatively assigned to cf. *Amphisauropus* isp. It is characterized by relatively large tracks (pes length of about 70 mm or 2.8 in) with plantigrade pes and semi-plantigrade manus imprints. The tracks are pentadactyl and ectaxonic. The pes imprint is about as long as wide, and the manus imprint is smaller and wider than long. The trackway is broad, and the pace angulation is very low (50–55°), a partial secondary overstep is observed, and the manus is directed inwards. This is the holotype of *Agostopus matheri* Gilmore, 1926, considered a *nomen dubium* because of its poor preservation (Marchetti and others, 2019b). *Amphisauropus* is generally regarded as the track of seymouriamorphs (Voigt, 2005; Marchetti and others, 2017a).

The ichnospecies *Ichniotherium sphaerodactylum* is more common in the Coconino Sandstone, being represented by 15 trackways found along the South Rim of GRCA (Dripping Springs, South Kaibab and Hermit trails) and the Mogollon Rim (Williams, Perkinsville and Seligman) (Francischini and others, 2019) (figures 16B–D). This material is characterized by pentadactyl, plantigrade and ectaxonic manus and pes imprints with an oval-shaped palm/sole impression. The digit IV impression is the longest, and digit II–IV impressions can be bent inwards. The digit V impression is relatively longer in *Ichniotherium sphaerodactylum* than in other ichnospecies of the same ichnogenus. Pes imprints are slightly larger than manus imprints (about 80%). Digit impressions are clawless and have a typical drumstick shape, with expanded tips. Two specimens (USNM 11137 and USNM 11138), both collected by Charles W. Gilmore at the Hermit Trail in 1924, were first described by Gilmore (1926) as the holotype and paratype of *Baropezia eakini*. The ichnogenus *Baropezia* was erected by Matthew (1903) for Pennsylvanian tracks of the Joggins Formation of Nova Scotia, Canada. Although further analysis is necessary to understand the validity of this ichnogenus, we consider here the ichnospecies *Baropezia eakini* as a junior synonym of *Ichniotherium*

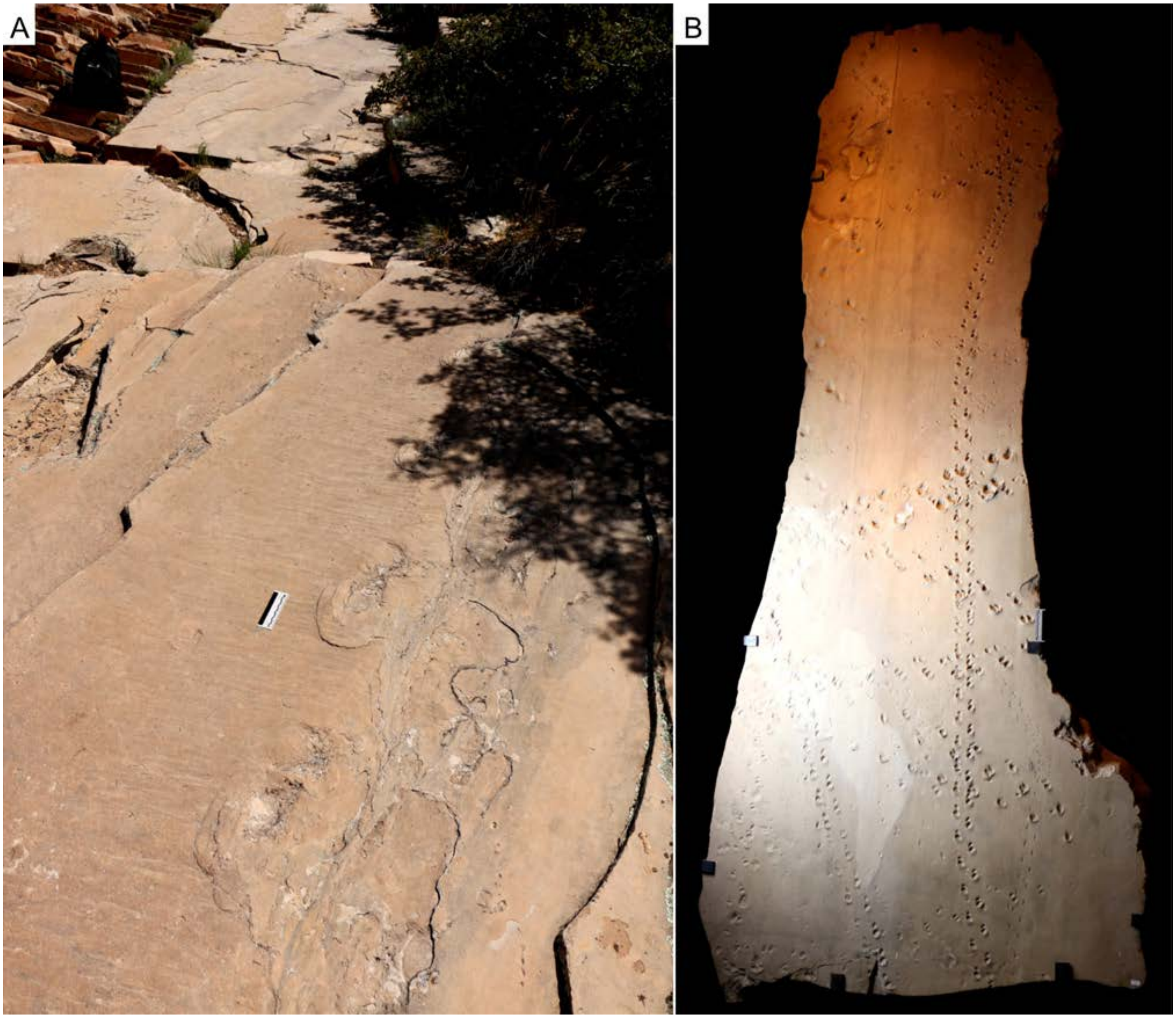

Figure 15. Tetrapod footprints from the Coconino Sandstone (LORENZO MARCHETTI & SPENCER LUCAS). ***A.*** *Trampled surface exposed along the Hermit Trail.* ***B.*** *Large slab RAM 244 showing more than 500 footprints, differently oriented trackways compared to the slope (upslope, downslope, transverse), and the longest trackway of the Paleozoic for number of footprints (almost 200), convex hyporelief.*

sphaerodactylum, in agreement with Francischini and others (2019) and Marchetti and others (2019b). The specimen USNM-V 11514, also from the Hermit Trail, is the holotype of *Baropus coconinoensis* (Gilmore, 1927), but was regarded as a junior synonym of *Baropezia eakini* by Haubold (1971). As with *Baropezia*, more information is needed to evaluate the validity of the ichnogenus *Baropus* (whose type materials come from the Coal Measures of Kansas; Marsh, 1894), but the ichnospecies *Baropus coconinoensis* is here regarded as a junior synonym of *Ichniotherium sphaerodactylum*, in agreement with Francischini and others (2019) and Marchetti and others (2019b). Some other *I. sphaerodactylum* specimens were previously assigned to *Baropus lentus* (UCMP 42945 and UCMP 42951), *Barypodus palmatus* (MNA-V 3386), *Chelichnus duncani* (USNM 11137 and USNM 11138), *Dolichopodus tetradactylus* (YPM 288), and *Laoporus noblei* (USNM-V 11508) (Gilmore, 1926; McKeever and Haubold, 1996). All of these ichnospecies are currently considered *nomina dubia* (Marchetti and others, 2019a). An incomplete specimen (GRCA 116801) found at the Hermit Trail was assigned to cf. *Ichniotherium* isp. (Francischini and others, 2019). *Ichniotherium* ichnospecies comprise one of the best examples of a strongly tied correlation between ichnotaxa and osteological taxa, representing tracks produced by diadectomorph reptiliomorphs. In particular, *I. sphaerodactylum* was assigned to the diadectid *Orobates pabsti*, based on complete trackways and skeletons from lower Permian (Rotliegend) of Germany (Voigt and oth-

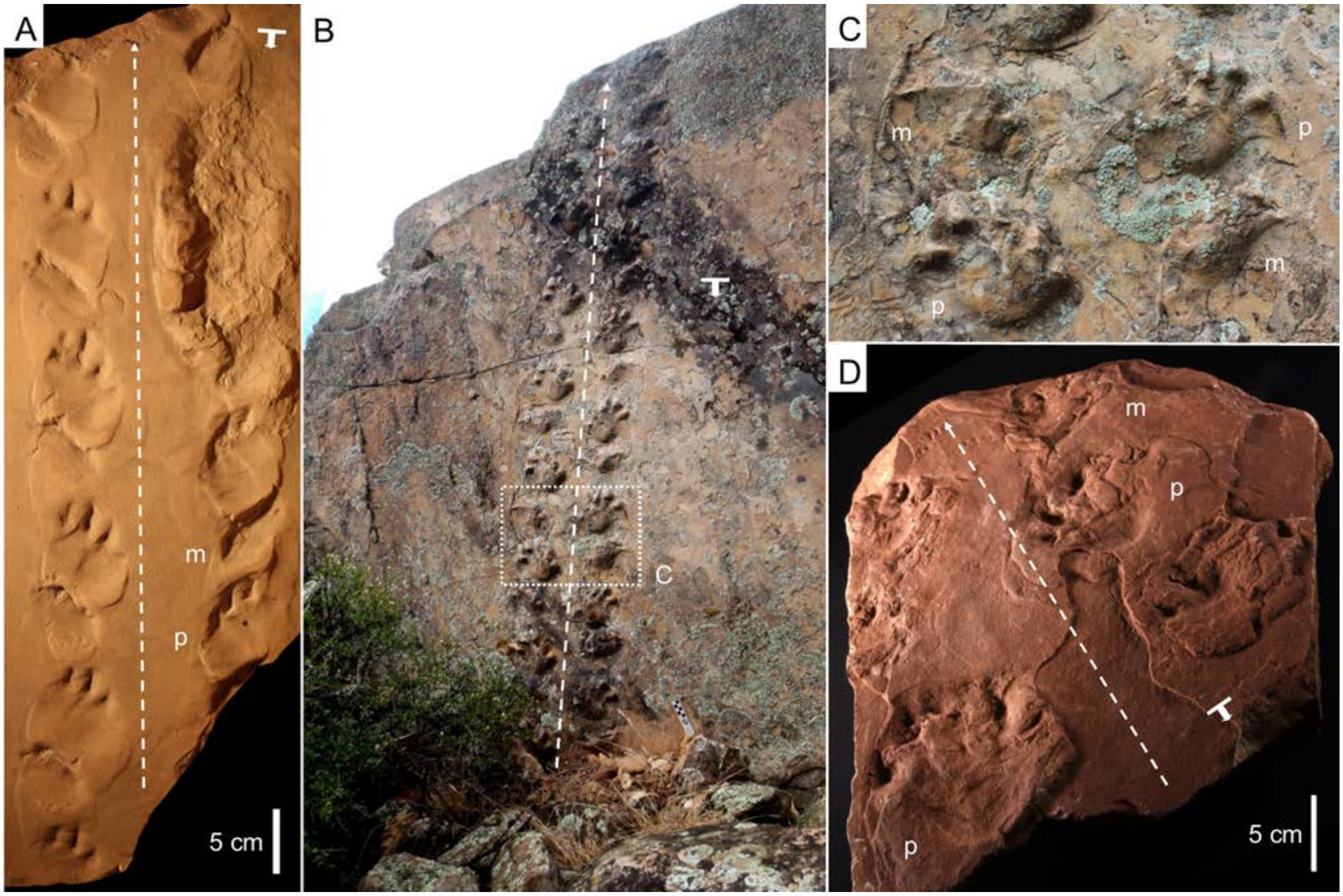

***Figure 16.** Anamniote footprints from the Coconino Sandstone (LORENZO MARCHETTI & SPENCER LUCAS). **A.** USNM 11135, Hermit Trail. cf.* Amphisauropus *isp., trackway, concave epirelief. Holotype of* Agostopus matheri *Gilmore, 1926,* nomen dubium. ***B.** Specimen in situ, Dripping Springs Trail.* Ichniotherium sphaerodactylum*, trackway, convex hyporelief. **C.** Detail of B, four tracks. **D.** GRCA 3065, Kaibab Trail.* Ichniotherium sphaerodactylum*, partial trackway, concave epirelief. Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint.*

ers, 2007). The specimens from the Coconino Sandstone are the youngest/last record of *Ichniotherium*.

Synapsid Tracks: The ichnogenus *Tambachichnium* is uncommon in the Coconino Sandstone, and only a few specimens were assigned to cf. *Tambachichnium* isp. by Marchetti and others (2019b). This material is characterized by relatively large tracks (foot length of about 50 to 100 mm, or 2.0 to 3.9 in) that are pentadactyl, ectaxonic and semi-plantigrade. The digit impressions are relatively thick and terminate in sharp claw marks. Digit I–IV impressions are superimposed and distally bent inwards. The digit V impression is proximal and oriented laterally. The manus imprint is smaller and less deeply impressed than the pes imprint. The trackways are broad and show a low pace angulation (50–95°) and possible secondary overstep. The most complete specimen is USNM 11506 (figures 17A and B), including a trackway with complete pes and manus impressions. This is the holotype of *Nanopus maximus* Gilmore, 1927, considered a *nomen dubium* by Marchetti and others (2019b). Other specimens include the trackway holotypes of *Barypodus metszeri* Gilmore, 1927 (USNM 11505) (figure 17C) and *Barypodus tridactylus* Gilmore, 1927 (USNM 11502) (figure 17D), considered *nomina dubia* by Marchetti and others (2019b) because of their poor preservation (incomplete tracks and digit drag marks). These three trackways are directed upslope, and those of specimens USNM 11505 and USNM 11506 also have a transverse component. An ichnotaxonomic revision of the ichnogenus *Tambachichnium* needs to be undertaken to definitively confirm the assignment of the Coconino material to this ichnogenus. This ichnotaxon is usually attributed to non-therapsid synapsids, such as the varanopids (e.g., Voigt, 2005).

Reptile Tracks: Only a few specimens from the Coconino Sandstone along the Mogollon Rim area are tentatively assigned to cf. *Dromopus* isp. (Marchetti and others, 2019b). This material is characterized by relatively small tracks (pes length of about 30 mm or 1.2 in) that are pentadactyl, markedly ectaxonic and semi-digitigrade. Digit impressions are long and slender and terminate in sharp claw marks. The digit I–IV impres-

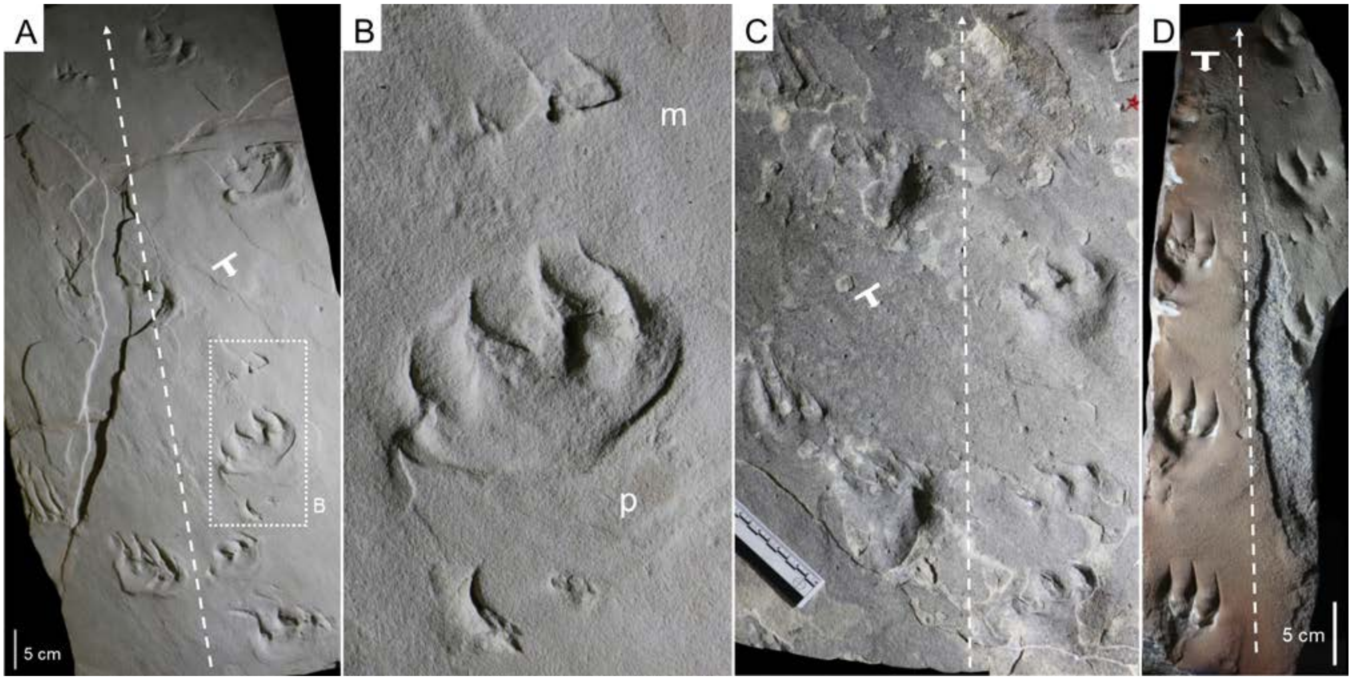

Figure 17. *Synapsid footprints from the Coconino Sandstone, Hermit Trail (LORENZO MARCHETTI & SPENCER LUCAS).* ***A.*** *USNM 11506. cf.* Tambachichnium *isp., trackway, concave epirelief. Holotype of* Nanopus maximus *Gilmore, 1927,* nomen dubium. ***B.*** *Detail of A, pes–manus couple.* ***C.*** *USNM 11505. cf.* Tambachichnium *isp., trackway, concave epirelief. Holotype of* Barypodus metszeri *Gilmore, 1927,* nomen dubium*.* ***D.*** *USNM 11502. cf.* Tambachichnium *isp., trackway, concave epirelief. Holotype of* Barypodus tridactylus *Gilmore, 1927,* nomen dubium*. Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression. p=pes imprint. m=manus imprint.*

sions are proximally superimposed and distally curved inwards, and the impression of digit V is proximal and oriented outwards. The manus imprint is smaller than the pes imprint. The trackways are broad, with low pace angulation (60–100°), the pes oriented outward and the possible occurrence of a thin tail impression. The specimen UCMP-V 159262 includes a trackway with a thin tail impression and superimposed tracks, differently positioned at the two sides of the trackway. The specimen UCMP-V 159265 (figure 18A) shows a trackway with superimposed pes-manus couples and superimposed digit impressions. Both trackways are directed upslope. This ichnotaxon is generally regarded as the track of araeoscelid diapsids or bolosaurid parareptiles (e.g., Voigt, 2005).

The ichnogenus *Erpetopus* is relatively uncommon in the Coconino Sandstone (Marchetti and others, 2019b). This material is characterized by small tracks (pes length 10 to 15 mm, or 0.39 to 0.59 in) that are pentadactyl, ectaxonic and semi-plantigrade. Digit impressions are long and slender and terminate in sharp claw marks. The digit I–IV impressions are distally bent inwards, and the impression of digit V is relatively short and distally bent outward. The manus imprint is slightly smaller than the pes imprint and wider than long; the pes imprint is about as long as wide. The trackways are broad or narrow, with variable pace angulation (60–125°); primary overstep can be observed, manus imprints are directed inward, and a thin tail impression may occur. The specimen USNM 11151 (figure 18B) includes a partial trackway clearly assignable to this ichnogenus. Other specimens from the Mogollon Rim area (figures 18C and D) include upslope-directed trackways assignable to this ichnogenus (MNA-V 3343 and MNA-V 3385). The upslope-directed trackway of USNM 11146, holotype of *Nanopus merriami* Gilmore, 1926, *nomen dubium* after Marchetti and others (2019b), is assignable to cf. *Erpetopus* isp. This track type is generally attributed to small captorhinomorph or parareptile producers (e.g., Haubold and Lucas, 2003; Marchetti, 2016).

The ichnotaxon *Varanopus curvidactylus* is by far the most common track type in the Coconino Sandstone (Marchetti and others, 2019b). This material is characterized by relatively small tracks (pes length 15 to 40 mm, or 0.59 to 1.6 in) that are pentadactyl, ectaxonic and semi-plantigrade. Digit impressions are long and slender and terminate in sharp claw marks. The digit I–IV impressions are distally bent inwards, and the pedal digit V impression is relatively long and straight. The manus imprint is slightly smaller than the pes imprint and wider than long; the pes imprint is about as long as wide. The trackways are broad to very narrow, with variable pace angulation (50–160°), can show primary overstep, and manus imprints are directed inward. Several specimens from the Mogollon Rim area (figures 18E and F) can be assigned to *Varanopus curvidactylus*: track-

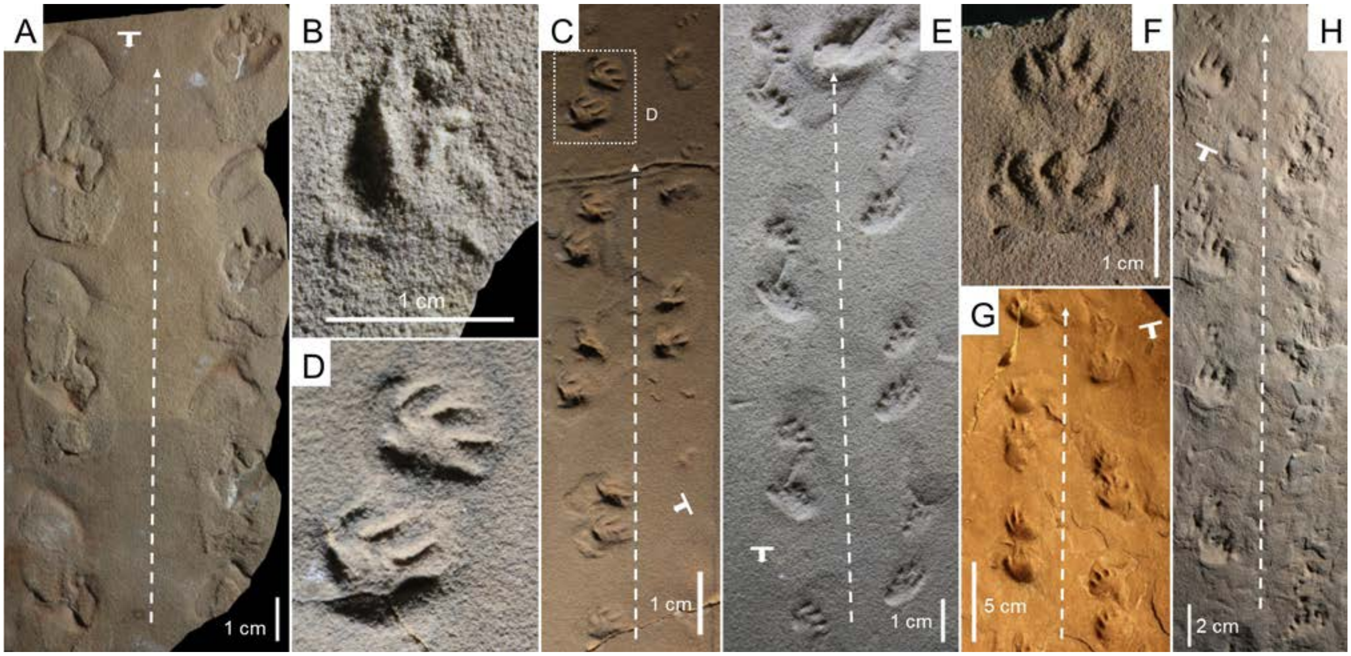

***Figure 18.** Reptile footprints from the Coconino Sandstone (LORENZO MARCHETTI & SPENCER LUCAS). **A.** UCMP-V 159265, Mogollon Rim. cf.* Dromopus *isp., trackway, concave epirelief. **B.** USNM 11151, Hermit Trail.* Erpetopus *isp., pes imprint, convex hyporelief. **C.** MNA-V 3385, Mogollon Rim.* Erpetopus *isp., trackway, concave epirelief. **D.** Detail of C, left pes–manus couple. **E.** RAM-NN 1, Mogollon Rim.* Varanopus curvidactylus*, trackway, convex hyporelief. **F.** MNA-V 5193, Mogollon Rim.* Varanopus curvidactylus*, right pes–manus couple, convex hyporelief. **G.** GRCA 2914, Hermit Trail.* Varanopus curvidactylus*, trackway, concave epirelief. **H.** YPM 2143, Hermit Trail. cf.* Varanopus *isp., trackway, concave epirelief. Holotype of* Laoporus schucherti *Lull, 1918,* nomen dubium*. Strike and dip symbols indicate the supposed dip of the inclined bedding plane, dashed arrows indicate the direction of progression.*

ways directed upslope (MNA-V 3327, MNA-V 3470, MNA-V 5193, RAM-NN 1, UCMP-V 36852, UCMP-V 42944), trackways directed upslope with a transverse component (MNA-V 3376, RAM 236, RAM 422, RAM-NN 1, UCMP-V 42932), trackways transverse to the slope (RAM 420) and trackways directed downslope (RAM-NN 1, UCMP-V 42944). Among the material coming from GRCA, the upslope-directed trackway of specimen GRCA 2914 (figure 18G) and a pes-manus couple with partial overstep of specimen GRCA 2939 can be assigned to this ichnotaxon. Because of the poor and incomplete preservation of the holotypes, the ichnotaxa *Laoporus schucherti* Lull, 1918 (YPM 2143, upslope-directed trackway) (figure 18H) and *Laoporus noblei* Lull, 1918 (YPM 2144, upslope-directed partial trackway) have been considered *nomina dubia*, and this material has been assigned to cf. *Varanopus* isp. (Marchetti and others, 2019b). *Varanopus curvidactylus* has generally been referred to relatively small captorhinomorph producers (e.g., Haubold and Lucas, 2003), but small parareptile trackmakers are also possible.

Undetermined Tracks: Several specimens are not assignable to an ichnotaxon but are holotypes of invalid ichnotaxa (Marchetti and others, 2019b). These specimens include the holotypes of: *Dolichopodus tetradactylus* Gilmore, 1926 (USNM 11123, downslope-directed trackway), *Palaeopus regularis* Gilmore, 1926 (USNM 11143, upslope-directed trackway), *Barypodus palmatus* Gilmore, 1926 (USNM 11134, possible pes-manus couple showing overstep), *Allopus*? *arizonae* Gilmore, 1926 (USNM 11132, large-sized trackway directed upslope with transverse component), *Agostopus medius* Gilmore, 1927 (USNM 11509, trackway directed upslope) and *Amblyopus pachypodus* Gilmore, 1927 (USNM 11511, possible trackway).

Discussion

The Coconino Sandstone yields an extensive track collection. Because of the presence of very long trackways differently oriented compared to the paleoslope, it is the ideal unit for the reconstruction of vertebrate locomotion on desert dunes. Some specimens, such as RAM 244 from the Mogollon Rim area (figure 15), are really remarkable: it includes the longest tetrapod trackway of the Paleozoic for the number of tracks (almost 200) and several trackways differently oriented compared to the slope. However, due to the effects of the locomotion on dune flanks, the track specimens useful for ichnotaxonomy are few, although significant (commonly grade 1.0–1.5 of the preservation scale, Marchetti and others, 2019a). According to Marchetti and others (2019b), the tetrapod ichnoassociation from the Coconino Sandstone includes (table 3): cf. *Amphisauropus* isp., cf. *Dromopus* isp., *Erpetopus* isp., *Ichniotherium sphaerodactylum*,

Table 3. *Museum collections, Coconino Sandstone. (continued on following page)*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
GRCA 2914	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	trackway	Sturdevant, G. E.	1927	Grand Canyon, Hermit Trail
GRCA 2939	*Varanopus curvidactylus*	N/A	N/A	N/A	convex hyporelief	pes–manus couple	Sturdevant, G. E.	1926	Grand Canyon, Hermit Trail
GRCA 3065	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	concave epirelief	partial trackway	Byrd, J.	1934	Grand Canyon, South Kaibab Trail
GRCA 116801	cf. *Ichniotherium* isp.	N/A	N/A	N/A	convex hyporelief	partial trackway	GRCA Staff	2017	Grand Canyon, Hermit Trail
MNA-V 3327	*Varanopus curvidactylus*	N/A	N/A	N/A	convex hyporelief	trackway	–	–	Sycamore Pass
MNA-V 3343	*Erpetopus* isp.	N/A	N/A	N/A	concave epirelief	trackway and tail impression	–	–	Ash Fork
MNA-V 3376	*Varanopus curvidactylus*	N/A	N/A	N/A	convex hyporelief	trackway	–	–	Seligman, Aubrey Cliffs
MNA-V 3385	*Erpetopus* isp.	N/A	N/A	N/A	concave epirelief	trackway	–	–	Sandflat, between Bear Canyon Road and Perkinsville
MNA-V 3386	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	concave epirelief	pes–manus couple	–	–	Sandflat, between Bear Canyon Road and Perkinsville
MNA-V 3470	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	trackway	–	–	Ash Fork
MNA-V 5193	*Varanopus curvidactylus*	N/A	N/A	N/A	convex hyporelief	trackway	–	–	Ash Fork
NMMNH-P 80306	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	convex hyporelief	trackway	Donated by a quarryman to Flagstaff Forest Service	1990s	Williams, commercial quarry
NMMNH-P 80307	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	concave epirelief	trackway	Donated by a quarryman to Flagstaff Forest Service	1990s	Williams, commercial quarry
RAM 236	*Varanopus curvidactylus*	N/A	N/A	N/A	convex hyporelief	two trackways	Alf, R. M.	N/A	Seligman

Table 3. *Continued*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
RAM 244	Undetermined tracks	N/A	N/A	N/A	convex hyporelief	several trackways	Alf, R. M.	N/A	Seligman
RAM 420	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	two trackways	Alf, R. M.	N/A	Seligman
RAM 422	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	trackway	Alf, R. M.	N/A	Seligman
RAM-NN 1	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	four trackways	Alf, R. M.	N/A	Seligman
UCMP-V 36852	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	trackway	Peabody, F. E.	1940	Yavapai County, Peach Springs
UCMP-V 42932	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	trackway	Kincade, S.	1940	Yavapai County, Peach Springs
UCMP-V 42944	*Varanopus curvidactylus*	N/A	N/A	N/A	concave epirelief	two trackways	–	–	Seligman
UCMP-V 42945	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	concave epirelief	trackway	–	–	–
UCMP-V 42951	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	convex hyporelief	trackway	Welles, S. P.	1949	Seligman
UCMP-V 159262	cf. *Dromopus* isp.	N/A	N/A	N/A	concave epirelief	trackway and tail impression	–	–	Yavapai County
UCMP-V 159265	cf. *Dromopus* isp.	N/A	N/A	N/A	concave epirelief	trackway	Richardson, F.	1938	Yavapai County
USNM 11123	Undetermined tracks	holotype	*Dolichopodus tetradactylus* Gilmore, 1926	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11132	Undetermined tracks	holotype	*Allopus? arizonae* Gilmore, 1926	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11134	Undetermined tracks	holotype	*Barypodus palmatus* Gilmore, 1926	*nomen dubium*	concave epirelief	pes–manus couple	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11135	cf. *Amphisauropus* isp.	holotype	*Agostopus matheri* Gilmore, 1926	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail

Table 3. *Continued*

Catalog #	Assignment	Type	Previous Ichnotaxon	Validity	Preservation	Description	Collector	Date	Locality
USNM 11137	*Ichniotherium sphaerodactylum*	holotype	*Baropezia eakini* Gilmore, 1926	junior synonym	concave epirelief and convex hyporelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11138	cf. *Ichniotherium* isp.	paratype	*Baropezia eakini* Gilmore, 1926	junior synonym	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11143	Undetermined tracks	holotype	*Paleopus regularis* Gilmore, 1926	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11146	cf. *Erpetopus* isp.	holotype	*Nanopus merriami* Gilmore, 1926	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11151	*Erpetopus* isp.	N/A	N/A	N/A	convex hyporelief	partial trackway	Gilmore, C. W.	1924	Grand Canyon, Hermit Trail
USNM 11502	cf. *Tambachichnium* isp.	holotype	*Barypodus tridactylus* Gilmore, 1927	*nomen dubium*	concave epirelief and convex hyporelief	trackway	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail
USNM 11505	cf. *Tambachichnium* isp.	holotype	*Barypodus metszeri* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail
USNM 11506	cf. *Tambachichnium* isp.	holotype	*Nanopus maximus* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11508	*Ichniotherium sphaerodactylum*	N/A	N/A	N/A	concave epirelief	trackway	Gilmore, C. W., Metzler, A.	1927	Grand Canyon, Hermit Trail
USNM 11509	Undetermined tracks	holotype	*Agostopus medius* Gilmore, 1927	*nomen dubium*	convex hyporelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11511	Undetermined tracks	holotype	*Amblyopus pachypodus* Gilmore, 1927	*nomen dubium*	concave epirelief	trackway	Gilmore, C. W.	1926	Grand Canyon, Hermit Trail
USNM 11514	*Ichniotherium sphaerodactylum*	holotype	*Baropus coconinoensis* (Gilmore, 1927)	junior synonym	concave epirelief	two pes–manus couples	Gilmore, C. W., Metzler, A.	1926	Grand Canyon, Hermit Trail

cf. *Tambachichnium* isp., and V*aranopus curvidactylus*. The co-occurrence of *Ichniotherium* and *Erpetopus* suggests a late Artinskian–Kungurian age (*Erpetopus* biochron) for the Coconino Sandstone, more likely a Kungurian age because of its stratigraphic position (e.g., Blakey and Knepp, 1989). The reptile tracks are very abundant and diverse, the anamniote tracks are less abundant and diverse, and the synapsid tracks are rare. This is in agreement with an early Permian low-latitude reptile radiation registered by the track record, that started during the Artinskian (Marchetti and others, 2019b).

The finding of ichnoassociations typical of the *Dromopus* biochron in Ghzelian eolian units such as the Wescogame Formation (this work) and ichnoassociations typical of the *Erpetopus* biochron in Kungurian desert units such as the Coconino and De Chelly Sandstones (Marchetti and others, 2019b) suggests a facies-crossing reptile radiation and gives strength to the tetrapod footprint biostratigraphy. Some comments can be presented on the ichnofaunal composition of the Coconino Sandstone compared with the underlying Hermit Shale (this work). Both of the ichnoassociations include abundant and diverse reptile tracks, rare synapsid tracks and belong to the *Erpetopus* footprint biochron. Noteworthy, the most abundant track is *Hyloidichnus* in the Hermit Shale and *Varanopus* in the Coconino Sandstone, and both are lacking in the other formation. The reptile tracks *Erpetopus* and *Dromopus* are instead similarly distributed. The difference in anamniote tracks is noteworthy: small temnospondyl tracks (*Batrachichnus*) are very abundant in the Hermit Shale, while they are absent in the Coconino Sandstone; diadectomorph tracks (*Ichniotherium*) are relatively abundant in the Coconino Sandstone, but rare in the Hermit Shale (also, the *Ichniotherium* ichnospecies is different). *Amphisauropus* (seymouriamorph tracks) has a similar distribution in both units. With regard to the synapsid tracks, the ichnogenus is different: *Dimetropus* occurs only in the Hermit Shale, and *Tambachichnium* occurs only in the Coconino Sandstone. These differences are probably not related to stratigraphy, because all the Hermit Shale ichnogenera occur in younger units, and all the Coconino Sandstone ichnogenera occur in older units (e.g., Voigt and Lucas, 2018; Marchetti and others, 2019b). Therefore, this seems to be due to a different paleoecology of the trackmakers that differentially occupied the floodplain (Hermit Shale) and desert (Coconino Sandstone) paleoenvironments. In this context, the non-occurrence of *Hyloidichnus*, *Batrachichnus* and *Dimetropus* in the Coconino Sandstone may have a paleoecological meaning, as does the non-occurrence of *Varanopus* and *Tambachichnium* in the Hermit Shale.

As mentioned above, the Coconino Sandstone is a unit deposited mainly by dunes of eolian origin intercalated with somewhat rare interdune deposits, representing a large erg located at low latitudes during the Kungurian. Since the Paleozoic, the tetrapod ichnological record of erg deposits is notoriously dominated by tracks of Amniota (i.e., eureptiles, parareptiles and synapsids) (e.g., Francischini and others, 2015; Krapovickas and others, 2015, 2016; Marchetti and others, 2019b, 2019c), but the Coconino Sandstone ichnoassociation is remarkable in containing two ichnotaxa (cf. *Amphisauropus* isp. and *Ichniotherium sphaerodactylum*) assigned to non-amniote tetrapods (Francischini and others, 2019; Marchetti and others, 2019b). *Amphisauropus* and *Ichniotherium* are considered to be seymouriamorph and diadectomorph (both reptiliomorph) tracks, and the presence of these ichnogenera in the Coconino Sandstone may represent the oldest record of anamniotes in desert environments and one of the oldest in eolian lithofacies (other occurrences are known from the Wescogame and De Chelly formations, Marchetti and others, 2019b and this work). This record suggests that the adaptations for living in arid settings could have appeared early in the Reptiliomorpha lineage, during the early Permian. Contrasting to this, the Coconino Sandstone lacks evidences of temnospondyl (Batrachomorpha lineage) tracks, such as *Batrachichnus* and *Limnopus*, which occur in the Wescogame Formation and Hermit Shale. Temnospondyl (including lissamphibian) tracks are still poorly known from eolian deposits (this work), and the colonization of arid settings by these tetrapods is an issue still to be investigated.

Hunt and Lucas (2005b, 2006, 2007, 2016) named the *Chelichnus* ichnofacies based on the now discredited interpretations of the ichnotaxonomy of the Coconino Sandstone and other Permian ichnofaunas of Arizona (De Chelly), and Colorado (Lyons) in the United States, Scotland, and Germany in Europe (as well as Late Triassic–Early Jurassic ichnofaunas of western North America which are in need of re-study: Hunt and Lucas, 1998, 2005b, 2007). Ichnofacies retain their name even if the name-bearing ichnotaxon is shown to be a *nomen dubium*, although it would be preferable to use a valid ichnotaxon actually typical of that ichnofacies (e.g., *Varanopus*, *Procolophonichnium*, *Brasilichnium*). Does the *Chelichnus* ichnofacies of the Coconino still have utility? In a biotaxonomic sense it can now be recognized as a relatively depauperate ichnofauna lacking ichnotaxa such as *Batrachichnus*, *Limnopus*, *Dimetropus* and *Hyloidichnus* and with a noteworthy abundance of *Varanopus*, relative to contemporary units (Marchetti and others, 2019b: figure 13). It arguably has more significance as an ethoichnofacies (*sensu* Hunt and Lucas, 2007), which reflects locomotor behavior such as digit drag marks and also as a taphofacies preserving features such as uni-directional ichnotaphonomic effects due to the slope direction (Marchetti and others, 2019b, 2019c). There is clearly a need to re-evaluate this ichnofacies.

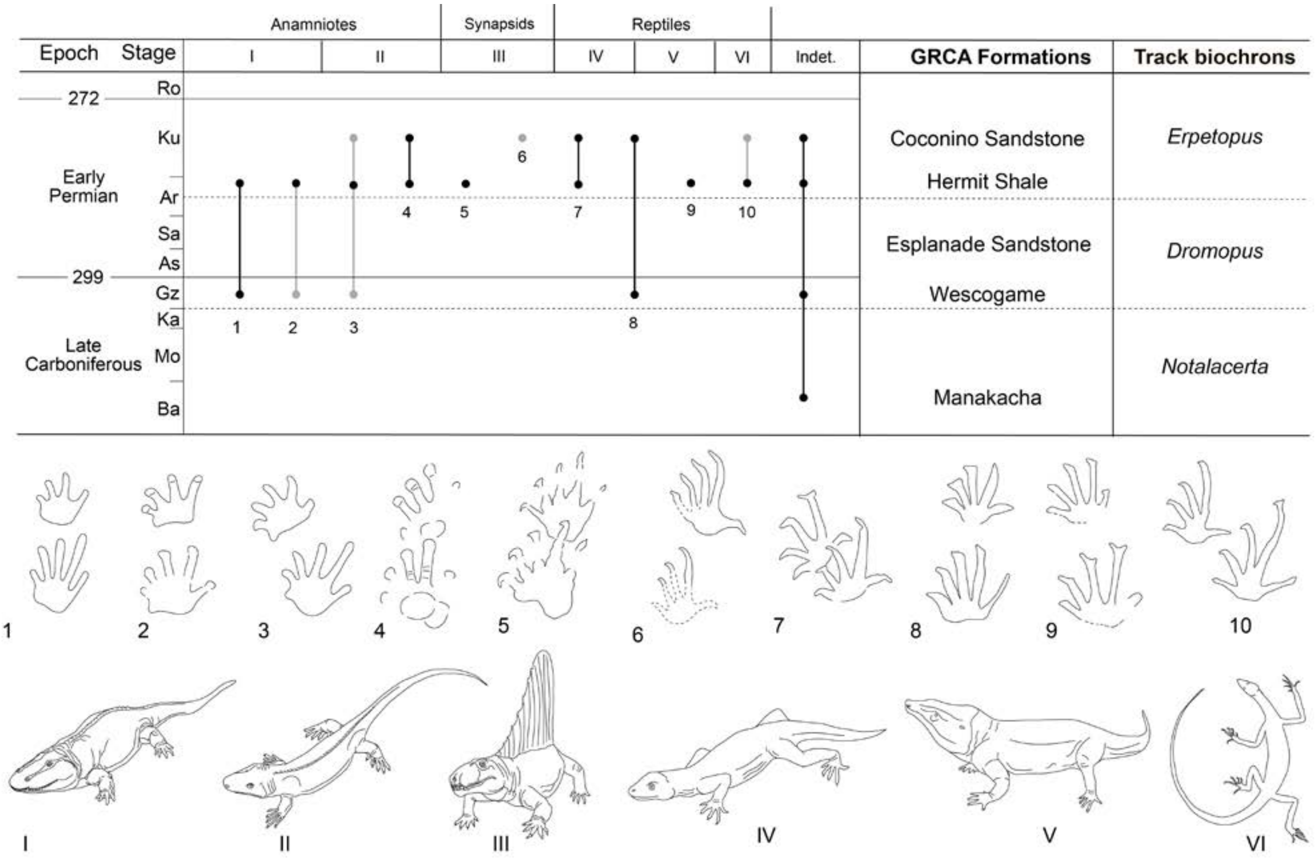

Figure 19. *Stratigraphic distribution of vertebrate tracks in the Paleozoic formations of GRCA (LORENZO MARCHETTI & SPENCER LUCAS). Gray lines and dots in the upper chart indicate uncertain occurrence.* ***1–10.*** *Tetrapod ichnogenera:* ***1.*** Batrachichnus*;* ***2.*** Limnopus*;* ***3.*** Amphisauropus*;* ***4.*** Ichniotherium*;* ***5.*** Dimetropus*;* ***6.*** Tambachichnium*;* ***7.*** Erpetopus*;* ***8.*** Varanopus*;* ***9.*** Hyloidichnus*;* ***10.*** Dromopus*.* ***I–VI.*** *Trackmaker groups:* ***I.*** *Temnospondyl anamniotes;* ***II.*** *Reptiliomorph anamniotes;* ***III.*** *Non-therapsid synapsids;* ***IV.*** *Parareptiles;* ***V.*** *Captorhinid eureptiles;* ***VI.*** *Diapsid eureptiles.*

CONCLUSIONS

The tetrapod ichnological record of the Grand Canyon and Mogollon Rim areas of Arizona is remarkable. Continental deposits are rare among the geological units of these areas and their Paleozoic vertebrate fossil record is restricted to tetrapod tracks of the Upper Pennsylvanian–lower Permian Manakacha Formation, Wescogame Formation, Hermit Shale and Coconino Sandstone (figure 19). The copious and variably preserved tetrapod track record of the Wescogame Formation, Hermit Shale and Coconino Sandstone is composed of non-amniote, synapsid and reptile tracks and trackways produced in marginal marine, alluvial plain and desert settings. On the other hand, the Manakacha Formation record is still scant and indeterminate, but it represents a potential new window for future important discoveries.

The Grand Canyon tetrapod track record is unique in recording several facies-crossing ichnotaxa, leading to a re-interpretation of some vertebrate ichnofacies. Among these ichnotaxa, *Amphisauropus* and *Ichniotherium* may represent the oldest colonization of arid environments by non-amniote tetrapods. In addition, the Artinskian–Kungurian Hermit Shale and Coconino Sandstone ichnoassociations suggest that those paleoenvironments were dominated by reptiles (i.e., parareptiles, araeoscelids and captorhinomorphs), contrasting with older ichnoassociations found worldwide, where these trackmakers are rarer. These are only a few examples of how the tetrapod track record can contribute to biostratigraphic, paleobiological, and evolutionary problems of the fossil record. In spite of the fact that tracks have been collected in the Grand Canyon from over a century, new findings and re-interpretations make it an important area for understanding the composition and diversity of Paleozoic continental tetrapods.

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MESOZOIC PALEONTOLOGY OF GRAND CANYON NATIONAL PARK—TRACE FOSSILS, STRATIGRAPHY, AND REGIONAL CORRELATIONS

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ABSTRACT

The only exposure of Mesozoic rocks at Grand Canyon National Park is found at Cedar Mountain near Desert View and is limited to the Triassic Moenkopi Formation and Shinarump Member of the Chinle Formation. Prior to this inventory, the only detailed geological study of Cedar Mountain occurred in 1922 (three years after the park was established), and the only fossils reported from the Mesozoic of Grand Canyon were petrified logs. We inventoried the Triassic rocks at Cedar Mountain in a two-day PaleoBlitz as part of the comprehensive paleontological inventory of Grand Canyon National Park. We determined that the Moenkopi Formation at Cedar Mountain consists of the Wupatki Member, the Moqui Member, and the Holbrook Member, similar to outcrops of the formation throughout the Little Colorado River Valley east of the park. We collected a specimen of *Rotodactylus* from the Wupatki Member at Cedar Mountain (the first Mesozoic fossil specimen collected for the park's museum collections), consisting of three to four partial pes tracks along a rippled surface, and we report the *Scoyenia* Ichnofacies from the Holbrook Member. We also observed numerous petrified logs and chert clasts in the Shinarump Member of the Chinle Formation that caps Cedar Mountain. Future surveys may recover more trace fossils from the Triassic rocks at Grand Canyon, but access to Cedar Mountain is difficult and the likelihood of finding anything new is low.

INTRODUCTION

The only Mesozoic strata found within the boundary of Grand Canyon National Park (GRCA) are the Triassic Moenkopi Formation and Shinarump Member of the Chinle Formation (figure 1). These Triassic rocks are best exposed at Cedar Mountain in eastern GRCA. An additional kilometer-thick section of later Mesozoic (Jurassic and Cretaceous) sedimentary rocks were once present in the region, but have eroded away as the Colorado Plateau continues to be uplifted (Flowers, 2010; Liu and Gurnis, 2010). Until this report, the only known paleontological resources of the Mesozoic section at GRCA were petrified logs in the Shinarump Member (Noble, 1922).

The Shinarump Member of the Chinle Formation has always been recognized in the region as a cliff-forming conglomerate containing fossil logs (Powell, 1873, 1876; Gilbert, 1875; Dutton, 1880), but other units have often been conflated or synonymized with it. The variegated finer beds above and below the "Shinarump Conglomerate" were first called the "Shinarump Group" (Powell, 1876:54); the "lower portion" of Powell's Shinarump Group was later removed from that unit and named the "Moencopie beds" (Walcott, 1880; Ward, 1901:17). The spelling later changed to "Moenkopi Formation" (Gregory, 1916:79), which has since been carried through the literature. Powell considered all of his "Shinarump Group" to be Triassic in age owing to the fossil logs, although once the "Moencopie beds" were removed from that group they were assigned to the Permian, because of the presence of supposed Permian-aged fossil plant impressions (Gregory, 1916, 1917). The organization and formalization of the "Shinarump Conglomerate" and "Moencopie beds" is detailed below

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Marsh, A.D., Parker, W.G., and Miller, A.E., 2021, Mesozoic Paleontology of Grand Canyon National Park—Trace Fossils, Stratigraphy, and Regional Correlations, *in* Santucci, V.L., and Tweet, J.S., editors, Grand Canyon National Park Centennial Paleontological Resources Inventory—A Century of Fossil Discovery and Research: Utah Geological Association Special Publication 1, p. 205-220.

in the overview of Triassic strata at GRCA. A marked unconformity is present between these units throughout the region and represents the Tr-3 unconformity between the Middle Triassic and Upper Triassic series (Pipiringos and O'Sullivan, 1978). The relatively hard Shinarump Member of the Chinle Formation "preserved the cliffs of the Moenkopi from destruction" (Gregory, 1917:38) where the upper part of the Moenkopi Formation crops out from Houck, Arizona, through Holbrook and Radar Mesa, and along the Little Colorado River Valley towards Cedar Mountain.

Here we present a review of the Triassic sedimentary rocks of GRCA, their regional correlations, and the trace and body fossils found in the area. We also present the results of a two-day PaleoBlitz (an abbreviated paleontological inventory), which represents the second and most comprehensive paleontological inventory of the Mesozoic section at GRCA since shortly after the park was established (Noble, 1922). These new data increase the fossil diversity of GRCA and shed light on an often-overlooked paleontological story in the park that chronicles an important change to the history of the area.

Institutional Abbreviations—GRCA, Grand Canyon National Park, Arizona; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **PEFO**, Petrified Forest National Park, Arizona; **UCMP,** University of California Museum of Paleontology, Berkeley, California; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **WASO**, Washington D.C. Area Support Office, National Park Service, Geological Resources Division, Washington, D.C.; **WUPA**, Wupatki National Monument, Arizona.

OVERVIEW OF TRIASSIC STRATA AT GRCA

Moenkopi Formation

Geology

The "Moencopie beds" were separated from the former "Shinarump Group" based on differences in fossil invertebrates (Walcott, 1880) within a succession of "dark reddish brown, soft, laminated, argillaceaous shales… highly charged with salt and gypsum" (Ward, 1901:403) below the Shinarump Member of the Chinle Formation near Moenkopi Wash, Arizona (~37 km or 23 mi southeast of Cedar Mountain). The type section of the Moenkopi Formation is located in northern Arizona near Tanner Crossing in Cameron, Arizona and includes nearly 122 m (400 ft) of irregular beds of sandstone and shale with frequent horizontal and vertical gypsum beds and a calcareous base (Gregory, 1917:23). The Moenkopi Formation at its type section sits unconformably over the Kaibab Formation and under the Shinarump Member of the Chinle Formation, just as it does at Cedar Mountain in GRCA (Gregory, 1917; Noble, 1922), although the section at Cedar Mountain is nearly 30 m (100 ft) thicker than the type section.

The Moenkopi Formation has different member-level divisions at various places in its outcrop belt in Colorado, New Mexico, Arizona, Utah, and Nevada. The formation thickens basinward to the northwest along the paleodrainage of a forearc basin east of the Cordilleran magmatic arc (McKee, 1954; Dickinson and Gehrels, 2008, 2009a). Exposures of the Moenkopi Formation north and west of the Canyon include the marginal marine Timpoweap Member, Virgin Limestone Member, Shnabkaib Member, and interspersed lower, middle, and upper "red members" (Gregory, 1948, 1952; Reeside and Bassler, 1922), and exposures south and east of the Canyon include prograding fluvial systems within the Wupatki Member, Moqui Member, and Holbrook Member (McKee, 1954; Repenning and others, 1969; Stewart and others, 1972b).

The Moenkopi Formation section at Cedar Mountain is most similar to the eastern exposures along the Little Colorado River Valley. The Wupatki Member is best exposed east of the Black Point Monocline at Wupatki National Monument (~65 km or 40 mi southeast of Cedar Mountain; McKee, 1954; Billingsley and others, 2007; Henderek and others, 2017). The Wupatki Member is characterized by "pale-reddish-brown, micaceous, horizontally and ripple-laminated siltstone that weathers to slopes" (Stewart and others, 1972b:7). The Moqui Member was named for the low badlands in the middle part of the Moenkopi Formation just west of Winslow, Arizona (McKee, 1954). The Moqui Member in the eastern outcrops of the Moenkopi Formation is most similar to the Shnabkaib Member found in the western outcrops in that they are both very fine grained with numerous gypsum beds, but the Moqui Member lacks the sabkha-like cyclicity found in the type section of the Shnabkaib Member in Warner Valley, Utah (McKee, 1954, 1964). The Moqui Member in the Little Colorado River Valley is characterized by "pale brown gypsiferous mudstone and siltstone beds" and is generally "a lighter shade of brown" than the rest of the section above and below it (Stewart and others, 1972b:8). The type section of the Holbrook Member occurs between Holbrook and Joseph City, Arizona (Hager, 1922), where it crops out as "pale-red thin- to thick-bedded channel deposits of sandstone" that are very fine to medium-grained, poorly sorted, trough cross-bedded, and rich in siltstone (Stewart and others, 1972b:9). Closer to Cameron, the Holbrook Member contains thin beds of calcareous cross-bedded sandstones. The contacts between the three major members discussed here are defined lithologically; the lower contact of the Moqui Member with the Wupatki Member

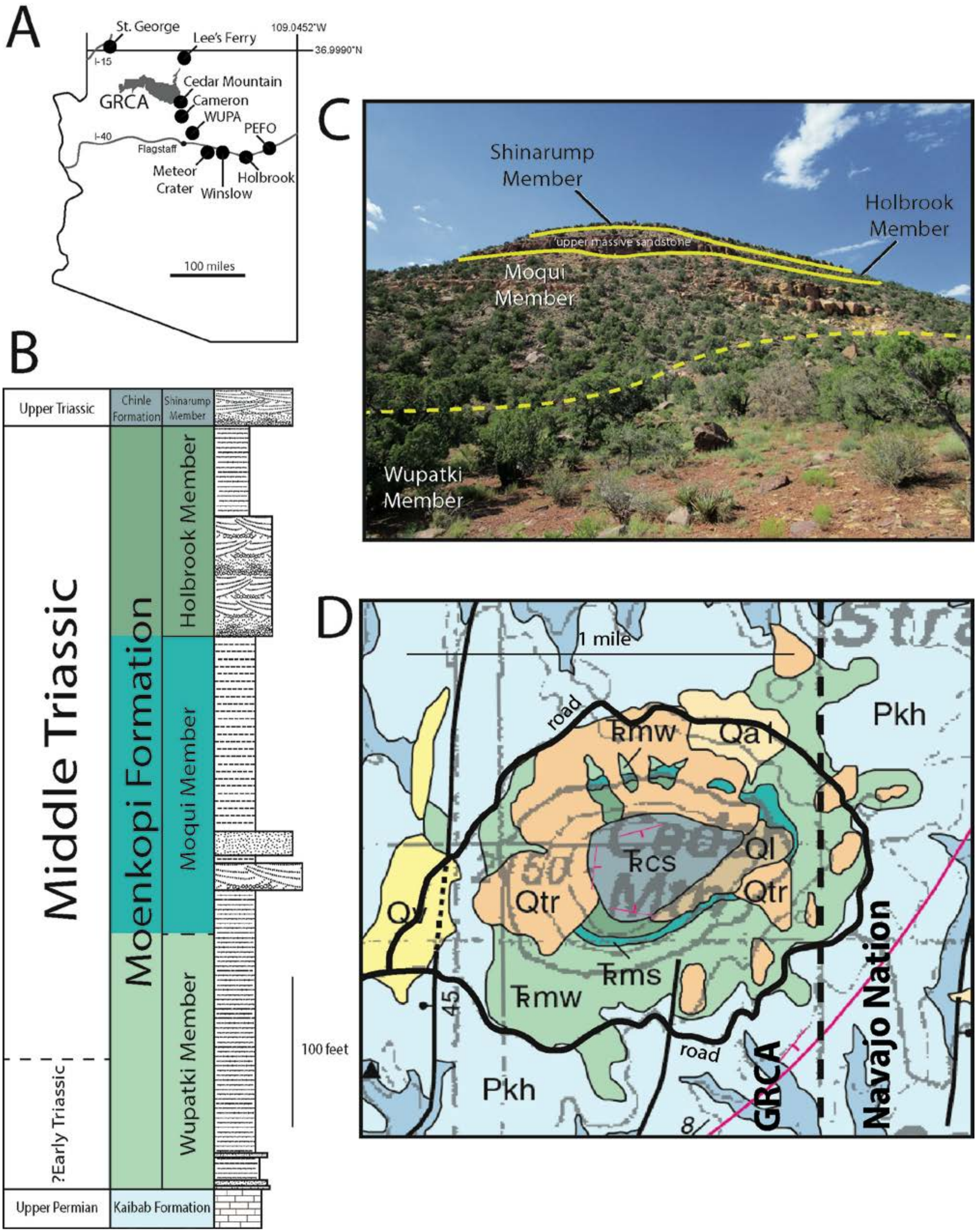

Figure 1. *Geographic location and stratigraphic section of Cedar Mountain, Grand Canyon National Park (NPS/MARSH ET AL.).* ***A.*** *Map of Arizona and southern Utah showing various locations discussed in the text.* ***B.*** *Stratigraphic section of the Mesozoic sedimentary rocks at Cedar Mountain, including the measured section of Noble (1922).* ***C.*** *Annotated view of the southwestern slope of Cedar Mountain.* ***D.*** *Geologic map of the Mesozoic section at Cedar Mountain (Billingsley and others, 2012).*

occurs just below the lowest gypsum bed, and the upper contact of the Moqui Member with the Holbrook Member occurs just above the highest gypsum bed (McKee, 1954; Stewart and others, 1972b; Morales, 1987).

Two prominent sandstone ledges within the Moenkopi Formation extend along the roughly east-to-west exposures throughout the Little Colorado River Valley. The "lower massive sandstone" occurs in the upper part of the Wupatki Member, and the "upper massive sandstone" occurs in the lower part of the Holbrook Member (McKee, 1954). The lower massive sandstone near Cameron (i.e., Cedar Mountain) is a prominent ledge-forming, very fine grained, well-sorted sandstone that is 3 to 9 m (10 to 30 ft) thick, nearly 23 m (75 ft) from the base of the formation (Stewart and others, 1972b). This ledge-forming sandstone has been traced throughout the area from Wupatki National Monument north to the Echo Cliffs and south to Meteor Crater. The upper massive sandstone is not well documented in the Cameron area, but it is well reported just west of Holbrook, Arizona, where it forms a 13 m (43 ft) thick, fine-grained sandstone bench nearly 18 m (60 ft) above the base of the member (Welles, 1947; McKee, 1954).

Continental redbeds such as the Moenkopi Formation and Shinarump Conglomerate are notoriously difficult to date to specific Triassic geochronological time bins, because those are defined by marine biostratigraphy. However, a combination of vertebrate and trace fossil biostratigraphy and radiometric dating support the hypothesis that the Moenkopi Formation is Early Triassic to early Middle Triassic in age (see below). Marcou (1858) first estimated the age of the Moenkopi Formation to be Triassic owing to its lithological similarity to the Triassic Bunter sandstone in Germany, but Newberry (1861) later estimated the unit to be Permian, because the underlying sedimentary rocks were considered to be Carboniferous (Dutton, 1882). Powell (1876) considered what is now the Moenkopi Formation in northwestern Arizona and southwestern Utah to be Triassic–Jurassic owing to the presence of brachiopods, crinoids, and bivalves in limestone beds in the lower part of the formation, but Walcott (1880) thought these fossils (and the strata) to be late Permian in age. Most researchers concurred with this designation (see discussion in McKee, 1954:8), except for Shimer (1919) who thought the fossils were Triassic in age, until vertebrate body and trace fossils were found throughout the formation along the Little Colorado River Valley (Welles, 1947; McKee, 1954).

Where the marine and marginal marine members of the Moenkopi Formation are exposed in eastern Nevada, they contain the Early Triassic *Meekoceras* ammonite zones (McKee, 1954; Ogg, 2012). The Moenkopi Formation between Holbrook and Cameron is quite fossiliferous in discrete stratigraphic horizons. Vertebrate fossils in the lower fossiliferous horizon occur in bonebeds of associated skeletons above the "lower massive sandstone" in the upper part of the Wupatki Member (exemplified by the UCMP locality V3835 near Meteor Crater; Nesbitt, 2005a) and include actinopterygian fish, mastodonsauroid and trematosaurian temnospondyls, and non-archosaur archosauromorphs such as tanystropheids (Welles, 1969, 1993; Nesbitt, 2005a, 2005b). Fossils in the upper fossiliferous horizon occur as disarticulated skeletal elements or isolated partial skeletons just underneath the "upper massive sandstone" in the Holbrook Member (exemplified by the UCMP locality V3922 near Holbrook; Nesbitt, 2000, 2005a, 2005b) and include sharks, actinopterygian and sarcopterygian fish, mastodonsauroid and brachyopid temnospondyls, and pseudosuchian archosaurs (Welles, 1947, 1969; McKee, 1954; Nesbitt, 2000, 2002, 2005a, 2005b). Invertebrate and vertebrate trace fossils are found on bedding planes in fluvial sandstones, are often associated with sedimentary structures such as ripples, mud cracks, and flute casts, and are concentrated in similar horizons as vertebrate body fossils (McKee, 1954; Klein and Lucas, 2010b) in the Wupatki Member and Holbrook Member. Trace fossils within the Moenkopi Formation include invertebrate burrows, arthropod tracks, and tetrapod tracks, many of which were collected from northern Arizona and are housed at the UCMP and MNA.

The most recent vertebrate biostratigraphy suggests that at least the eastern terrestrial outcrops of the Holbrook Member are as young as the early Middle Triassic (Lucas, 2010) based on the presence of the capitosaurid temnospondyl *Eocyclotosaurus*. This age estimate is supported by the presence of the tetrapod ichnogenera *Rotodactylus* and *Chirotherium* within the Holbrook Member; these ichnotaxa arguably only occur in the Middle Triassic (McKee, 1954; Klein and Lucas, 2010a; Henderek and others, 2017; see Brusatte and others, 2011 and Niedźwiedzki and others, 2013 for a possible Early Triassic record of cf. *Rotodactylus* isp.). Owing to the presence of Cordilleran magmatic arc-derived zircon grains incorporated into the prograding terrestrial Moenkopi–Chinle deposystems, U-Pb geochronology (either LA-ICP-MS or high-resolution CA/ID-TIMS) has been particularly effective in inferring the maximum depositional ages of these rocks. A detrital zircon sample from the Holbrook Member of the Moenkopi Formation (Dickinson and Gehrels, 2009b) suggests that it may have been deposited as late as the early Late Triassic (Carnian, ~230 Ma), which is at least 10 million years later than what vertebrate biochronology suggests (Cohen and others, 2013). A horizon near the top of the Moenkopi Formation at PEFO was recently dated to 241.10 ± 0.43 Ma using high-resolution CA-TIMS on the youngest single zircon grain (Rasmussen et al., 2020).

Previous Studies

The complete section of the Moenkopi Formation at Cedar Mountain in GRCA is important for determining the fluvial facies distribution across the aerial extent of the formation, because it is one of the only complete sections between the western marginal marine facies and the eastern fluvial facies. When it was first measured and described, the Moenkopi Formation exposed at Cedar Mountain was not differentiated into member-level units owing to vegetative cover (Noble, 1922); however, it was subsequently mapped as including the Wupatki Member, Shnabkaib Member, and Holbrook Member (Billingsley and others, 2012).

Noble (1922:72) noted a thin (0 to 1.2 m, 0 to 4 ft) "curious gnarly [conglomeratic] cherty bed" near the base of the section, which compares favorably to a similar bed found at the base of the Moenkopi Formation at Lee's Ferry (McKee, 1954; Stewart and others, 1972b) that may represent the southeastern most expression of the Timpoweap Member (Blakey and others, 1993). However, similar cherty conglomeratic beds are also present at the top of the Kaibab Formation (McKee, 1954), so the presence of the Timpoweap Member at Cedar Mountain is unlikely. Rather than being the Shnabkaib Member, the slope-forming, gypsiferous middle portion of Cedar Mountain represents the Moqui Member, as its lithology is inconsistent with the cyclic sabkha-like deposits of the type section of the Shnabkaib Member at St. George, Utah (Reeside and Bassler, 1922). As Stewart and others (1972b) noted, the Moqui Member of northern Arizona overlies the "lower massive sandstone" within the Moenkopi Formation (as it does at Cedar Mountain), but this sandstone occurs near the top of the Shnabkaib Member in southern Utah. Noble named a massive sandstone near the top of Cedar Mountain the "De Chelly sandstone" (1922:72), but this unit represents the "upper massive sandstone" of the Holbrook Member, and not the De Chelly Sandstone Member of the Permian Cutler Formation found within the Navajo Nation in northeastern Arizona (McKee, 1933; Read and Wanek, 1961).

GRCA Resources

There are no fossils previously reported from the Moenkopi Formation at Cedar Mountain, and Noble (1922) reported looking for, but not finding any fossils during his study. We collected a specimen referred to *Rotodactylus* isp. (GRCA 33186; figure 2), located numerous sedimentary structures, and identified the ichnotaxon *Scoyenia* cf. *gracilis* from the Wupatki Member and Holbrook Member, respectively, from Cedar Mountain (see "Results" below).

Paleontological Potential

Medium; much of the Moenkopi Formation in northern and northeastern Arizona is fossiliferous if specific stratigraphic horizons are targeted (however, this may be a function of the lack of comprehensive surveying). For example, fossils are unknown in the slope-forming Moqui Member (McKee, 1954 reported plant impressions found at Moqui Wash near Winslow, but it is unclear whether they actually came from the Moqui Member there). The two stratigraphic horizons that produce vertebrate fossils described above are present at Cedar Mountain, but are either largely covered by talus or vegetation (the upper part of the Wupatki Member) or are strongly cliff-forming (the "upper massive sandstone" of the Holbrook Member) along the section. Depending on if the Timpoweap Member is indeed present at the base of the Moenkopi Formation (see above), the ammonite genus *Meekoceras* may be present (McKee, 1954; Stewart and others, 1972b), but the contact between the lowest part of the Moenkopi Formation and the uppermost Kaibab Formation is poorly exposed. Invertebrate and vertebrate trace fossils are possible in fallen sandstone blocks from the Wupatki Member and Holbrook Member, but finding these in situ is unlikely.

Chinle Formation (Shinarump Member)

Geology

What is now accepted as the Shinarump Member of the Chinle Formation has long been recognized as a significant sedimentary unit throughout the Colorado Plateau, though its definition and lithological diagnosis have undergone substantial revision since its first conception (Powell, 1873, 1876; Gilbert, 1875). Recognized as the basal unit of the Chinle Formation (Stewart, 1957; Repenning and others, 1969; Stewart and others, 1972a), the Shinarump Member unconformably overlies the Moenkopi Formation and often deeply scours the top of that unit, eroding down into the Holbrook Member in large trough-stratified channels. Throughout the Little Colorado River Valley and near Cameron, the primary lithology of the Shinarump Member is usually characterized as a lightly colored sandstone with substantial conglomeratic lenses containing at least 50% clasts of 5 cm (2 in) in diameter (Gregory, 1917) and large petrified conifer logs. The unit is approximately 8 m (25 ft) thick at Cedar Mountain (Nobel, 1922), but its deposited thickness is nearly impossible to determine at a given outcrop unless overlying Chinle Formation strata are present. The typical conglomeratic facies of the Shinarump Member can grade laterally into finer-grained facies formally recognized as the Mesa Redondo Member (Cooley, 1958), but these are likely syndepositional overbank deposits correlative to the channelized fluvial system of the Shinarump Member (Irmis and others, 2011; Riggs and others, 2016; Martz and others, 2012, 2017). Regionally, the upper portions of the Shinarump Member and Mesa Redondo Member have been heavily pedogenically modified, and this can be used to recognize these units locally (Irmis and others, 2011, supp.). This may be the same as the post-depositional "mottling" described by Stewart and others (1972a), which is

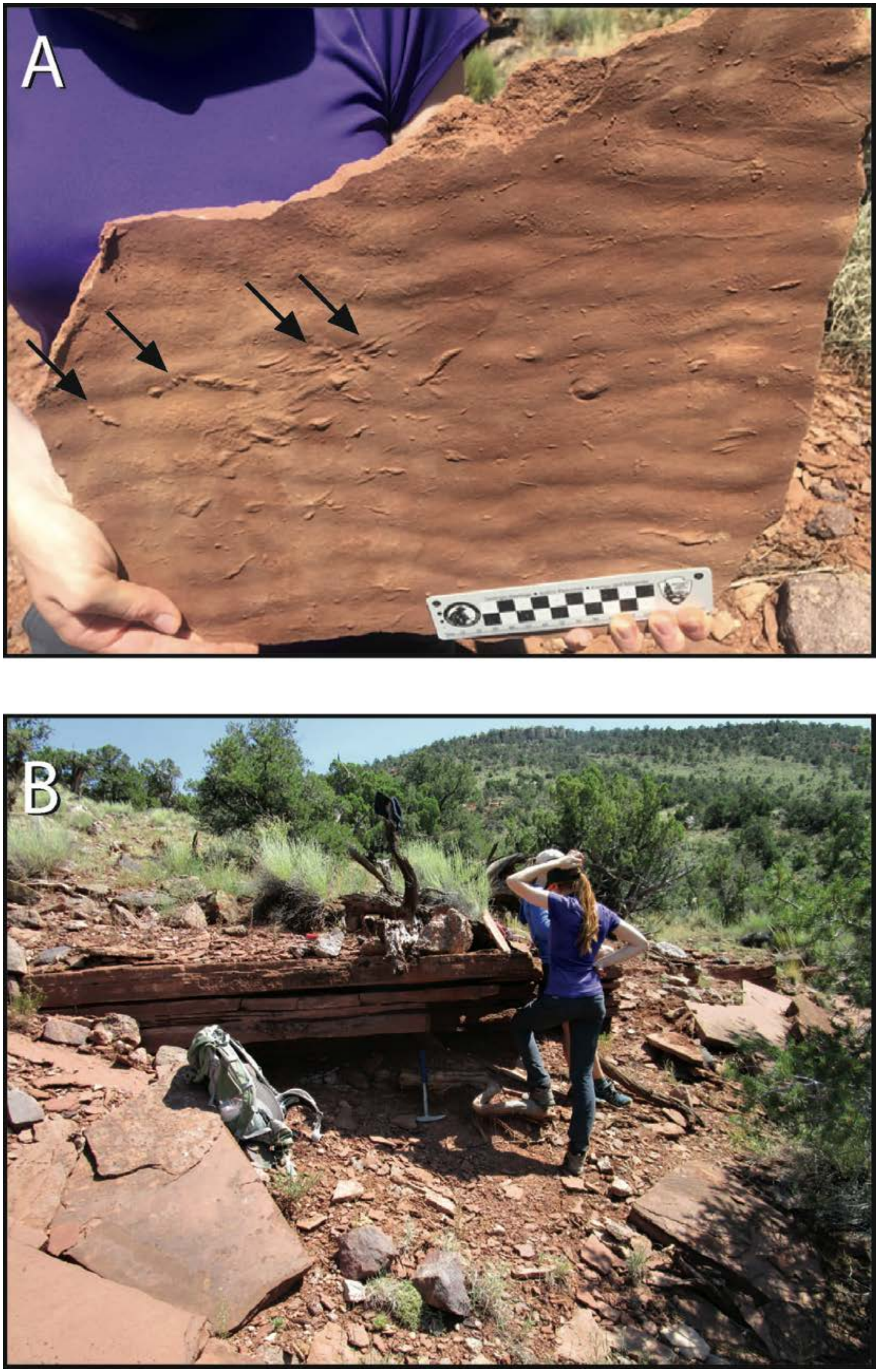

Figure 2. *GRCA 33186,* Rotodactylus *isp. from the Wupatki Member, Moenkopi Formation at Cedar Mountain (NPS/MARSH ET AL.).* ***A.*** *Trackway with arrows showing individual prints.* ***B.*** *Photo of locality where the* Rotodactylus *trackway was found (hammer at approximate location of fallen block).*

a pedogenic alteration of the top of the Moenkopi Formation and parts of the Shinarump Member. At Cedar Mountain the top of the Shinarump Member is weathered off and the upper mottled horizon is not preserved or was never present.

Whereas the Shinarump Member of the Chinle Formation lacks diagnostic vertebrate fossils, it contains wood fossils similar to "*Araucarioxylon*" (figure 7) and it stratigraphically underlies lower Chinle Formation members that have been removed by erosion here. These removed overlying units, such as the Blue Mesa Member, are Late Triassic (Norian) in age owing to the presence of non-pseudopalatine leptosuchomorph phytosaurs and the absence of the aetosaur *Typothorax* at PEFO and other regional localities (Lucas, 2010; Martz and Parker, 2017). Detrital zircon samples from the Shinarump Member of the Chinle Formation in that study (Dickinson and Gehrels, 2009b) do not seem to contain the youngest deposition-age grains, but a high-resolution U-Pb date from the laterally equivalent Mesa Redondo Member supports a Late Triassic age (Norian, ~228 Ma) for the Shinarump Member (Atchley and others, 2013; Riggs and others, 2016). Lithostratigraphic correlation of the Shinarump Member to the base of the Dockum Group of Texas also suggests an early Norian age based on the presence of basal phytosaurs in the latter unit (Martz and Parker, 2017).

Previous Studies

The Shinarump Member was originally recognized as the capping sandstone at Cedar Mountain (Noble, 1922), but at the time the unit was not recognized as the basal unit of the Chinle Formation in the area. Noble (1922) described the Shinarump Member as a hard, poorly sorted, cross-bedded conglomerate with chert clasts and sedimentary clasts that do not resemble any units in the underlying Moenkopi Formation. At the time, the Shinarump Member was considered Late Triassic in age owing to the presence of large petrified logs (see below) and its correlation to other Shinarump Member outcrops in the region that underlie other sedimentary units with Late Triassic vertebrate fossils (i.e., the rest of the Chinle Formation).

GRCA Resources

Noble (1922) described in situ petrified logs from the Shinarump Member at Cedar Mountain, and several pieces of petrified wood were previously documented by GRCA interns in 2011 as weathered talus and in situ. We observed numerous pieces of petrified wood ex situ and in situ (figure 7; see "Results" below).

Paleontological Potential

Low; the taxonomy of the petrified wood found in the Shinarump Member in northern Arizona is in need of revision, and the rare vertebrate bones that have been reported from the unit (Martz and others, 2017) are too fragmentary to determine identifications beyond major clades (e.g., Temnospondyli, Phytosauria). The finer-grained lateral equivalent of the Shinarump Member, the Mesa Redondo Member, is not fossiliferous where it crops out near PEFO (Martz and others, 2012, 2017).

FIELD METHODS

The two-day PaleoBlitz at Cedar Mountain occurred on July 15 and 16, 2019 as part of the GRCA Paleontological Resource Inventory (study no. GRCA-00745, permit no. GRCA-2019-SCI-0002). Access to Cedar Mountain was provided by a difficult two-track dirt road that does not seem to have been improved since Noble first described it as "rather poor" (1922:71). Any future excursions to Cedar Mountain will require a high clearance, short-bed 4x4 vehicle to best navigate the patches of boulders, ruts, and narrow switchbacks on the road. Instead of surveying the slope of the mesa in a systematic fashion (which is largely made up of the unfossiliferous Moqui Member), we targeted the specific horizons in the Wupatki Member and Holbrook Member that have the best potential for fossil preservation, as described above (figure 1D).

The locations of sedimentary structures and fossils were documented using a Garmin GPS MAP64S and a resource-grade GNSS receiver, and digital photographs were taken with a Canon Powershot ELPH 150 IS and iPhone camera. We surveyed for body fossils by inspecting split pieces of sandstone and looking for bones weathering out of softer units, and we surveyed for trace fossils by inspecting the underside of sandstone overhangs and flipping blocks of fallen sandstone. Field consolidant was not used on any specimens. Copies of field notes, photographs, and GPS data are on file at GRCA and the WASO Paleontology Archives. The fossil potential for the Triassic units at GRCA described above in the overview of Triassic strata at GRCA include low (lacks fossils or contains fossils with little scientific significance), medium (contains fossils in equivalent sections regionally), and high potential (contains scientifically significant fossils).

RESULTS

Moenkopi Formation

Wupatki Member

The Wupatki Member is best exposed in low relief along small drainages, which incise into the alternating layers of siltstone and sandstone that characterize the member. We could not locate an extensive "lower massive sandstone" in the unit and thus were not able to determine our exact stratigraphic position within the member at a given location. However, the incised outcrops in the drainages expose innumerable slabs of ripple-laminated sandstone; most of the ripples are asymmetrical and indicative of uni-directional flow. We were not able to discern the upper contact with the Moqui Member in outcrop owing to the coverage of juniper.

Rotodactylus Peabody, 1948

Type species—*Rotodactylus cursorius* Peabody, 1948.

Type specimen—UCMP 37794, trackway of 11 pes-manus sets.

Type locality and horizon—UCMP V3835, near Meteor Crater, Arizona; Wupatki Member, Moenkopi Formation.

Diagnosis—Semi-bipedal, long-striding trackway of a small five-toed reptile; when present, the manus is closer to the midline than the pes (Peabody, 1948); digit IV longer than digit III in the pes (Haubold, 1967, 1971). Brusatte and others (2011) suggested that the ichnogenera *Prorotodactylus* and *Rotodactylus* were made by dinosauromorphs, which would extend the origin of Dinosauromorpha at least into the Middle Triassic 5–10 million years before the appearance of the oldest dinosauromorph body fossil (Ezcurra and others, 2017; Marsh and Parker, 2020).

Rotodactylus

Referred specimen—GRCA 33186 (figure 2).

Location—Cedar Mountain, GRCA (figure 1).

Description—This specimen was collected as a small sandstone slab (figure 2A) that fell a short distance from its source horizon in the Wupatki Member at Cedar Mountain (figure 2B). It includes three to four partial pes tracks that run obliquely along a rippled surface. The front two prints appear to include ungual drag marks, and the rest of the rippled surface contains flute casts and other drag marks. It is not possible to determine the ichnospecies because the prints are too subtle and do not preserve enough anatomy, but the presence of the ichnogenus *Rotodactylus* is characteristic of the Wupatki Member in northern Arizona (Peabody, 1948; Klein and Lucas, 2010b).

Moqui Member

We found a few sedimentary structures within the thin sandstone lenses in the Moqui Member at Cedar Mountain, but we did not locate any fossils. The fine-grained, gypsum-rich slopes that make up most of the outcrop of this member are mostly covered by juniper and are weakly bedded in the better exposures around the mesa. One location in the upper part of the Moqui Member included a local sandstone unit that protects the softer underlying beds in the member. We found mud cracks superposed on bi-directional ripples in a laminated sandstone from that channel (figure 3). We were also able to locate primary gypsum beds below this prominent sandstone, indicating that the Wupatki Member–Moqui Member contact is lower than this horizon and that this sandstone is not the "lower massive sandstone" that is found near the top of the Wupatki Member elsewhere in the region.

Figure 3. *Mud cracks superposed on bi-directional ripples in a sandstone from the Moqui Member of the Moenkopi Formation at Cedar Mountain. Hammer is 40 cm (16 in) long (NPS/ MARSH ET AL.).*

Holbrook Member

We were unable to locate a bench-forming conglomeratic layer within the Holbrook Member at Cedar Mountain, which would have been the most likely bed to yield vertebrate fossils. We determined that the second unit of Noble's measured section (1922:72) is the "upper massive sandstone" found throughout the Little Colorado River Valley; this cliff-former is difficult to navigate around the mesa, but provides a gentle slope above it containing interspersed exposures of orthogonal ripple-laminated sandstones (figure 4). One location yielded internal molds of invertebrate burrows, but they were found ex situ and their orientation is impossible to determine. The burrows are straight, circular in cross section, have weak transverse striations on the outer surface, and a few appear to taper in one direction (figure 5).

Figure 4. Hand sample of orthogonal ripples in alternating layers of laminated sandstone from the Holbrook Member of the Moenkopi Formation at Cedar Mountain (NPS/MARSH ET AL.).

Figure 5. Internal molds of burrows found ex situ in the Holbrook Member of the Moenkopi Formation at Cedar Mountain (NPS/MARSH ET AL.).

Scoyenia White, 1929

Type species—*Scoyenia gracilis* White, 1929.

Type specimen—USNM 201869, straight to slightly curved, horizontally overlapping burrows considered to be a deposit feeding or dwelling structure, potentially made by insects (White, 1929; see Paleozoic Invertebrate Ichnology contribution by Miller and others in this inventory).

Type locality and horizon—GRCA 8538, Grand Canyon National Park, Arizona; lower part of Hermit Formation (Permian).

Diagnosis—Horizontal, narrow, and curved burrows; unbranched (White, 1929; Frey and others, 1984; MacEachern and others, 2010).

Scoyenia cf. *gracilis*

Referred specimen—Nothing collected; several hand samples observed but left in the field (figure 6).
Location—Cedar Mountain, GRCA.

Description—These hand samples were observed as ex situ surface float in a talus pile of associated ripple-laminated sandstones above the "upper massive sandstone" in the Holbrook Member at Cedar Mountain. They include horizontal, gently curved burrows that generally trend in the same direction, but can overlap one another. The sedimentological and ichnological fabric of this portion of the Holbrook Member (and much of the Moenkopi Formation in northern Arizona) is consistent with the *Scoyenia* Ichnofacies (Buatois and Mángano, 1995, 2004), which is characterized by horizontal feeding and locomotory traces, fish fin markings, vertical and horizontal dwelling structures, arthropod and vertebrate trackways, and plant root traces (MacEachern and others, 2010). These occur in low-energy terrestrial systems with alternating periods of flooding and subaerial conditions, which describes much of the depositional setting of the continental fluvial system of the Moenkopi Formation in northern Arizona (McKee, 1954; Stewart and others, 1972b; MacEachern and others, 2010).

Chinle Formation

Shinarump Member

We found numerous fragments of petrified wood and impressions of wood in Shinarump Member clasts (figure 7). The in situ logs within the Shinarump Member at Cedar Mountain are several meters in length and often have chert clasts silicified onto the outer surface of the wood. Mud rip-up clasts with concentric bands in cross section are commonly associated with the petrified wood near the base of fining-upward channel sequences in the Shinarump Member.

CONCLUSIONS

The Triassic sedimentary rocks at Cedar Mountain are the only Mesozoic units within the boundary of GRCA, and beneath the juniper cover are quite similar to equivalent units in the region. The Moenkopi Formation at GRCA includes the Wupatki Member, Moqui Member (but not the Shnabkaib Member), and Holbrook Member, all of which are similar with respect to sedimentary architecture and sedimentary structures to the same units at Cameron, WUPA, Meteor Crater, and Holbrook, Arizona. We were able to match Noble's measured section to the outcrop at Cedar Mountain (1922), which allowed

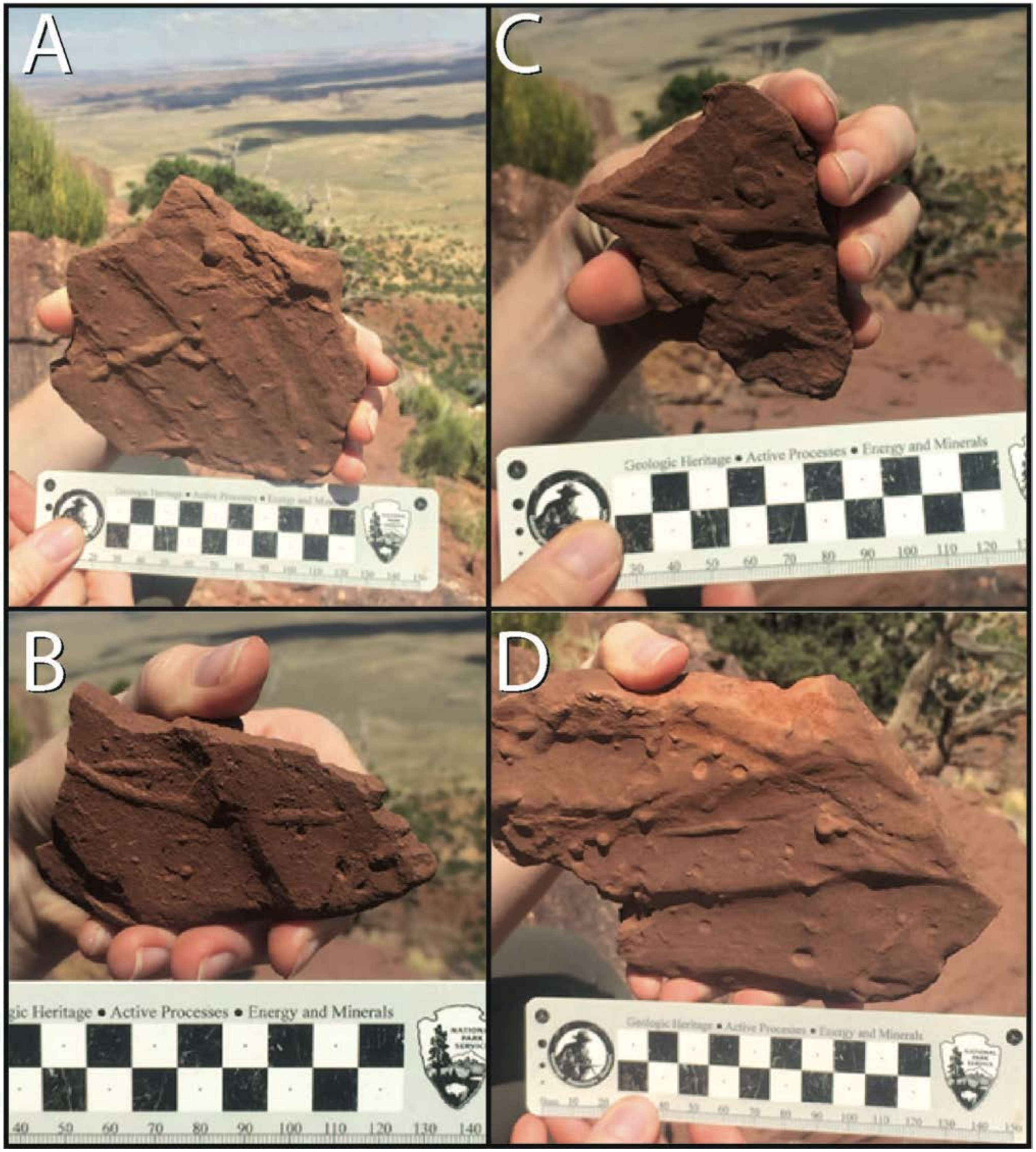

Figure 6. *Hand samples of* Scoyenia *cf.* gracilis *found in the Holbrook Member of the Moenkopi Formation at Cedar Mountain (A–D) (NPS/MARSH ET AL.).*

us to target specific areas for a two-day paleontological survey. The discovery of *Rotodactylus* in the Wupatki Member at GRCA is the first Mesozoic fossil specimen found in the park to be collected for the park's museum collections, and it confirms the presence of a small reptilian trackmaker (possibly a dinosauromorph; Brusatte and others, 2011) in the Middle Triassic similar to those reported from other sites in northern Arizona. Similarly, we confirm the presence of the *Scoyenia* Ichnofacies in the Holbrook Member, which is typical of the fluvial and overbank depositional settings of the eastern exposures of the Moenkopi Formation. Large pieces of

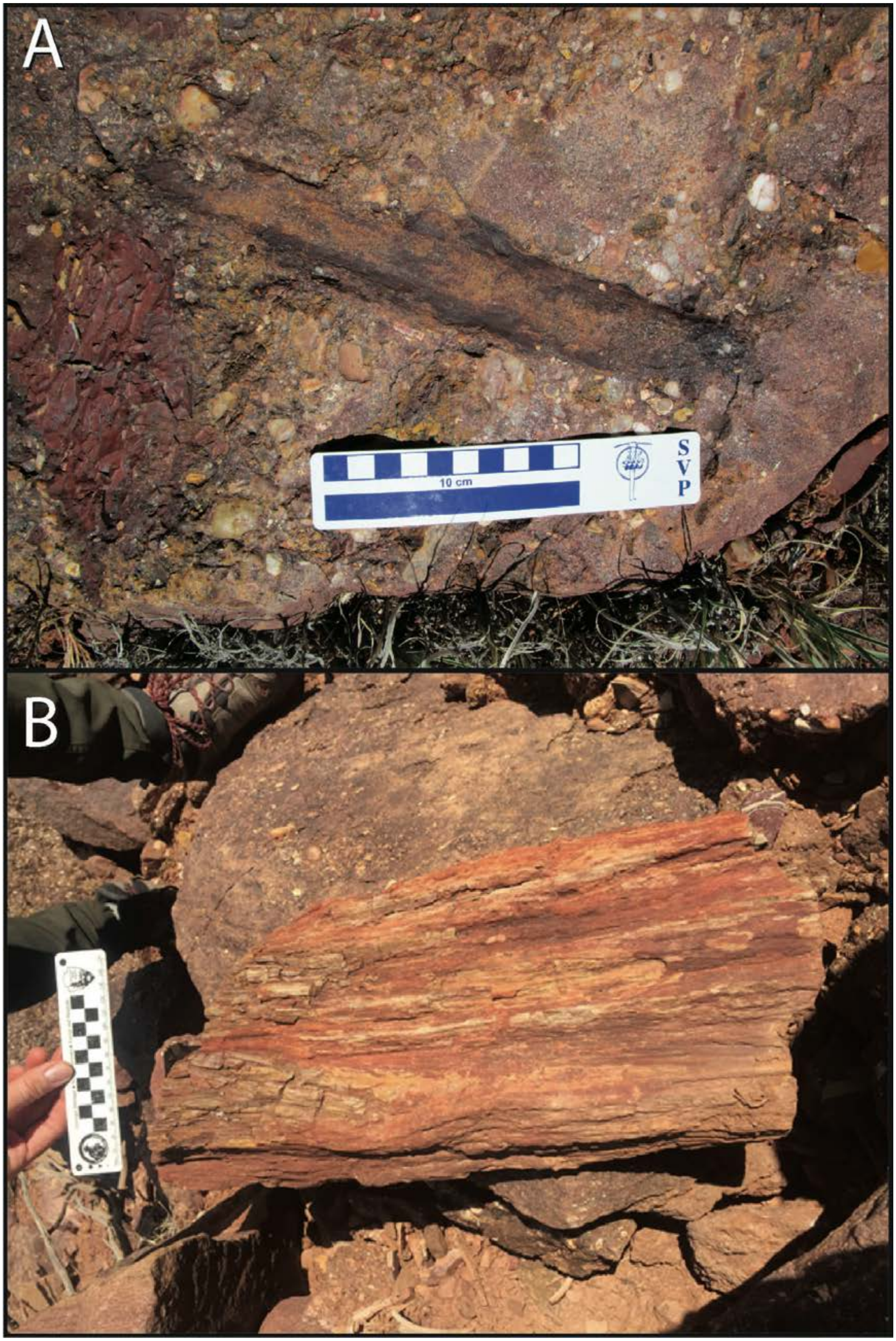

Figure 7. *Plant fossils from the Shinarump Member of the Chinle Formation at Cedar Mountain (NPS/MARSH ET AL.).* ***A.*** *Impression of a stem or small log in a fallen block, exhibiting the chert pebble conglomerate and mud rip-up clasts of the member.* ***B.*** *Fragment of conifer log that eroded from the Shinarump Member.*

petrified wood are common in the Shinarump Member of the Chinle Formation, which caps Cedar Mountain and covers much of its slopes as talus.

Given the difficult access to Cedar Mountain as well as the low to medium potential to find exposed fossil resources, the Mesozoic section at GRCA needs very little monitoring in the future. More of the fallen sandstone slabs of the Holbrook Member and incised drainages in the Wupatki Member may be surveyed for additional trace and/or body fossils, but the likelihood of finding anything new is low. If future surveys or monitoring efforts are to take place, we suggest navigating the road from Desert View as few times as possible, camping at the base of Cedar Mountain for the duration of the trip, and contacting the Navajo Nation for permission to use the eastern road to access the site.

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SHASTA GROUND SLOTH

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Shasta Ground Sloth
Scientific Name: *Nothrotheriops shastensis*
Geologic Age: 11,000 years ago (Pleistocene)
Geologic Formation: Cave deposits

Interactive 3D models

Stable and dry environments in caves preserve organic materials like fur.

During the last Ice Age, it was cooler and wetter than today, allowing vegetation to flourish. This provided plenty of food for large herbivores, like the bear-sized Shasta ground sloth. Analysis of plant material in fossil dung, or coprolites, tells us what these ground sloths ate.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

2 of 9

Grand Canyon National Park Fossil Trading Card featuring bones, hair, and coprolites of the fossil ground sloth Nothrotheriops shastensis *from Pleistocene cave deposits (NPS).*

PLEISTOCENE/HOLOCENE CAVE FOSSILS FROM GRAND CANYON NATIONAL PARK—ICE AGE (PLEISTOCENE) FLORA, FAUNA, ENVIRONMENTS, AND CLIMATE OF THE GRAND CANYON, ARIZONA

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ABSTRACT

Here we review the Ice Age (Pleistocene) floras and faunas found within the Grand Canyon and adjacent Coconino, Kaibab, Kanab, Uinkaret, Shivwits, Hualapai plateaus, and the Marble Platform. These Pleistocene fossils are predominantly discovered in and recovered from the dry caves created in the numerous limestone rock formations (mainly the Redwall Formation). What makes the greater Grand Canyon region unique in the Southwest is the abundance of dry caves. A unique set of fossils comes from the urine-cemented middens (debris piles) made by packrats. These middens are created in caves, crevices, overhanging rock ledges, and rockshelters. As long as the middens are protected from direct precipitation, the contents are preserved. Materials for these middens include a diversity of plant remains (leaves, twigs, flowers, thorns, bark, seeds), invertebrates (mollusks, arthropods), dung, raptor pellets, and bones (mammals, birds, reptiles)—all gathered from within 100 m (330 ft) of the nest. Some of the earliest paleoecological studies of the American Southwest using packrat middens began in the Grand Canyon. Select caves with diverse fossil records and chronologies are discussed in detail, including: Stanton's, Sandblast, Kaetan, Bida, Double Bopper, Rampart, and Vulture caves. The Ice Age record is biased towards those deposits that can be radiocarbon-dated, typically less than 50,000 years before present. Select alluvial and fluvial deposits in the Colorado River corridor hold a biotic record but have issues with precise age assessments; many such deposits have been flushed from the river corridor by periodic massive floods. The fossil record is also biased toward the eastern portion of the Grand Canyon and the far western sector (predominantly within the river corridor), leaving the majority of the Grand Canyon not surveyed and not sampled for assessment of the environmental and climatic changes through the Pleistocene.

INTRODUCTION

The Colorado Plateau is a distinct physiographic province in western North America covering an area of roughly 337,000 km^2 (130,115 mi^2) across parts of Arizona, Colorado, New Mexico, and Utah. Elevations range from about 360 m (1,180 ft) in the overall Grand Canyon (GC; which includes the Grand Canyon National Park, GRCA) river corridor to an average at the eastern South Rim of 2,072 m (6,800 ft) to 3,850 m (12,630 ft) on the nearby San Francisco Peaks at Flagstaff, Arizona, with an average elevation of 1,525 m (5,000 ft). The Colorado River of Grand Canyon is located along the southwestern portion of the Colorado Plateau in Arizona and is renowned for its dramatic display of geomorphic effects created by fluvial incision and its unique dry-preservation of fossils from the Ice Age (late Pleistocene and Holocene [Quaternary]; most recent 2.58 million years). Although there were at least 22 glacial-interglacial cycles during the Ice Age, this dis-

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cussion is limited to the most recent episode (called the Wisconsinan Glaciation), which includes the transition to the modern climate (latest Pleistocene and Holocene; the most recent 50,000 years of geologic history).

Due to its range in elevations and physiographic position in western North America, the Colorado Plateau (CP; along with its GC river corridor) plays a key role in the continental monsoons much in the same way that the Tibetan Plateau affects the Southeast Asian monsoon climate (Tang and Reiter, 1984; Adams and Comrie, 1997). In general, precipitation decreases from high elevations to lower elevations. Summer precipitation decreases from the southern Colorado Plateau northward which correlates to the strength of the summer monsoon. These relationships have important consequences for modern and Ice Age biotic distributions in the Grand Canyon and on the surrounding plateaus (Mock, 1996; Higgins and others, 1997; Anderson and others, 2000, among others).

Here we review the Ice Age floras and faunas found predominantly within the GC but also on adjacent rims made by the Coconino, Kaibab, Kanab, Uinkaret, Shivwits, and Hualapai plateaus in addition to the Marble Platform at the up-river end of GC. The Grand Canyon includes land administered by the Havasupai, Hualapai, and Navajo Indian tribes along with federal lands managed by National Park Service (Grand Canyon National Park, Lake Mead National Recreation Area), Bureau of Land Management (Grand Canyon-Parashant National Monument), and US Forest Service (Coconino and Kaibab National Forests). The GC and its Colorado River corridor extends nearly 448 km (278 mi) in length and encompasses an area of about 4,921 km^2 (1,900 mi^2).

The preservation potential of Ice Age fossil deposits within the confines of the GC is limited due to active downcutting, steep canyon walls, abundant mass wasting, and periodic catastrophic flooding. Occasionally one can find some perched Ice Age alluvium that has been spared being flushed by subsequent floods down to the Gulf of Mexico. What has been the "gold mine" for Ice Age preservation are the dry caves created in the numerous limestone rock formations coupled with the arid climate. For details about the geology and overall history of the region, see the Stratigraphy article by Connors and others in this publication or Beus and Morales (2003).

There are a variety of geochemical analyses used to assess the age of the various deposits found throughout the GC. For the Ice Age fossils of preserved organic remains researchers typically use radiocarbon dating (^{14}C, radiometric dating). This isotopic dating technique is accurate for only about the most recent 50,000 years. Over the past couple of decades the technique has been refined and now researchers refer to ages in "calibrated" (or corrected) years before present (cal yr BP). "Before present" is expressed as pre-1950 (pre-atomic bomb) and can be thought of in terms of "years ago". In the 1970s and 1980s a researcher would need enough organic remains to fill an old 35-mm film can in order to obtain an accurate radiocarbon age. Now, with a technique called accelerator mass spectrometry (AMS), a researcher can use a single seed or piece of wood the size of a pin head (Van Devender and others, 1985). In the review below of fossil localities, the established age range will be presented. The interested reader who wants to know more details about the chronology will need to go to the original publications provided in the literature cited.

PRESERVATION SCENARIOS (TAPHONOMY)

River Corridor Sediments

Much has been written about the Colorado River and its evolution in the GC region (e.g., chapters in Young and Spamer, 2001; Beus and Morales, 2003). Tobin and others (in press) provide a detailed overview of the karst system model as one of the primary drivers of canyon development and stream piracy. Critical for the preservation of the fossil record is a preserved depositional environment. The fairly narrow river corridor offers few places where fluvial and alluvial sediments can persist for a long period of time. Periodic floods have occurred along the river corridor, especially related to the series of lava dams that were positioned in the west region of the GC (Hamblin, 1994; Fenton and others, 2002). Damming with sediment infilling (along with outburst-flood deposits) within the GC has permitted select side canyons to preserve some of the perched alluvial deposits (although some of these observed units might be related to spring-fed deposition and not flood debris; see Kaufman and others, 2002 and references within). These rare sedimentary deposits hold a record of select Grand Canyon past environments.

Dry Caves

Cave morphology throughout the GC can be separated into two distinct groups: 1) caves formed under confined hydrogeologic conditions (i.e., phreatic zone, saturated, below water table) and 2) those formed under unconfined conditions (i.e., vadose, unsaturated zone; Hill and Polyak, 2010). Those formed under confined conditions are typically older, dry today, and removed from current hydrologic processes and are typically assumed to have formed either during or prior to river corridor incision. Unconfined caves are being formed currently, are a part of the karst groundwater system of the region and are actively recharged from precipitation on the surrounding plateaus. These differing conditions have resulted in a dichotomy of cave morphology in GC (Huntoon, 2000).

Some of the oldest and most impressive cave systems in the area are formed in the upper members of the Redwall Limestone (see overview in Tobin and others in press). Dating of mammillary cave formations in some of these caves places their formation prior to 1.6 to 3.7 million years ago (Polyak and others, 2008). These caves form along regional fracture patterns, resulting in two-dimensional maze caves with minimal vertical development, except in rare cases. These "maze caves" formed under phreatic conditions (Hill and Polyak, 2010) and follow regional hydrologic gradients, ultimately emerging in the canyon. As the canyon incised, the water table dropped, resulting in the dewatering of these cave systems and exposing cave entrances along canyon walls. There are competing hypotheses on their formation with observations supporting both: epigenic processes (Huntoon, 2000) versus hypogenic processes (Hill and Polyak, 2010).

Due to the dry nature of these "confined" caves, they often provide the best environment for preservation of paleontological resources from the Pleistocene to recent times. The nature of the known entrances to these caves also plays a major role in what species are most likely to be preserved within them. Since these caves were exposed to the surface environment due to canyon incision, the entrances are typically in cliff faces with hundreds of feet of cliff above and below. This results in a limited variety of species that can actively use them. These species typically include birds, bats, packrats, ringtails, and an extinct mountain goat. When these dry caves have easier access, evidence of a wider array of species can be found that utilized them, including ground sloths, carnivores of many types, tortoises, and other forms of Pleistocene fauna.

Ongoing cave development is evident throughout the region as well. While these "unconfined" caves are more sporadically distributed throughout the park, many large springs are tied to them. The speleogenesis of these caves is much simpler than the confined systems, following the typical model of epigenic karst development. As with caves at the top of the Redwall Limestone, these caves follow regional structural patterns. Water is sourced directly from precipitation that recharges the aquifer via sinkholes on the surrounding plateaus. These regional aquifers appear to have a distributary pattern (Jones and others, 2018), with individual sinkholes tied to multiple springs. Springs on either side of the Colorado River have distinct flow patterns (Tobin and others, 2018), resulting in vastly different spring morphologies, with only aquifers on the north side of the Colorado River having significant cave development. Due to the increased moisture in these caves, they typically have minimal paleontological resources, with the majority that have been noted tied to packrat (typically nearer the drier entrance) and bat use.

What makes the greater Grand Canyon region unique in the Southwest is the abundance of dry caves. The development of these confined caves helps keep the cave and its contents dry, but having the climate and environment outside arid is equally as critical for preservation of Pleistocene-age fossils. A case in point: a horizontal crevice a mere 20 cm (8 in) in from the dripline can preserve packrat middens (see below) for over 30,000 years.

Packrat Middens

Packrats (trade rats, woodrats) are a genus of rodent (Rodentia, Cricetidae, *Neotoma*) with about 20 species with distributions from Alaska to southern Mexico (Vaughan, 1990). There are more species of packrats whose distributions include the greater Grand Canyon area than any other region for the genus. They all have the habit of making a nest and den along with the construction of debris piles over the living areas (Dial and Czaplewski, 1990; Finley, 1990). Materials for these debris piles include a wide diversity of plant remains (such as leaves, twigs, flowers, thorns, bark, and seeds), dung, bones, and rocks—typically all gathered from within 100 m (330 ft) of the nest (Spaulding and others, 1990). Faunal remains recovered from the debris piles are not all necessarily of local origin (especially when sourced from carnivore dung, regurgitated pellets, and raptor and vulturid nests; figure 1) (Mead, 2005). These nests and dens can be created in caves, crevices, overhanging rock ledges, and rockshelters. As long as the middens are protected from direct precipitation, the contents are preserved.

As the packrat uses the den and nest, it cleans the passageways and reassembles the pile of debris on top. In so doing, what looks like a mine tailing dump develops along the edge of the constructed mound. Over time this mound, containing all of the contents collected by the packrat along with its dung is incorporated into a mixed heap of debris and then is scent-marked with its urine. Repeated urination on the debris pile ultimately cements all the material into a rock-hard mass (concentrated urine is called "amberat"); the cemented debris pile is called a "midden" (figure 2).

Some of the earliest paleoecological studies of the American Southwest using packrat middens began in the GC (Phillips and Van Devender, 1974; Van Devender and Mead, 1976). The entire GC has not been assessed for packrat middens and their paleoecological data; rather, research has been limited to select regions primarily in the eastern half. Major study areas are typically along the river corridor and in side canyons and include Stanton's Cave (Dryer, 1994), Little Nankoweap Canyon (Mead and others, 2003), Chuar (Cole, 1982, 1990a, 1990b), Hance Canyon and Horseshoe Mesa (Cole, 1982, 1990a,

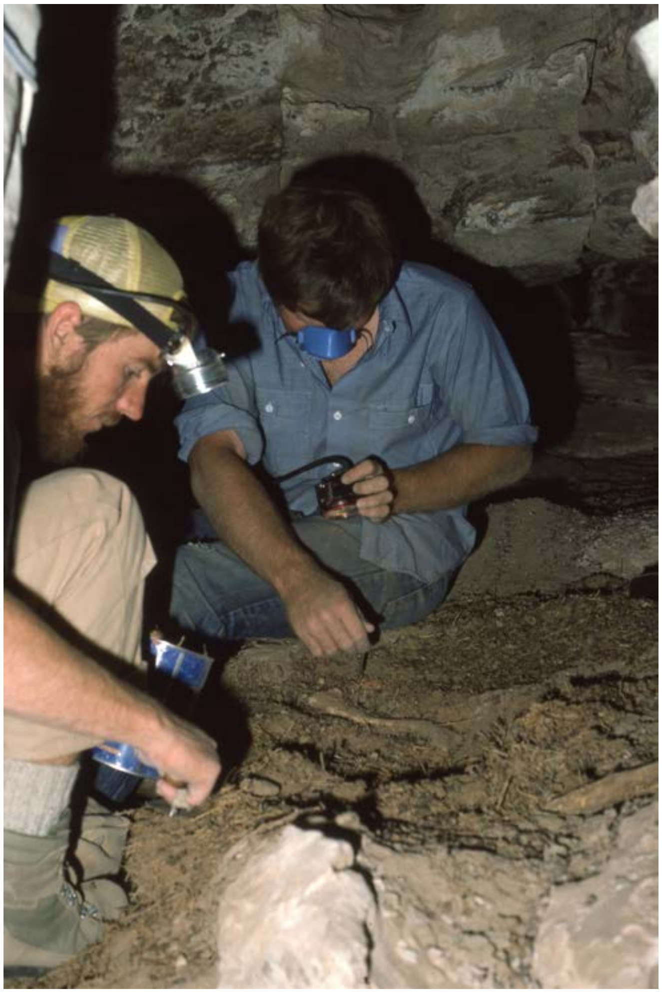

Figure 1. *Steve Emslie (right) and Larry Coats (left) excavating a condor (*Gymnogyps*) nest and skeletal remains reclaimed by a packrat and made into a midden, Sandblast Cave, 1984 (EMILEE MEAD).*

1990b), and Rampart Cave, Vulture Cave, and surrounding canyons (Phillips and Van Devender, 1974; Mead and Phillips, 1981; Phillips, 1984; Spaulding and others, 1990).

These preserved middens are valuable for a number of reasons. Each can be accurately radiocarbon dated. They contain abundant macrobotanical remains typically from within the home range of less than 100 m (330 ft) (Spaulding and others, 1990). Multiple species of macrobotanical remains can be independently radiocarbon dated to produce accurate coeval habitat reconstructions. Microfaunal fossils found associated with botanical remains often include the delicate skeletal remains of the local herpetofauna, species often not found in typical alluvial localities due to the abrasive nature of deposition. Interestingly, radiocarbon-dated packrat middens were used to determine the rates of cliff retreat in the eastern GRCA (Cole and Mayer, 1982).

TAXONOMIC GROUPS

Appendix A presents a list of known biotic remains recovered from Pleistocene deposits in the GC region. The list presents taxa by primary publication resource and not by locality (which can be determined from the primary reference).

Plants

Due to the numerous dry cave and rockshelter localities coupled with the overall arid environment, Pleistocene-age plant remains are plentiful within each packrat midden unit. Packrats are basically browsers, over-selecting the woody and herbaceous plants but

Figure 2. *A juvenile extinct Harrington's mountain goat (*Oreamnos harringtoni*) skull in a packrat midden, Stevens Cave, 1984 (EMILEE MEAD).*

typically underrepresenting the graze species such as the grasses. Although equally as well-preserved as the macrobotanical fossils, pollen remains from the region have been less frequently utilized for paleoenvironmental reconstructions. Martin and others (1961) recovered pollen from Shasta ground sloth dung in Rampart Cave. Pollen frequencies recovered from sediments were compared to pollen counts from artiodactyl dung pellets and macrobotanical remains from the same sediments from test pits in Bida and Kaetan caves (see below; O'Rourke and Mead, 1985). Pollen and microhistological remains from dung were also compared to fossils from test pits in Stanton's Cave (Robbins and others, 1984; see Hansen, 1974 about technique). Pollen assemblages and associated plant macrofossils from packrat middens do reflect similar vegetation signals but this still needs to be further assessed for future paleoecological reconstructions (Anderson and Van Devender, 1991). Ideally one would sample the macrobotanical remains and pollen from packrat middens and also assess the pollen and microhistological remains from dung also in the midden, hopefully selecting not only packrat pellets but also dung from potential grazers.

Invertebrates

The recovery and study of Ice Age and Holocene-age mollusks from the GC is still in its infancy. The extant taxa and their distributions are well studied from a few localities, primarily from the work of Pilsbry and Ferriss (1911). Spamer and Bogan (1993) provided a critical overview of the extant taxa. Spamer (1993) and Spamer and Bogan (1993) synthesized the known late Pleistocene malacofaunas (molluscan faunas) and emphasized that much is yet to be understood about the mollusks of the region dating to the last glacial and early Holocene. Kaufman and others (2002) provide a few more records but still illustrate that the Pleistocene molluscan faunas are not adequately studied. Mollusks have also been incorporated into packrat middens (Cole and Mead, 1981). Ostracodes are equally as poorly understood in the GC region (Kaufman and others, 2002). The record of Pleistocene arthropods is restricted to those fossils recovered from dry-preserved packrat midden and cave sediment localities (Elias and others, 1992), and again, the group as a whole for the Ice Age is poorly understood. The single discussion about nematodes comes from a study of dry-preserved sloth dung from Rampart Cave (Schmidt and others, 1992).

Vertebrates

The recovery and study of vertebrates from the GC is much more voluminous and well understood than the invertebrates. **Appendix A** provides an extensive list of the fossils and relevant citations. The first study of the Pleistocene vertebrates in the GC occurred at Rampart Cave (see below) following the discovery of Shasta ground sloth dung (Evans, 1936; Laudermilk and Munz, 1938; Hansen, 1978). Vertebrate remains include skeletal elements, dung, hair, dermal scales, and occasionally entire mummified animals (figure 3). These fossils are recovered from cave sediments, dung mats (both bat and artiodactyl), packrat middens, owl pellets, raptor nests, and ringtail refuse areas (e.g., Mead and Van Devender, 1981; Mead, 2005).

A number of studies have been made of the Pleistocene vertebrate remains but there is only one comprehensive, albeit outdated, overview (Mead, 1981; see review in Kenworthy and others, 2004). The Pleistocene record of amphibians (anurans and salamanders) is non-existent for the GC. The record of turtles is exceedingly rare and occurs only from cave and midden deposits in the far western river corridor (Rampart and Vulture caves; see below). Lizards and snakes are abundant in the record due to the presence of their remains in dry cave deposits and packrat middens from throughout the GC. Some of the first or only fossil records of select squamate species come from packrat middens. Birds are fairly well represented due to the in-depth records from Rampart and Stanton's caves and localities in the Sandblast Cave area (see below; Emslie, 1988), but there is a bias toward the river corridor avifauna.

Mammals are equally as well represented as the birds. Entrances to a number of the cave localities is inaccessible to most mammals due to their locations high on cliff faces (figure 4). Only the best cliff climbers (mountain goats, packrats, ringtails) and fliers (bats) gain entrance to some of these caves. With all the caves in the GC, studies of extant and ancient bats and their guano (dung) deposits are abundant (e.g., Wurster and others, 2008; Pape, 2014), with a number of mummified remains beginning to be studied in detail (e.g., Mead and Mikesic, 2001; see Double Bopper Cave below). A number of medium to large mammals (some extinct) are reported from various caves throughout the GC region, both within the river corridor and above the Tonto Platform mid-canyon, including Shasta ground sloth (*Nothrotheriops shastensis*), camel (*Camelops* sp.), Harrington's mountain goat (*Oreamnos harringtoni*), bighorn (*Ovis canadensis*), bison (*Bison* sp.), and horse (*Equus* sp.) (Mead, 1981).

SELECT LOCALITIES

Not all caves and packrat midden localities will be described here, only those with a more complex, unusual, and/or diverse fossil assemblage story. The descriptions below are arranged based on their approximate down-canyon/river location, beginning up-river.

Stanton's Cave and Skull Cave

Stanton's Cave (named after Robert Brewster Stanton) is a large Redwall Limestone (Mississippian) cavern along

Figure 3. *A mummified myotid bat at its last perch among the gypsum crystals in Double Bopper Cave (NPS/SHAWN THOMAS).*

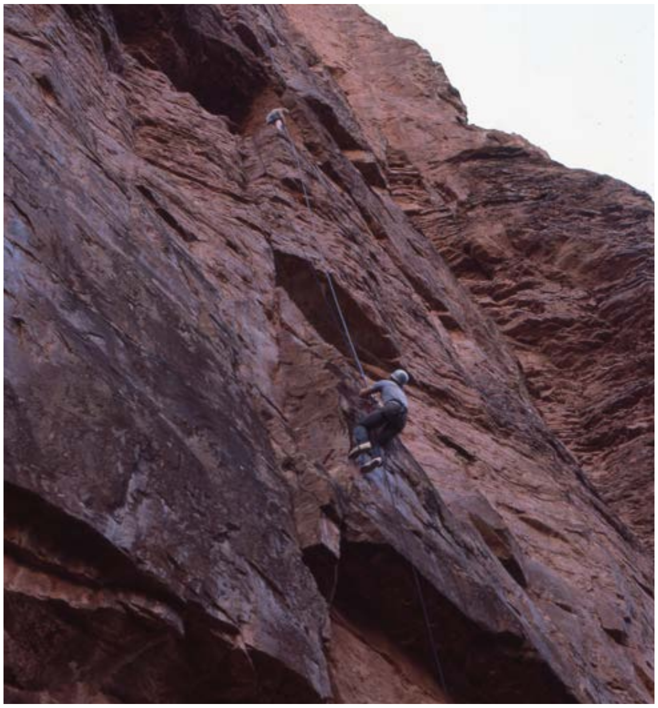

Figure 4. *Ascending into Skylight Cave, 1984 (EMILEE MEAD).*

the Marble Canyon river corridor. Nearby is Vasey's Paradise (named after George Vasey, a friend of John Wesley Powell), a gushet spring flowing into the river (Springer and others, 2008) that appears to show how Stanton's Cave was formed in the distant past. The cave has a long history of use in part due to easy access from the river and from the canyon rim country above via nearby South Canyon. Euler (1984) provides a synthesis of the historic and prehistoric use of the cave. Much of the surface deposit is composed of Holocene-age sediments containing bighorn (*Ovis canadensis*) dung and archaeological artifacts. Excavations in 1969–1970 produced a wealth of archaeological and paleontological information (see chapters in Euler, 1984). Dryer (1994) produced a research project on the packrat middens recovered from the back room of the cave—an area not thoroughly studied previously. The dry environment within the cave provided a wealth of information about the extinct *Oreamnos harringtoni* with the preservation of horn sheaths and dung (Mead and others, 1986a, 1986b; Mead and Lawler, 1994). Today, a large steel lattice keeps human visitors from entering the cave but bats and other animals can still utilize the cave.

Packrat middens from the back of the cavern produced ^{14}C ages ranging from about 11,000 to 35,000 years ago (Dryer, 1994). Radiocarbon dates on dung, wood, and a bone of an extinct bird (*Teratornis*) produced ages ranging from as young as 1,500 to as old as about 17,000 (uncorrected) yr B.P.; driftwood at the base of the sediments dated to >35,000 years old (Robbins and others, 1984).

Skull Cave is a rather small cavern that divides into three separate passages (Emslie, 1988). Analysis of three test pits indicated that for the most part the cave was used by packrats and birds, producing an impressive avifauna (Emslie, 1988). Only a few radiometric ages provide a preliminary chronology via a uranium series date on anhydrite from test pit sediments and AMS ages obtained from packrat pellets. All ages are less than 20,000 yr B.P.

Sandblast Cave and Nearby Caves

A series of cliff-entrance caves can be found in the exposed Redwall Limestone in the Marble Canyon river corridor. Probably the most significant locality is Sandblast Cave (figure 5) which is a grouping of crevices and tunnels (Emslie, 1988). Excavations produced important data about the condor (*Gymnogyps californianus*, including a preserved nest; figure 1) in addition to specimens of the extinct mountain goat, bison, camel, and horse, along with the only reported mammoth remains from the GC; these large mammal remains are thought to be remnants of food items brought in by condors (Emslie, 1987, 1988; Mead and others, 2003). Other caves with fossils in the corridor stretch include Skylight (figure 4) and Hummingbird caves, among others (Emslie, 1987). Radiocarbon ages on *Gymnogyps* skeletal remains range from about 10,000 to 13,000 (uncorrected) yr B.P. ^{14}C ages on packrat middens and *Oreamnos* dung are all older than 30,000 and wood dating in excess of 40,000 yr B.P. (Emslie, 1987; Mead and others, 2003).

Little Nankoweap

The Little Nankoweap drainage is known to have countless caves, many containing important archaeological and paleontological remains (Emslie and others, 1987; Mead and Lawler, 1994; Emslie and others, 1995). Crescendo (CC:5:1), Rebound (CC:5:5), Left and Right Eye, Five-Windows (CC:5:2), Shrine (CC:5:3), and Stevens (CC:5:4; figure 6) caves have been the most intensely studied and described, but many chambers and passageways in these caves still contain numerous areas and deposits that remain to be fully analyzed. Besides data on condors (Emslie, 1987, 1988), a series of packrat middens produced copious plant macrofossils (Coats and others, 2008) and faunal remains (Carpenter and Mead, 2000; Mead and others, 2003). The entrances to most of these caves are on the sheer cliff face of the Redwall Limestone well out of the main river corridor. Some of the flora and fauna (e.g., extinct camel and the extinct shrubox *Euceratherium collinum*) recovered from these cave deposits likely represent inhabitants of the flat plateau surface immediately above (figure 7), which also provide access to the higher plateaus of the North Rim, and not the narrow, steep river corridor and side-canyons. A number of the caves have multiple packrat middens and *Oreamnos* dung remains dating from about 11,000 to 46,000 yr B.P. (Mead and others, 2003).

Hance Canyon and Horseshoe Mesa

A series of packrat middens from Bida Cave were described by Cole (1982, 1985). Faunal remains from the middens were reported in Cole and Mead (1981). Surface remains and a test pit produced a wealth of information about the skeleton, diet, and habitat of *Oreamnos harringtoni* (Mead, 1983; O'Rourke and Mead, 1985; Mead and others, 1986a, 1986b; Mead and Lawler, 1994). The cave is extensive, with the lower

Figure 5. *Close-up of the entrance to Sandblast Cave showing the series of openings, 1984 (EMILEE MEAD).*

Figure 6. *Stevens Cave entrance located high on the cliff face of the Redwall Limestone, 1984 (EMILEE MEAD).*

entrance a large, gaping cavern. At the point where the main cavern turns and narrows into a tunnel and all outside light ceases, bedding depressions are littered with *O. harringtoni* dung (Mead, 1983). The cave system goes through a series of small tubes and large rooms, many with additional fossil and subfossil remains that have yet to be fully documented and studied. Ultimately the cave emerges at the top of the Redwall Limestone as a small entrance providing rare access through the cliff to the Inner Gorge region.

Multiple packrat middens have been dated from Bida Cave ranging from 8,000 to about 13,000 (uncorrected) yr B.P. (Cole, 1982). *Oreamnos* dung and keratinous horn sheaths range in ^{14}C age from 12,000 to about 25,000 (uncorrected) yr B.P. (Mead, 1983; Mead and others, 1986a).

The caves and dry crevices of Horseshoe Mesa up Hance and Cottonwood canyons have been studied speleologically and to a certain extent archaeologically (see Farmer and deSaussure, 1955), but are poorly known paleontologically. Ancient packrat middens were recovered from many areas in these two canyons and a few across the river (Cole, 1985). Cole (1982, 1990a, 1990b) reviews all the radiocarbon ages from multiple packrat midden dating from about 10,000 to 35,000 (uncorrected) years old.

Cremation Creek Caves

The first realization that many caves preserve organic remains for a long period of time came with the report of split-twig figure artifacts at sites on Cremation Creek (Farmer and deSaussure, 1955). The greater Cremation Creek provides a number of caves that were explored in the early 1950s and found to contain Ice Age fossils. Marmot (*Marmota*) remains (not found in the region today at these elevations) were recovered in Tse-an Olje, Cylinder, Tse-an Kaetan, and Tooth caves (Lange, 1956; among other caves across the river). Caves being explored in the 1950s were to be kept secret so the names applied by Lange (1956) and deSaussure (1956) were given in the Navajo (Dinéh) language; tsé’áán refers to “rock cave”.

***Figure 7.** An expansive flat region exists above the Redwall Limestone caves in the Little Nankoweap Canyon region. With access from the higher North Rim plateau region above, large artiodactyls such as camels (*Camelops*), shrubox (*Euceratherium*), and bison (*Bison*), not cliff-climbers, were able to easily enter into portions of the eastern Grand Canyon (JIM MEAD).*

Only Kaetan Cave ("prayer stick cave"; figure 8) in this area is fairly well studied; it is a small cavern with abundant archaeological material in the entrance chamber (Schwartz and others, 1958). Although the cave has a dry entrance chamber, it becomes wet further in with pools. Because of the exploration in 1955 for split-twig figurines, Schwartz and others (1958) also provided the earliest Ice Age palynological analysis in the GC. This then pointed the way for further work in the cave in the late 1970s (Mead, 1983; O'Rourke and Mead, 1985). An owl roost deposit in the cave was sampled but never studied and remains to be examined. As with Bida Cave, *Oreamnos harringtoni* remains were abundant (Mead and Lawler, 1994). Packrat middens with plant and micromammal remains are ^{14}C 15,000 to 19,000 (uncorrected) yr B.P. A stratified test pit produced uncorrected ages from 14,000 to 30,000 yr B.P. An owl roost deposit may date back to 21,000 yr B.P. (Mead, 1983).

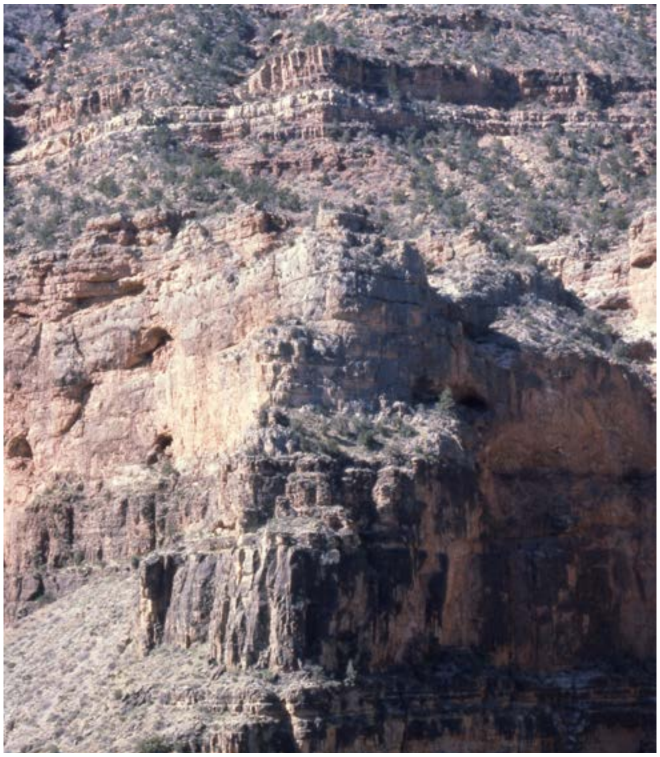

***Figure 8.** Entrance to Kaetan Cave, 1980 (JIM MEAD).*

Double Bopper Cave

Double Bopper Cave is the longest known cave in GRCA. This cave developed in Redwall Limestone, and is located in a remote part of the north rim (figure 9). Difficult to access and largely hidden from view, the

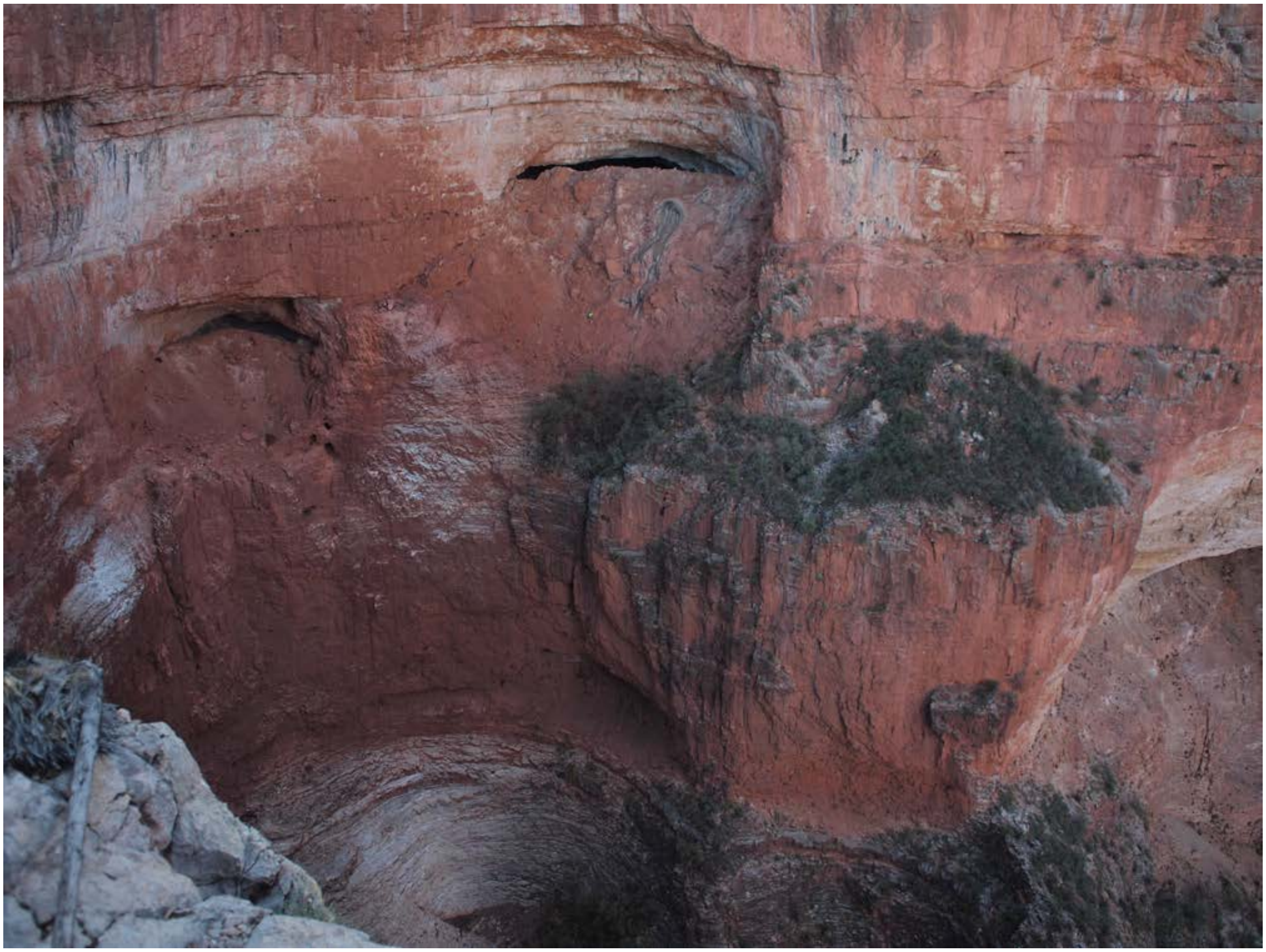

Figure 9. *The two main entrances to Double Bopper Cave. Only the best of climbers and fliers can enter the cave via these entrances (NPS/SHAWN THOMAS).*

cave was only discovered in 2008. Annual expeditions have mapped over 64 km (40 mi) of passage, making it the longest known cave in Arizona and among the 50 longest caves in the world. The cave is still being actively mapped, so the length will continue to increase with future exploration. Double Bopper Cave is a maze cave characterized by rectilinear, joint-controlled passage development (see Tobin and others, in press). Parallel primary passages are large and relatively easy to travel through. Between these primary corridors, smaller passages connect the parallels, sometimes with dense and complicated cave development. The cave is predominantly horizontal, though there is multi-level development in a few isolated areas with vertical passages connecting the levels. The massive extent of the cave and diversity of passage sizes provides a considerable amount of habitat for subterranean wildlife.

One of the most unique features of Double Bopper Cave is the abundance of mummified bats, which are typically rare or altogether absent from other GRCA caves. Bats still actively use the cave with flyways indicated by fresh guano deposits. However, live bats are rarely seen in the cave aside from bats exiting the main entrance at dusk and occasional solitary individuals in torpor. Mummified bats occur throughout the cave, especially along the larger parallel passages. Mummies are typically found clinging to walls and secondary gypsum formations but are also found scattered on the ground. The stable microclimate conditions in the cave, with low relative humidity (typically 35–45%), have likely persisted for thousands of years, making for excellent preservation of specimens. Most mummified bats can be identified to species, possessing intact skin and fur, and many mummy specimens "roosting" on walls cannot immediately be distinguished from live bats without closer examination (figure 3).

Though a complete census has not been conducted, estimates from survey teams suggest the cave contains many hundreds to thousands of bat mummies. At least eight bat species have been identified in the cave. Townsend's big-eared bat (*Corynorhinus townsendii*), a cave-obligate species, is the most common. Less abundant but still commonly observed are pallid bats (*Antrozous pallidus*), big brown bats (*Eptesicus fuscus*), and myotid species (*Myotis* spp.). Canyon bats (*Parastrellus hesperus*) and free-tailed bats (*Tadarida brasiliensis* and possibly *Nyctinomops femorosaccus*) are also present. The rarest species, consisting of only a few specimens, include hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*), which is unusual in that these species are typically considered tree-dwelling bats. A nearby cave, Leandras Cave, also contains abundant bat mummies but with a suspected higher proportion of hoary bats and silver-haired bats (future inventory work is being planned to answer this question). Radiocarbon dating of a subset of bat mummy tissues collected from Double Bopper Cave yielded ages ranging from 3,500 to 33,650 yr B.P., demonstrating long-term use of the cave by bats.

Double Bopper Cave also contains mummified remains of other mammals. Packrats (*Neotoma* spp.) are far outnumbered by bats but still common. Several ringtail (*Bassariscus astutus*) specimens have been found deep in the cave in excellent states of preservation (figure 10) but have not been radiocarbon dated yet. Other skeletonized specimens have yet to be fully assessed, including one gray fox (*Urocyon cinereoargenteus*; figure 11). Inventory and carbon dating continue for paleontological resources in Double Bopper Cave.

Rampart, Muav, and Vulture Caves

Rampart, Muav, and Vulture caves are located in the far western end of the GC not far from where the river exits the Colorado Plateau and heads across the Basin and Range Province. This series of caves and packrat midden studies are about 305 km (190 mi) west of the other well-known fossil localities mentioned above. Only a few packrat midden localities have been found in between (Van Devender and Mead, 1976; Cole, 1985).

The entrance to Rampart Cave is a fair distance up a long, steep talus slope from the Colorado River. Today there is a short inclined climb into the cave, but there may have been more of a subtle ramp into the cave dur-

Figure 10. *A mummified ringtail (*Bassariscus astutus*) from Double Bopper Cave. With the carcass still with all its hair and it only being slightly modified in color, the age of this individual is likely fairly recent. Other carcasses of this taxon in the cave will be radiocarbon dated (NPS/SHAWN THOMAS).*

Figure 11. *An articulated gray fox skeleton (not radiocarbon dated) from Double Bopper Cave (NPS/SHAWN THOMAS).*

ing the Pleistocene based on the occurrence of Shasta ground sloth and tortoise remains in the deposit.

The cave was the first location studied in the GC for Pleistocene biotic remains. In 1936 the CCC (Civilian Conservation Corp) produced a few test pits (figure 12). Laudermilk and Munz (1938) described the plant remains from the dry-preserved dung. Subsequent excavation in the cave was made by Remington Kellogg of the National Museum of Natural History in 1942. Preliminary description of the faunal remains was published by Wilson (1942) and Harington (1972). Martin and others (1961) provided the first detailed paleoenvironmental and chronological study of cave contents with the analysis of dung from the 1956 Shutler Profile. A detailed analysis of radiocarbon-dated sloth dung was produced by Long and Martin (1974; Long and others, 1974). Fortunately, the Kellogg test trench was excavated to the limestone cave floor, because in 1976–1977 the bulk (~70%) of the deposit was destroyed by a smoldering fire set by an unauthorized visitor. The test trench produced a fire break saving some of this non-renewable fossil deposit. An exhaustive history of the various field studies in the cave (including field notes, early photographs, and the relocation of field maps) and an assessment of the remaining, unburned deposit was presented in Carpenter (2003). The entrance today requires permission and a key to open the steel gate. Studies of packrat middens from Rampart Cave and a multitude of isolated limestone crevice localities in a number of nearby canyons were published by Phillips (Phillips and Van Devender, 1974; Mead and Phillips, 1981; Phillips, 1984). Sloth dung from the 1.5 m (5 ft) deep deposit produced ages from as young at 11,000 (uncorrected) years old, back to greater than 40,000 (Long and Martin, 1974).

Muav Caves is a series of small tubes just above the pre-dam river level and now just above the high-stand of Lake Mead. The caves are best known for the remains of Shasta ground sloth (Long and Martin, 1974; Long and others, 1974). Although some test pits were made in the cave entrance long ago, very little is understood about the contents of the deposits. In some crevices below these caves are a series of packrat middens and ringtail refuse den deposits in the Whipple Cliffs, but these remains have not

Figure 12. *Rampart Cave in the 1930s.* ***A.*** *Photograph by the CCC (Civilian Conservation Corp) of the Shasta ground sloth (*Nothrotheriops shastensis*) dung deposit prior to excavation in the 1930s and the fire in 1975–1976.* ***B.*** *Photograph of the CCC excavating a Shasta ground sloth skeleton from the dung deposit in the 1930s.*

been published at this time (Mead and others in progress). Vulture Cave is primarily a low crawlway along short passageways, but all areas are heavily congested with a multitude of packrat middens, floor deposits, and ringtail den debris (Mead and Phillips, 1981; Mead and Van Devender, 1981). Besides remains of *Gymnogyps californianus*, *Cathartes aura* (turkey vulture), and *Camelops* sp. the deposits provided a wealth of information about the Ice Age desert and woodland herpetofauna (Mead and Phillips, 1981). Packrat midden contents ranged in age from 1,100 to 33,000 (uncorrected) yr B.P. (Mead and Phillips, 1981). Important herpetological data came from a ringtail den ^{14}C dated to 2,000 yr B.P. (Mead and Van Devender, 1981).

ENVIRONMENTS AND CLIMATE DISCUSSION

When one thinks of the GC, it is often visualized as an uncomplicated, sinuous, deep gorge east to west, with high elevations with forests at the rims, and low elevations with hot desert habitats along the roaring river at its spine down below. Conceptually this viewpoint may be good, but the real understanding is that the modern canyon is truly complex in all aspects, and this was equally true during the Pleistocene. The eastern region is distinctly different from the western end—climatically, ecologically, and geologically. The differences are in the details. To understand the record of the Pleistocene (Ice Age), preservation is at the core of the recovery of the details. Any cave or shelter with the occurrence of split-twig figurines (e.g., Farmer and deSaussure, 1955; Emslie and others, 1995) illustrates that preservation of these Archaic cultural remains in the chamber is ideal enough that Ice Age remains are more than likely also present and the cavern should be assessed for them as well. Split-twig figurines are part of the Archaic culture that occurred throughout the GC region and elsewhere on the Colorado Plateau, all since the Ice Age and within the Holocene. Overviews of this cultural period as it relates to the GC region can be found in Geib (1995), Huckell (1996), and Janetski and others (2012).

The CP is a distinct physiographic province, straddling the present transition between summer-wet climatic regimes to the south and summer-dry climatic regimes to the north. With the tremendous topographic diversity of the region, there are extremes in available habitats and plant communities today; and these attributes were certainly expressed with the Ice Age climate regimes. Anderson and others (2000) provides a detailed synthesis of many southern CP late Ice Age localities for paleoclimatic and paleobotanic reconstructions.

The data about world-wide changes in temperature are derived from deep sea core samples. A multitude of fossil forms have been used to create a world-wide record of climate and temperature changes. Different phases are grouped into like clusters termed marine isotope stages (MIS) or oxygen isotope stages (OIS) (see Cronin, 2010; Bradley, 2015, 3rd edition). For the GC region, the preserved dataset permits one to examine MIS 1 (14,059 cal. yr BP to present), MIS 2 (27,500–14,060 cal yr BP, and MIS 3 (59,000–27,501 cal yr BP). Clearly much of the Pleistocene (~2.59 million to 11,000 years ago) is not understood. More is known for other regions on the CP, but these deposits are not to be recovered in the GC.

Some of the best high elevation paleoecological data comes from stratified sediment cores taken from lakes that are not found within the limestone region of the GC, but elsewhere on the southern CP (Potato Lake, Anderson, 1993; Walker Lake, see Anderson and others, 2000, for detailed discussion of dataset; Hay Lake, Jacobs, 1985).

Data about MIS 2 and MIS 3 plant communities above about 2,800 m (9,190 ft) elevation are presently not fully understood. Lake-core pollen records at about 2,700 m (8,860 ft) suggest that during MIS 3 high-elevation pine species (perhaps bristlecone and or limber) mixed with Engelmann spruce and subalpine fir created an open forest, possibly with sagebrush growing in open areas. Calculated average summer temperatures were about 3–4°C cooler during MIS 3 than at present (Anderson and others, 2000).

The knowledge of plant communities between 1,600–2,100 m (5,250–6,890 ft) elevation is minimal due to the lack of fossil data. One thing is consistent with the preserved macrobotanical record: there is a lack of ponderosa pine from MIS 3–2. Below 1,500 m (4,940 ft) elevation to about 450 m (1,380 ft) a juniper-desertscrub open woodland persisted, including sagebrush, prickly pear cactus, agave, and, lower down, saltbush. Looking down into the GC during the Ice Age, one would be overwhelmed with this open woodland desertscrub community growing clear to the river's edge. Side canyons would have stands of Douglas fir and white fir in the wetter habitats. A mixed-conifer forest (montane conifers) with limber pine, white fir, and Douglas fir occupied the upper slopes, buttes, and rim county.

The transition from MIS 2 to MIS 1 (~14,000 cal yr BP) occurred with a major reorganization of the plant communities from rim to river. Many species of mixed-conifer forest retreated upslope to attain their near-current elevation distributions. Ponderosa pine quickly became established across middle elevations, as they are today. At lower elevations desertscrub communities replaced the juniper woodlands. All species did not move in concert to these climate-induced changes; instead, what is observed is a mosaic change. Figure 13 shows diagrammatically the inferred elevational distribution of plant communities in and adjacent to the GC

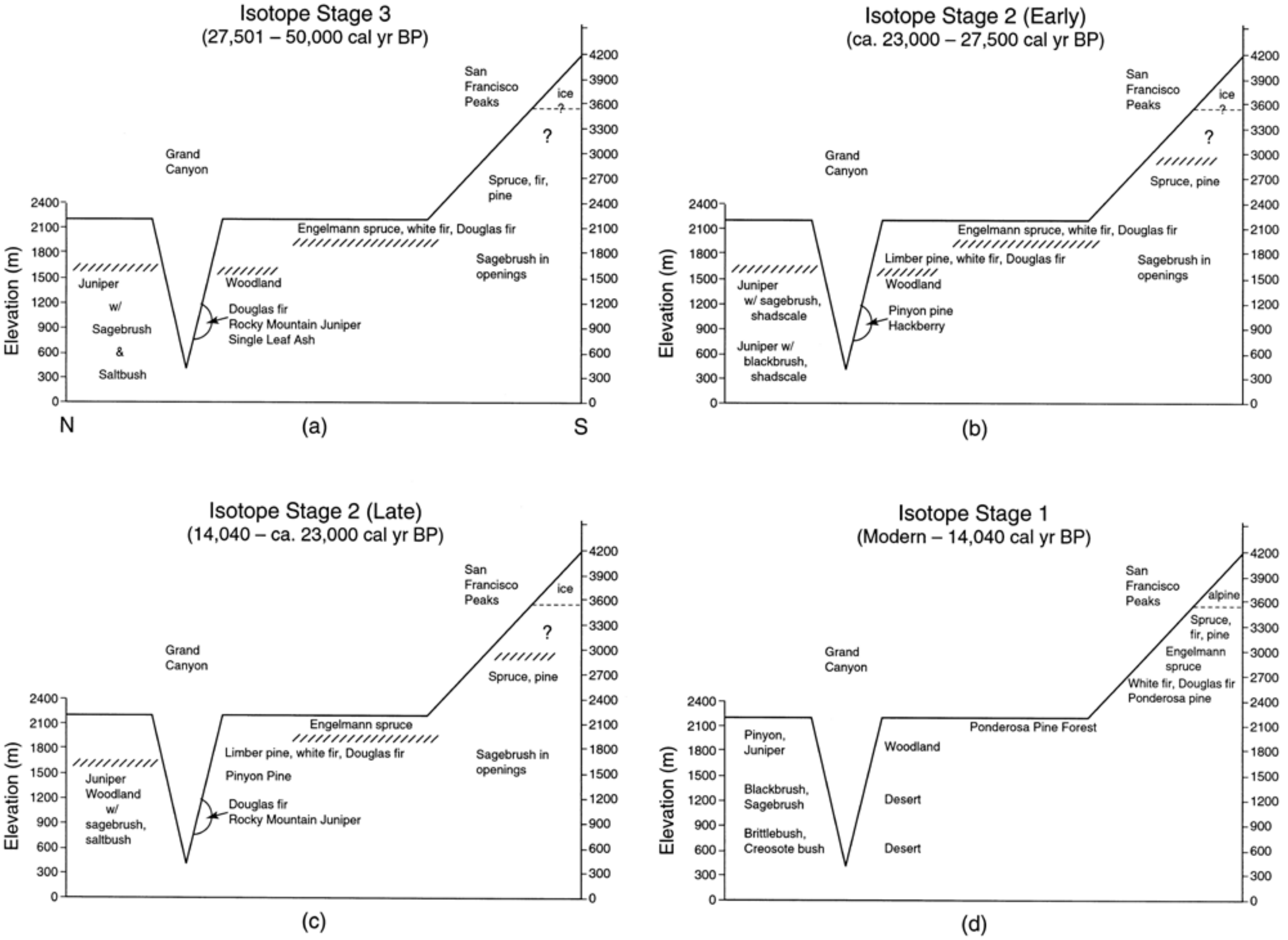

Figure 13. *Inferred elevational distribution of plant communities within and adjacent to the Grand Canyon during the most recent 50,000 years. Cross-section is a line oriented from the San Francisco Peaks north through the Grand Canyon to the North Rim region (Anderson and others, 2000: figure 8).*

during the most recent approximately 50,000 years. The data seem to imply that during the last glacial, the southern position of the jet stream, a cooler tropical ocean, and a heavy spring snowpack over the CP and adjacent Colorado Rocky Mountains probably conspired to suppress the monsoonal flow pattern (Anderson and others, 2000). During this time the seasonality of precipitation appears to have been dampened to predominate during the winter storms. The change to a summer precipitation maximum at the beginning of MIS 1 may be recorded by the sudden appearance and rapid migration of ponderosa pine across the southern CP. Data suggest that the mean depression of late glacial temperatures was at least 5° C (~9° F) colder than today (Anderson and others, 2000).

The vertebrate species were likewise responding not only to the temperature and precipitation changes (i.e., they are affected directly by these parameters) as discussed above but also to the modifications to the local plant community changes (i.e., their food source and/or their habitat requirements). Some species were not directly affected by these parameters and have not changed their distribution within the greater GC region, such as the bighorn, possibly the bison, and Gila monster (*Heloderma suspectum*). Other species appear to have moved up in elevation but stayed within the overall region (some species of voles), or moved out of the GC region to other areas of the continent (*Gymnogyps californianus*), or died out completely (extinction occurred), such as *Oreamnos harringtoni*, *Euceratherium collinum*, *Nothrotheriops shastensis*, *Camelops* sp., and likely some carnivores.

The trends in climate and climate-induced biotic changes over the most recent 50,000 years are based on the data discussed above. It must be remembered that these statements are based on an incomplete fossil record, both through time and for the length of the GC. Packrat midden and dry-preserved cave data have at least a 360 km (190 mi) gap beginning in the eastern GC and going throughout much of the western GC. Most of the above data is really the eastern GC. Data are sparse to almost non-existent for the Hualapai Plateau on the southwest end of the GC. The topographic structure of the northwestern GC (Shivwitts and Uinkaret plateaus) is completely different than the eastern GC so it should be expected that biotic communities and climate responses would have been different over the past 50,000 years. Much still needs to be recovered and assessed to understand the details surrounding this rapid and critical change in climate along with plant community distributional changes for the greater GC.

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Appendix A

GRCA Ice Age Taxa

The following is a list of plants and animals from various Ice Age fossil deposits in the greater Grand Canyon, Arizona. The list is set up taxonomically and refers to the publication(s) that discuss each taxon (see References in the article). Those publications listed can be referred to, to better understand the fossils and the fossil locality. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Plants

Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Polypodiopsida	
Family Equisetaceae	
Equisetum sp.	Hansen, 1978; Robbins and others, 1984
Family Pteridaceae	
Adiantum capillus-veneris	Laudermilk and Munz, 1938
Adiantum sp.	Hansen, 1978; Robbins and others, 1984
Gnetophyta	
Family Ephedraceae	
Ephedra nevadensis	Laudermilk and Munz, 1938; Hansen, 1978
Ephedra nevadensis/viridis	Cole, 1985
Ephedra torreyana	Robbins and others, 1984; Dryer, 1994
Ephedra viridis	Cole and Mead, 1981
Ephedra cf. *E. nevadensis*	Long and others, 1974; Phillips and Van Devender, 1974
Ephedra sp.	Euler, 1978; Mead and Phillips, 1981; Hevly, 1984; Phillips, 1984; Robbins and others, 1984; O'Rourke and Mead, 1985; Cole, 1990a, 1990b; Dryer, 1994
Pinophyta	
Family Cupressaceae	
Juniperus communis	Cole, 1990a, 1990b; Coats, 1997; Coats and others, 2008
Juniperus monosperma	Coats and others, 2008
Juniperus monosperma and/or *J. osteosperma*	Phillips and Van Devender, 1974
Juniperus osteosperma[1]	Hansen, 1978; Cole and Mead, 1981; Cole, 1982, 1990a, 1990b; Coats, 1997; Coats and others, 2008; Cole and others, 2013
Juniperus scopulorum	Dryer, 1994; Coats, 1997
Juniperus cf. *J. monosperma*	Cole, 1985, 1990a, 1990b
Juniperus cf. *J. osteosperma*	Cole, 1985; O'Rourke and Mead, 1985

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[1] *Juniperus californicus* var. *osteosperma* = *Juniperus osteosperma*

Juniperus sp.	Martin and others, 1961; Van Devender and Mead, 1976; Van Devender and others, 1977; Euler, 1978; Mead and others, 1978, 1986a; Mead and Phillips, 1981; Cole, 1982; Ferguson, 1984; Hevly, 1984; Phillips, 1984; O'Rourke and Mead, 1985; Dryer, 1994; Cole and others, 2013
Cupressaceae undetermined	Hansen, 1978
Family Pinaceae	
Abies concolor	Mead and others, 1978; Cole and Mead, 1981; Cole, 1985, 1990a, 1990b; O'Rourke and Mead, 1985; Cole and others, 2013
Abies sp.	O'Rourke and Mead, 1985; Mead and others, 1986a; Dryer, 1994
Picea engelmannii	Cole, 1985
Picea engelmannii/pungens	Cole, 1990a, 1990b
Picea cf. *P. pungens*	Dryer, 1994
Picea sp.	Euler, 1978; Cole and Mead, 1981; Cole, 1982; Hevly, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a
Pinus cf. *P. contorta*	O'Rourke and Mead, 1985
Pinus edulis	Van Devender and Spaulding, 1979; Cole and Mead, 1981; Ferguson, 1984; Cole, 1990a, 1990b; Dryer, 1994; Cole and others, 2013
Pinus cf. *P. edulis* (late Holocene)	O'Rourke and Mead, 1985
Pinus edulis var. *fallax*	Cole and others, 2013
Pinus flexilis	Cole and Mead, 1981; Cole, 1982, 1985, 1990a, 1990b; Van Devender and others, 1985; Coats, 1997; Coats and others, 2008
Pinus cf. *P. flexilis*	O'Rourke and Mead, 1985
Pinus monophylla	Van Devender and Spaulding, 1979
Pinus ponderosa	Cole, 1982, 1985, 1990a, 1990b; O'Rourke and Mead, 1985
Pinus sp.	Euler, 1978; Hevly, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a; Coats, 1997
Pseudotsuga menziesii	Euler, 1978; Mead and others, 1978; Cole and Mead, 1981; Cole, 1982, 1985, 1990a, 1990b; Ferguson, 1984; O'Rourke and Mead, 1985; Dryer, 1994; Coats, 1997; Coats and others, 2008
Pseudotsuga sp.	O'Rourke and Mead, 1985; Mead and others, 1986a
Magnoliophyta	
Family Amaranthaceae	
Amaranthus cf. *A. palmeri*	Coats, 1997
Amaranthus sp.	Long and others, 1974

Amaranthus spp.	Hansen, 1978
Atriplex confertifolia	Van Devender and Mead, 1976; Van Devender and others, 1977; Van Devender and Spaulding, 1979; Cole and Mead, 1981; Mead and Phillips, 1981; Cole, 1982, 1985, 1990a, 1990b; Phillips, 1984; Dryer, 1994; Coats, 1997
Atriplex cf. *A. confertifolia*	Long and others, 1974
Atriplex cf. *A. jonesi* (Holocene)	Robbins and others, 1984
Atriplex sp.	Laudermilk and Munz, 1938; Robbins and others, 1984; Mead and others, 1986a; Dryer, 1994; Coats, 1997
Atriplex spp.	Hansen, 1978
Chenopodium sp. (Holocene only?)	Robbins and others, 1984
Eurotia lanata	Hansen, 1978
Tidestromia oblongifolia	Long and others, 1974
Tidestromia spp.	Hansen, 1978
Cheno-am pollen	Euler, 1978; Hevly, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a
Family Anacardiaceae	
Rhus trilobata	Van Devender and Mead, 1976; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; O'Rourke and Mead, 1985; Coats, 1997
Rhus sp.	O'Rourke and Mead, 1985; Mead and others, 1986a; Emslie and others, 1987; Cole, 1990a, 1990b; Dryer, 1994; Coats, 1997
Family Apiaceae	
Caucalis microcarpa	Phillips, 1984
Cymopterus sp.	Mead and others, 1986a
Lomatium sp.	Dryer, 1994
Apiaceae (or "Umbelliferae") undetermined (pollen)	Mead and others, 1986a
Family Apocynaceae	
Amsonia eastwoodiana	Van Devender and others, 1977
Amsonia tormentosa	Phillips, 1984
Amsonia sp.	Mead and Phillips, 1981
Family Asparagaceae	
Agave utahensis	Van Devender and Mead, 1976; Mead and others, 1978; Cole and Mead, 1981; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; Cole, 1985, 1990a, 1990b; O'Rourke and Mead, 1985; Van Devender and others, 1985; Cole and others, 2013
Agave cf. *A. utahensis*	Long and others, 1974
Agave sp.	Mead and others, 1978; Robbins and others, 1984; Dryer, 1994; Coats, 1997; Coats and others, 2008

Agave spp.	Hansen, 1978
Nolina microcarpa	Van Devender and others, 1977; Hansen, 1978; Mead and others, 1978; Van Devender and Spaulding, 1979; Mead and Phillips, 1981; Phillips, 1984
Nolina cf. *N. parryi*	Phillips and Van Devender, 1974
Nolina sp.	Laudermilk and Munz, 1938; Long and others, 1974; Van Devender and Mead, 1976
Yucca angustissima	Robbins and others, 1984; Cole, 1990a, 1990b; Dryer, 1994
Yucca baccata	Van Devender and Mead, 1976; Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; Coats, 1997
Yucca brevifolia	Van Devender and others, 1977
Yucca mohavensis	Laudermilk and Munz, 1938
Yucca schidigera	Mead and Phillips, 1981
Yucca cf. *Y. newberryi*	Long and others, 1974
Yucca sp.	Mead and others, 1978, 1986a; Hevly, 1984; Robbins and others, 1984; Coats, 1997
Yucca spp.	Hansen, 1978
Agave and *Yucca* undifferentiated	Hevly, 1984
Family Asteraceae	
Ambrosia sp	O'Rourke and Mead, 1985; Dryer, 1994
cf. *Ambrosia* (pollen)	O'Rourke and Mead, 1985; Mead and others, 1986a
Artemisia ludoviciana	Cole, 1990a, 1990b
Artemisia tridentata	Hansen, 1978; Robbins and others, 1984; Cole, 1985, 1990a, 1990b; Coats, 1997;Coats and others, 2008
Artemisia cf. *A. ludoviciana*	Van Devender and Mead, 1976
Artemisia sp	Euler, 1978; Cole, 1982; Hevly, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a
Artemisia spp	Dryer, 1994
Aster sp.	Robbins and others, 1984
Aster spp.	Hansen, 1978
Baccharis sergiloides	Robbins and others, 1984
Baccharis sp.	Dryer, 1994
Bahia sp	Coats, 1997
Bahia spp	Hansen, 1978
Brickellia atractyloides	Coats, 1997
Brickellia cf. *B. scabra*	Coats, 1997
Brickellia sp.	Mead and Phillips, 1981; Hevly, 1984; Robbins and others, 1984; Dryer, 1994; Coats, 1997
Chrysopsis cf. *C. hispida*	Robbins and others, 1984
Chrysothamnus nauseosus	Hansen, 1978

Chrysothamnus cf. *C. viscidiflorus*	Coats, 1997; Coats and others, 2008
Chrysothamnus sp.	Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; Dryer, 1994; Coats, 1997
Cirsium sp.	Mead and Phillips, 1981; Phillips, 1984
Cirsium spp.	Dryer, 1994
cf. *Cirsium* (pollen)	Mead and others, 1986a
Coreopsis sp.	Dryer, 1994
Dyssodia pentachaeta	Robbins and others, 1984
Dyssodia sp.	Robbins and others, 1984
Encelia farinosa	Van Devender and Mead, 1976; Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984; Cole, 1990a, 1990b
Encelia sp.	O'Rourke and Mead, 1985
Encelia spp.	Hansen, 1978
Erigeron sp.	Mead and Phillips, 1981
Franseria confertifolia	Phillips, 1984
Gutierrezia lucida	Phillips and Van Devender, 1974; Van Devender and others, 1977; Hansen, 1978; Mead and Phillips, 1981
Gutierrezia microcephala	Phillips, 1984
Gutierrezia sp.	Long and others, 1974; Robbins and others, 1984; Dryer, 1994
Haplopappus sp. (Holocene)[2]	Robbins and others, 1984
cf. *Helianthus* (pollen)	Mead and others, 1986a
Hofmeisteria pluriseta	Hansen, 1978
Hofmeisteria sp.	Long and others, 1974
Laphamia congesta	Robbins and others, 1984
Lygodesmia exigua	Robbins and others, 1984
Peucephyllum schottii	Hansen, 1978
Solidago sp.	Robbins and others, 1984
Tetradymia canescens?	Robbins and others, 1984
cf. *Brickellia* and *Cirsium*	Hevly, 1984
Asteraceae (or "Compositae") undetermined (pollen)	Euler, 1978; Hevly, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a
Family Berberidaceae	
Berberis repens (Holocene)	Robbins and others, 1984
Berberis sp.	O'Rourke and Mead, 1985; Dryer, 1994
Family Betulaceae	
Alnus sp. (pollen)	Euler, 1978; Hevly, 1984
Betula sp. (pollen)	Euler, 1978; Hevly, 1984
Ostrya knowltoni	Van Devender and others, 1977; Mead and Phillips, 1981;

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[2] *Aplopappus* = *Haplopappus*

Phillips, 1984; O'Rourke and Mead, 1985; Cole, 1990a, 1990b; Coats, 1997

Ostrya sp. (pollen)................................... O'Rourke and Mead, 1985; Mead and others, 1986a

Family Boraginaceae

Amsinckia intermedia.. Hansen, 1978; Mead and Phillips, 1981

Amsinckia sp. .... Van Devender and Mead, 1976

Coldenia hispidissima ....Robbins and others, 1984

Coldenia sp. ....Robbins and others, 1984

Cryptantha pterocarya .... Mead and Phillips, 1981

Cryptantha virginensis .... Mead and Phillips, 1981; Phillips, 1984

Cryptantha cf. *C. confertiflora* .... Coats, 1997

Cryptantha cf. *C. recurvata* .... Dryer, 1994

Cryptantha cf. *C. torreyana* .... Coats, 1997

Cryptantha cf. *C. virginensis* .... Coats, 1997

Cryptantha sp. .... Robbins and others, 1984; Mead and others, 1986a; Dryer, 1994; Coats, 1997

Cryptantha spp. ....Hansen, 1978

Lappula occidentalis .... Dryer, 1994; Coats, 1997

Lappula redowskii .... Van Devender and Mead, 1976

Lithospermum incisum .... Coats, 1997; Coats and others, 2008

Pectocarya spp. ....Hansen, 1978

Phacelia crenulata .... Mead and Phillips, 1981; Phillips, 1984

Phacelia sp. ....Long and others, 1974

Phacelia spp. ....Hansen, 1978

Tiquilia sp. .... Coats, 1997

cf. *Trixis* (pollen)... Mead and others, 1986a

Coldenia–Cryptantha...Robbins and others, 1984

Family Brassicaceae

Descurainia pinnata..Hansen, 1978

Draba cuneifolia ....Hansen, 1978

Lepidium sp. .... Long and others, 1974; Mead and Phillips, 1981; Phillips, 1984; Dryer, 1994; Coats, 1997

Lepidium spp. ....Hansen, 1978

Lesquerella sp. .... Robbins and others, 1984; Mead and others, 1986a

cf. *Lesquerella* (pollen) .... Mead and others, 1986a

Streptanthella longirostris .... Dryer, 1994

Thysanocarpus amplectens .... Phillips, 1984

Brassicaceae (or "Cruciferae") undetermined................ Hevly, 1984; Mead and others, 1986a

Family Cactaceae

Cylindropuntia sp. .... Dryer, 1994; Coats, 1997

Echinocactus polycephalus .... Phillips and Van Devender, 1974;

Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984

Echinocactus sp. .... Martin and others, 1961; Phillips, 1984

Echinocereus sp. .... Mead and Phillips, 1981; Coats, 1997

Ferocactus acanthodes .... Van Devender and Mead, 1976; Mead and Phillips, 1981; Phillips, 1984

Ferocactus wislizeni .... Coats, 1997

Opuntia basilaris .... Phillips and Van Devender, 1974; Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; Cole, 1990a, 1990b

Opuntia chorotica .... Van Devender and Mead, 1976

Opuntia erinacea .... Mead and Phillips, 1981; Phillips, 1984; Cole, 1985, 1990a, 1990b

Opuntia macrorhiza .... Mead and Phillips, 1981

Opuntia phaeacantha .... Van Devender and Mead, 1976; Cole, 1990a, 1990b

Opuntia whipplei .... Phillips and Van Devender, 1974;Van Devender and Mead, 1976; Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984; Dryer, 1994

Opuntia cf. *O. whipplei* .... Mead and others, 1978

Opuntia (*Platyopuntia*) sp.[3] .... Coats, 1997

Opuntia sp. .... Laudermilk and Munz, 1938; Long and others, 1974; Mead and Phillips, 1981; Hevly, 1984; Cole, 1985, 1990a, 1990b; O'Rourke and Mead, 1985; Dryer, 1994; Coats, 1997; Coats and others, 2008

Cactaceae undetermined .... Hansen, 1978; Dryer, 1994; Coats, 1997

Family Cannabaceae

Celtis reticulata .... Van Devender and Mead, 1976; Hansen, 1978; Mead and Phillips, 1981; O'Rourke and Mead, 1985; Dryer, 1994

Celtis sp. (Holocene) .... Hevly, 1984

Family Caprifoliaceae

Lonicera sp. .... Mead and others, 1986a

Symphoricarpos sp. .... Van Devender and others, 1977; Van Devender and Spaulding, 1979; Mead and Phillips, 1981; Phillips, 1984; Mead and others, 1986a; Cole, 1990a, 1990b; Dryer, 1994; Coats, 1997; Coats and others, 2008

Family Caryophyllaceae

Arenaria fendleri .... Robbins and others, 1984

Arenaria sp. .... Robbins and others, 1984

Caryophyllaceae undetermined (pollen) .. O'Rourke and Mead, 1985; Mead and others, 1986a

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[3] *Platypuntia* of Coats (1997) accepted as *Opuntia* (*Platyopuntia*)

Family Celastraceae	
Mortonia scabrella	Phillips and Van Devender, 1974; Van Devender and others, 1977; Mead and others, 1978; Mead and Phillips, 1981
Mortonia scabrella var. *utahensis*	Phillips, 1984
Pachystima myrsinites	Cole, 1990a, 1990b
Family Convolvulacea	
Convolvulus sp.	Robbins and others, 1984
Family Crossosomaceae	
Crossosoma bigelovii	Hansen, 1978; Mead and Phillips, 1981; Phillips, 1984
Crossosoma sp.	Long and others, 1974
Glossopetalon nevadense	Hansen, 1978
Glossopetalon sp.	Mead and others, 1986a
Family Cucurbitaceae	
Cucurbita sp.	Van Devender and Mead, 1976
Family Cyperaceae	
Carex sp.	Long and others, 1974; Robbins and others, 1984; Mead and others, 1986a
Eleocharis sp.	Robbins and others, 1984
Cyperaceae undetermined	Hansen, 1978
Family Elaeagnaceae	
Shepherdia sp.	Hevly, 1984
Shepherdia spp.	Hansen, 1978
Family Euphorbiaceae	
Argythamnia sp.	Dryer, 1994
Euphorbia cf. *E. fendleri*	Coats, 1997
Euphorbia sp.	Van Devender and Mead, 1976; Robbins and others, 1984; Dryer, 1994
Tragia sp.	Robbins and others, 1984
Family Fabaceae	
Acacia greggii	Long and others, 1974; Hansen, 1978; Mead and Phillips, 1981; Phillips, 1984
Acacia sp.	Mead and others, 1986a
Astragalus nutallianus	Phillips, 1984
Astragalus sp.	Hansen, 1978; Robbins and others, 1984; O’Rourke and Mead, 1985; Dryer, 1994
Astragalus-type pollen	Mead and others, 1986a
Cassia sp.	Laudermilk and Munz, 1938
Cercis occidentalis	O’Rourke and Mead, 1985; Cole, 1990a, 1990b
Lotus spp.	Hansen, 1978
Prosopis juliflora	Long and others, 1974; Hansen, 1978; Cole, 1990a, 1990b
Fabaceae (or “Leguminosae”) undetermined (pollen)	Mead and others, 1986a
Fabaceae undetermined (driftwood)	Ferguson, 1984

“Legume a and b”	Hevly, 1984
Family Fagaceae	
Quercus turbinella	Mead and Phillips, 1981; Cole, 1982, 1985, 1990a, 1990b
Quercus sp.	Euler, 1978; Hansen, 1978; Hevly, 1984;O’Rourke and Mead, 1985; Mead and others, 1986a
Family Grossulariaceae	
Ribes montigenum	Van Devender and others, 1977; Van Devender and Spaulding, 1979; Mead and Phillips, 1981; O’Rourke and Mead, 1985
Ribes pinetorum	Coats and others, 2008
Ribes cf. *R. pinetorum*	Coats, 1997
Ribes sp.	Cole, 1985, 1990a, 1990b; Coats, 1997
cf. *Ribes* sp.	Dryer, 1994
Family Hydrangeaceae	
Fendlera rupicola	Cole, 1990a, 1990b
Family Juglandaceae	
Juglans sp. (Holocene body fossils)	Hevly, 1984
Juglans sp. (pollen)	Euler, 1978; Hevly, 1984
Family Krameriaceae	
Krameria parvifolia	Hansen, 1978
Family Lamiaceae	
Hedeoma diffusum	Robbins and others, 1984
Hedeoma sp.	Robbins and others, 1984
Salvia dorrii	Mead and Phillips, 1981; Phillips, 1984
Lamiaceae (or “Labiatae”) undetermined (pollen)	Mead and others, 1986a
Family Liliaceae	
Liliaceae undetermined (pollen)	Mead and others, 1986a
Family Linaceae	
Linum sp. (pollen)	Mead and others, 1986a
Family Loasaceae	
Eucnide urens	Hansen, 1978
Mentzelia puberula	Mead and Phillips, 1981
Mentzelia sp.	Phillips, 1984; Robbins and others, 1984; Dryer, 1994
Family Malpighiaceae	
Janusia gracilis	Van Devender and Mead, 1976
Janusia sp.	Hansen, 1978
Family Malvaceae	
Malvastrum rotundifolium	Hansen, 1978
Sida sp.	Mead and others, 1986a
Sphaeralcea ambigua	Laudermilk and Munz, 1938; Van Devender and others, 1977; Hansen, 1978
Sphaeralcea cf. *S. laxa*	Long and others, 1974

Sphaeralcea sp.	Martin and others, 1961; Van Devender and Mead, 1976; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a; Dryer, 1994
Family Nyctaginaceae	
Abronia sp.	Hansen, 1978
Allionia incarnata	Hansen, 1978; Phillips, 1984
Allionia sp.	Long and others, 1974
Boerhavia coulteri	Mead and Phillips, 1981
Boerhavia sp.	Van Devender and Mead, 1976
Mirabilis multiflora	Coats, 1997
Oxybaphus sp.	O'Rourke and Mead, 1985
Family Oleaceae	
Fraxinus anomala	Long and others, 1974; Phillips and Van Devender, 1974; Van Devender and Mead, 1976; Van Devender and others, 1977; Hansen, 1978; Mead and others, 1978; Van Devender and Spaulding, 1979; Mead and Phillips, 1981; Cole, 1982, 1985, 1990a, 1990b; Phillips, 1984; O'Rourke and Mead, 1985; Coats, 1997; Coats and others, 2008
Fraxinus cf. *F. anomala*	Dryer, 1994
Fraxinus sp.	Laudermilk and Munz, 1938
Fraxinus spp.	Hansen, 1978
Family Onagraceae	
Oenothera cavernae	Phillips, 1984
Oenothera sp.	Robbins and others, 1984; Mead and others, 1986a
Oenothera spp.	Hansen, 1978
Family Orobanchaceae	
Castilleja cf. *C. miniata*	Coats, 1997
Castilleja sp.	Coats, 1997
Castilleja spp.	Hansen, 1978
Castilleja or *Orthocarpus*	Van Devender and Mead, 1976
Family Papaveraceae	
Argemone sp.	Mead and Phillips, 1981; Phillips, 1984; O'Rourke and Mead, 1985; Dryer, 1994; Coats, 1997
Family Phrymaceae	
Mimulus sp.	Robbins and others, 1984
Family Plantaginaceae	
Penstemon eatonii	Phillips, 1984
Penstemon sp.	Van Devender and Mead, 1976; Mead and Phillips, 1981
Plantago sp.	Dryer, 1994
Family Poaceae	

Agropyron sp.	Robbins and others, 1984; Mead and others, 1986a
Agropyron spp.	Hansen, 1978
Andropogon sp.	Robbins and others, 1984
Aristida glauca	Robbins and others, 1984
Aristida longiseta	Robbins and others, 1984
Aristida sp.	Laudermilk and Munz, 1938; Long and others, 1974; Robbins and others, 1984; Mead and others, 1986a; Dryer, 1994
Aristida spp.	Hansen, 1978
Bouteloua eripoda (Holocene)	Robbins and others, 1984
Bouteloua gracilis	Robbins and others, 1984
Bouteloua simplex	Robbins and others, 1984
Bouteloua trifida	Robbins and others, 1984
Bouteloua sp.	Robbins and others, 1984; Mead and others, 1986a
Bouteloua spp.	Hansen, 1978
Bromus sp.	Long and others, 1974; Robbins and others, 1984; Mead and others, 1986a
Bromus spp.	Hansen, 1978
Enneapogon desvauxii	Robbins and others, 1984
Festuca arizonica	Hansen, 1978
Festuca sp.	Robbins and others, 1984; Mead and others, 1986a
Hilaria rigida	Hansen, 1978
Lycurus phleoides (Holocene)	Robbins and others, 1984
Muhlenbergia sp.	Long and others, 1974; Hansen, 1978
Oryzopsis hymenoides	Mead and Phillips, 1981; O’Rourke and Mead, 1985; Coats, 1997; Coats and others, 2008
Oryzopsis sp.	Hansen, 1978; Mead and others, 1986a
Panicum huachucae	Robbins and others, 1984
Phragmites communis	Laudermilk and Munz, 1938; Hansen, 1978
Phragmites sp.	Long and others, 1974; Robbins and others, 1984
Poa sp.	Mead and others, 1986a
Poa spp.	Hansen, 1978
Schedonnardus paniculatus	Robbins and others, 1984
Schizachyrium scoparium	Dryer, 1994
Sporobolus flexuosus	Robbins and others, 1984
Sporobolus texanus	Robbins and others, 1984
Sporobolus cf. *S. cryptandrus*	Robbins and others, 1984
Sporobolus sp.	Robbins and others, 1984; Mead and others, 1986a
Sporobolus spp.	Hansen, 1978
Stipa arida	Robbins and others, 1984
Stipa hymenoides	Dryer, 1994
Stipa cf. *neomexicana*	Dryer, 1994

Stipa sp.	Long and others, 1974; Mead and others, 1986a
Stipa spp.	Hansen, 1978
Tridens pulchellus	Robbins and others, 1984
Tridens sp	Long and others, 1974; Hansen, 1978
Tridens spp.	Hansen, 1978
Zea mays (late Holocene)	Cole, 1982
Gramineae A	Robbins and others, 1984
Poaceae (or "Gramineae") undetermined.	Euler, 1978; Hevly, 1984; Robbins and others, 1984; O'Rourke and Mead, 1985; Mead and others, 1986a
Family Polemoniaceae	
Gilia sp.	Hevly, 1984
cf. *Leptodactylon* (pollen)	Mead and others, 1986a
Linanthus demissus	Hansen, 1978
Phlox sp. (pollen)	Mead and others, 1986a
Phlox/*Leptodactylon*	Mead and others, 1986a
Polemoniaceae undetermined (pollen)	O'Rourke and Mead, 1985
Family Polygonaceae	
Eriogonum deflexum	Robbins and others, 1984
Eriogonum sp.	Robbins and others, 1984; Mead and others, 1986a
Eriogonum spp.	Hansen, 1978
Polygonum sp.	Dryer, 1994
Rumex sp.	Dryer, 1994
Polygonaceae undetermined (pollen)	O'Rourke and Mead, 1985; Mead and others, 1986a
Family Ranunculaceae	
Anemone tuberosa	Hansen, 1978; Phillips, 1984
Anemone sp.	Van Devender and Mead, 1976
Aquilegia chrysantha	Hansen, 1978
Caltha sp. (pollen)	Mead and others, 1986a
Clematis ligusticifolia	Robbins and others, 1984
Ranunculus sp.	Dryer, 1994
Ranunculaceae undetermined (pollen)	O'Rourke and Mead, 1985; Mead and others, 1986a
Family Rhamnaceae	
Rhamnus betulaefolia	Phillips, 1984
Rhamnus sp. (late Holocene)	O'Rourke and Mead, 1985
Rhamnaceae undetermined (pollen)	O'Rourke and Mead, 1985
Family Rosaceae	
Amelanchier sp.	Hevly, 1984; Robbins and others, 1984; Coats, 1997
Cercocarpus intricatus	Van Devender and others, 1977; Van Devender and Spaulding, 1979; Phillips, 1984; Robbins and others, 1984; O'Rourke and Mead, 1985; Cole, 1990a, 1990b; Coats, 1997; Coats and others, 2008

Cercocarpus montanus .... Hansen, 1978
Cercocarpus sp. (pollen) .... Mead and others, 1986a
cf. *Cercocarpus* (pollen) .... O'Rourke and Mead, 1985
Chamaebatiaria millefolium .... Cole, 1990a, 1990b; Coats, 1997; Coats and others, 2008
Coleogyne ramosissima .... Phillips and Van Devender, 1974;Van Devender and others, 1977; Mead and Phillips, 1981; Phillips, 1984; O'Rourke and Mead, 1985; Cole, 1990a, 1990b; Coats, 1997; Coats and others, 2008
Cowania mexicana .... O'Rourke and Mead, 1985; Cole, 1990a, 1990b; Coats, 1997
Fallugia paradoxa .... Van Devender and Mead, 1976; Robbins and others, 1984
Geum spp. .... Hansen, 1978
Holodiscus dumosus .... Cole, 1990a, 1990b; Coats, 1997
Potentilla spp. .... Hansen, 1978
Prunus fasciculata .... Phillips and Van Devender, 1974; Van Devender and others, 1977; Hansen, 1978; Mead and others, 1978; Phillips, 1984; Robbins and others, 1984; Cole, 1990a, 1990b
Prunus virginiana .... Dryer, 1994; Coats, 1997
Prunus sp. .... Laudermilk and Munz, 1938; Long and others, 1974; Mead and others, 1986a
Purshia mexicana .... Dryer, 1994
Purshia sp. .... Hevly, 1984
Rosa cf. *R. arizonica* .... O'Rourke and Mead, 1985
Rosa stellata .... Coats and others, 2008
Rosa cf. *R. stellata* .... Cole, 1985, 1990a, 1990b; Dryer, 1994; Coats, 1997
Rosa sp. .... O'Rourke and Mead, 1985; Dryer, 1994; Coats, 1997
Rubus sp. .... Cole, 1990a, 1990b; Dryer, 1994;Coats, 1997
Rosaceae undetermined (pollen) .... Mead and others, 1986a

Family Rubiaceae

Galium sp. .... Van Devender and Mead, 1976; Mead and Phillips, 1981; Phillips, 1984; Robbins and others, 1984
Galium spp. .... Hansen, 1978

Family Rutaceae

Ptelea trifoliata .... Coats, 1997; Coats and others, 2008
Ptelea trifoliata var. *pallida* .... Cole, 1985, 1990a, 1990b; O'Rourke and Mead, 1985
Thamnosma montana .... Dryer, 1994
Thamnosma sp. .... Mead and Phillips, 1981; Hevly, 1984

Family Salicaceae

Populus fremontii .... Hansen, 1978
Populus fremontii? .... Euler, 1978
Populus sp. .... Laudermilk and Munz, 1938; Ferguson, 1984; Mead and others, 1986a
Salix sp. (pollen) .... Euler, 1978; Hevly, 1984; Mead and others, 1986a

    - *Populus* and *Salix* (Holocene body fossils)............Hevly, 1984
  - Family Santalaceae
    - *Phoradendron californicum*............Phillips, 1984
    - *Phoradendron* sp............Long and others, 1974; Hansen, 1978; Mead and Phillips, 1981; Robbins and others, 1984
  - Family Sapindaceae
    - *Acer glabrum*............Coats, 1997; Coats and others, 2008
    - *Acer* sp. (pollen)............Euler, 1978; Hevly, 1984
  - Family Sarcobataceae
    - *Sarcobatus vermiculatus*............Robbins and others, 1984
    - *Sarcobatus* sp. (pollen)............Euler, 1978; Hevly, 1984
  - Family Saxifragaceae
    - *Mitella* sp............Dryer, 1994
    - cf. *Saxifraga* (pollen)............Mead and others, 1986a
    - Saxifragaceae undetermined (pollen)............O'Rourke and Mead, 1985
  - Family Solanaceae
    - *Datura metaloides* (GRCA: Holocene)............Van Devender and Mead, 1976; Robbins and others, 1984
    - *Lycium andersonii*............Phillips, 1984
    - *Lycium* sp............Dryer, 1994
    - cf. *Lycium* (pollen)............Mead and others, 1986a
    - *Physalis fendleri*............Robbins and others, 1984
    - *Physalis* sp............Laudermilk and Munz, 1938; Van Devender and Mead, 1976; Mead and Phillips, 1981; Phillips, 1984
    - Solanaceae undetermined (pollen)............Mead and others, 1986a
  - Family Urticaceae
    - *Urtica* sp............Robbins and others, 1984
  - Family Verbenaceae
    - *Aloysia wrightii*............Robbins and others, 1984; Cole, 1990a, 1990b
    - *Verbena* sp............Van Devender and Mead, 1976
  - Family Vitaceae
    - *Vitis arizonica*............Mead and Phillips, 1981; Phillips, 1984
    - *Vitis* sp............Mead and others, 1978
  - Family Zygophyllaceae
    - *Kallstroemia* sp............Van Devender and Mead, 1976
    - *Larrea divaricata*............Laudermilk and Munz, 1938
    - *Larrea tridentata*............Martin and others, 1961; Hansen, 1978; Mead and Phillips, 1981; Phillips, 1984
  - *Ceanothus*/*Cercocarpus*............Mead and others, 1986a
- Undetermined wood............Emslie, 1988; Dryer, 1994; Kaufman and others, 2002
- Undetermined plants............Phillips and Van Devender, 1974; Mead and others, 1978,

	1986a; Hevly, 1984; Emslie and others, 1987; Emslie, 1988; Kaufman and others, 2002
Invertebrates	
Phylum Mollusca	
Class Bivalvia	
Pisidium cf. *P. casertanum*	Kaufman and others, 2002
Pisidium cf. *P. nitidum*	Kaufman and others, 2002
Pisidium cf. *P. subtruncatum*	Kaufman and others, 2002
Pisidium cf. *P. walkeri*	Kaufman and others, 2002
Pisidium sp.	Kaufman and others, 2002
Class Gastropoda	
Catinella cf. *C. vermeta*[4]	Spamer, 1993; Kaufman and others, 2002
Catinella sp.	Kaufman and others, 2002
Cionella lubrica[5]	Spamer, 1993; Kaufman and others, 2002
Fossaria dalli	Kaufman and others, 2002
Fossaria sp.	Kaufman and others, 2002
Gyraulus parvus	Kaufman and others, 2002
Oreohelix yavapai[6]	Spamer and Bogan, 1993; Kaufman and others, 2002
Oxyloma cf. *O. haydeni kanabensis*	Kaufman and others, 2002
Oxyloma sp.	Kaufman and others, 2002
Physella cf. *P. humerosa*	Kaufman and others, 2002
Physella cf. *P. virgata*	Kaufman and others, 2002
cf. *Sonorella* sp.	Cole and Mead, 1981
Vertigo ovata	Kaufman and others, 2002
Mollusca undetermined	Hevly, 1984
Phylum Nematoda	
*Agamofilaria oxyura**	Schmidt and others, 1992
*Strongyloides shastensis**	Schmidt and others, 1992
Nematoda unspecified	Laudermilk and Munz, 1938
Phylum Arthropoda	
Class Arachnida	
Order Ixodida	
Family Ixodidae	
Dermacentor andersoni	Elias and others, 1992
Dermacentor sp.	Elias and others, 1992

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[4] *Catinella* cf. *C. avara* = *Catinella* cf. *C. vermeta*

[5] *Cochlicopa lubrica* = *Cionella lubrica*

[6] Subspecies of *Oreohelix yavapai*, such as *O. y. fortis** Cockerell (1927) are now generally subsumed in *Oreohelix yavapai*

Order Scorpiones	
Family Buthidae	
Centruroides sp.	Elias and others, 1992
Class Diplopoda	
Diplopoda undetermined	Elias and others, 1992
Class Insecta	
Order Coleoptera	
Family Carabidae	
Agonum (*Rhadine*) *perlevis* (late Holocene)	Elias and others, 1992
Agonum (Rhadine) sp.	Elias and others, 1992
Calosoma cf. *C. scrutator* (late Holocene)	Elias and others, 1992
Family Chrysomelidae	
Chaetocnema sp. (late Holocene)	Elias and others, 1992
Lema trilinea	Elias and others, 1992
Chrysomelidae undetermined	Elias and others, 1992
Family Cleridae	
Acanthoscelides sp.	Elias and others, 1992
Family Curculionidae	
Apleurus angularis	Elias and others, 1992
Cleonidus trivittatus or *C. quadrilineatus*	Elias and others, 1992
Ophryastes sp.	Elias and others, 1992
Orimodema protracta (late Holocene)	Elias and others, 1992
Sapotes sp.	Elias and others, 1992
Scyphophorus acupunctatus	Elias and others, 1992
Cleridae undetermined	Elias and others, 1992
Family Dermestidae	
Dermestidae undetermined	Elias and others, 1992
Family Elateridae	
Elateridae undetermined	Elias and others, 1992
Family Histeridae	
Histeridae undetermined	Elias and others, 1992
Family Melandryidae	
Anaspis rufa	Elias and others, 1992
Family Meloidae	
Meloidae undetermined	Elias and others, 1992
Family Nitidulidae	
Nitidulidae undetermined	Elias and others, 1992
Family Ptinidae	
Niptus cf. *N. ventriculus*	Elias and others, 1992
Ptinis sp.	Elias and others, 1992
Ptinidae undetermined	Cole and Mead, 1981
Family Scarabaeidae	

Aphodius near *A. ruficlarus*	Elias and others, 1992
Aphodius sp.	Elias and others, 1992
Diplotaxis sp.	Elias and others, 1992
Onthophagus sp.	Elias and others, 1992
Phyllophaga sp.	Elias and others, 1992
Serica sp.	Elias and others, 1992
Scarabaeidae undetermined	Elias and others, 1992
Family Scotylidae	
Scotylidae undetermined	Elias and others, 1992
Family Silphidae	
Thanatophilus truncatus (late Holocene)	Elias and others, 1992
Family Tenebrionidae	
Coniontis sp.	Elias and others, 1992
Eleodes cf. *E. nigrina*	Elias and others, 1992
Eleodes spp.	Elias and others, 1992
Tenebrionidae undetermined	Hevly, 1984
Order Diptera	
Diptera undetermined	Elias and others, 1992
Order Hemiptera	
Hemiptera undetermined	Elias and others, 1992
Order Homoptera	
Family Cicadidae	
Cicadidae undetermined	Elias and others, 1992
Order Hymenoptera	
Superfamily Apoidea	
Apoidea undetermined	Elias and others, 1992
Order Lepidoptera	
Lepidoptera undetermined	Elias and others, 1992
Order Neuroptera	
Family Myrmelodontidae	
Myrmelodontidae undetermined	Elias and others, 1992
Order Orthoptera	
Family Acrididae	
Acrididae undetermined	Elias and others, 1992
Insecta undetermined	Cole and Mead, 1981; Mead and Phillips, 1981
Class Ostracoda	
Candona sp. (late Holocene)	Kaufman and others, 2002
Cypridopsis okeechobei	Kaufman and others, 2002
Cypridopsis vidua	Kaufman and others, 2002
Darwinula stevensoni	Kaufman and others, 2002
Heterocypris incongruens	Kaufman and others, 2002
Ilyocypris bradyi	Kaufman and others, 2002

Strandesia meadensis	Kaufman and others, 2002
Arthropoda undetermined	Mead and Van Devender, 1981; Hevly, 1984

Vertebrates

Class Osteichthyes	
Catostomus discobolus	Miller and Smith, 1984
Catostomus latipinnis (possibly Holocene)	Miller and Smith, 1984
Gila cypha (probably Holocene)	Miller and Smith, 1984
Gila elegans (probably Holocene)	Miller and Smith, 1984
Ptychocheilus lucius (probably Holocene)	Miller and Smith, 1984
Osteichthyes undetermined	Hevly, 1984; Emslie, 1988; Dryer, 1994
Class Amphibia	
Order Anura	
Bufo sp.	Spamer, 1988
Hyla sp.	Spamer, 1988
Scaphiopus sp.	GCM
Order Urodela	
Ambystoma tigrinum (late Holocene)	Mead, 2005
Class Reptilia	
Order Testudines	
Gopherus agassizii	Wilson, 1942; Van Devender and others, 1977; Mead, 1981, 2005; Hunt and Lucas, 2018
Gopherus morafkai	Hunt and Lucas, 2018
Order Squamata	
Cnemidophorus tigris	Mead, 2005
Cnemidophorus cf. *C. tigris*	Van Devender and others, 1977; Mead, 1981
Cnemidophorus sp.	Cole and Van Devender, 1976; Van Devender and others, 1977; Cole and Mead, 1981
Coleonyx variegatus	Van Devender and others, 1977; Mead, 1981, 2005
Crotaphytus collaris	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981
Crotaphytus cf. *C. collaris*	Cole and Mead, 1981
Crotaphytus sp.	Cole and Van Devender, 1976
Heloderma suspectum (uncertain age)	Mead, 2005
Phrynosoma hernandesi	Mead and others, 2003; Mead, 2005
cf. *Phrynosoma*	Mead and others, 2003
Sauromalus ater[7]	Wilson, 1942; Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981; Hunt and Lucas, 2018
Sceloporus magister	Hunt and Lucas, 2018

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[7] *Sauromalus obesus = Sauromalus ater*

Sceloporus tristichus	Hunt and Lucas, 2018
Sceloporus undulatus	Mead, 2005
Sceloporus cf. *S. magister*	Van Devender and others, 1977; Mead, 1981; Mead and Phillips, 1981
Sceloporus cf. *S. undulatus*	Van Devender and others, 1977; Cole and Mead, 1981; Mead, 1981; Mead and Phillips, 1981; Hunt and Lucas, 2018
Sceloporus sp.	Van Devender and others, 1977; Cole and Mead, 1981
Sceloporus spp.	Cole and Van Devender, 1976
Uta stansburiana	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981
Undetermined lizard	Emslie, 1988; Dryer, 1994; Emslie and others, 1995
Suborder Serpentes	
Coluber or *Masticophis* (late Holocene)	Mead and Phillips, 1981
Crotalus mitchelli or *C. viridis*	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981
Crotalus sp.	Van Devender and others, 1977
Diadophis punctatus	Mead and others, 2003; Mead, 2005
Hypsiglena torquata	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981
Lampropeltis getula[8]	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981; Olsen and Olsen, 1984; Hunt and Lucas, 2018
Lampropeltis pyromelana	Mead, 1981, 2005; Mead and Phillips, 1981
Lampropeltis triangulum (late Holocene)	Mead and Phillips, 1981; Mead, 2005
cf. *Lampropeltis*	Mead and others, 2003
Pituophis catenifer	Hunt and Lucas, 2018
Pituophis melanoleucus	Van Devender and others, 1977; Mead, 1981, 2005
Rhinocheilus lecontei	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981; Hunt and Lucas, 2018
Salvadora cf. *S. hexalepis* (late Holocene)	Mead and Phillips, 1981
Sonora semiannulata	Van Devender and others, 1977; Mead, 1981, 2005; Mead and Phillips, 1981
Thamnophis sp.	Mead, 1981
Trimorphodon bisulcatus (late Holocene)	Mead and Phillips, 1981
Serpentes undetermined	Emslie, 1988; Dryer, 1994; Mead and others, 2003
Reptilia undetermined	Hevly, 1984
Class Aves	
Order Accipitriformes	
Accipiter striatus (Holocene general)	Mead, 1981; Hevly, 1984
Aquila chrysaetos	Hevly, 1984; Carpenter, 2003; Hunt and Lucas, 2018

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[8] *Lampropeltis getulus* = *Lampropeltis getula*

Buteo jamaicensis	Hevly, 1984; Hunt and Lucas, 2018
Buteo regalis (Holocene general)	Mead, 1981
Buteo sp.	Emslie, 1988
cf. *Buteo jamaicensis*	Carpenter, 2003
Buteogallus anthracinus (Holocene general)	Mead, 1981; Hevly, 1984
Circus cyaneus	Emslie, 1988
cf. *Circus cyaneus* (Holocene general)	Hevly, 1984
Hawk similar to *Buteo jamaicensis*	Miller, 1960
Order Anseriformes	
Aix sponsa (Holocene general)	Mead, 1981; Hevly, 1984
Anas acuta (Holocene general)	Mead, 1981; Hevly, 1984
Anas americana	Hevly, 1984; Emslie, 1988
Anas clypeata	Hevly, 1984; Emslie, 1988
Anas crecca	Emslie, 1988
Anas crecca carolinensis?	Mead, 1981
Anas crecca cf. *carolinensis* (Holocene general)	Hevly, 1984
Anas cyanoptera (Holocene general)	Mead, 1981; Hevly, 1984
Anas discors	Rea and Hargrave, 1984
Anas platyrhynchos	Rea and Hargrave, 1984; Emslie, 1988
Anas strepera (Holocene general)	Mead, 1981; Hevly, 1984
Anas sp.	Emslie, 1988; Emslie and others, 1995
Aythya americana (Holocene general)	Mead, 1981; Hevly, 1984
Aythya affinis	Hevly, 1984; Emslie, 1988
Aythya marila (Holocene general)	Mead, 1981; Hevly, 1984
Aythya valisineria (Holocene general)	Mead, 1981; Hevly, 1984
Aythya sp.	Emslie, 1988
Aythya sp.? (Holocene general)	Hevly, 1984
Branta canadensis (Holocene general)	Mead, 1981; Hevly, 1984
Bucephala albeola (Holocene general)	Mead, 1981; Hevly, 1984
Bucephala clangula (Holocene general)	Mead, 1981
Chen caerulescens	Hevly, 1984; Emslie, 1988
cf. *Clangula hyemalis* (Holocene general)	Hevly, 1984
Mergus cucullatus (Holocene general)	Mead, 1981; Hevly, 1984
Mergus merganser (Holocene general)	Mead, 1981; Hevly, 1984
Olor columbianus (Holocene general)	Mead, 1981
cf. *Olor columbianus* (Holocene general)	Hevly, 1984
Oxyura jamaicensis (Holocene general)	Mead, 1981; Hevly, 1984
Order Apodiformes	
Aeronautes saxatalis	Emslie, 1988
Order Cathartiformes	
Cathartes aura	Mead, 1981; Hevly, 1984; Emslie, 1988; Mead and Phillips, 1981
?*Cathartes aura*	Carpenter, 2003

Coragyps atratus	Carpenter, 2003; Hunt and Lucas, 2018
Coragyps occidentalis	Hunt and Lucas, 2018
Gymnogyps amplus?	deSaussure, 1956
Gymnogyps californianus	*see text*
Gymnogyps sp.	Rea and Hargrave, 1984
Teratornis merriami	Mead, 1981; Rea and Hargrave, 1984
Teratornis cf. *T. merriami*	Dryer, 1994
Teratornis sp.	Lindsay and Tessman, 1974
Order Charadriiformes	
Actitis macularia	Rea and Hargrave, 1984
Calidris melanotos	Rea and Hargrave, 1984
Capella gallinago	Mead, 1981; Rea and Hargrave, 1984
Larus pipixcan (Holocene general)	Hevly, 1984
Larus sp.	Emslie, 1988
Numenius americanus (Holocene general)	Mead, 1981; Hevly, 1984
Phalaropus fulicarius	Rea and Hargrave, 1984
Phalaropus lobatus	Rea and Hargrave, 1984; Emslie, 1988
Phalaropus cf. *fulicarius*	Mead, 1981
Recurvirostra americana	Hevly, 1984; Emslie, 1988
Tringa semipalmata[9]	Emslie and others, 1995
Order Columbiformes	
Zenaida macroura	Hevly, 1984; Emslie, 1988; Emslie and others, 1995
Order Falconiformes	
Falco femoralis	Miller, 1960; Carpenter, 2003; Hunt and Lucas, 2018
Falco mexicanus	Hevly, 1984; Emslie, 1988
Falco peregrinus	Emslie, 1988
Falco sparverius	Rea and Hargrave, 1984; Emslie, 1988; Emslie and others, 1995
Order Galliformes	
Centrocercus urophasianus (Holocene general)	Mead, 1981; Hevly, 1984
cf. *Colinus virginianus*	Emslie, 1988
Meleagris crassipes (Holocene general)	Mead, 1981; Hevly, 1984
Order Gruiformes	
Fulica americana	Emslie, 1988
Gallinula chloropus (Holocene general)	Mead, 1981; Hevly, 1984
cf. *Porzana carolina*	Emslie, 1988
Order Passeriformes	
Agelaius phoeniceus	Emslie, 1988
Aphelocoma caerulescens (Holocene general)	Mead, 1981
cf. *Aphelocoma caerulescens* (Holocene general)	Hevly, 1984
Catherpes mexicanus (Holocene general)	Mead, 1981; Hevly, 1984

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[9] *Catoptrophorus semipalmatus = Tringa semipalmata*

Cinclus mexicanus .... Rea and Hargrave, 1984
Contopus sordidulus (Holocene general) .... Mead, 1981; Hevly, 1984
Corvus corax .... Hevly, 1984; Emslie, 1988
Corvus corax sinuatus (Holocene general) .... Mead, 1981
Corvus sp. .... Emslie, 1988; Emslie and others, 1995
Dendroica coronata (Holocene general) .... Mead, 1981; Hevly, 1984
Empidonax sp.? (Holocene general) .... Hevly, 1984
Eremophila alpestris .... Mead, 1981; Hevly, 1984
Hirundo sp. (Holocene general) .... Mead, 1981
Hirundo sp.? (Holocene general) .... Hevly, 1984
Icterus galbula (Holocene general) .... Hevly, 1984
Icterus sp. (Holocene general) .... Mead, 1981
Junco hyemalis .... Mead, 1981; Rea and Hargrave, 1984
cf. *Junco* sp. .... Emslie, 1988
Lanius excubitor (Holocene general) .... Mead, 1981; Hevly, 1984
Loxia cf. *L. curvirostra* .... Mead, 1981
Myadestes townsendi (Holocene general) .... Mead, 1981; Hevly, 1984
Passerella iliaca (Holocene general) .... Hevly, 1984
Passerina sp. (Holocene general) .... Hevly, 1984
Pica hudsonia (Holocene general)[10] .... Hevly, 1984
Salpinctes obsoletus (Holocene general) .... Hevly, 1984
Salpinctes obsoletus? .... Mead, 1981
Sayornis nigricans (Holocene general) .... Hevly, 1984
Sayornis saya (Holocene general) .... Mead, 1981; Hevly, 1984
Sialia currucoides (Holocene general) .... Mead, 1981; Hevly, 1984
Turdus grayi (Holocene general) .... Hevly, 1984
Turdus migratorius (Holocene general) .... Hevly, 1984
Turdus migratorius? .... Mead, 1981
Turdus sp.? .... Mead, 1981
Zonotrichia cf. *Z. leucophrys* (Holocene general) .... Hevly, 1984
cf. Fringillidae (late Holocene) .... Mead and Van Devender, 1981
Passeriformes undetermined .... Emslie, 1988; Dryer, 1994; Emslie and others, 1995

Order Pelecaniformes

Ardea herodias (Holocene general) .... Mead, 1981; Hevly, 1984
Nycticorax nycticorax .... Hunt and Lucas, 2018
cf. *Nycticorax nycticorax* .... Carpenter, 2003
Ardeidae undetermined .... Carpenter, 2003

Order Piciformes

Colaptes auratus .... Emslie, 1988
Sphyrapicus varius .... Emslie, 1988

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[10] *Pica pica hudsonica* = *Pica hudsonia*

Picidae undetermined	Emslie, 1988
Order Podicipediformes	
Aechmophorus occidentalis	Hevly, 1984; Emslie, 1988
Podiceps auritus (Holocene general)	Mead, 1981
Podiceps nigricollis (Holocene general)	Mead, 1981; Hevly, 1984
cf. *Podiceps nigricollis*	Emslie, 1988
Podilymbus podiceps	Emslie, 1988
Order Strigiformes	
Bubo virginianus	Mead, 1981; Mead and Van Devender, 1981; Rea and Hargrave, 1984
Otus asio (Holocene general)	Mead, 1981; Hevly, 1984
Tyto alba	Miller, 1960; Carpenter, 2003; Hunt and Lucas, 2018
Aves undetermined	Cole and Mead, 1981; Mead and Phillips, 1981; Hevly, 1984; Emslie, 1988; Dryer, 1994
Class Mammalia	
Order Pilosa	
Nothrotheriops shastensis[11]	*see text*
Order Eulipotyphla	
Notiosorex crawfordi	Mead, 1981; Mead and Phillips, 1981; Mead and Van Devender, 1981; Emslie, 1988
Order Rodentia	
Ammospermophilus cf. *A. leucurus* (late Holocene)	Mead and Van Devender, 1981
Castor canadensis (Holocene general)	Mead, 1981; Olsen and Olsen, 1984
Dipodomys sp.	Lindsay and Tessman, 1974; Mead, 1981; Mead and Van Devender, 1981; Hunt and Lucas, 2018
Erethizon dorsatum	Van Devender and others, 1977; Mead, 1981; Mead and Phillips, 1981; Hunt and Lucas, 2018
Eutamias sp.	Lindsay and Tessman, 1974; Cole and Mead, 1981; Hunt and Lucas, 2018
Lemmiscus curtatus	Mead and others, 2003
Marmota flaviventris	Lange, 1956; Van Devender and others, 1977; Hunt and Lucas, 2018
Marmota flaviventris cf. *M. f. engelhardti*	Wilson, 1942
Marmota cf. *M. flaviventris*	Mead, 1981; Mead and Phillips, 1981
Marmota sp.	Lindsay and Tessman, 1974; Emslie and others, 1995
Microtus sp.	Cole and Mead, 1981; Mead, 1981; Mead and Phillips, 1981; Emslie, 1988; Mead and others, 2003
Neotoma cinerea	Mead and others, 2003
Neotoma devia or *N. lepida*	Hunt and Lucas, 2018
Neotoma lepida	Van Devender and others, 1977; Mead, 1981; Hunt and

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[11] *Nothrotherium shastense = Nothrotheriops shastensis*

	Lucas, 2018
Neotoma mexicana	Mead, 1981; Hunt and Lucas, 2018
Neotoma stephensi	Van Devender and others, 1977; Mead, 1981; Hunt and Lucas, 2018
Neotoma cf. *N. cinerea*	Cole and Mead, 1981
Neotoma cf. *N. lepida*	Cole and Mead, 1981
Neotoma cf. *N. mexicana*	Van Devender and others, 1977
Neotoma sp.	Lindsay and Tessman, 1974; Van Devender and others, 1977; Cole and Mead, 1981; Olsen and Olsen, 1984; Emslie, 1988; Dryer, 1994; Mead and others, 2003
Neotoma spp.	Mead, 1981; Mead and Phillips, 1981
Ondatra zibethicus (Holocene general)	Mead, 1981; Olsen and Olsen, 1984
Perognathus cf. *P. intermedius*	Mead, 1981; Mead and Phillips, 1981
Perognathus sp.	Emslie, 1988
Peromyscus sp.	Van Devender and others, 1977; Cole and Mead, 1981; Mead and Phillips, 1981; Olsen and Olsen, 1984; Emslie, 1988; Dryer, 1994; Mead and others, 2003; Hunt and Lucas, 2018
Peromyscus spp.	Mead, 1981; Mead and Van Devender, 1981
cf. *Reithrodontomys*	Cole and Mead, 1981
Sciurus sp. (Holocene?)	Olsen and Olsen, 1984
cf. *Sciurus* sp.	Emslie, 1988
Spermophilus variegatus	Mead, 1981; Mead and Phillips, 1981
Spermophilus sp.	Lindsay and Tessman, 1974; Mead and others, 2003; Hunt and Lucas, 2018
Tamias sp.	Hunt and Lucas, 2018
Thomomys sp.	Lindsay and Tessman, 1974; Cole and Mead, 1981; Hunt and Lucas, 2018
Sciuridae undetermined	Emslie and others, 1995
Rodentia undetermined	Hevly, 1984
Order Lagomorpha	
Lepus californicus	Mead, 1981; Olsen and Olsen, 1984
Lepus near *L. californicus*	Wilson, 1942
Lepus sp.	Lindsay and Tessman, 1974; Emslie, 1988; Emslie and others, 1995; Hunt and Lucas, 2018
Sylvilagus cf. *S. audubonii*	Olsen and Olsen, 1984
Sylvilagus sp.	Lindsay and Tessman, 1974; Van Devender and others, 1977; Mead, 1981; Emslie, 1988; Emslie and others, 1995; Mead and others, 2003; Hunt and Lucas, 2018
Lagomorpha undetermined	Hevly, 1984
Order Chiroptera	
Antrozous pallidus	Emslie, 1988

Desmodus stocki	Ray and others, 1988; Carpenter, 2003; Hunt and Lucas, 2018
Eptesicus cf. *E. fuscus*	Olsen and Olsen, 1984
Euderma maculatum	Mead and Mikesic, 2005
Eumops sp.	Carpenter, 2003; Hunt and Lucas, 2018
Lasiurus cinereus	*see text*
Lasionycteris noctivagens	*see text*
Myotis sp. (possibly Holocene)	Olsen and Olsen, 1984
cf. *Myotis* sp.	Emslie, 1988
Pipistrellus hesperus [*Parastrellus*]	Emslie, 1988
Plecotus townsendi [*Corynorhinus*]	Emslie, 1988
Tadarida brasiliensis	Carpenter, 2003; Hunt and Lucas, 2018
Chiroptera undetermined	Van Devender and others, 1977
Order Carnivora	
Bassariscus astutus	Wilson, 1942; Mead, 1981; Mead and Phillips, 1981; Hunt and Lucas, 2018
Bassariscus sp.	Lindsay and Tessman, 1974
Canis latrans (Holocene general)	Mead, 1981; Olsen and Olsen, 1984
Canis sp. (wolf)	Emslie, 1988
Lontra canadensis	Mead, 1981; Olsen and Olsen, 1984
Lynx rufus	Mead, 1981
Lynx sp.	Wilson, 1942; Hunt and Lucas, 2018
Miracinonyx truemani	Hodnett and others, in press
Mustela sp.	Lindsay and Tessman, 1974; Hunt and Lucas, 2018
Procyon lotor (Holocene general)	Mead, 1981; Olsen and Olsen, 1984
Puma concolor[12]	Mead, 1981; Mead and others, 2003; Hunt and Lucas, 2018
Puma concolor?	Wilson, 1942
Spilogale putorius	Emslie, 1988
Spilogale gracilis or *S. putorius*	Hunt and Lucas, 2018
Spilogale sp.	Lindsay and Tessman, 1974
Urocyon cinereoargenteus (Holocene general)	Mead, 1981; Olsen and Olsen, 1984
Vulpes vulpes	Carpenter, 2002
Canidae undetermined	Carpenter and Mead, 2000
Order Proboscidea	
Mammuthus sp.	Emslie, 1987, 1988
Order Perissodactyla	
Equus sp. (*E. conversidens*?)	Harington, 1984
Equus sp.	Wilson, 1942; Mead, 1981; Emslie, 1987, 1988; Carpenter, 2003; Mead and others, 2003; Hunt and Lucas, 2018
Order Artiodactyla	
Antilocapra americana	Mead, 1981; Mead and Phillips, 1981

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[12] *Felis concolor* = *Puma concolor*

Bison sp. .... Harington, 1984; Emslie, 1987, 1988; Mead and others, 2003; Martin, 2014; Martin and others, 2017
Camelops hesternus .... Mead and others, 2003
Camelops cf. *C. hesternus* .... Mead, 1981; Mead and Phillips, 1981
?*Camelops* sp. .... Emslie, 1987
cf. *Camelops* sp. .... Emslie, 1988
Euceratherium collinum .... Mead and others, 2003; Kropf and others, 2007
cf. *Euceratherium collinum* .... Mead and others, 2003
Odocoileus hemionus (Holocene general) .... Mead, 1981; Olsen and Olsen, 1984
Odocoileus sp. .... Mead, 1981; Mead and Phillips, 1981
Oreamnos harringtoni .... *see text*
Oreamnos sp. (probably Holocene) .... Harington, 1984
Oreamnos or *Ovis* .... Emslie, 1988
Ovis canadensis .... Mead, 1981; Mead and Phillips, 1981; Olsen and Olsen, 1984; Harington, 1984; Carpenter, 2003; Mead and others, 2003; Hunt and Lucas, 2018
Ovis sp. .... Wilson, 1942
Bovidae undetermined .... Carpenter, 2003
Artiodactyla undetermined .... Cole and Mead, 1981; Harington, 1984; Dryer, 1994; Carpenter, 2003
Undetermined large mammal .... Emslie, 1988; Emslie and others, 1995
Mammalia undetermined .... Hevly, 1984
Vertebrata undetermined .... Hevly, 1984

Ichnofossils and Reproductive Traces

Invertebrates

Dipteran pupal case .... Hevly, 1984
“Helminth” eggs .... Schmidt and others, 1992
Nematode eggs .... Laudermilk and Munz, 1938

Vertebrates

Artiodactyl dung .... Mead and Swift, 2012; Hunt and Lucas, 2018
Bassariscus astutus dung .... Mead and Swift, 2012; Hunt and Lucas, 2018
Bat guano .... *see text*
Bison sp. dung .... Mead and Swift, 2012
Equus sp. dung .... Mead and Swift, 2012
Erethizon dorsatum dung .... Mead and Swift, 2012
Large felid dung .... Mead and Swift, 2012; Hunt and Lucas, 2018
cf. *Lepus* sp. dung .... Mead and Swift, 2012; Hunt and Lucas, 2018
Neotoma spp. dung .... abundant in *Neotoma* middens; *see text*
Nothrotheriops shastensis dung (*Castrocopros martini**) .... *see text*
Oreamnos harringtoni dung .... *see text*

Ovis canadensis dung	Robbins and others, 1984; O'Rourke and Mead, 1985; Mead and Swift, 2012; Hunt and Lucas, 2018
Peromyscus sp. dung	Emslie, 1988
Rabbit dung	Hevly, 1984
Rodent dung	Hevly, 1984; Mead and Swift, 2012; Hunt and Lucas, 2018
Sauromalus dung (age not stated)	Mead and Swift, 2012
cf. *Sylvilagus* sp. dung	Mead and Swift, 2012; Hunt and Lucas, 2018
Bird regurgitation pellets	Emslie and others, 1995; Mead and Swift, 2012
Bassariscus astutus middens (late Holocene)	Mead, 1981; Mead and Phillips, 1981
Neotoma spp. middens	*see text*
Cathartes aura eggshells	Miller, 1960; Harington, 1975
Gymnogyps californianus eggshells	Emslie, 1987
Gymnogyps nest	Martin, 2014

Other Fossils

Phylum Apicomplexa	
Class Conoidasida	
Subclass Coccidia	
*Archaeococcidia antiquus**	Schmidt and others, 1992
*Archaeococcidia nothrotheriopsae**	Schmidt and others, 1992
Fungal spores	Robbins and others, 1984; Schmidt and others, 1992

BRACHIOPODS

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Brachiopod
Scientific Name: *Peniculauris bassi*
Geologic Age: 270 million years ago (Permian)
Geologic Formation: Kaibab Limestone

Interactive 3D model

Stick-type bryozoans attached to the sea floor to filter feed.

Brachiopods such as, *Penicularis, Meekella,* and *Derbyia,* were members of a robust and diverse marine community including sponges, crinoids, coral, bryozoans, and pelecypods. These filter feeders thrived with abundant sunlight, food, and habitat. Look for these organisms along the rim of the canyon.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

7 of 9

Grand Canyon National Park Fossil Trading Card featuring the fossil brachiopod Peniculauris bassi *from the Permian Kaibab Formation (NPS).*

GRAND CANYON NATIONAL PARK PALEONTOLOGICAL RESOURCES MANAGEMENT AND PROTECTION

Diana Boudreau[1], Vincent Santucci[2], Klara Widrig[1], Mark Nebel[1], Anne Miller[1],
Ronnie Colvin[1], Kim Besom[1], and Colleen Hyde[1]

ABSTRACT

Grand Canyon National Park (GRCA) contains a multitude of paleontological resources that reveal the history of life on Earth. Since 2009, these resources are required to be managed and preserved by the National Park Service under the Paleontological Resources Preservation Act (PRPA). Within this article, background information and current GRCA procedures regarding resource management, protection, and conservation of fossils are addressed. At the forefront of managing fossil resources are inventorying and monitoring. These tasks utilize the latest in geospatial techniques to properly document new and historic fossil localities and their conditions to establish baseline data. GRCA's paleontological resources attract external researchers from around the world, leading to a robust research and permitting system operated by the park. In addition, historic fossil collections, as well as more recently collected specimens, are properly curated and housed within the park and are made available to outside researchers upon request. Fossil resources provide unique opportunities for resource managers to collaborate with other divisions within the park. Well-known and publicly accessible fossil localities within the park allow for the development of unique interpretive and educational programming. However, the accessibility of these localities has led to issues of vandalism and theft, requiring communication between Law Enforcement Officers and Resource Management staff. Managing fossil resources is a multidimensional process that requires regular interdepartmental collaboration to ensure these non-renewable resources will continue to be monitored, conserved, and protected into the future.

INTRODUCTION

Paleontological resources are an integral part of Grand Canyon National Park (GRCA). As stated in the park's foundation statement, one of the purposes of GRCA is to preserve and protect Grand Canyon's unique geologic, paleontologic, and other natural and cultural features for the benefit and enjoyment of the visiting public. Furthermore, paleontological resources are considered a fundamental resource, warranting primary consideration during planning and management, contributing to the park's significance, and helping achieve the park's purpose (NPS, 2017).

The foundation document also highlights fossil resources of particular interest, such as the diverse invertebrate and vertebrate trace fossils in the Coconino Sandstone, Precambrian stromatolites, Pleistocene vertebrate fossils found in cave deposits, and the large assemblages of marine invertebrate fossils in the Redwall Limestone, Surprise Canyon Formation, and Kaibab Formation. While it is known that GRCA contains an extremely diverse and complete fossil record, visitor use trends and site conditions for heavily visited fossil localities are lacking. The foundation statement supports the development of this paleontology inventory report and paleontological resource protection plan in order to preserve paleontological resources and support the park's purpose (NPS, 2017).

In previous years, there have been a few dedicated paleontologists studying fossil tracks, cave fossils, vertebrates,

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and other fossil resources found at GRCA; however, they are often outside researchers who do not work directly for the NPS. During the 2019 Paleontology Inventory, GRCA preserved and protected paleontological resources by building a park-based team and partnering with paleontologists from the NPS Geologic Resources Division. Therefore, 2019 has been an important year that demonstrated that establishing a team of dedicated paleontologists can greatly advance the knowledge and protection of fossil resources in NPS units and provide valuable outreach opportunities for the public.

GRCA PALEONTOLOGICAL RESOURCE INVENTORY

The inventory of paleontological resources is one of the most fundamental resource management activities that can be undertaken by a park. Baseline paleontological resource inventories help identify the scope, significance, distribution, and resource management issues associated with fossils. The information gained through the inventory of park fossils enables park management to incorporate this information into park planning, programming, and decision-making.

Paleontological resource inventories are specifically identified in Section 6302 of the Paleontological Resources Preservation Act of 2009 (16 USC 470aaa–1), in Section 4302 of the Federal Cave Resources Protection Act of 1988 (16 USC 4301), and in NPS policy. The NPS Paleontology Program provides assistance to parks, including GRCA, by documenting and preserving paleontological resource information in the NPS Paleontology Archives and Library.

Between 1970 and 2010, most of the paleontology-related activities undertaken at GRCA were primarily related to research and collecting by outside academic paleontologists and geologists working in the park. Jim Mead and students from the Quaternary Studies Program at Northern Arizona University coordinated paleontological research and collecting at Rampart Cave and other caves in GRCA (Mead, 1981; Mead and Van Devender, 1981; Mead and Phillips, 1982; Mead and others, 2003; Carpenter, 2003). In 2001, an inventory of paleontological resources associated with NPS caves, including those in GRCA, was undertaken by the NPS Geologic Resources Division (Santucci and others, 2001). This work later led to a GRCA-focused inventory of cave paleontological resources (Kenworthy and others, 2004). A more comprehensive inventory of paleontological resources at GRCA was included in a report documenting the fossils of the Southern Colorado Plateau Inventory and Monitoring Network in 2009 (Tweet and others, 2009). Between 2012 and 2018 a trans-boundary and collaborative project known as the Greater Grand Canyon Landscape Assessment (GGCLA) was undertaken to assess cave resources, including cave fossils, in and around the park. This project was expanded to include a Resource Condition Assessment (RCA) for the cave resources evaluated in the GGCLA project (Stortz, 2018).

A number of paleontology interns were hired at GRCA after Deanna Greco was hired as the GRCA Physical Science Program Manager in 2010. Cassi Knight, Jeff Dobbins, James Super, Robyn Henderek, and Anne Miller served as Geoscientists-in-the-Parks (GIP) paleontology interns at GRCA and assisted with a variety of paleontological resource inventory projects. The work completed by these paleontology interns, along with their field notes, are incorporated into the GRCA museum and resource management archives.

In preparation for GRCA's centennial in 2019, the NPS Paleontology Program (Vincent Santucci) initiated communication with GRCA staff (Jeanne Calhoun) in early 2018 proposing the development of a park specific paleontological resource inventory for GRCA in conjunction with the park's centennial. This proposal was met with support from GRCA leadership and is the basis for this report.

In addition to the publication of this paleontology resource inventory report, GRCA staff conducted several surveys to document fossil localities as part of the second ever NPS PaleoBlitz (the first was conducted at CHIC in 2016). A few stratigraphic units at GRCA were the focus of these PaleoBlitz activities; Chinle Formation, Moenkopi Formation, Kaibab Formation, Coconino Sandstone, and Bright Angel Shale. Paleontologists Adam Marsh and Bill Parker from Petrified Forest National Park (PEFO) assisted in surveying the Mesozoic strata. JP Hodnett, program coordinator for the Maryland-National Capital Park and Planning Commission (M-NCPPC) Dinosaur Park (MD) and National Fossil Day coordinator, conducted surveys for vertebrate material in the Kaibab Formation on the North and South Rims. The GRCA Paleontology Team (Mark Nebel, Anne Miller, Diana Boudreau, Klara Widrig, and Jered Hansen) conducted targeted surveys of, primarily, the Coconino Sandstone and, to a lesser degree, the Kaibab and Toroweap Formations and the Bright Angel Shale, throughout the 2019 season, and discovered a number of previously unknown track localities (figure 1). Each survey used a combination of field notebooks, paper locality forms, and digital data collection devices leveraging the ArcGIS Online and Collector technologies to physically and digitally collect locality and site information, setting the stage for faster and more efficient data entry for future paleontology surveys.

Figure 1. *The GRCA paleontology team documenting a new fossil track locality in the Coconino Sandstone during the 2019 PaleoBlitz (left to right: Klara Widrig, Anne Miller, Diana Boudreau, and Jered Hansen) (NPS/MARK NEBEL).*

GRCA PALEONTOLOGICAL RESOURCE MONITORING

The monitoring of in situ paleontological resources is another important resource management tool for the NPS. Paleontological resource monitoring enables the long term assessment of fossil stability through the use of a variety of techniques (Santucci and Koch, 2003; Santucci and others, 2009). Monitoring strategies may be developed for each fossil locality to consider the site specific variables, either natural or anthropogenic, which may threaten the paleontological resources and their values. Paleontological monitoring prescriptions are developed to determine the site specific monitoring activities such as 1) how frequently to monitor the fossil locality; 2) which monitoring methods are to be used; 3) when conditions warrant the collection of fossils from the locality; and other considerations.

The most common technique to monitor paleontological sites is repeat photography. GRCA archives contain many images of known fossil sites, many of which would benefit from monitoring. Many of these images have recently been linked to GRCA's paleontology geodatabase for ease of access and ability to spatially analyze paleontology site and locality data. Recreating these images would allow GRCA staff to assess the vulnerability of those sites due to natural or anthropogenic effects. Photogrammetry is another great option for monitoring. By taking a series of photographs and stitching them together to create 3D models, it is possible to preserve large specimens, such as trackways, to establish a baseline condition. However, neither of these techniques are quantitative in nature. Miller and others developed a methodology, based on paleontological sites from GRCA, that uses clearly defined indices to quantitatively identify high-priority sites for monitoring (2018). Both quantitative and qualitative methods should be utilized to monitor paleontological resources.

There are a number of natural processes, environmental conditions, and other natural factors beyond human management that affect the stability of paleontological sites at GRCA. Fossils are primarily affected by weathering and erosion, particularly at GRCA where unvegetated outcrops and seasonal climate are common. Freeze-thaw cycles contribute to increased fracturing and monsoonal precipitation can increase rates of erosion. Winds transporting sediments can also gradually abrade fossils already exposed. Fossils found near creeks and streams at GRCA are threatened by flash flood activity that could abrade exposed fossils or wash fossils out of geologic context and deeper into the canyon. Sudden geologic processes, such as rock falls, may also reveal, cover, or damage fossil resources. Biological activity, such as lichen growth, plant growth, or trampling by deer, elk, or bighorn, could impact the visibility or quality of those fossils.

In addition to natural processes, anthropogenic or human caused impacts, both intentional and unintentional, can lead to degradation of fossil sites. Unintentional harm could be done by individuals that are not aware of the fossils or those who don't understand that their actions negatively impact fossil stability. Despite the fossil protection provided by the Paleontological Resources Preservation Act (PRPA), fossils are still intentionally disturbed, removed, or vandalized. Due to these impacts, determining the monitoring plan for a fossil site should factor in ease of public access, visitor use near or at the site, potential for any ground disturbing activities, such as trail maintenance or construction work, and other factors that may contribute to theft or vandalism (Miller and others, 2018: table 4).

GRCA PALEONTOLOGICAL RESOURCE PROTECTION

Paleontological resources are threatened by natural processes such as erosion, as well as anthropogenic impacts, such as unauthorized collecting and vandalism. These threats impact the fossils' inherent scientific and educational value, as removing fossils from their geologic context impairs scientists' ability to accurately understand a fossil's significance in the geologic record. For resource management and protection, patrols of known paleontological sites and resources should be conducted to identify any indirect or direct human or natural impacts.

In 2009, the Paleontological Resources Preservation Act (PRPA) was signed into law as part of the Omnibus Public Land Management Act of 2009. New paleontology legislation is currently being drafted by an interagency coordination team including representatives from the Bureau of Land Management (BLM), Bureau of Reclamation (BOR), National Park Service (NPS), and U.S. Fish & Wildlife Service (FWS) within the Department of the Interior (DOI). This legislation will provide guidance related to fossil inventories, monitoring, public education, research and collecting permits, curation, and criminal prosecution on DOI lands. For more information regarding this act, visit **https://www.nps.gov/subjects/fossils/fossil-protection.htm**.

History of Paleontological Resource Protection at GRCA

Fossil theft and vandalism at GRCA have not been frequently reported. Few incident reports have been filed regarding paleontology theft and vandalism. However, anecdotal evidence from Law Enforcement Officers (LEO) in South Rim, Inner Canyon, and North Rim districts indicate that damage to fossils may occur more frequently than the incident report records show (figures 2 and 3). Most fossil incidents occur within the Canyon District, because more fossils are exposed in that district.

The first record of fossil vandalism was in 1946. Superintendent Harold Bryant saw threats to park resources, including fossils, and compiled a list including abused signs, interpretive displays, trees, shrubbery, and graffiti, as well as noting damaged or stolen binoculars and a fossil specimen from the Yavapai Observation Station (now renamed Yavapai Geology Museum). Bryant's efforts emboldened staff to prevent, as he called them, "such vicious acts of destruction." In addition, this was the start of littering fines and proactive measures to lessen harm to park resources (Anderson, 2000).

More recently, there have been continued reports of fossil theft and vandalism. In 2007 or 2008, law enforcement investigated a report of a fossil track block that was stolen off of North Kaibab Trail. During Spring Break of 2017, the Fossil Fern Exhibit along South Kaibab Trail at Cedar Ridge and fern impressions surrounding the exhibit were heavily vandalized (figures 4 and 5). Most of the damage involved scratching rocks and the plexiglass covering the exhibit. Part of the plexiglass was broken, exposing the fossils housed inside the exhibit. Fossil specimens may have been removed from the area by visitors, but this has not been confirmed.

On May 20, 2019 two individuals were caught collecting approximately 13.5 kg (30 lbs.) of specimens from the fossil beds along the western Rim Trail (figure 6). They were reported by a visitor, and law enforcement responded in time to apprehend the individuals. The couple appeared to be avid rock collecting hobbyists and used small hammers and picks to collect specimens. All fossil specimens were confiscated and are being held as evidence.

Paleontological Resource Protection Recommendations

Canyon Rangers, law enforcement, and GRCA staff should be attentive during their regular duties for individuals attempting to take or deface specimens. Many

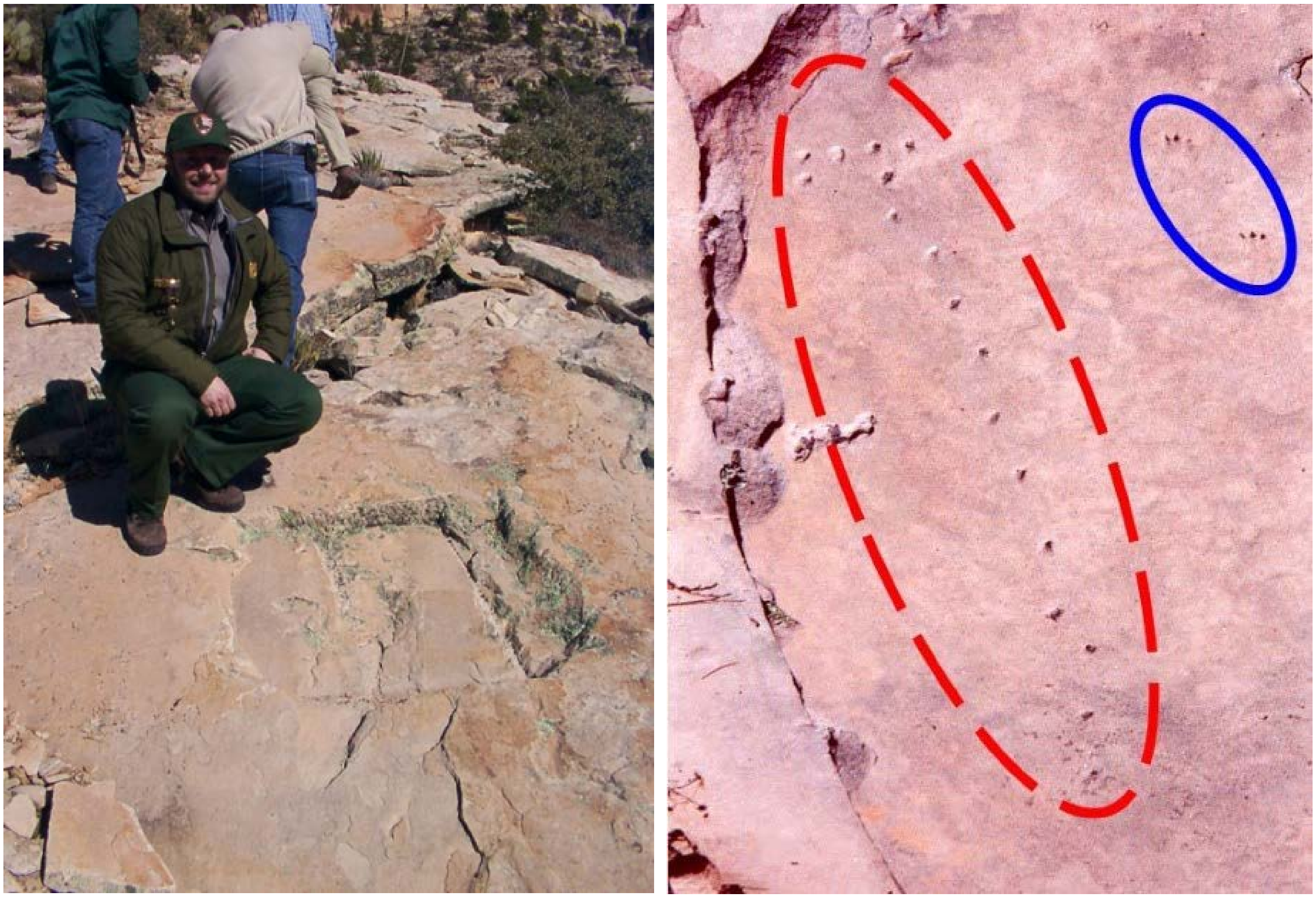

Figure 2. *Track blocks have been chiseled out and removed from the Coconino Sandstone along Hermit Trail (left). Individuals have attempted to remove other trackways (solid blue oval), but did not complete the task, leaving behind chisel marks (dashed red oval) (NPS/VINCENT SANTUCCI).*

Figure 3. *A nail was used by a visitor attempting to pry this brachiopod fossil from the Kaibab Formation (NPS/VINCENT SANTUCCI).*

Figure 4. *Scratch marks on the Fossil Fern Exhibit structure along the South Kaibab Trail in 2017 (NPS/ANNE MILLER).*

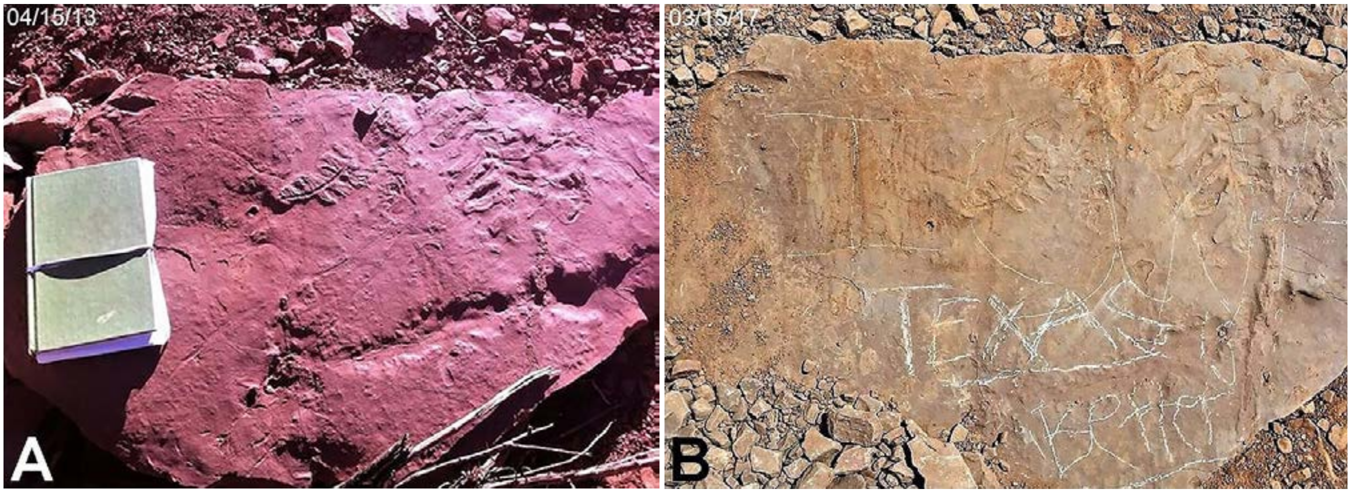

Figure 5. *Photographs from 2013* ***(A)*** *and 2017* ***(B)*** *of the same fossil fern impressions near the exhibit showing vandalism that occurred during Spring Break in 2017 (NPS).*

well-preserved specimens are close to the main trails in the park and are therefore at a higher risk of damage or theft due to ease of access. Regular patrols should be conducted near heavily visited paleontological localities.

Fossil theft and vandalism trainings can better prepare staff to identify, report, and manage fossil theft and vandalism incidents. For more information on Paleontology Resource Protection trainings, contact Vincent Santucci (vincent_santucci@nps.gov). Regular training of LEOs and interpretive staff can help reduce the number of fossil theft or vandalism incidents. However, active recruitment of paleontological research scientists should also be considered a management strategy.

Figure 6. *Rock and fossil specimens found in suspect's backpack after GRCA law enforcement apprehended them removing specimens from park land in 2019 (NPS).*

If fossil specimens are found during regular patrols by staff or visitors, follow these steps:

- Do not collect, remove, or disturb the fossils without consulting the Chief of Resources or individual responsible for paleontological resources at GRCA.
- Record locality information, including, but not limited to, geographic location, nearest trail or natural feature, GPS coordinates, and description of fossil within the rock.
- Take photos of the fossil specimen itself with a scale, a wider view of the fossil in the surrounding rock, and images looking up trail, down trail, and/or with identifiable landmarks in frame. Use an item for scale in each photo (e.g., another hiker, backpack, water bottle, coin).
- Reach out to individuals responsible for paleontological resources at GRCA to notify them of the resource and provide them with the associated information.

GRCA PALEONTOLOGICAL RESOURCE RESEARCH AND PERMITS

Internal Permits

Several internal blanket permits were issued to past Chiefs of Resources to facilitate study and interpretation of geological and paleontological resources within the park. Permit GRCA-2011-SCI-0034 was issued to Deanna Greco to facilitate a paleontological inventory of Grand Canyon National Park with Geoscientists-in-the-Parks (GIP) interns Jeff Dobbins and James Super. Judy Helmich was issued permit GRCA-2003-SCI-0085 that allowed interpretive staff to collect specimens while in the field to use in their programs. Both of these permits are now expired.

On October 18, 2019, the GRCA Paleontology Program received a programmatic Categorical Exclusion (CE) (PEPC 90271) to guide ongoing paleontology work in the Park. The CE describes routine, ongoing paleontology inventory and monitoring work and resource mitigations for performing this work.

Previous Research Permits

Jim Mead and Mary Carpenter were issued permit GRCA-1999-SCI-0001 for their project "*Late Pleistocene Vertebrate Communities in the Lower Grand Canyon, Arizona: Rampart and Muav Caves.*" This work supported Mary Carpenter's thesis (Carpenter, 2003) and an abstract (Carpenter and Mead, 1999).

John Foster was issued permit GRCA-2009-SCI-0032 in an attempt to relocate historic trilobite quarry locations. The permit was for in situ research only. He was unsuccessful in relocating the Cameron-Walcott quarry site, but the McKee Quarry was relocated in 2009. His findings were published in the Museum of Northern Arizona bulletins (Foster, 2011).

Jessica Metcalfe was issued permit GRCA-2013-SCI-0001 for her dissertation project, "*Late Pleistocene Paleoecology of the Colorado Plateau.*" The overall goal of this study was to reconstruct late Pleistocene paleoecology on the Colorado Plateau using isotopic analysis to examine feeding and migratory patterns. No collections were made as part of this project, which instead relied on GRCA and MNA museum collections (Metcalfe, 2018).

Permit GRCA-2017-SCI-0054 was issued to Stephen Rowland for the study of fossil trackways in the Supai Formation. Research was focused on a trackway along the Bright Angel Trail, which may represent the oldest vertebrate trackway in the park. This research has been published as Rowland and others (2020).

Anne Miller was issued permit GRCA-2017-SCI-0059 for her Master's thesis at Northern Arizona University "*Ichnology of the Bright Angel Shale Formation, Grand Canyon, AZ: Indicators for Middle Cambrian Paleoecology*." This research is still ongoing.

A complete list of paleontology research permits issued in Grand Canyon National Park from 1999 to 2019 can be found in **appendix A**.

Current Permits

Permit GRCA-2019-SCI-0002 was issued to Vincent Santucci for the Grand Canyon National Park 2019 Paleontological Resource Inventory and PaleoBlitz. All field activities related to this report were authorized by this permit. Field activity is focused on the documentation and assessment of paleontological localities; however, surface collection of exceptional specimens is permitted.

GRCA PALEONTOLOGICAL RESOURCE CURATION AND MUSEUM COLLECTIONS

Museum collections at GRCA are stored at 2C Albright Avenue, Grand Canyon, Arizona, 86023. This storage facility was completed in 1999. It contains 6,000 ft^2 (557 m^2) of climate-controlled storage and houses over 1.6 million objects. Items are cataloged using the Interior Collections Management System (ICMS), version 8.20.48.3660 as of April 29, 2019.

Scope of Paleontological Collections

Grand Canyon National Park's paleontology collection includes a total of 13,428 catalog numbers. Of these, the vast majority were found within the park. Specimens collected from outside the park were once brought into the collections for teaching, research, exhibit, or other purposes, with the majority being from Arizona. This practice was discontinued in 1978, when the service's management policies stated "a scope of collection statement, in which the limits of museum collection are detailed, must be prepared and approved for every park." Fossils from other NPS units that remain in the GRCA collections include: 12 specimens from Harpers Ferry Center, one of which was returned to the Harpers Ferry Center museum storage facility; 38 specimens from Lake Mead National Recreation Area (LAKE); 45 specimens from Petrified Forest National Park (PEFO); and 239 specimens from Grand Canyon-Parashant National Monument (PARA). Most of the non-GRCA fossils are from areas in the vicinity of the park in northern Arizona. It should be noted that some Grand Canyon fossil specimens come from lands formerly part of GRCA, but now within the Havasupai Indian Reservation, which may lead to some confusion, because the original locality information may report that they are from the park. With 2,857 cataloged specimens, brachiopods are the most common fossil type in the collection, followed by mammals (2,177), trilobites (1,438), and bivalves (1,006). When considering the rock unit of origin, the greatest number of fossils in the collection were found in Quaternary deposits (4,994 catalog numbers), followed by the Kaibab Formation (3,302) and the Bright Angel Shale (1,669).

At least 167 fossil taxa have been named from specimens (holotypes, syntypes, etc.) collected within the modern boundaries of GRCA **(supplemental information part A)**. An additional 13 taxa are based on specimens potentially collected within GRCA, but the provenance information is too vague to know for certain (**supplemental information part B**) (Tweet and others, 2016). Four holotype specimens are stored in a locked cabinet separate from the rest of the paleontology collections for added security.

Notable Contributors to Paleontological Collections

Many of the fossils housed at Grand Canyon were collected by notable geologists and paleontologists including: Raymond Alf, Merrill Beal, Stan Beus, Major L. F. Brady, Jim Mead, Kenneth L. Cole, Arthur L. Lang, Raymond deSaussure, Steve Emslie, Bob Euler (archeologist), Lawrence Goebels, Paul Martin, Edwin D. McKee, Larry Coates, Charles Merriam, Arthur Phillips, Allen Phillips, Larry Powers, Louis Schellbach, Edward T. Schenk, Adolf Seilacher, Glen Sturdevant, and David White.

Paleontological Collections in Outside Repositories

Numerous GRCA specimens are housed at outside institutions. The exact number of these institutions will probably never be known. There are several reasons for this. Among the most important factors are the following: the Grand Canyon region has long been a popular area for geological and paleontological field trips; undocumented collecting frequently occurred before the permitting system was implemented; the park boundaries have changed several times; standards for reporting locality information were formerly more relaxed, so that fossils collected from within GRCA are undoubtedly lost behind provenance information limited to "Grand Canyon" or "Arizona"; provenance information has been partially or entirely lost when material from smaller collections has been absorbed by other institutions; and many fossil specimens are easily accessible, portable, and therefore prone to illegal collecting. Because of these and other factors, it would not be surprising to find a small quantity of Grand Canyon fossils in any large paleontological collection.

A list of institutions containing GRCA specimens has been compiled from the literature. This list is based on mentions of definite GRCA specimens in specific collections (particularly type and figured specimens). This is not an exhaustive list.

- Academy of Natural Sciences of Drexel University (ANSP, formerly the Academy of Natural Sciences of Philadelphia; Philadelphia, Pennsylvania)
- American Museum of Natural History (AMNH; New York, New York)
- Brigham Young University (BYU; Provo, Utah)
- California Academy of Sciences, including material from the former collections of Stanford University (CAS; San Francisco, California)
- Carnegie Museum of Natural History (CMNH; Pittsburgh, Pennsylvania)
- Cincinnati Museum Center, including material from the former collections of the University of Minnesota (CMC; Cincinnati, Ohio)
- Columbia University (CU; New York, New York)
- Field Museum of Natural History (FMNH; Chicago, Illinois)
- Harvard University Herbaria (HUH; Cambridge, Massachusetts)
- Lake Mead National Recreation Area (LAKE; Boulder City, Nevada)
- Lund University (UL; Lund, Sweden)
- Museum of Comparative Zoology (MCZ; Harvard, Massachusetts)
- Museum of Northern Arizona (MNA; Flagstaff, Arizona)
- Natural History Museum of Los Angeles County, including material from the former collections of the California Institute of Technology and University of California at Los Angeles (LACM; Los Angeles, California)
- Raymond Alf Museum (RAM; Claremont, California)
- Smithsonian National Museum of Natural History (USNM; Washington, D.C.)
- University of Arizona Laboratory of Paleontology (UALP; Tucson, Arizona)
- University of California Museum of Paleontology (UCMP; Berkeley, California)
- University of Notre Dame (UND; Notre Dame, Indiana)
- University of Tübingen (Eberhard Karls University) (UT; Tübingen, Germany)
- Western Archeological and Conservation Center (WACC; Tucson, Arizona)
- Yale Peabody Museum (YPM; New Haven, Connecticut)

USNM houses significant material from GRCA, including the holotypes of 138 of the 167 fossil species named from GRCA material. Notable non-holotype specimens include a complete vampire bat skull (*Desmodus stocki*) found in Rampart Cave (USNM V 25478). The Smithsonian also houses the GRCA collections of Charles Doolittle Walcott, Charles Gilmore's track collections, David White's fossil plants, and Rampart Cave collections.

Photographic Archives

The GRCA Museum Collection maintains an image index database of historical photos related to paleontology in the park. This collection includes 247 photos, the oldest of which is an 1858 portrait of J. S. Newberry, the first geologist to describe fossils from Grand Canyon. Other notable geologists and paleontologists in the image database include David White, John Merriam, George Hesemann, Edwin McKee, and Charles Doolittle Walcott. Many of the photographs in the database document fieldwork and ichnofossils throughout the canyon. As such, they are useful for relocating historic sites and providing comparative photos for site monitoring and management. The oldest of these field photographs was taken in 1913, by Francois Matthes, and documents vertebrate tracks in the Coconino Sandstone. In 1930, a series of photographs of ichnofossils in the Coconino Sandstone were taken by George Grant. Civilian Conservation Corps (CCC) projects in the late 1930s were well documented via photography. These projects included the construction of the Fossil Fern Exhibit on the South Kaibab (Yaki) Trail, construction of trilobite exhibits near Indian Garden, and work at Rampart Cave. The CCC project at Rampart Cave was photographed by Michael Bobko and includes photographs of sloth dung filling the cave and the CCC crew excavating fossil bones. Kaibab fossils within the Museum Collection were also extensively photographed in the 1930s.

The image index database also includes a handful of photographs from outside the park. Photos of dinosaur tracks near Moenkopi, Cameron, and Tuba City can be found in the archives. Two photos of modern animal tracks in a sand dune north of Kanab, Utah, were added for comparison with fossil trackways. Other notable photos include petrified wood from PEFO and a human skeleton at Willow Beach photographed during the CCC expedition to Rampart Cave. Western portions of GRCA were once within the boundary of Lake Mead National Recreation Area (LAKE), so additional archival items may be found within LAKE's archives.

Digital Archives

3D models produced by photogrammetry techniques are an excellent way to make fossils available to the general public and remote researchers. A total of 15 photogrammetry models have been created from GRCA specimens using this technique. Two models can be found on the Smithsonian 3D Digitization webpage. Both specimens were originally from GRCA and are now housed at USNM.

In April 2019, a project with Geology and Photogrammetry Specialist Jack Wood (GRD) was initiated to digitize additional museum specimens to display as online 3D models for National Fossil Day. These models have been uploaded to the National Park Service Geologic Resource Division Sketchfab page (**https://sketchfab.com/grd_nps/models**), GRCA photogrammetry series website (**https://www.nps.gov/articles/series.htm?id=A9E62040-AC6F-A6D7-BE564A036F1D6146**), and photos and files associated with each 3D model have been archived on IRMA. For a complete list of specimens with photogrammetry 3D models see **appendix B**.

Very few photographic records exist for fossils within the collections. Although it would be a lengthy undertaking, photographing each item in the collection would be extremely useful for archival and research purposes. It would also be valuable to digitize more museum objects via 3D photogrammetry. This would make the museum collections far more accessible to visitors and researchers, the vast majority of whom do not have the opportunity to tour or visit the museum collection.

Outreach

The GRCA Museum Collection is a storage and research facility that is open to the public by appointment only. All tours of the collections must be requested in advance. Museum curators normally give 50 to 60 tours each year. The main audiences for these tours are school groups, park staff, and members of other affiliated organizations, such as Xanterra and the Grand Canyon Conservancy. A yearly art exhibition is held in mid-September, where the museum hosts a three-hour open house to display the art collection.

GRCA PALEONTOLOGICAL RESOURCE INTERPRETATION, EDUCATION, AND OUTREACH

The fossils preserved in the rock layers of GRCA are an integral part of explaining the geologic history of the canyon to the public. Their presence helps scientists better understand past depositional environments and how the landscape and lifeforms of this region have changed over time. There are many ranger-led programs, self-guided hikes, brochures, booklets, and educational programs at GRCA that focus on fossils and paleontological resources. All of the programs, handouts, and available resources are compiled here to better prepare interpretation and education staff. While most events are localized to the South Rim, any large interpretive event or program that is developed by the park should extend to the North Rim, Desert View, and Inner Canyon districts as often as possible. This can be accomplished by distributing flyers, cards, stickers, posters, or by adapting programs for use at these other locations.

Current Long Range Interpretive Plan

There is no current or proposed long range interpretive plan for paleontology at GRCA.

Current Paleontological Interpretive Programs

Ranger-Led Programs

Fossil Walk—Summer Only: The Fossil Walk program takes visitors on a journey back in time to discover what fossils can tell us about this part of the continent 270 million years ago. Visitors join a Park Ranger for a hike along the western Rim Trail from Bright Angel Trailhead to visit the fossil beds preserved in the Kaibab Formation. Fossils are abundant in this area including *Meekella* and productid brachiopods, crinoid stem segments, stick and lacy bryozoans, burrows, horn corals, and sponges. This locality is also very close to the rim, providing an excellent opportunity to discuss other fossiliferous units in the canyon and the significance of the fossil record.

Geo-Glimpse—Year-Round: This 20-minute ranger-led program explains how Grand Canyon formed while exploring the canyon rim near Yavapai Geology Museum. Although fossils are not a central part of this program, paleontological topics are woven into the geologic history of the Grand Canyon to better understand paleoenvironments and the canyon we see today. A 45-minute version of this program is offered spring to fall as a Geo-Walk Ranger Program.

Junior Ranger Family Program—Summer Only: During summer months, in Grand Canyon Village on the South Rim, special family-friendly programs are offered with youth and Junior Rangers in mind. Two of these programs, Family Adventure Hike and Natural Wonders, highlight the paleontological resources found within the layered rocks of Grand Canyon. Family Adventure Hike guides individuals down the Hermit Trail for a two-hour hike to explore the canyon's resources first hand. Natural Wonders is a 30-minute Park Ranger presentation on the historic El Tovar Hotel Canyon-side porch.

Evening Programs—Summer Only: Evening programs presented by Park Rangers cover a wide variety of topics. Occasionally, programs discuss paleontology and geology of GRCA.

Self-Guided Hikes

Trail of Time Geology Walk—South Rim, Year-Round: The Trail of Time is a self-guided walking timeline trail along the South Rim that prompts visitors to understand the complex and long geologic history of Grand Canyon without having to leave the rim (figure 7). Examples of each of the major rock layers are displayed along the trail, some of which contain fossil resources such as stromatolites, trace fossils, and invertebrate body fossils. A number of wayside signs explain paleontological concepts such as evolution, deep time, depositional environments, and erosion of past fossil-bearing strata. A Trail of Time companion booklet was compiled to provide visitors with a more in-depth interpretive experience. Self-guided materials for school groups or other larger groups are also available for teachers who could not schedule a ranger-led field trip.

Widforss Trail—North Rim, April through October: The Widforss Trail provides access to many views of the canyon along the North Rim. The interpretive brochure available at the trailhead or Visitor Center provides visitors with paleontology information at stops 2 and 9. Stop 2 encourages visitors to examine the fossils preserved in the Kaibab Formation beneath their feet including crinoids and other small marine creatures (figure 8). Stop 9 identifies the cliff-forming Coconino Sandstone from a particularly scenic overlook. Visitors are informed of the wealth of fossil tracks preserved in this prominent geologic unit and the brochure includes an image of fossil vertebrate tracks.

Figure 7. *Entrance portal along the Trail of Time near the Grand Canyon Headquarters building (NPS/DIANA BOUDREAU).*

Curriculum-Based Programs

Ranger-Led Field Trips—Spring and Fall: Each year the Environmental Education Branch of Grand Canyon National Park offers many ranger-led field trips for grades 3–12. Students from Arizona, and across the world, sign up for these free, curriculum-based programs. “Stories in Stone” is a two-and-a-half-hour trip focused on teaching introductory geology and paleontology, how fossils form, how to interpret ancient environments, and the importance of field work and making observations. “Grand Canyon Rocks” is a similar field trip to “Stories in Stone”, but it includes more exercises related to geology rather than paleontology. “Dynamic Earth” is a five-hour field trip that combines the information presented in these two programs. During each of these field trips, students fill out a journal with guiding questions and exercises to introduce new geologic and paleontological terms and concepts (figure 9).

Classroom Ranger Visits—Winter Only: During the winter months, Park Rangers make classroom visits to nearby schools in Arizona and surrounding states to educate students about a variety of topics, including paleontology and geology of GRCA.

Distance Learning—Year-Round: These programs are available year-round to classrooms or anyone with an internet connection. One of the distance learning programs is the “Ancient Life Program” which aims to teach 3rd–5th grade students about fossils. This program introduces students to the National Park Service, orients them to the geographic location of GRCA, familiarizes students with examples of GRCA fossils and rock units that contain fossils, relates rock types to depositional environments, explains environmental change over geologic time, and introduces students to the vast amount of time represented by the rock layers in the Grand Canyon. Students also better understand fossil bias in the rock record by playing a card game in which students are either turned into fossils or not, depending on the cards they are dealt.

Junior Paleontologist Program—Year-Round: This nationwide program targets kids age 5–12 and encour-

Figure 8. *Crinoid stems, stick and lacy bryozoans, and shell fragments from exposures of the Kaibab Formation can be found along the rim of the canyon (NPS/DIANA BOUDREAU).*

Figure 9. *Students identify fossils in the Kaibab Formation at the fossil beds during the "Stories in Stone" field trip (NPS/RONNIE COLVIN).*

ages them to explore, learn about, and protect fossil resources in National Parks, including those at Grand Canyon. The NPS Geologic Resources Division can provide Junior Paleontologist Activity Program supplies including activity booklets, badges, posters, and other fossil-related educational resources. Contact Vincent Santucci for more details (vincent_santucci@nps.gov).

Grand Canyon Field Institute and School Programs

There are a number of outside companies that offer guided trips into the canyon, such as the Grand Canyon Field Institute that is run by the park's non-profit partner, Grand Canyon Conservancy. Some of these guided trips take time to educate their groups on the geology and fossil resources found within the park.

Canyon Field School is a partnership between the Grand Canyon Conservancy and the National Park Service and offers unique opportunities for youth to experience the great outdoors at Grand Canyon National Park. They offer overnight camps that center around scientific discovery and learning at Grand Canyon National Park.

National Fossil Day Event

National Fossil Day is an annual event that takes place nationwide on Wednesday of the second full week in October, which is also Earth Science Week. Grand Canyon National Park has hosted a National Fossil Day event on the South Rim for the past five years (figure 10). In the past, Park Rangers have led a fossil walk program, scheduled fossil themed games and activities for kids, hosted a Q&A session with fossil experts, remotely toured the Kaibab Formation fossil beds and interacted with rangers and fossil experts using "Facebook Live", and presented a fossil themed evening program focused on National Fossil Day and GRCA fossil resources. The NPS Geologic Resources Division can assist the park with planning for National Fossil Day activities and provide Junior Paleontologist Activity Program supplies including activity booklets, badges, posters, and other fossil-related educational resources. Contact Vincent Santucci for more details (vincent_santucci@nps.gov).

The 2019 National Fossil Day Celebration was a larger event compared to previous years, as an opportunity to commemorate the park's 100th anniversary (figure 11). In 2019, Grand Canyon National Park hosted a number of outside researchers and partners on the South Rim on September 27 and 28. The festivities started off with a mini Paleontology Symposium on Friday, September 27, 2019. Four guest speakers shared their research on GRCA paleontology and specimens from the museum were on display during the symposium (figure 12). During the National Fossil Day Celebration on September 28, visitors could participate in ranger-led programs to the fossil beds, create fossil-themed crafts during children's activities at the Yavapai Geology Museum, and were even able to ask paleontologists questions virtually through a special Facebook Live event. Twelve partner organizations participated with informational booths at the Grand Canyon Visitor Center plaza, including a green-screen photobooth provided by the American Geosciences Institute (figure 13). A welcome ceremony for the event took place at the Mather Amphitheater with guest speakers Bruce MacFadden (President of the Paleontological Society) and Vincent Santucci (NPS Senior Paleontologist), Science and Resource Management's Chief of Resources, Jeanne Calhoun, and an Arizona State Greeting for the National Fossil Day event (figure 14). The National Fossil Day Celebration was capped by a special paleontology evening program given by NPS Senior Paleontologist and Paleontology Program Coordinator Vincent Santucci. For more in-depth information on the National Fossil Day Celebration, refer to the 2019 Paleontology Project After Action Report (Boudreau, 2020).

Below are some statistics concerning visitation during the National Fossil Day Celebration:

- Approximately 110 visitors attended the Paleontology Symposium on Friday, September 27, 2019
- 85 visitors attended the Paleontology Evening Program given by Vincent Santucci on Saturday, September 28, 2019
- Ask-A-Scientist social media livestream reached 7,617 individuals, a maximum of 104 individuals viewed simultaneously, and 116 viewers submitted comments or questions
- Fossil Bed social media livestream event reached 23,788 individuals, over double the viewership compared to last year which reached 10,756 individuals. This livestream peaked at 290 viewers and received 116 comments and questions.

A number of new interpretive materials were developed specifically for the 2019 National Fossil Day event. Interpretation and education staff designed a portable pop-up exhibit, highlighting fossils from GRCA with paleo environments, to use for events hosted at GRCA, such as National Fossil Day, or for classroom ranger visits (figure 15). This pop-up exhibit was unveiled on September 27, 2019, and was on display at the Grand Canyon Visitor Center for two months following the event. A set of nine GRCA fossil-themed trading cards and National Fossil Day informational postcards were also developed for distribution at fossil events.

Figure 10. *Park Rangers talk with the public about fossils at the 2016 National Fossil Day celebration at Grand Canyon National Park (NPS).*

Figure 11. *NPS paleontologists and educators who assisted with the 10th Annual National Fossil Day activities and programs on the South Rim of Grand Canyon National Park on September 28, 2019. Left to right (front): Jeremy Childs, Jennifer Glennon, Anne Miller, Hazel Wolfe, Celia Dubin, Kevin Garcia, John-Paul Hodnett, Vincent Santucci, Mary Carpenter, Jim Mead, Joel Despain, Adam Blankenbicker, Chris Symons, Jason Kenworthy, and Justin Tweet. Left to right (back): Grace Lilly, Janet Gillette, David Gillette, Tom Olson, Richard McMichael, Don Weeks, Anne Scott, Eleanour Snow, Andy Grass, Sequoyah McGee, Robyn Henderek, Sandy Croteau, Erin Eichenberg, Diana Boudreau, Sherman Mohler, Mary Ontiveros, Doug Wolfe, Maria Rodriguez, Veronica Colvin, Joel Kane, and Bryan Maul (NPS/MICHAEL QUINN).*

Interpretive Signs and Exhibits

Permanent Signs and Exhibits

South Rim: There are a number of fossil interpretive signs on the South Rim in Grand Canyon Village. The largest concentration of paleontological interpretation is at the Yavapai Geology Museum. There is a small wall case that contains real and replica fossil specimens, such as brachiopods, stromatolites, trilobites, worm burrows, and a cast of a dragonfly wing. Many interpretive signs within the museum explain past depositional environments at Grand Canyon and have models of fossils from the canyon, including a trilobite with tracks, brachio-

Grand Canyon National Park

National Park Service
U.S. Department of the Interior

Paleontology Symposium

Friday, September 27, 2019
7:30 pm
Shrine of the Ages Auditorium

Jaws of the Grand Canyon

Fossil Sharks of Grand Canyon

John-Paul Hodnett is the National Fossil Day Coordinator, and the paleontologist and coordinator for the M-NCPPC Dinosaur Park in Maryland. His research focuses on the evolution and ecology of sharks and mammalian carnivores.

No Bones About It...

Grand Canyon's Invertebrate Fossils

Linda Sue Lassiter is a researcher of evolutionary biology studying Early Paleozoic fossil groups including vertebrates, eurypterid arthropods, and interactions of ancient species. She teaches Paleontology at Northern Arizona University.

An Ice Age in Grand Canyon

Cave Paleontology of Grand Canyon

Dr. Jim Mead is the Research Director at South Dakota's Mammoth Site, specializing in Pleistocene mammal, reptile, and amphibian fossils in the Black Hills, Grand Canyon, Sonora (Mexico), Abaco (Bahamas), and Guangxi (China).

Paleozoic Tracks and Traces of the Grand Canyon

Grand Canyon's Vertebrate Trace Fossils

Dr. Spencer G. Lucas' research focuses on biostratigraphic problems of the late Paleozoic, Mesozoic and early Cenozoic. He is the Curator of Geology and Paleontology at the New Mexico Museum of Natural History and Science.

Join us for an evening of fossil discovery and learning with paleontologists!

Programs are subject to cancellation. See bulletin boards, visitor centers, or nps.gov/grca for a complete list of park ranger programs. Take a picture for reference.

Figure 12. *Advertisement for the four speakers at the Paleontology Symposium on Friday September 27, 2019 at the Shrine of the Ages (NPS).*

Grand Canyon

National Park Service
U.S. Department of the Interior

Grand Canyon National Park

National Fossil Day Celebration

Schedule of Activities

Friday, September 27

7:30 pm to 9 pm ● **Paleontology Symposium**
Join us for an evening of fossil discovery and learning with visiting paleontologists. Four speakers will highlight some of Grand Canyon's most notable fossil specimens.
Shrine of the Ages Auditorium

Saturday, September 28

9 am to 10 am ● **Fossil Walk**
Learn about Grand Canyon's ancient life through its fossil history. This easy walk along the Rim Trail explores the marine fossils of an ancient Permian Sea.
Meet at Bright Angel Trailhead

10 am to 11 am ● **Ask a Scientist!**
How do fossils form? What's a trace fossil? Ask your questions to Grand Canyon's scientists!
Yavapai Geology Museum

10 am to 12 pm ● **Fun with Fossils!**
Discover why fossils are important. Fun fossil games and activities for kids of all ages! Meet some of Grand Canyon's scientists and ask your questions!
Yavapai Geology Museum

10 am to 3 pm ● **All Day Events**
Meet with partner organizations such as American Geosciences Institute, Museum of Northern Arizona, Southwestern Paleontological Society, and more!
Grand Canyon Visitor Center Plaza

1 pm to 2 pm ● **Welcome Ceremony**
Join Park Rangers for a welcome ceremony, event proclamation, and remarks by Grand Canyon Superintendent and visiting paleontologists.
Mather Point Amphitheater

4:30 pm to 5:30 pm ● **Facebook Live!**
Can't be at Grand Canyon today? No worries! You can join us live for a tour of the Fossil Beds via Facebook Live!

7:30 pm to 8:30 pm ● **Paleontology Evening Program**
Join NPS Paleontology Program Coordinator, Vincent Santucci, for a special evening program about the rich paleontology resources found at Grand Canyon.
Shrine of the Ages Auditorium

Figure 13. *Advertisement for the National Fossil Day Celebration event at the South Rim of Grand Canyon National Park (NPS).*

Figure 14. *Speakers at the Welcome Ceremony at Mather Amphitheater at the National Fossil Day Celebration on September 28, 2019. Left to right: Jeanne Calhoun, Ronnie Colvin, Bruce MacFadden, and Vincent Santucci (JOHN-PAUL HODNETT).*

Figure 15. *A large pop-up exhibit highlighting Grand Canyon National Park fossils was developed for the 2019 National Fossil Day Celebration at Grand Canyon (NPS/DIANA BOUDREAU).*

pods, and *Chelichnus* tetrapod trackway (figure 16). A cast of the Shasta Ground Sloth skull and dung are on exhibit in the main lobby of the Grand Canyon Visitor Center. A regularly scheduled program about the formation of the Grand Canyon titled "The Canyon World" plays in the Science on the Sphere exhibit at the Grand Canyon Visitor Center and highlights the fossil record.

The Rim Trail between the Grand Canyon Visitors Center and the Yavapai Geology Museum is void of interpretive signage; however, traveling west along the Rim Trail from the Yavapai Geology Museum, visitors explore the "Trail of Time." See the Trail of Time section above for more information. The Rim Trail is often bordered by a small stone wall that contains large chunks of petrified wood. Most notable is the section of wall across from Verkamp's Visitors Center (figure 17); it also has two large sections of petrified wood placed by the entrance ramp.

A number of other localities on the South Rim expose the public to GRCA's rich fossil assemblage. Bright Angel Lodge has a historic geology fireplace designed by Mary Colter (figure 18A). Visitors can see stromatolites and a coiled nautiloid embedded in the rock fireplace. In the central courtyard of GRCA Headquarters, a few track blocks have been placed in the benches and stone floor (figure 18B). In the main lobby, a small exhibit, compiled by a previous GIP, contains paleo environment images, fossil specimens, and an explanation of the fossil history of GRCA. These are examples of paleontological resources in cultural contexts; see Kenworthy and Santucci (2006) for further information on similar occurrences.

North Rim: The North Rim has one interpretive sign that outlines the paleoenvironments of the Kaibab, Coconino, Hermit, and Supai formations. The sign is located along a paved path between the North Rim Lodge and Bright Angel Point, providing an opportunity for visitors to read about past depositional environments of the canyon. Visitors can also learn about erosion, geologic time, and lack of Mesozoic strata and dinosaurs in the park on an interpretive sign at Point Imperial.

Desert View: There is no paleontological signage at Desert View. However, a coiled nautiloid that was found in the Kaibab Formation during the construction of the Desert View Watchtower was placed in a small glass wall case with other cultural and historic artifacts on the second floor of the watchtower with a small descriptive label (figure 19).

Canyon District: Most of the paleontological interpretation within the canyon district occurs via ranger programs. However, interpretive staff are planning to restore and add interpretive signage to the historic Fossil Fern Exhibit along the South Kaibab Trail at Cedar Ridge. For more information on this exhibit see the Historic Interpretive Sites section.

Future Signs and Exhibits: There are a few ongoing projects to update and add to paleontological interpretation at Grand Canyon. A proposed wayside exhibit for the fossil beds site would provide visitors with information for that site year-round, however there are concerns about fossil theft and vandalism at the site. Staff also plan to restore the historic Cedar Ridge CCC Fossil Fern Exhibit along the South Kaibab Trail, produce an interactive fossil component for the GRCA park app, and develop a mini program to display at the Grand Canyon Visitor Center's "Science on the Sphere". Construction on the Maswick South Lodging Complex began in 2019 and each of the four new lodging buildings will be named for fossils (Trilobite, Shasta, Fern, and Burrow). Xanterra plans to incorporate paleontological interpretive and outreach elements into the construction and landscaping of these buildings.

Historic Interpretive Sites

Cedar Ridge CCC Fossil Fern Exhibit: Located along the South Kaibab Trail at Cedar Ridge approximately 2.4 km (1.5 mi) down trail, the CCC Fossil Fern Exhibit resides at the edge of a cliff (figure 20). During the construction of the South Kaibab Trail (formerly called the Yaki Trail) in the 1930s, trail workers uncovered well-preserved fossil ferns in the Hermit Formation. Recognizing their importance, the trail crew constructed an exhibit case to display and protect the well-preserved fossil plant materials. Since that time, little has been done to maintain and protect this exhibit. Therefore, the paleontology, interpretation, and outreach staff will work along with volunteers to rebuild this historic site in future years.

"Lost" Trilobite Exhibit: A trilobite exhibit was built near Indian Garden in 1935 along the Bright Angel Trail by the CCC. There are no indicators on the trail today that this site ever existed. A team from the Museum of Western Colorado relocated one quarry using historic images in 2011 (Foster, 2011). This exhibit was developed near a known fossil locality along the Tonto Trail. A total of three quarries were excavated; however, only the third quarry proved suitable for an exhibit. Unfortunately, the exhibit case did not protect the fossils from water and erosional processes. The Bright Angel Shale is very friable in nature, which caused the overlying shales to fall on top of the exhibit, obscuring the fossil trilobites. Noticing this threat to fossil resources, the park superintendent requested the exposed fossils be removed from the exhibit before it was completely buried. These specimens are now housed in GRCA museum collections. The location of the trilobite quarries is not entirely known by GRCA staff.

Figure 16. *Paleozoic exhibit at the Yavapai Geology Museum (NPS/DIANA BOUDREAU).*

Figure 17. *Two large chunks of petrified wood used as building materials for the wall along the Rim Trail outside the Verkamp's Visitor Center on the South Rim (NPS/DIANA BOUDREAU).*

***Figure 18. A.** The geology fireplace in the Bright Angel Lodge designed by Mary Colter exhibits geology and paleontology of the Grand Canyon (NPS/MICHAEL QUINN). **B.** Fossil trackway slab used as building material for a bench in the Grand Canyon Headquarters courtyard. (NPS/DIANA BOUDREAU).*

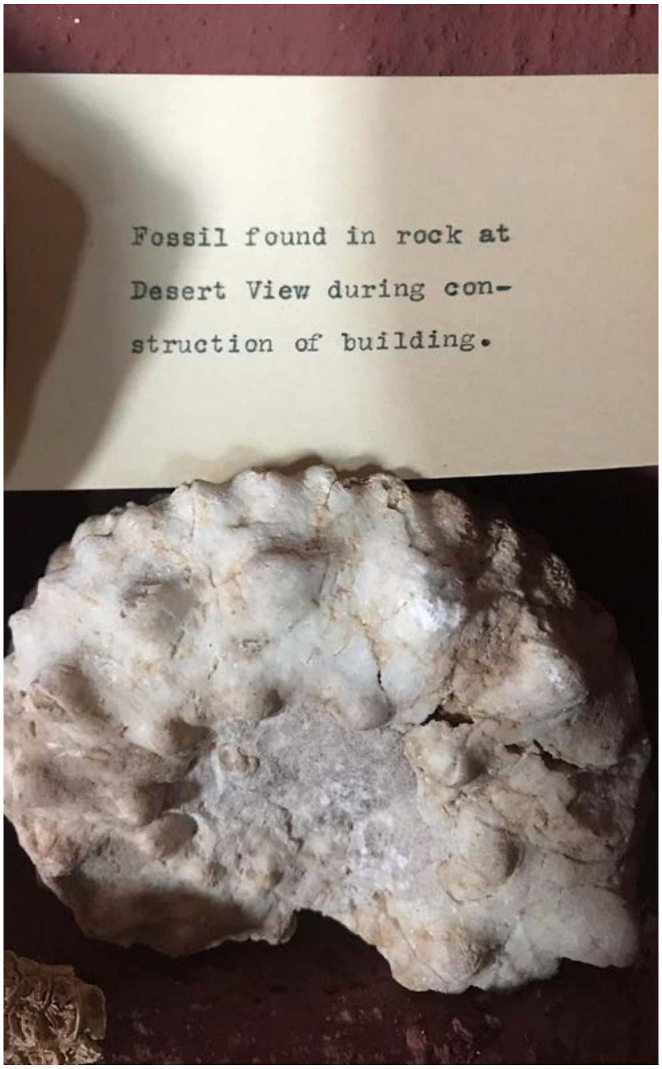

***Figure 19.** A coiled nautiloid found in the Kaibab Formation during construction of the Desert View Watchtower on display at Desert View (NPS/SALLY CARTTAR).*

Interpretive Handouts, Site Bulletins, Books, and Brochures

2015. Grand Canyon National Park. Journey Through Time: Grand Canyon Geology. PDF File.

Thayer, D. 2009. An Introduction to Grand Canyon Fossils. Grand Canyon Association. 64 p.

Karlstrom, K, and L. Crossey. 2019. The Grand Canyon Trail of Time Companion: Geology Essentials for your Canyon Adventure. Four Colour Printing, Korea. 142 p.

Interpretive Staff Training and Resources

Paleontology Trainings

No formal paleontological training is provided to seasonal or permanent interpretive staff. However, Ronnie Colvin, Interpretive Park Ranger, provides a “Fossil 101” training upon request for incoming interpretive staff with an interest in fossils and paleontology. There are also teacher workshops available upon request that are taught by Ronnie Colvin and the Education Branch staff (figure 21). In addition, interpreters and others interested in paleontological training may contact the park paleontologist to explore participating in field work.

Paleontological Interpretation Resources

There are a number of tools and resources available for the interpretive staff. A cache of fossil specimens from GRCA are available for use in public programs and outreach events. The education and interpretation department has a few items located within the park. These specimens were deaccessioned from the museum collections and made available to the interpretation divi-

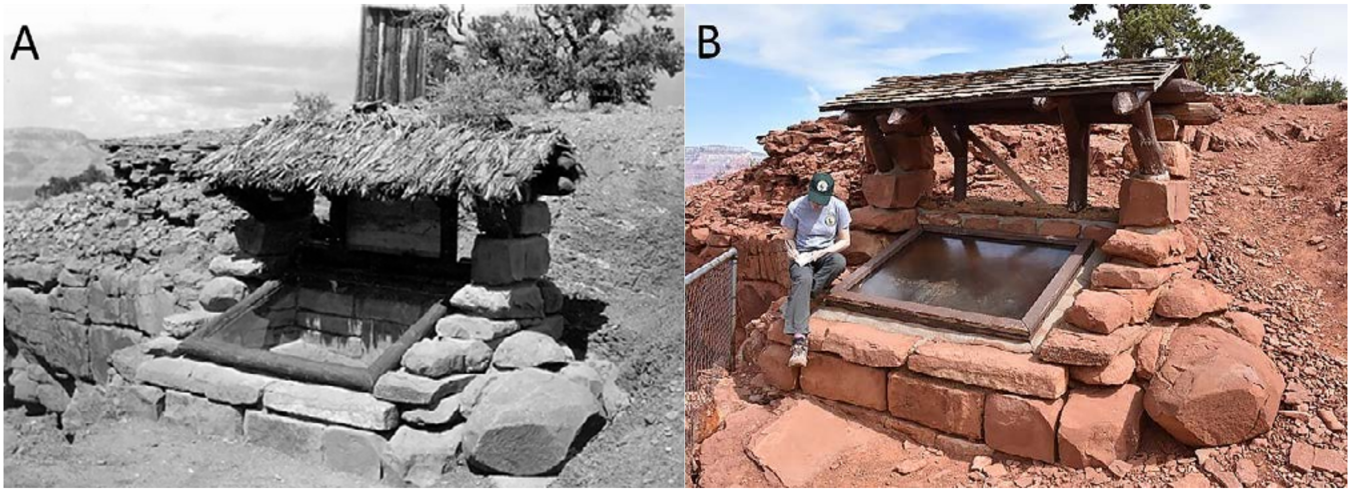

Figure 20. *Fossil Fern Exhibit at Cedar Ridge on South Kaibab Trail in the 1930s* ***(A)*** *and in the spring of 2019* ***(B)*** *(NPS).*

Figure 21. *Teacher workshop at the fossil beds site along the Rim Trail (NPS).*

sion. Contact GRCA Museum Specialists Kim Besom (x7766) or Colleen Hyde (x7769) for more information. In previous years, a collection permit was provided for the interpretation staff to acquire more educational materials; however the permit has since expired and should be updated if more materials are needed.

As technology advances, examples of fossil resources are also available in digital forms. During the 2019 paleontology inventory, a number of important museum specimens were imaged to create 3D models which could then be 3D printed or viewed online as interactive models. See **appendix B** for a detailed list of available 3D specimens. Contact Vincent Santucci (vincent_santucci@nps.gov) or GRCA Museum Specialists Kim Besom (x7766) and Colleen Hyde (x7769) for more information.

Park websites were produced by the Geologic Resources Division to compile information about the 2019 Paleontology Inventory, PaleoBlitz, National Fossil Day Celebration, and links to available 3D specimens. See **https://www.nps.gov/subjects/fossils/100-years-of-paleontological-discoveries-at-the-grand-canyon.htm**, **https://www.nps.gov/articles/park-paleo-fall-2019-grand-canyon.htm**, and **https://www.nps.gov/grca/learn/nature/fossils.htm** for more information.

All paleontology programs developed by Park Rangers should instruct visitors on how to be paleontologically aware while in the park. The following topics should be highlighted when mentioning fossils in interpretive programs:

- When paleontologists survey for fossils, an important tool is a geologic map. Paleontological resources are more common in certain geologic units, so knowing where those units are exposed is important for a successful survey. Other field paleontology tools include small picks and brushes, appropriate glues and consolidants, GPS, camera, topographic maps, and appropriate First Aid and safety equipment. It might be helpful to provide examples of these items for visitors during an interpretive talk, if available.
- If fossils are found in the park by a visitor, they should photograph it, note the coordinates, and notify a ranger of where the resource was found, but most importantly they should leave the fossil where they found it. It is extremely important for scientific and resource management purposes for original location information to be preserved. Visitors should be informed that park fossils are non-renewable resources that are protected by federal law (Paleontological Resources Preservation Act, 2009).

GRCA PALEONTOLOGICAL RESOURCE DATA MANAGEMENT

GRCA has been a focal point of paleontology research even before its designation as a National Park 100 years ago, leading to a wealth of data and resources that need to be properly managed. In addition, the Paleontological Resources Preservation Act (PRPA) mandates the management of fossils and associated data using scientific principles and expertise. Information regarding paleontological resources at GRCA, such as field notes, publications, and paleontology locality datasheets, are managed within the Park's internal network. Field data collected at paleontological sites and localities are maintained within a geospatial database. NPS Paleontology Archives and Library has a copy of all these files. These databases and archives have been fully updated as part of the 2019 Paleontology Inventory.

GRCA Paleontology Archives

GRCA maintains a paleontology archive and library to organize all documents related to paleontology resources at the park. Items such as field notes, publications, historic photos, maps, research permits, and museum collection documents can be found within the archives. Due to the sensitive nature of paleontological resources, paleontology archives are restricted access only. To request access to information within the archives, contact Mark Nebel (mark_nebel@nps.gov) or Anne Miller (anne_miller@nps.gov).

NPS Paleontology Program Archives (WASO)

The National Park Service Paleontology Program (WASO) maintains a copy of all digital and hardcopy field notes, sketches, photographs, maps, reports, publications, and lists of archived fossil specimens at GRCA (Santucci and others, 2018). This ensures the safety of paleontological resource data in the event either GRCA or WASO archives are lost. To request access to materials in the WASO Paleontology Archives contact Vincent Santucci (vincent_santucci@nps.gov) or Justin Tweet (justin_tweet@nps.gov).

E&R Files

E&R files (from "Examination and Report on Referred Fossils") are unpublished internal USGS documents. For more than a century, USGS paleontologists identified and prepared informal reports on fossils sent to the survey by other geologists, for example to establish the relative age of a formation or to help correlate beds. The system was eventually formalized as a two-part process including a form sent by the transmitting geologist and a reply by the survey geologist. Sometimes the fossil identifications were incorporated into publications, but in many cases this information is unpublished. These E&R files include documentation of numerous fossil localities within GRCA, including from L. F. Noble's and Edwin McKee's work. Extensive access to the original files was granted to the NPS by the USGS beginning in 2014 (Santucci and others, 2014).

McKee and Walcott Archives

Paleontological research has a long history at GRCA. Two individuals, Edwin McKee and Charles Walcott, were heavily involved in recording and studying fossils in the canyon and created extensive archives. The McKee Archives, housed at USGS in Denver, include hand drawn stratigraphic columns, specimen lists, and correspondence with outside researchers. The Walcott Archives, housed at the Smithsonian Institute, are almost entirely composed of his field notes and sketches from 1930. To request access to these archives, contact Vincent Santucci (vincent_santucci@nps.gov), Justin Tweet (justin_tweet@nps.gov), Mark Nebel (mark_nebel@nps.gov), or Anne Miller (anne_miller@nps.gov).

Geospatial Database

Earle E. Spamer originally created, for his own personal and professional use, a *Paradox* database in the 1980s to track published data, and some unpublished theses, on paleontological resources of the Grand Canyon region and their related taxonomy. This database was later migrated to an Access database format that was presented by Spamer to the National Park Service (NPS) in 2003.

GRCA GIS Program Manager Mark Nebel and Geologist Steve Rice initially developed a spatial paleontology geodatabase for GRCA in 2011, adapting and significantly modifying the framework of Spamer's *Access* database, specifically for use at GRCA. The primary motivation for this effort was the imminent arrival, after many years without a paleontology program, of two Geoscientists-in-Parks (GIP) paleontology interns at GRCA. This initial GRCA geodatabase consisted of a single point feature class for paleontology localities. This was the primary database used and populated by a series of GIP interns at GRCA from 2011 into 2017.

Beginning in early 2017, GRCA Paleontology (Anne Miller) and GIS (Mark Nebel) staff recognized many shortcomings of the existing database and the need for development of a more comprehensive and systematic paleontology geodatabase for tracking data on paleontological resources in the park. After more than a year of development, including a needs assessment, database schema design, development, and field testing, the new GRCA paleontology geodatabase was deployed for park use in 2019. This database was accompanied by the development and testing of new field forms. GIS layer files (.lyr) have also been developed to provide a consistent map symbology for all feature classes in the geodatabase. This geodatabase can be adapted for use at other NPS units. For more information, contact Mark Nebel (mark_nebel@nps.gov).

The GRCA paleontology geodatabase is an ESRI file geodatabase that currently contains five feature classes (Paleontology Localities, Sites, Photopoints, Survey Lines, and Survey Polygons) and two related geodatabase tables (Paleontology Photos and Collected Specimens) (figure 22). Photograph files are managed separately through a GRCA internal file system. All features in the paleontology database and all photographs have unique record IDs and are subject to naming conventions.

A ***PaleontologyLocality*** is a contiguous fossiliferous area (polygon) of a known minimum extent, based on field observations, and characterized by a unique geographic location, geology, and fossil assemblage. "In Context" ***PaleontologyLocality*** polygons include fossils that are in place within bedrock ("In Situ"), or situated loose on underlying bedrock of the formation from which the fossils are directly derived. Minor weathering out or local transport may have occurred. "Float" ***PaleontologyLocality*** polygons include fossils that are out of context, i.e., derived from a geologic formation different from that on which they are situated or located, having been transported to their current location.

A ***PaleontologySite*** point can be either a ***PaleontologyLocality*** discovery point, a specific fossil or fossil assemblage to be noted or monitored, or a fossil specimen collection point. ***PaleontologySite*** features are always within a ***PaleontologyLocality.***

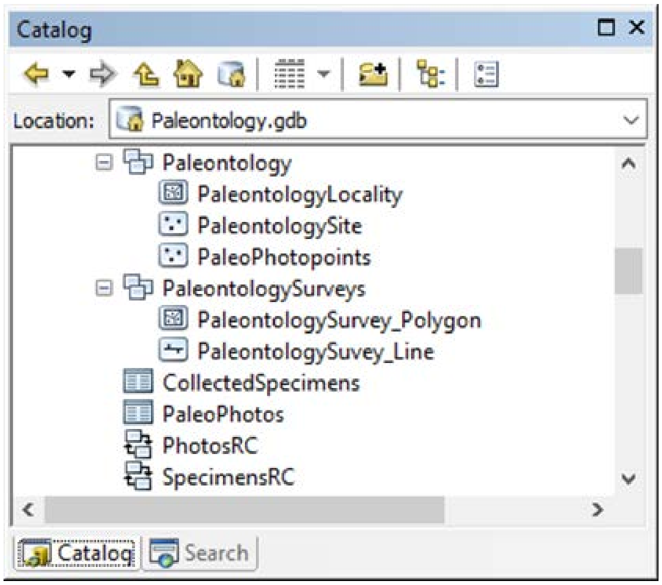

Figure 22. *Screenshot from ArcCatalog showing the structure of the GRCA Paleontology geodatabase (NPS).*

PaleoPhotopoints are points that represent the locations from which ***PaleontologyLocality*** photographs are taken, including photos of representative fossils, outcrop or outcrop-scale photos, and photos of setting or location. They are referenced to a ***PaleontologyLocality*** (as opposed to a ***PaleontologySite***), but do not need to be within a locality polygon (figure 23). Photographs provide scientific documentation of the resource and provide a baseline for monitoring their condition over time. Photographs are hot-linked in the geodatabase, so that they can be viewed directly from an ArcGIS map application connected to the GRCA network file system.

PaleontologySurvey (line and polygon) features delineate areas where systematic paleontology surveys have been undertaken.

PaleoPhotos and ***CollectedSpecimen*** geodatabase tables record any photographs or collected specimens, respectively, that are associated with the Localities, Photopoints, and Sites, as appropriate, and are linked to the respective features via geodatabase relationship classes. Photographs are hot-linked to their respective ***PaleoPhotopoints*** via the GRCA network file system.

The geodatabase was designed initially to be compatible with Trimble GPS data collection devices, data dictionaries, and workflows. GRCA is currently developing and migrating to new protocols that leverage the ArcGIS Online and Collector software environments and GNSS data collection devices. The GRCA Paleontology geodatabase, definitions, protocols, naming conventions, and schema, field forms, etc. are evolving documents. To obtain the most current version of these documents contact Mark Nebel (GIS Program Manager; mark_nebel@nps.gov).

The following evolving GRCA paleontology documents are available upon request:

1. Geodatabase Documentation (.docx)
2. Geodatabase Schema and Domains (.xlsx)
3. Paleontology Field Form and Guide (.docx or .pdf)

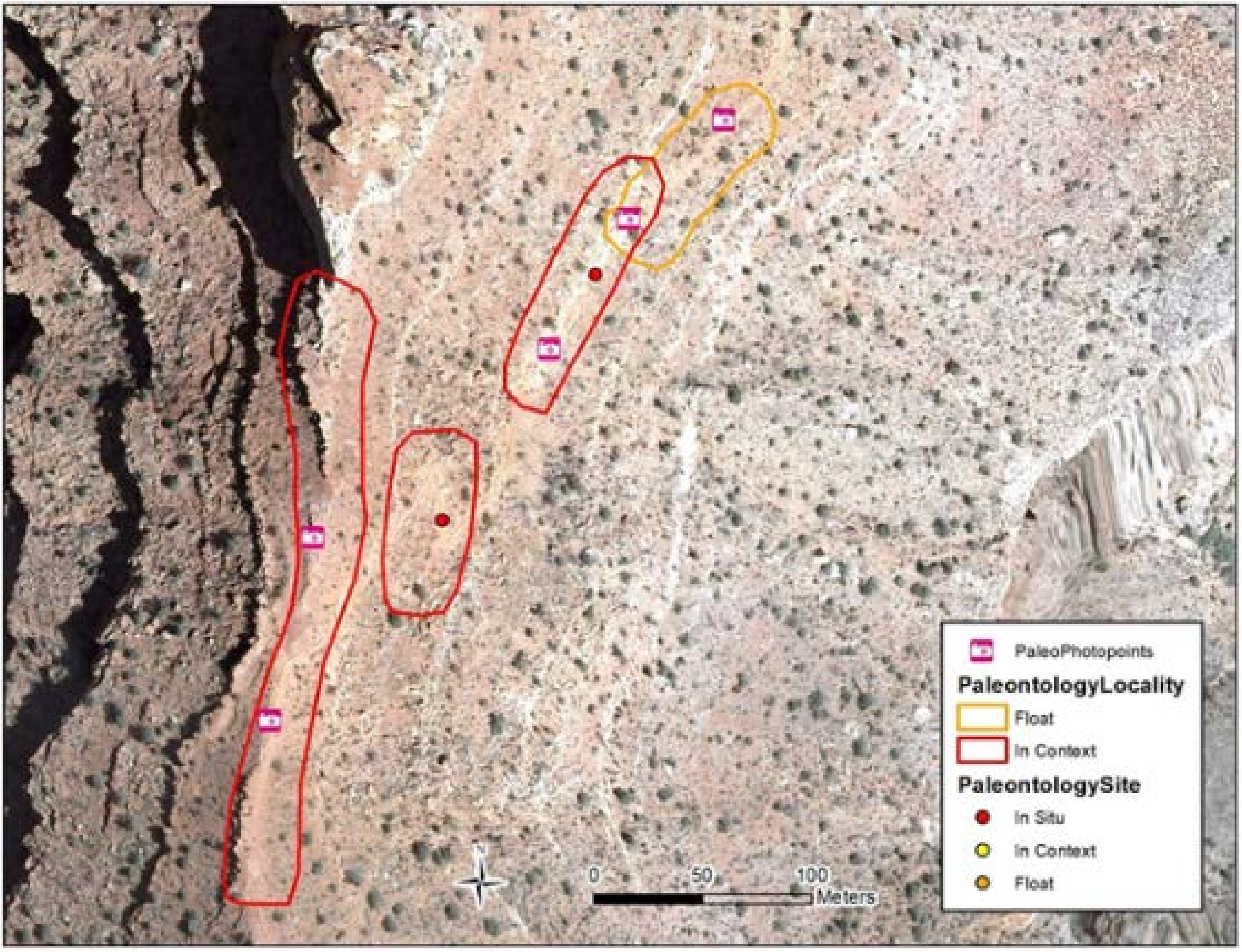

Figure 23. *Screenshot from ArcMap showing an example of a Paleontology Locality with associated Sites and Photopoints (NPS).*

CONCLUSIONS

As illustrated in the many thematic articles of this paleontological resources inventory and the after-action report (Boudreau, 2020), 2019 has been an important year in establishing a comprehensive baseline for paleontological resource stewardship and science at Grand Canyon National Park. Collectively, the paleontology-focused projects undertaken and accomplishments achieved at GRCA during 2019 represents the largest collaborative effort for paleontology in National Park Service history. This unprecedented work will help guide and inform future paleontological resource planning and activities for other NPS areas. In addition, the concurrence of this 2019 project with the celebration of GRCA's centennial, 10th anniversary of National Fossil Day, and the Department of Interior's final rulemaking for the Paleontological Resources Preservation Act (2009) bolstered each management action and supports continued affirmative paleontological resource management and stewardship within the park.

Despite the paleontology program at Grand Canyon being understaffed for many decades, great strides have been made, building upon 150 years of dedicated individuals who observed, recorded, preserved, and promoted the paleontological resources found within the Grand Canyon. In recent years, the park's paleontology projects have been primarily accomplished through the supervision of Geoscientists-in-the-Parks interns and as collateral duties by physical science or GIS staff members, with guidance and assistance from the WASO NPS Paleontology Program. The establishment of a committed, multi-disciplinary team for the 2019 paleontology project provided an opportunity for the development of goals and projects to advance the paleontological knowledge of the park on behalf of science, public education, and resource stewardship. The GRCA Paleontological Resource Inventory provides the essential foundation for current and future park leaders to ensure that the non-renewable paleontological resources at GRCA will continue to be monitored, conserved, and protected into the future.

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Appendix A

GRCA Paleontology Research Permits 1999–2019

Appendix Table A-1. *List of paleontological research permits issued from 1999 to 2019. Study titles are verbatim. IAR = Investigator Annual Report. Continued on following page.*

Permit Number	Year	Investigator(s)	Study Title	IAR/Report Published
GRCA-1999-SCI-0001	1999–2004	Jim Mead, Mary Carpenter	Late Pleistocene Vertebrate Communities in the Lower Grand Canyon, Arizona: Rampart and Muav Caves	IAR: 2001, 2004 Publications: Carpenter, M. C. 2003. Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Grand Canyon, Arizona. Thesis. Northern Arizona University, Flagstaff, Arizona. Carpenter, M. C., and J. I. Mead. 1999. Late Pleistocene vertebrate communities of the lower Grand Canyon: Rampart and Muav caves. Journal of Vertebrate Paleontology 19(supplement to 3):36A.
GRCA-2001-SCI-0002	2001–2002	Steven Austin	Sedimentary Model for Canyon-Length Mass Kill and Burial of Large Orthocone Nautiloids, Redwall Limestone (Lower Mississippian), Grand Canyon, Arizona: A Proposal for Research	IAR: 2001
GRCA-2003-SCI-0085	2003–2005	Judy Hellmich	Research and Education in Grand Canyon National Park	IAR: 2004, 2005
GRCA-2009-SCI-0005	2009	Karl Karlstrom	The Trail of Time at Grand Canyon: synthesis of Proterozoic research and studies of Quaternary geology of Grand Canyon	IAR: 2009
GRCA-2009-SCI-0032	2009	John Foster	Trilobite Taphonomy of a Quarry in the Middle Cambrian Bright Angel Shale, Grand Canyon National Park	IAR: 2009 Foster, J. R. 2011. Trilobites and other fauna from two quarries in the Bright Angel Shale (Middle Cambrian, Series 3; Delamaran), Grand Canyon National Park, Arizona. Pages 99–120 *in* J. S. Hollingsworth, F. A. Sundberg, and J. R. Foster, editors. Cambrian stratigraphy and paleontology of northern Arizona and southern Nevada. Museum of Northern Arizona, Flagstaff, Arizona. Bulletin 67.

Appendix Table A-1. *Continued*

Permit Number	Year	Investigator(s)	Study Title	IAR/Report Published
GRCA-2010-SCI-0001	2010–2011	Paul Strother, John H. Beck, Eben Rose	Investigations of the Earliest Land Plants: The Collection of Microfossils from the Bright Angel Shale at Red Canyon	IAR: 2010, 2011
GRCA-2010-SCI-0017	2010–2011	Karl Karlstrom, Owen Shufeldt, Jake McDermott, Ryan Crow, Laura Crossey	The Trail of Time at Grand Canyon: synthesis of Proterozoic research and studies of Quaternary geology of Grand Canyon	IAR: 2010, 2011
GRCA-2010-SCI-0027	2010	Jill Allen	Grand Canyon Rocks	IAR: 2010
GRCA-2010-SCI-0039	2010–2012	Leonard Brand, John Whitmore	Coconino Sandstone fossil trackways: relationship to sedimentological features	IAR: 2010, 2011, 2012
GRCA-2011-SCI-0034	2011–2013	Deanna Greco, Erica Clites, James Super, Jeff Dobbins	Paleontological Inventory of Grand Canyon National Park	IAR: 2011
GRCA-2012-SCI-0021	2012–2013	Steve Dworkin, Stacy Atchley, Lee Nordt	Reconstructing Paleozoic Climates Using Paleosols in the Grand Canyon	IAR: 2012
GRCA-2013-SCI-0001	2013–2014	Jessica Metcalfe, Michael Richards	Late Pleistocene Paleoecology of the Colorado Plateau	IAR: 2013, 2014
GRCA-2013-SCI-0052	2013–2014	Jeffrey Martin, Jim Mead	Holocene and late-Pleistocene Bison of the Grand Canyon and the Colorado Plateau	IAR: 2013, 2014
GRCA-2015-SCI-0011	2015–2016	Jessica Metcalfe, Michael Richards	Late Pleistocene Paleoecology of the Colorado Plateau	IAR: 2015, 2016 Publication: Metcalfe, J. Z. 2018. Pleistocene hairs: microscopic examination prior to destructive analysis. PaleoAmerica, DOI: 10.1080/20555563.2017.1413529
GRCA-2017-SCI-0054	2017–2018	Steve Rowland	Fossil Trackways in the Supai Formation in GRCA	IAR: 2017, 2018
GRCA-2017-SCI-0059	2018–2019	Anne Miller, David Elliott	Ichnology of the Bright Angel Shale Formation, Grand Canyon, AZ: Indicators for Middle Cambrian Paleoecology	IAR: 2018 Ongoing Masters thesis work
GRCA-2018-SCI-0030	2018	Chris Doughty	A metagenomics study of extinct sloth dung	IAR: 2018
GRCA-2019-SCI-0002	2019	Vincent Santucci, Anne Miller, Justin Tweet, Mark Nebel	Grand Canyon National Park Paleontological Resource Inventory and Paleoblitz	In Progress

Appendix B

GRCA Photogrammetry 3D Models

3D photogrammetry models can be viewed on the National Park Service Geologic Resource Division Sketchfab page (https://sketchfab.com/grd_nps/models) or GRCA photogrammetry series website (https://www.nps.gov/articles/series.htm?id=A9E62040-AC6F-A6D7-BE564A036F1D6146).

All photos and files associated with each 3D model have been archived on IRMA and within the GRCA and WASO paleontology archives.

Appendix Table B-1. *GRCA specimens which have been documented as 3D photogrammetry models.*

Specimen ID	Scientific Name	Common Name
NMNH 25478	*Desmodus stocki*	Stock's Vampire Bat Skull
GRCA 56441	*Oreamnos harringtoni*	Harrington's Goat Skull
GRCA 55908	*Gymnogyps californianus*	California Condor Beak
GRCA 21734	*Miracinonyx trumani*	American Cheetah Maxilla
GRCA 21751	*Nothrotheriops shastensis*	Shasta Ground Sloth Skull
USNM PAL 617525	*Nothrotheriops shastensis*	Shasta Ground Sloth Coprolite
GRCA 20214	*Tainoceras schellbachi*	Coiled Nautiloid Holotype
GRCA 21372	*Productus bassi*	Brachiopod
GRCA 14466	Undetermined	Crinoid Columnal Block
GRCA 33184	*Platysomus*	Phyllodont Fish Tooth Plate
[no catalog number]	*Chelichnus*	Vertebrate Trackway Block (Field)
[no catalog number]	*Ichniotherium*	Vertebrate Trackway Block (Field)
GRCA 3217	Undetermined	Permian Seed Fern
USNM PAL 38033	*Supaia merriami*	Permian Seed Fern Holotype
GRCA 3090	*Typus whitei*	Griffinfly Wing Holotype
GRCA 17187	*Dolichometopus productus*	Trilobite

BURROWS

Grand Canyon National Park

GRAND CANYON NATIONAL PARK

Common Name: Burrows

Scientific Name: *Scoyenia gracilis*

Geologic Age: 285 million years ago (Permian)

Geologic Formation: Hermit Formation

Interactive 3D model

This trace fossil formed as an animal plowed through sediment to feed.

Trace fossils, like these burrows, help scientists better understand how organisms behaved and moved within their enviornment. Insects that made *Scoyenia* traces burrowed horizontally and vertically in soft river banks and swampy muds to feed and seek shelter.

Fossils are non-renewable natural resources protected by federal law. Please don't take or vandalize these precious resources.

8 of 9

Grand Canyon National Park Fossil Trading Card featuring fossil invertebrate traces of the ichnotaxon Scoyenia gracilis *from the Permian Hermit Formation (NPS).*

Grand Canyon National Park Paleontological Supplemental Information: Part A Fossil Taxa Named From GRCA

Complied by Justin S. Tweet

Befitting a park with such a long history of paleontological investigations and diversity of fossiliferous rocks, GRCA has been the source for numerous type specimens. At least 167 fossil species have been named from fossils discovered within 2020 GRCA boundaries (table A-1), a number which is exceeded only by Florissant Fossil Beds National Monument, Guadalupe Mountains National Park, John Day Fossil Beds National Monument, and Yellowstone National Park. They are also among the most diverse groups of species named from an NPS unit. An additional 13 potentially based on GRCA fossils (Part B). The great majority of these taxa were collected and named during the National Park era (1919–present), although not all of the discovery localities were within GRCA at the time of discovery due to park boundary changes. For example, some type specimens recovered from what is now far western GRCA during the 1930s were then within Lake Mead National Recreation Area (LAKE). Pre-1919 taxa are primarily Walcott's Cambrian invertebrates and a few species from the very early era of exploration. Some land once in southern GRCA was transferred to the Havasupai Indian Reservation in 1975; some fossil sites given in the literature as within GRCA are affected by this, but apparently not any type specimens. Two bibliographies by Spamer (1984, 1988) were invaluable for creating this supplement and Part B.

Although GRCA is justly famous for its Paleozoic plants and vertebrate ichnofossils, its type record is dominated by invertebrates, particularly trilobites, brachiopods, and ostracode-like crustaceans. Taxa from nearby but not within GRCA were omitted. Three names that would otherwise fall within this table are omitted: the pseudofossil or dubiofossil *Brooksella canyonensis* (Bassler, 1941); the controversial "algae" *Rivularites permiensis* (White, 1929); and the *nomen nudum* or "naked name" *Agostopus robustus*, accidentally created by Gilmore (1927) as he recognized a year later (Gilmore, 1928). The table is divided into plants, invertebrates, vertebrates, invertebrate ichnofossils, vertebrate ichnofossils, other ichnofossils, and other fossils. Within each group, sorting is by general type of fossil, and then alphabetically by taxa. No evaluation of validity or preferred taxonomy is intended; only corrections of preoccupied names are included.

Institutional Abbreviations—**ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **GCNPM**, Grand Canyon National Park Museum, Grand Canyon, Arizona, USA; **HUPC**, Paleobotanical Collections of Harvard University Herbaria, Cambridge, Massachusetts, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **LO**, Lund University (Lunds universitet), Lund, Sweden; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **NGS**, Nebraska Geological Survey (now at UNSM); **UCLA**, University of California Los Angeles (now at LACM); **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska, USA; **USNM**, National Museum of Natural History, Washington, D.C., USA; **USNMPC**, U.S. National Museum Parasite Collection, Beltsville, Maryland, USA; **UT**, Eberhard Karls University, Tübingen (Eberhards Karls Universität Tübingen), Tübingen, Germany; **YPM**, Peabody Museum of Natural History, New Haven, Connecticut, USA.

Table A-1. *Fossil taxa named from specimens found within GRCA. (continued on the following page)*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Plants	*Brachyphyllum arizonicum*	White, 1929	Permian, Hermit	USNM 38060	Conifer
	Brachyphyllum tenue	White, 1929	Permian, Hermit	Syntypes USNM 38061, 312783, and 312784	Conifer
	Pagiophyllum dubium	White, 1929	Permian, Hermit	Syntypes USNM 38062 and 312790–312792	Conifer
	Palaeotaxites praecursor	White, 1929	Permian, Hermit	Syntypes USNM 38058, 38060, and 324560–324564	Conifer
	Voltzia dentiloba	White, 1929	Permian, Hermit	Syntype USNM 38056	Conifer
	Walchia dawsoni	White, 1929	Permian, Hermit	Syntypes USNM 38052 and 312796–312798	Conifer
	Walchia gracillima	White, 1929	Permian, Hermit	Syntypes USNM 38053 and 312793–312795	Conifer
	Brongniartites? *aliena*	White, 1929	Permian, Hermit	Syntypes USNM 38043 and 312785–312789	Pteridophyte
	Brongniartites? *yakiensis*	White, 1929	Permian, Hermit	Syntypes USNM 38042, 312807–312812 and 324554–324559	Pteridophyte
	Sphenophyllum gilmorei	White, 1929	Permian, Hermit	Syntypes USNM 38025 and 324567–324575	Pteridophyte
	Supaia anomala	White, 1929	Permian, Hermit	Syntypes USNM 38035 and 324581–324588	Pteridophyte
	Supaia breviloba	White, 1929	Permian, Hermit	Syntype USNM 38037	Pteridophyte
	Supaia compacta	White, 1929	Permian, Hermit	Syntypes USNM 38034 and 324590–324593	Pteridophyte
	Supaia linearifolia	White, 1929	Permian, Hermit	Syntypes USNM 38036 and 324594	Pteridophyte
	Supaia merriami	White, 1929	Permian, Hermit	Syntype USNM 38033	Pteridophyte
	Supaia rigida	White, 1929	Permian, Hermit	Syntypes USNM 38031, 324595, and 324596	Pteridophyte

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Plants (continued)	*Supaia sturdevantii*	White, 1929	Permian, Hermit	Syntypes USNM 38032 and 324597	Pteridophyte
	Supaia subgoepperti	White, 1929	Permian, Hermit	USNM 38038	Pteridophyte
	Supaia thinnfeldioides	White, 1929	Permian, Hermit	Syntypes USNM 38030 and 324598–324603	Pteridophyte
	Yakia heterophylla	White, 1929	Permian, Hermit	Syntypes USNM 38044 and 312799–312804	Pteridophyte
	Taeniopteris angelica	White, 1929	Permian, Hermit	Syntypes USNM 38048, 324565, 324566, and 342587	Pteridophyte or gingko
	Callipteris arizonae	White, 1929	Permian, Hermit	Syntype USNM 38027	Pteridophyte?
	Cyclocarpon angelicum	White, 1929	Permian, Hermit	Syntype USNM 38063	Seed/fruit
	Eltovaria bursiformis	White, 1929	Permian, Hermit	Syntype USNM 38066	Seed/fruit
Invertebrates	*Avonia subhorrida newberryi*	McKee, 1938	Permian, Kaibab	USNM 102301	Brachiopod
	Billingsella obscura	Walcott, 1905	Cambrian, Bright Angel	USNM 52258a	Brachiopod
	Chonetes quadratus	King, 1931	Permian, Kaibab	YPM 10830a	Brachiopod
	Composita arizonica	McKee, 1938	Permian, Kaibab	Syntypes USNM 102303, 102304, and 102305	Brachiopod
	Derbyia regularis	McKee, 1938	Permian, Kaibab	Syntypes USNM 102290 and 102291	Brachiopod; preoccupied, renamed *Derbyia arizonensis* (McKee, 1941)
	Dictyonina arizonaensis	Resser, 1945	Cambrian, Bright Angel?	USNM 108557	Brachiopod
	Finkelnburgia noblei	Walcott, 1924	Cambrian, Muav	USNM 69750–69752	Brachiopod
	Iphidea crenistria	Walcott, 1897	Cambrian, Bright Angel	USNM 26431a	Brachiopod
	Iphidea superba	Walcott, 1897	Cambrian, Bright Angel?	USNM 26429a	Brachiopod

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrates (continued)	*Lingulella kanabensis*	Resser, 1945	Cambrian, Bright Angel / Muav	USNM 33829a	Brachiopod
	Lingulella mckeei	Resser, 1945	Cambrian, Bright Angel	USNM 108561a	Brachiopod
	Nisusia (*Jamesella*) *kanabensis*	Walcott, 1908	Cambrian, Bright Angel / Muav	USNM 52300	Brachiopod
	Obolus (*Lingulella*) *chuarensis*	Walcott, 1898	Cambrian, Bright Angel?	USNM 57020a	Brachiopod
	Obolus (*Lingulella*) *euglyphus*	Walcott, 1898	Cambrian, Bright Angel	USNM 27316a	Brachiopod
	Obolus (*Lingulella*) *lineolatus*	Walcott, 1898	Cambrian, Bright Angel?	USNM 27325a	Brachiopod
	Obolus (*Lingulella*) *spatulus*	Walcott, 1902	Cambrian, Bright Angel	USNM 35290a	Brachiopod
	Obolus (*Lingulella*) *zetus*	Walcott, 1898	Cambrian, Bright Angel	USNM 27347b	Brachiopod
	Obolus (*Westonia*) *themis*	Walcott, 1905	Cambrian, Bright Angel	USNM 51732a	Brachiopod
	Bascomella subsphaerica	Condra and Elias, 1944	Permian, Kaibab	NGS 449 (not found on May 2016 visit to UNSM)	Bryozoan
	Girtypora maculata	McKinney, 1983	Permian, Kaibab	FMNH PE 24301	Bryozoan
	Bicorbula arizonica	Condra and Elias, 1945a	Permian, Kaibab	NGS 264 (not found on May 2016 visit to UNSM)	Bryozoan or bryozoan-algal consortium; preoccupied, renamed *Bicorbis arizonica* (Condra and Elias, 1945b)
	Conularia kaibabensis	McKee, 1935	Permian, Kaibab	USNM 102289 (originally GCNPM FK211)	Conulariid
	Eocrinus multibrachiatus	Kirk (in Resser, 1945)	Cambrian, Bright Angel	USNM 108556a	Eocrinoid

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrates (continued)	*Oreohelix yavapai fortis*	Cockerell, 1927	Pleistocene?, “red earth”	ANSP 141875	Gastropod
	Typus gilmorei	Carpenter, 1927	Permian, Hermit	USNM 71279	Insect (meganeurid wing); generic name now corrected to *Tupus* (ICZN, 1985)
	Typus whitei	Carpenter, 1928	Permian, Hermit	USNM 71713	Insect (meganeurid wing); generic name now corrected to *Tupus* (ICZN, 1985)
	Agamofilaria oxyura	Schmidt and others, 1992	Pleistocene	USNMPC 82076	Nematode
	Strongyloides shastensis	Schmidt and others, 1992	Pleistocene	USNMPC 82075	Nematode
	Bradoria tontoensis	Ulrich and Bassler, 1931	Cambrian, unspecified	USNM 81377	Ostracode-like crustacean
	Dielymella appressa	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56506	Ostracode-like crustacean
	Dielymella dorsalis	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56505	Ostracode-like crustacean
	Dielymella nasuta	Ulrich and Bassler, 1931	Cambrian, Bright Angel	Cotypes USNM 56508 and 56509	Ostracode-like crustacean
	Dielymella recticardinalis	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56510	Ostracode-like crustacean
	Dielymella recticardinalis angustata	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56511	Ostracode-like crustacean
	Indiana curta	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56466	Ostracode-like crustacean
	Indiana faba	Ulrich and Bassler, 1931	Cambrian, Bright Angel?	USNM 56458	Ostracode-like crustacean
	Indiana faba intermedia	Ulrich and Bassler, 1931	Cambrian, Bright Angel?	USNM 56462	Ostracode-like crustacean

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrates (continued)	*Indiana impressa*	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56463	Ostracode-like crustacean
	Tontoia kwaguntensis	Walcott, 1912	Cambrian, Bright Angel?	USNM 57660	Ostracode-like crustacean
	Walcottella apicalis	Ulrich and Bassler, 1931	Cambrian, Bright Angel?	Cotypes USNM 56477 and 56478	Ostracode-like crustacean
	Walcottella breviuscula	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56481	Ostracode-like crustacean
	Walcottella concentrica	Ulrich and Bassler, 1931	Cambrian, Bright Angel?	Cotypes USNM 56479 and 56480	Ostracode-like crustacean
	Walcottella leperditoides	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56484	Ostracode-like crustacean
	Walcottella limatula	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56488	Ostracode-like crustacean
	Walcottella longula	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56491	Ostracode-like crustacean
	Walcottella nitida	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56485	Ostracode-like crustacean
	Walcottella oblonga	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56486	Ostracode-like crustacean
	Walcottella obsoleta	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56487	Ostracode-like crustacean
	Walcottella pulchella	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56483	Ostracode-like crustacean
	Walcottella scitula	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56482	Ostracode-like crustacean
	Walcottella subtruncata	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56490	Ostracode-like crustacean
	Walcottella ventrosa	Ulrich and Bassler, 1931	Cambrian, Bright Angel	USNM 56489	Ostracode-like crustacean

Table A-1. Continued

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrates (continued)	*Scenella hermitensis*	Resser, 1945	Cambrian, Muav	USNM 108568a	Scenellid (described as a gastropod)
	Acrocephalops? arizonaensis	Resser, 1945	Cambrian, Bright Angel	USNM 108624	Trilobite
	Albertella schenki	Resser, 1945	Cambrian, Bright Angel	USNM 108583	Trilobite
	Alokistocare althea	Walcott, 1916a	Cambrian, Bright Angel	Lectotype USNM 61574	Trilobite
	Bolaspis aemula	Resser, 1945	Cambrian, Muav	USNM 108602a	Trilobite
	Clavaspidella kanabensis	Resser, 1945	Cambrian, Bright Angel / Muav	USNM 108578a	Trilobite
	Delaria macclintocki	Cisne, 1971	Permian, Kaibab	GCNPM 3949	Trilobite
	Dolichometopus tontoensis	Walcott, 1916b	Cambrian, Bright Angel	Lectotype USNM 62685	Trilobite
	Ehmaniella arizonaensis	Resser, 1945	Cambrian, Bright Angel	USNM 108603a	Trilobite
	Ehmaniella hebes	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108612a	Trilobite
	Elrathia nitens	Resser, 1945	Cambrian, Bright Angel	USNM 108625	Trilobite
	Elrathiella? insueta	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108621a	Trilobite
	Glossopleura mckeei	Resser, 1935	Cambrian, Bright Angel	USNM 62714	Trilobite
	Glyphaspis tecta	Resser, 1945	Cambrian, Muav	USNM 108596a	Trilobite
	Glyphaspis vulsa	Resser, 1945	Cambrian, Bright Angel	USNM 108595a	Trilobite
	Glyphaspsis kwanguntensis	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108618a	Trilobite
	Kochina? angustata	Resser, 1945	Cambrian, Bright Angel / Muav	USNM 108610	Trilobite

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrates (continued)	*Kootenia mckeei*	Resser, 1945	Cambrian, Bright Angel / Muav	USNM 108588a	Trilobite
	Kootenia schenki	Resser, 1945	Cambrian, Muav	USNM 108586a	Trilobite
	Kootenia simplex	Resser, 1945	Cambrian, Bright Angel	USNM 108591a	Trilobite
	Pachyaspis fonticola	Resser, 1945	Cambrian, Bright Angel	USNM 108608	Trilobite
	Parehmania kwaguntensis	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108620a	Trilobite
	Parehmania nitida	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108613a	Trilobite
	Parehmania tontoensis	Resser, 1945	Cambrian, Bright Angel	USNM 108614	Trilobite
	Solenopleurella diligens	Resser, 1945	Cambrian, Bright Angel / Muav	USNM 108627a	Trilobite
	Solenopleurella erosa	Resser, 1945	Cambrian, Muav	USNM 108616a	Trilobite
	Solenopleurella porcata	Resser, 1945	Cambrian, Muav	USNM 108626a	Trilobite
	Spencia tontoensis	Resser, 1945	Cambrian, Bright Angel	USNM 108611a	Trilobite
	Trachycheilus typicale	Resser, 1945	Cambrian, Bright Angel or Muav	USNM 108619	Trilobite
Vertebrates	*Megactenopetalus kaibabanus*	David, 1944	Permian, Kaibab	MNA G2.2280	Chondrichthyan
Invertebrate Ichnofossils	*Scoyenia gracilis*	White, 1929	Permian, Hermit	USNM 201869	Invertebrate trail
	Walpia hermitensis	White, 1929	Permian, Hermit	Syntypes USNM 263675 and 263676	Invertebrate trail
	Unisulcus sinuosus	Gilmore, 1927	Permian, Coconino	USNM 11498	Invertebrate trail
	Octopodichnus didactylus	Gilmore, 1927	Permian, Coconino	USNM 11501	Invertebrate track
	Paleohelcura tridactyla	Gilmore, 1926	Permian, Coconino	USNM 11145	Invertebrate track
	Stipsellus annulatus	Howell, 1957	Cambrian, Tapeats	GCNPM 8538	Invertebrate trail
	Cruziana arizonensis	Seilacher, 1970	Cambrian, Tapeats	UT Ic 1329/9	Invertebrate trace

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Invertebrate Ichnofossils (continued)	*Mesichnium benjamini*	Gilmore, 1926	Permian, Coconino	USNM 11155	Invertebrate track
	Triavestigia niningeri	Gilmore, 1927	Permian, Coconino	USNM 11510	Invertebrate track
	Angulichnus alternipes	Elliott and Martin, 1987	Cambrian, Bright Angel	MNA N3862	Invertebrate trail
Vertebrate Ichnofossils	*Castrocopros martini*	Hunt and Lucas, 2018	Pleistocene	USNM PAL 720155	*Nothrotheriops* coprolite
	Agostopus matheri	Gilmore, 1926	Permian, Coconino	USNM 11135	Vertebrate track
	Agostopus medius	Gilmore, 1927	Permian, Coconino	USNM 11509	Vertebrate track
	Allopus? *arizonae*	Gilmore, 1926	Permian, Coconino	USNM 11132	Vertebrate track
	Amblyopus pachypodus	Gilmore, 1927	Permian, Coconino	USNM 11511	Vertebrate track
	Ammobatrachus turbatans	Gilmore, 1928	Pennsylvanian, Wescogame	USNM 11691	Vertebrate track
	Anomalopus sturdevanti	Gilmore, 1927	Pennsylvanian, Wescogame	USNM 11577	Vertebrate track
	Baropezia eakini	Gilmore, 1926	Permian, Coconino	USNM 11137	Vertebrate track
	Baropus coconinoensis	Gilmore, 1927	Permian, Coconino	USNM 11514	Vertebrate track
	Barypodus metszeri	Gilmore, 1927	Permian, Coconino	USNM 11505	Vertebrate track
	Barypodus palmatus	Gilmore, 1926	Permian, Coconino	USNM 11134	Vertebrate track
	Barypodus tridactylus	Gilmore, 1927	Permian, Coconino	USNM 11502	Vertebrate track
	Batrachichnus obscurus	Gilmore, 1927	Permian, Hermit	USNM 11529	Vertebrate track
	Collettosaurus pentadactylus	Gilmore, 1927	Permian, Hermit	USNM 11527	Vertebrate track
	Dolichopodus tetradactylus	Gilmore, 1926	Permian, Coconino	USNM 11123	Vertebrate track
	Dromillopus parvus	Gilmore, 1927	Permian, Hermit	USNM 11537	Vertebrate track
	Exocampe? *delicatula*	Lull, 1918	Permian, Hermit	YPM 2146	Vertebrate track
	Hyloidichnus bifurcatus	Gilmore, 1927	Permian, Hermit	USNM 11518	Vertebrate track
	Hyloidichnus whitei	Gilmore, 1928	Permian, Hermit	USNM 11692	Vertebrate track
	Hylopus hermitanus	Gilmore, 1927	Permian, Hermit	USNM 11517	Vertebrate track
	Ichniotherium gilmorei	Haubold, 1971	Permian, Hermit	USNM 11707 (now lost)	Vertebrate track

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Vertebrate Ichnofossils (continued)	*Laoporus noblei*	Lull, 1918	Permian, Coconino	YPM 2144	Vertebrate track
	Laoporus schucherti	Lull, 1918	Permian, Coconino	YPM 2143	Vertebrate track
	Megapezia? *coloradensis*	Lull, 1918	Permian, Hermit	YPM 2145	Vertebrate track
	Nanopus maximus	Gilmore, 1927	Permian, Coconino	USNM 11506	Vertebrate track
	Nanopus merriami	Gilmore, 1926	Permian, Coconino	USNM 11146	Vertebrate track
	Palaeopus regularis	Gilmore, 1926	Permian, Coconino	USNM 11143	Vertebrate track
	Stenichnus yakiensis	Gilmore, 1927	Pennsylvanian, Wescogame	USNM 11533	Vertebrate track
	Tridentichnus supaiensis	Gilmore, 1927	Pennsylvanian, Wescogame	USNM 11534	Vertebrate track
Other Ichnofossils	*Cryptozoon*? *occidentale*	Dawson, 1897	Neoproterozoic, Kwagunt	USNM 33799 (USNM 60710 and 60711 per Rezak, 1957)	Stromatolite
Other Fossils	*Archeococcidia antiquus*	Schmidt and others, 1992	Pleistocene	USNMPC 82073	Coccidian oocyst
	Archeococcidia nothrotheriopsiae	Schmidt and others, 1992	Pleistocene	USNMPC 82074	Coccidian oocyst
	Endothyra baileyi poloumera	Skipp, 1969	Mississippian, Redwall	USNM 641727	Foraminifera
	Septaglomospiranella rossi	Skipp, 1969	Mississippian, Redwall	USNM 641578	Foraminifera
	Chuaria circularis	Walcott, 1899	Neoproterozoic, Kwagunt	Lectotype USNM 33800	Organic-walled microfossil
	Kaibabia gemmulella	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36082a	Organic-walled microfossil
	Microlepidopalla mira	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36104b	Organic-walled microfossil
	Vandalosphaeridium walcottii	Vidal and Ford, 1985	Neoproterozoic, Kwagunt	LO 5661	Organic-walled microfossil
	Volleyballia dehlerae	Porter and Riedman, 2016	Neoproterozoic, Galeros	UCMP 36080d	Organic-walled microfossil

Table A-1. *Continued*

Category	Taxon	Citation	Age, Formation	Type Specimen	Classification
Other Fossils (continued)	*Bombycion micron*	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62988	Vase-shaped microfossil
	Bonniea dacruchares	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64409	Vase-shaped microfossil
	Bonniea pytinaia	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64410	Vase-shaped microfossil
	Cycliocyrillium simplex	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64455	Vase-shaped microfossil
	Cycliocyrillium torquata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64453	Vase-shaped microfossil
	Hemisphaeriella ornata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62990	Vase-shaped microfossil
	Melanocyrillium fimbriatum	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58968 (now LACM?)	Vase-shaped microfossil
	Melanocyrillium hexodiadema	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58959 (now LACM?)	Vase-shaped microfossil
	Melanocyrillium horodyskii	Bloeser, 1985	Neoproterozoic, Kwagunt	UCLA 58976 (now LACM?)	Vase-shaped microfossil
	Melicerion poikilon	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62990	Vase-shaped microfossil
	Palaeoarcella athanata	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 62988	Vase-shaped microfossil
	Trachycyrillium pudens	Porter and others, 2003	Neoproterozoic, Kwagunt	HUPC 64413	Vase-shaped microfossil

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Grand Canyon National Park Paleontological Supplemental Information: Part B
Fossil Taxa Potentially Named From GRCA

Complied by Justin S. Tweet

A small number of taxa have been named from fossils discovered somewhere in the Grand Canyon area, but with insufficient provenance information to determine the exact location. Some, all, or none of the type specimens may have come from GRCA (table B-1).

Institutional Abbreviations—**CU**, Columbia University, New York City, New York; **GCNPM**, Grand Canyon National Park Museum, Grand Canyon, Arizona; **USNM**, National Museum of Natural History, Washington, D.C.

Table B-1. *Fossil taxa named from specimens possibly found within GRCA.*

Category	Taxon	Citation	Age, Formation	Type Specimen	Notes
Invertebrates	*Avonia dorsoconcava*	McKee, 1938	Permian, Kaibab	GCNPM 9993	Brachiopod
	Chonetes kaibabensis	McKee, 1938	Permian, Kaibab	Syntypes USNM 102292, 102293, and 102294	Brachiopod
	Marginifera meridionalis	McKee, 1938	Permian, Kaibab	Syntype USNM 102302	Brachiopod
	Productus (*Dictyoclostus*) *bassi*	McKee, 1938	Permian, Kaibab	Lectotype USNM 102295a	Brachiopod
	Productus (*Dictyoclostus*) *paraindicus*	McKee, 1938	Permian, Kaibab	Lectotype USNM 102297	Brachiopod
	Productus ivesi	Newberry, 1861	Permian, Toroweap	Syntypes USNM 5356a–c	Brachiopod
	Archaeocidaris gracilis	Newberry, 1861	Permian, Toroweap / Kaibab	Syntypes CU 604 and USNM 5412	Echinoid
	Archaeocidaris longispinus	Newberry, 1861	Permian, Toroweap / Kaibab	CU 6419G	Echinoid
	Archaeocidaris ornatus	Newberry, 1861	Permian, Toroweap / Kaibab	Syntypes CU 6000G	Echinoid; preoccupied, renamed *Archaeocidaris coloradensis* (Jackson, 1912)
	Kootenia havasuensis	Resser, 1945	Cambrian, Muav	USNM 108601a	Trilobite
	Pachyaspis moorei	Resser, 1945	Cambrian, Muav	USNM 108606a	Trilobite
Invertebrate Ichnofossils	*Cruziana linnarsoni*	White, 1874	Cambrian, Tonto Group	Syntype USNM 8614	Invertebrate (crustacean?) trace
	Cruziana rustica	White, 1874	Cambrian, Tonto Group	Syntype USNM 8615	Invertebrate (crustacean?) trace

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Grand Canyon National Park Paleontological Supplemental Information: Part C Stratigraphic Tables of GRCA Paleozoic Taxa

Complied by Justin S. Tweet

The following tables collate known Paleozoic taxa reported from localities verified as within GRCA, based on the literature and Grand Canyon National Park museum records. They provide a synoptic look at the groups of fossils in a stratigraphic format. Taxonomically, it was not possible to critically evaluate every cited occurrence. There are undoubtedly instances where the same taxon has been listed more than once due to differing interpretations or general changes in taxonomic usage. In addition, it was not within the scope of the project to evaluate every potential synonymy and genus-species combination. The most recent name employed in Grand Canyon literature for a given taxon is generally used, with usage in the other articles of this volume serving as the ultimate arbitrator. Older combinations are included in a section following the tables to facilitate translation between different references. Some cited taxa have outdated names, but the author did not provide enough information to determine more appropriate names. In these cases, the taxonomy is left as the author gave it.

The tables are organized with the first column providing the taxa and the last column providing references, with the intervening tables showing presence or absence. Groups are separated by darker gray rows; within groups, taxa are sorted alphabetically by genus and species, with reports not assigned to a genus placed after those that are. Taxon presence in a given formation is denoted by "Y" in the appropriate cell. Taxon absence is denoted by "–". If there is some question about an occurrence, a "?" is used. Some taxa are present in multiple formations; in these cases, the listed references may apply to one or all of the formations. "GCM" as a reference refers to GRCA collections; only unique results unreported in the literature are included. Names employed these otherwise unattested records should be taken with some caution. Due to the number of taxa and formations, entries have been split into four tables, incorporating the following formations in ascending order:

Acronyms used for Table C-1: Cambrian

- Ctt = Tapeats Sandstone
- Ctba = Bright Angel Shale (* = possibly Muav Limestone instead)
- Ctm = Muav Limestone
- Ctu = Undivided Tonto Group (presumably mostly the Bright Angel Shale and Muav Limestone
- Cu = Frenchman Mountain Dolostone

Acronyms used for Table C-2: Devonian and Mississippian

- Dtb = Temple Butte Formation
- Mr = Redwall Limestone
- Msc = Surprise Canyon Formation

Acronyms used for Table C-3: Supai Group

- IPswa = Watahomigi Formation
- IPsm = Manakacha Formation
- IPswe = Wescogame Formation
- Pse = Esplanade Sandstone

Acronyms used for Table C-4: post-Supai Permian

- Ph = Hermit Formation
- Pc = Coconino Sandstone
- Pt = Toroweap Formation
- Pk = Kaibab Formation

Table C-1. *Cambrian fossil taxa. Ctt = Tapeats Sandstone, Ctba = Bright Angel Shale (* = possibly Muav Limestone instead), Ctm = Muav Limestone, Ctu = Undivided Tonto Group (presumably mostly the Bright Angel Shale and Muav Limestone), and Cu = Frenchman Mountain Dolostone.*
(continued on following page)

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Plants	Cryptogam spores, various morphologies	–	Y	–	–	–	Strother and Beck, 2000; Taylor and Strother, 2008
Invertebrates	**Overall Invertebrates**	**Y**	**Y**	**Y**	**Y**	**–**	**–**
Invertebrates: Porifera	Archaeocyatha undetermined?	–	?	Y	–	–	Resser, 1945; GCM
	Sponge spicules	–	–	Y	–	–	Resser, 1945 (potentially *Chancelloria*)
Invertebrates: Brachiopoda	**Overall Brachiopoda**	**Y**	**Y**	**Y**	**Y**	**–**	**–**
	Acrothele sp.	–	–	–	Y	–	Walcott, 1890
	Acrotreta? sp.	–	–	Y	–	–	Noble, 1922
	Clitambonites sp.	–	–	Y	–	–	Noble, 1922
	Dictyonina arizonaensis	–	Y	–	–	–	Walcott, 1912a; Noble, 1922; Resser, 1945; Bonde and others, 2018
	Dictyonina sp.	–	–	?	–	–	Resser, 1945
	Diraphora impressions?	–	Y	–	–	–	Resser, 1945
	Discina sp.	–	–	Y	–	–	Noble, 1922
	Finkelnburgia sp.	–	–	Y	–	–	Noble, 1922
	Iphidea ornatella	–	–	–	Y	–	Walcott, 1890
	Lingula sp.	–	Y	Y	–	–	Noble, 1922; Strother and Beck, 2000
	Lingula monticula?	–	Y	–	–	–	Frech, 1893
	Lingulella acutangula	–	Y	–	–	–	Walcott, 1912a; Noble, 1922
	Lingulella chuarensis	–	Y	–	–	–	Walcott, 1898, 1912a, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1945; Foster, 2011
	Lingulella euglypha	–	Y	–	–	–	Walcott, 1898, 1912a, 1916a; Resser, 1945
	Lingulella kanabensis	–	–	–	Y	–	Resser, 1945
	Lingulella lineolata	–	Y	–	–	–	Walcott, 1898, 1912a, 1916a; Noble, 1922; Resser, 1945
	Lingulella mckeei	–	Y	–	–	–	Resser, 1945; Foster, 2011; Bonde and others, 2018
	Lingulella spatula	–	Y	–	–	–	Walcott, 1902, 1912a; Noble, 1922; Resser, 1945
	Lingulella themis	–	Y	–	–	–	Walcott, 1905, 1912a; Noble, 1922; Resser, 1945
	Lingulella winona convexa	–	–	–	Y	–	Walcott, 1912a
	Lingulella zetus	–	Y	–	Y	–	Walcott, 1898, 1912a, 1916a; Resser, 1945

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Brachiopoda (continued)	*Lingulella* n. sp.	–	Y	–	–	–	Schenk and Wheeler, 1942
	Lingulella sp.	–	Y	–	Y	–	Walcott, 1890; Resser, 1945
	Lingulepis prima?	–	–	Y	–	–	Noble, 1922
	Lingulepis sp.	–	–	Y	–	–	Walcott, 1883, 1890; Noble, 1922
	Micromitra pealei	–	Y	–	–	–	Walcott, 1912a, 1916a
	Micromitra (*Paterina*) *crenistria*	–	Y	–	Y	–	Walcott, 1897, 1912a, 1916a; Resser, 1945
	Micromitra (*Paterina*) *superba*	–	Y	–	–	–	Walcott, 1897, 1912a, 1916a; Noble, 1922; Resser, 1945
	Nisusia kanabensis	–	–	–	Y	–	Walcott, 1908, 1912a; Resser, 1945
	Nisusia noblei	–	–	Y	–	–	Walcott, 1924; Resser, 1945
	Nisusia noblei?	–	Y	Y	–	–	Resser, 1945; GCM
	Nisusia obscura	–	Y	–	–	–	Walcott, 1905, 1912a, 1916a; Resser, 1945
	Nisusia sp.	–	Y	Y	–	–	Schenk and Wheeler, 1942; Palmer E&R, 1963/10/17; Bonde and others, 2018
	Nisusia? sp.	–	Y	Y	–	–	Resser, 1945; Palmer E&R, 1963/10/17
	Obolella polita?	–	Y	–	–	–	Frech, 1893
	Obolella sp.	–	Y	–	–	–	Frech, 1893
	Obolella sp.?	–	Y	–	–	–	Frech, 1893
	Obolus sp.	–	Y	–	–	–	GCM
	Paterina? sp.	–	Y	–	–	–	Resser, 1945
	Protorthis sp.	–	–	–	Y	–	Walcott, 1912a
	Syntrophia sp.	–	–	Y	–	–	Noble, 1922
	Trematis sp.	–	–	Y	–	–	Noble, 1922
	Wimanella sp.	–	Y	–	–	–	GCM
	Obolidae undetermined	Y	–	–	–	–	Schuchert, 1918a
	Brachiopoda undetermined	–	Y	Y	–	–	McKee, 1945; GCM
Invertebrates: Hyolitha	*Hyolithes primordialis*?	–	–	Y	–	–	Noble, 1922
	Hyolithes sp. (small)	–	Y*	–	–	–	Resser, 1945
	Hyolithes sp.	–	Y	Y	Y	–	Walcott, 1890, 1916a; Noble, 1922; Schenk and Wheeler, 1942; Resser, 1945; Foster, 2011; Bonde and others, 2018
	Hyolithes sp. (two species)	–	Y*	–	–	–	Resser, 1945
	Hyolithes? sp.	–	–	Y	–	–	Resser, 1945

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Mollusca: Helcionelloida	*Helcionella* sp.	–	–	Y	–	–	Palmer E&R, 1963/10/17; Bonde and others, 2018
Invertebrates: Mollusca: Gastropoda	Gastropoda undetermined	–	Y	–	–	–	GCM
Invertebrates: Arthropoda: Trilobita	**Overall Trilobita**	**?**	**Y**	**Y**	**Y**	**–**	**–**
	Acrocephalops? *arizonaensis*	–	Y	–	–	–	Resser, 1945
	Albertella schenki	–	Y	–	–	–	Resser, 1945
	Albertella n. sp.	–	Y	–	–	–	Schenk and Wheeler, 1942
	Albertella sp.	–	Y	–	–	–	Bonde and others, 2018
	Alokistocare lepida	–	Y	–	–	–	Schenk and Wheeler, 1942
	Alokistocare sp.	–	Y	Y	–	–	Schenk and Wheeler, 1942; Resser, 1945
	Alokistocare?	–	Y	–	–	–	Schenk and Wheeler, 1942
	Alokistocare sp. or *Ehmaniella* sp.	–	Y	–	–	–	Bonde and others, 2018
	Amecephalus althea	–	Y	–	–	–	Walcott, 1916a, 1916b; Schuchert, 1918a; Noble, 1922; Schenk and Wheeler, 1942; Resser, 1945; Foster, 2011
	Amecephalus cf. *A. althea*	–	Y	–	–	–	Schenk and Wheeler, 1942
	Amecephalus sp. cf. *A. packi*	–	Y	–	–	–	Foster, 2011
	Anomocarella sp.	–	–	Y	–	–	Noble, 1922
	Anoria n. sp.	–	Y	–	–	–	Schenk and Wheeler, 1942
	Anoria sp.	–	Y	Y	–	–	Schenk and Wheeler, 1942; Resser, 1945
	“Anoria” *tontoensis*	–	Y	–	–	–	Walcott, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1945; Foster, 2011
	Antagmus arizonaensis	–	Y	–	–	–	Resser, 1945; Bonde and others, 2018
	Antagmus sp.	–	Y	–	–	–	GCM
	Athabaskia kanabensis	–	–	–	Y	–	Resser, 1945
	Athabaskia sp.	–	Y	Y	–	–	Resser, 1945
	Bathyurus? sp.	–	–	Y	–	–	Noble, 1922
	Bolaspis aemula	–	–	Y	–	–	Resser, 1945
	Bolaspis? sp.	–	–	Y	–	–	Resser, 1945
	Dolichometopus sp.	–	–	–	Y	–	Walcott, 1890

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Arthropoda: Trilobita (continued)	*Dorypyge* sp.	–	–	Y	–	–	Stoyanow, 1936
	Ehmaniella arizonaensis	–	Y	–	–	–	Resser, 1945
	Ehmaniella basilica	–	Y	–	–	–	Bonde and others, 2018
	Ehmaniella hebes	–	–	–	Y	–	Resser, 1945
	Ehmaniella sp.	–	Y	–	–	–	Bonde and others, 2018
	Elrathia nitens	–	Y	–	–	–	Resser, 1945
	Elrathia n. sp.	–	Y	–	–	–	Schenk and Wheeler, 1942
	Elrathia sp.	–	Y	–	–	–	Schenk and Wheeler, 1942; Resser, 1945
	Elrathiella? *insueta*	–	–	–	Y	–	Resser, 1945
	Glossopleura boccar	–	Y	–	Y	–	Walcott, 1916a; Schuchert, 1918a; Noble, 1922; Resser, 1935; Schenk and Wheeler, 1942; Resser, 1945; Palmer E&R, 1963/10/17; Foster, 2011; Bonde and others, 2018
	Glossopleura meriwitica	–	Y	–	–	–	GCM
	Glossopleura walcotti?	–	Y	–	–	–	Foster, 2011
	Glossopleura sp.	–	Y	Y	Y	–	Schenk and Wheeler, 1942; Resser, 1945; Palmer E&R, 1963/10/17; Elliott and Martin, 1987a; Bonde and others, 2018
	Glossopleura? sp.	–	Y	–	–	–	GCM
	Glossopleura sp. or *Anoria* sp.	–	–	Y	–	–	Resser, 1945
	Glyphaspis kwaguntensis	–	–	Y	Y	–	Resser, 1945; GCM
	Glyphaspis tecta	–	–	Y	–	–	Resser, 1945
	Glyphaspis vulsa	–	Y	–	–	–	Resser, 1945
	Glyphaspis sp.	–	Y	Y	–	–	Schenk and Wheeler, 1942; Resser, 1945
	Glyphaspis? sp.	–	–	Y	–	–	Resser, 1945
	Kochina? *angustata*	–	–	–	Y	–	Resser, 1945
	Kootenia havasuensis	–	–	?	–	–	Resser, 1945
	Kootenia mckeei	–	–	Y	Y	–	Resser, 1945
	Kootenia schenki	–	–	Y	–	–	Schenk and Wheeler, 1942; Resser, 1945; Palmer E&R, 1963/10/17; Bonde and others, 2018
	Kootenia simplex	–	Y	Y	–	–	Resser, 1945
	Kootenia sp.	–	Y	Y	Y	–	Schenk and Wheeler, 1942; Resser, 1945; Palmer E&R, 1963/10/17; Foster, 2011

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Arthropoda: Trilobita (continued)	*Kootenia*? sp.	–	–	Y	–	–	Resser, 1945
	Neolenus sp.	–	–	Y	–	–	Noble, 1922
	Olenellus sp.	?	Y	–	–	–	Schenk and Wheeler, 1942; Resser, 1945
	Olenoides sp.	–	–	–	Y	–	Walcott, 1890
	Pachyaspis fonticola	–	Y	–	–	–	Resser, 1945
	Pachyaspis moorei	–	Y	?	–	–	Resser, 1945; Bonde and others, 2018
	Pachyaspis sp.	–	Y*	–	–	–	Resser, 1945
	Pagodia? sp.	–	–	Y	–	–	Noble, 1922
	Parehmania kwaguntensis	–	Y	–	Y	–	Bonde and others, 2018
	Parehmania nitida	–	–	–	Y	–	Resser, 1945
	Parehmania tontoensis	–	Y	–	–	–	Resser, 1945
	Parehmania sp.	–	Y*	–	–	–	Resser, 1945
	Ptarmigania sp.	–	Y	–	Y	–	Resser, 1945
	Ptychoparia sp.	–	–	Y	–	–	Walcott, 1883, 1890; Noble, 1922
	Ptychoparia? sp.	–	–	Y	–	–	Noble, 1922
	Saukia sp.	–	–	Y	–	–	Noble, 1922
	Spencella diligens	–	–	–	Y	–	Resser, 1945
	Spencella erosa	–	–	Y	–	–	Resser, 1945
	Spencella porcata	–	–	Y	–	–	Schenk and Wheeler, 1942; Resser, 1945; Palmer E&R, 1963/10/17; Bonde and others, 2018
	Spencella sp.	–	–	Y	Y	–	Resser, 1945; GCM
	Spencia tontoensis	–	Y	–	–	–	Resser, 1945
	Trachycheilus typicale	–	–	–	Y	–	Resser, 1945
	Zacanthoides cf. *walapai*	–	Y	–	–	–	Resser, 1945
	Zacanthoides sp.	–	Y	Y	–	–	Resser, 1945; GCM
	Olenellidae undetermined	–	Y	–	–	–	Bonde and others, 2018
	Trilobita undetermined	–	Y	Y	–	–	Stoyanow, 1936; Palmer E&R, 1963/10/17; GCM
Invertebrates: Arthropoda: Bradoriida	**Overall Bradoriida**	**–**	**Y**	**–**	**Y**	**–**	**–**
	"*Bradoria tontoensis*"	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Dielymella appressa	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Dielymella dorsalis	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945

***Table C-1.** Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Arthropoda: Bradoriida (continued)	*Dielymella nasuta*	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Dielymella recticardinalis	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Dielymella recticardinalis angustata	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Indianites curtus	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Indianites faba	–	Y*	–	–	–	Noble, 1922; Ulrich and Bassler, 1931a; Resser, 1945
	Indianites impressus	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Indianites intermedius	–	Y*	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella apicalis	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella breviuscula	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella concentrica	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella leperditoides	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella limatula	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella longula	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella nitida	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella oblonga	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella obsoleta	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella pulchella	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella scitula	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella subtruncata	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Walcottella ventrosa	–	Y	–	–	–	Ulrich and Bassler, 1931a; Resser, 1945
	Three species of "*Leperditia*"	–	–	–	Y	–	Walcott, 1890
Invertebrates: Echinodermata: Eocrinoidea	*Eocystites*? undetermined sp.	–	Y	–	–	–	Walcott, 1916a; Noble, 1922
	Gogia longidactylus	–	Y	–	–	–	GCM
	Gogia ?longidactylus	–	Y	–	–	–	Foster, 2011
	Gogia multibrachiatus	–	Y	–	–	–	Resser, 1945; Foster, 2011
	"Cystoid" (interpreted as Eocrinoidea undetermined)	–	–	Y	–	–	GCM
Invertebrates: Other Invertebrates	*Chancelloria* cf. *C. eros*	–	–	Y	–	–	Schenk and Wheeler, 1942
	Chancelloria sp.	–	Y	–	–	–	Elliott and Martin, 1987a
	"Echinoid imprint?"	–	Y	–	–	–	GCM
	Margaretia sp.	–	Y	–	–	–	GCM

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Invertebrates: Other Invertebrates (continued)	*Margaretia*? sp. (misspelled *Margaritia*)	–	Y	–	–	–	Schenk and Wheeler, 1942
	"Pelecypod" (bradoriid?)	–	Y	–	–	–	GCM
	Scenella hermitensis	–	–	Y	–	–	Resser, 1945
	Tontoia kwaguntensis	–	Y	–	–	–	Walcott, 1912b; Resser, 1945
Ichnofossils	**Overall Ichnofossils**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
Ichnofossils: Microbial Trace Fossils	Wrinkle structures	–	Y	–	–	–	Strother and Beck, 2000; Baldwin and others, 2004
Ichnofossils: Invertebrate Trace Fossils	**Overall Invertebrate Trace Fossils**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
	Angulichnus alternipes	–	Y	–	–	–	Martin, 1985; Elliott and Martin, 1987b
	Arenicolites isp.	Y	Y	–	–	–	Baldwin and others, 2004; Hagadorn and others, 2011
	Belorhaphe isp.	–	Y	–	–	–	Martin, 1985
	Bergaueria aff. *B. perata*	–	Y	–	–	–	Martin, 1985
	Bergaueria isp.	–	Y	–	–	–	Miller and others, this volume
	Cruziana arizonensis	Y	–	–	–	–	Seilacher, 1970
	Cruziana linnarssoni	–	Y	–	–	–	White, 1874
	Cruziana cf. *C. rusiformis*	–	Y	–	–	–	GCM
	Cruziana rustica	–	Y	–	–	–	White, 1874
	Cruziana "*grandcanyonensis*/*rusiformis*"	–	Y	–	–	–	Martin, 1985; Rose, 2003
	Cruziana isp.	Y	Y	–	Y	–	Walcott, 1886; Frech, 1893; Palmer E&R, 1963/10/17; Elliott and Martin, 1987b; Baldwin and others, 2004; Hagadorn and others, 2011
	Dimorphichnus isp.	–	Y	–	–	–	Martin, 1985; Baldwin and others, 2004
	Diplichnites isp.	Y	Y	–	–	–	Miller and others, this volume; GCM
	Diplocraterion yoyo	–	Y	–	–	–	Martin, 1985
	Diplocraterion isp.	Y	Y	Y	–	–	Elliott and Martin, 1987a, 1987b; Baldwin and others, 2004; Miller and others, this volume
	Diplocraterion or *Rhizocorallium*	Y	–	–	–	–	Miller and others, this volume
	"*Flectostriatus imporcatus*"	–	Y	–	–	–	Martin, 1985
	"*Fodichnites bitumulus*"	–	Y	–	–	–	Martin, 1985

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Ichnofossils: Invertebrate Trace Fossils (continued)	*Monocraterion* isp.	–	Y	–	–	–	Baldwin and others, 2004
	Monomorphichnus lineatus var. *giganticus*	–	Y	–	–	–	Miller and others, this volume
	Monomorphichnus isp.	Y	Y	–	–	–	Martin, 1985; Baldwin and others, 2004; Hagadorn and others, 2011
	Nereites isp.	–	Y	–	–	–	Martin, 1985; Miller and others, this volume
	Palaeophycus aff. *P. striatus*	–	Y	–	–	–	Martin, 1985
	Palaeophycus isp.	Y	Y	–	–	–	Schuchert, 1918a; Elliott and Martin, 1987a, 1987b; Baldwin and others, 2004
	"*Pholetichnus circinatus*"	–	Y	–	–	–	Martin, 1985
	Phycodes aff. *P. circinnatum*	–	Y	–	–	–	Martin, 1985
	Phycodes isp.	–	Y	Y	–	–	Elliott and Martin, 1987b; Baldwin and others, 2004; Miller and others, this volume
	Planolites isp.	Y	Y	–	–	–	Baldwin and others, 2004; Hagadorn and others, 2011
	Rusophycus didymus	Y	Y	–	–	–	Miller and others, this volume
	Rusophycus cf. *R. dispar*	–	Y	–	–	–	GCM
	Rusophycus "*biungis*"	–	Y	–	–	–	Martin, 1985
	Rusophycus isp.	Y	Y	–	Y	–	Elliott and Martin, 1987b; Baldwin and others, 2004; Bonde and others, 2018; Miller and others, this volume
	Scolicia isp.	–	Y	–	–	–	Martin, 1985
	Sinusites isp.	–	Y	–	–	–	Miller and others, this volume
	Skolithos annulatus	Y	–	–	–	–	Howell, 1957; Alpert, 1974
	Skolithos linearis	–	Y	–	–	–	Martin, 1985
	Skolithos cf. *S. linearis*	Y	–	–	–	–	GCM
	Skolithos isp.	Y	Y	–	–	–	Frech, 1893; McKee, 1945; Elliott and Martin, 1987a; Baldwin and others, 2004; Hagadorn and others, 2011
	Spirophycus isp.	–	Y	–	–	–	Martin, 1985
	Teichichnus rectus	–	Y	–	–	–	Martin, 1985
	Teichichnus isp.	Y	Y	–	–	–	Elliott and Martin, 1987a; Baldwin and others, 2004; Hagadorn and others, 2011
	Teichichnus isp. large	–	Y	–	–	–	Miller and others, this volume
	Teichichus isp. small	–	Y	–	–	–	Miller and others, this volume

Table C-1. *Continued*

Category	Taxon Observed	Ctt	Ctba	Ctm	Ctu	Cu	References
Ichnofossils: Invertebrate Trace Fossils (continued)	Cf. *Teichichnus* isp.	–	Y	–	–	–	GCM
	Treptichnus pedum	–	Y	Y	–	–	Martin, 1985; Buatois, 2018; GCM
	Treptichnus cf. *T. pedum*	–	–	Y	–	–	GCM
	Treptichnus isp.	Y	–	–	–	–	Hagadorn and others, 2011
	“Fucoids” (including “seaweeds”)	Y	Y	Y	–	–	Noble, 1922; White, 1928, 1929; McKee, 1932, 1945
	Indeterminate horizontal burrows	–	Y	–	–	–	Martin, 1985
	Invertebrate tracks	–	–	–	Y	–	Palmer E&R, 1963/10/17
	Reticulate burrow	–	–	Y	–	–	GCM
	Spiral trace fossil	–	Y	–	–	–	Martin, 1985
	Trilobite trails	Y	Y	–	Y	–	Schenk and Wheeler, 1942; McKee, 1945; Palmer E&R, 1963/10/17
	Trilobite? crawling and resting traces	–	Y	–	–	–	Beus, 1987
	Vertical tubes	–	–	Y	–	–	GCM
	Worm borings and trails	Y	Y	Y	–	Y	Noble, 1922; Schenk and Wheeler, 1942; McKee, 1945
	Unspecified invertebrate trace fossils	–	Y	Y	–	–	Beus, 1987; GCM
Other Fossils	**Overall Other Fossils**	**Y**	**Y**	**Y**	**–**	**–**	**–**
	“*Eophyton*”? (a type of tool mark made by organisms dragged by currents)	–	–	Y	–	–	GCM
	“Fossil spine-like structures”	Y	–	–	–	–	GCM (possibly Muav instead)
	Girvanella structures/spheres	–	–	Y	–	–	McKee, 1945
	Large metazoan fragments	–	Y	–	–	–	Baldwin and others, 2004
	Leiospheres	–	Y	–	–	–	Baldwin and others, 2004
	Mats of filaments resembling *Nematothallus*	–	Y	–	–	–	Baldwin and others, 2004
	Non-marine cryptospores	–	Y	–	–	–	Baldwin and others, 2004
	Organic impression	Y	–	–	–	–	GCM
	Terrestrial algal cell clusters	–	Y	–	–	–	Baldwin and others, 2004
	Undetermined fossil	–	Y	–	–	–	GCM

Cambrian Taxonomic Notes

[Genus] sp. and [Genus] sp. undet. as used in McKee and Resser (1945) are consolidated as [Genus] sp.

Stratigraphy for many of Walcott's records follows Resser (1945).

Stratigraphy of Schenk and Wheeler (1942) revised after McKee and Resser (1945). Similarly, Palmer (E&R 1963/10/17) and Bonde and others (2018) describe Schenk's Cambrian collections as all Bright Angel Shale, when they actually include both Bright Angel Shale and Muav Limestone collections.

- *Alokistocare althea* = *Amecephalus althea*
- *Billingsella obscura* = *Nisusia obscura*
- *Clavaspidella enucleata* Resser as mentioned in Schenk and Wheeler (1942) and repeated in Bonde and others (2018) appears to be the only use of this name, suggesting Resser had proposed it but later dropped it; the same site in Resser (1945) has *Clavaspidella* sp. (=*Athabaskia*), and it is assumed that this was Resser's final identification
- *Clavaspidella kanabensis* = *Athabaskia kanabensis*
- *Corophioides* = *Diplocraterion*
- *Dolichometopus productus* (in part) = *Dolichometopus tontoensis* (in part) = *Glossopleura mckeei* = *Glossopleura boccar*
- *Dolichometopus tontoensis* (in part) = *Anoria tontoensis*
- *Ehmaniella basilica* = *Proehmaniella basilica*
- *Ehmaniella hebes* = *Proehmaniella hebes*
- *Eocrinus* = *Gogia*
- *Finkelnburgia noblei* = *Nisusia noblei*
- *Glossopleura mckeei* = *Glossopleura boccar*
- Species of *Indiana* named in Ulrich and Bassler (1931a) moved to *Indianites* in Ulrich and Bassler (1931b)
- *Iphidea crenistria* = *Micromitra* (*Paterina*) *crenistria*
- *Iphidea superba* = *Micromitra* (*Paterina*) *superba*
- *Isopodichnus* = *Cruziana*
- *Kootenia* n. sp. of Schenk and Wheeler (1942) = *Kootenia schenki*
- *Lingulella perattenuata* ("*attenuata*" of Resser, 1945) = *Lingulella spatula*
- *Lingulepis* and *Crepicephalus*/*Ptychoparia* zone of Walcott (1883, 1890) is Muav Limestone per Noble (1922)
- *Micromitra* (*Iphidella*) *pannula* (in part) = *Dictyonina arizonaensis*
- *Nisusia*? (*Jamesella*) *kanabensis* = *Nisusia kanabensis*
- *Obolus* (*Lingulella*) *chuarensis* = *Obolus* (*Westonia*) *chuarensis* = *Lingulella chuarensis*
- *Obolus* (*Lingulella*) *euglyphus* = *Obolus* (*Westonia*) *euglyphus* = *Lingulella euglypha*
- *Obolus* (*Lingulella*) *lineolatus* = *Lingulella lineolata*
- *Obolus* (*Lingulella*) *spatulus* = *Lingulella attenuata* (in part) = *Lingulella* (*Lingulepis*) *spatula* = *Lingulepis spatula* = *Lingulella spatula*
- *Obolus* (*Lingulella*) *zetus* = *Lingulella zetus*
- *Obolus* (*Westonia*) *themis* = *Lingulella themis*
- *Orthisina* = *Clitambonites*
- *Phycodes pedum* = *Treptichnus pedum*
- *Scalarituba* = *Nereites*
- *Solenopleurella diligens* = *Spencella diligens*
- *Solenopleurella erosa* = *Spencella erosa*
- *Solenopleurella porcata* = *Spencella porcata*
- *Solenopleurella* n. sp. of Schenk and Wheeler (1941) = *Solenopleurella porcata* = *Spencella porcata*
- *Stipsellus annulatus* (sometimes misspelled *Stripsellus*) = *Skolithos annulatus*

Table C-2. *Devonian and Mississippian fossil taxa. Dtb = Temple Butte Formation, Mr = Redwall Limestone, and Msc = Surprise Canyon Formation. (continued on following page)*

Category	Taxon Observed	Dtb	Mr	Msc	References
Plants	**Overall Plants**	**–**	**–**	**Y**	**–**
Plants: Equisetopsida	*Calamites* (*Mesocalamites*) *cistiformis*	–	–	Y	Tidwell and others, 1992
	Calamites sp.	–	–	Y	Tidwell and others, 1992; Beus, 1999
Plants: Isoetopsida	*Lepidodendron* sp.	–	–	Y	Beus, 1990a, 1995; Beus, 1999; Billingsley and Beus, 1999a
	Lepidostrobophyllum sp.	–	–	Y	Tidwell and others, 1992; Beus, 1999
Plants: Other Plants	Carbonized wood	–	–	Y	Hodnett and Elliott, 2018
	Undetermined wood	–	–	Y	Billingsley and Beus, 1999a
	Undetermined plant fossils	–	–	Y	Beus, 1995; Billingsley and Beus, 1999a; Hodnett and Elliott, 2018
Invertebrates	**Overall Invertebrates**	**Y**	**Y**	**Y**	**–**
Invertebrates: Cnidaria: Anthozoa	**Overall Anthozoa**	**Y**	**Y**	**Y**	**–**
	Anthozoa undetermined	Y	Y	Y	Noble, 1922; McKee and Gutschick, 1969a; Billingsley and Beus, 1985, 1999a; Hodnett and Elliott, 2018; GCM
	Anthozoa undetermined?	–	Y	–	GCM
Invertebrates: Cnidaria: Anthozoa: Tabulata	**Overall Tabulata**	**–**	**Y**	**Y**	**–**
	Michelinia sp.	–	–	Y	Billingsley and McKee, 1982; Beus, 1999
	Syringopora aculeata	–	Y	–	McKee and Gutschick, 1969b; Sando, 1969
	Syringopora surcularia	–	Y	–	Sando E&R, 1963/10/14; Bonde and others, 2018
	Syringopora aff. *S. surcularia*	–	Y	–	Sando E&R, 1963/10/14
	Syringopora cf. *S. surcularia*	–	Y	–	Schuchert, 1918b
	Syringopora sp.	–	Y	–	McKee and Gutschick, 1969b; Sando and Bamber, 1985
	Tabulata undetermined	–	Y	–	GCM
Invertebrates: Cnidaria: Anthozoa: Rugosa	**Overall Rugosa**	**Y**	**Y**	**Y**	**–**
	Amplexizaphrentis sp.	–	Y	–	Sando and Bamber, 1985
	Amplexus sp.	–	–	Y	Beus, 1999
	Barytichisma sp.	–	–	Y	Beus, 1999
	Clisiophyllum sp.	–	Y	–	Schuchert, 1918b
	Diphyphyllum? sp.	–	Y	–	Noble, 1922
	Diphyphyllum (*Lithostrotion*?) sp.	–	Y	–	Noble, 1922

Table C-2. Continued

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Cnidaria: Anthozoa: Rugosa (continued)	*Dorlodotia inconstans*	–	Y	–	Easton and Gutschick, 1953
	Dorlodotia inconstans?	–	Y	–	Easton and Gutschick, 1953
	Dorlodotia sp.?	–	?	–	Sando and Bamber, 1985
	Homalophyllites paucicinctus	–	?	–	Easton and Gutschick, 1953
	Homalophyllites subcrassus	–	Y	–	McKee and Gutschick, 1969b; Sando, 1969
	Menophyllum excavatum	–	Y	–	Schuchert, 1918b
	Streptelasma? sp.	?	–	–	Schenk and Wheeler, 1942
	Sychnoelasma sp.	–	Y	–	Sando and Bamber, 1985
	Vesiculophyllum incrassatum	–	Y	–	Easton and Gutschick, 1953; Sando E&R, 1963/10/14; McKee and Gutschick, 1969b; Sando, 1969; Bonde and others, 2018
	Vesiculophyllum sp.	–	Y	–	Sando and Bamber, 1985
	Zaphrentites persimilis	–	Y	–	Sando E&R, 1963/10/14; Bonde and others, 2018
	“Cyathophylloids”	Y	–	–	Walcott, 1883
	Probable “cup corals”	Y	–	–	Noble, 1922
	Undetermined horn corals	–	Y	Y	McKee and Gutschick, 1969b; Billingsley and Beus, 1999a
Invertebrates: Bryozoa	**Overall Bryozoa**	**–**	**Y**	**Y**	**–**
	Archimedes sp.	–	–	Y	Beus, 1999
	Cladochonus? sp.	–	Y	–	Noble, 1922
	Cystodictya sp.	–	Y	–	McKee and Gutschick, 1969b
	Dichotrypa n. sp.	–	Y	–	Duncan, 1969
	Dichotrypa sp.	–	Y	–	McKee and Gutschick, 1969b
	Fenestella sp.	–	Y	–	Schuchert, 1918b; Noble, 1922
	Fenestella fine mesh	–	Y	–	McKee and Gutschick, 1969b
	Fenestella medium mesh	–	Y	–	McKee and Gutschick, 1969b
	Fenestella moderately coarse mesh	–	Y	–	McKee and Gutschick, 1969b
	Fenestella coarse mesh	–	Y	–	McKee and Gutschick, 1969b
	Fenestella fine mesh?	–	Y	–	McKee and Gutschick, 1969b
	Fenestella medium mesh?	–	Y	–	McKee and Gutschick, 1969b
	Fenestella coarse mesh?	–	Y	–	McKee and Gutschick, 1969b
	Fenestralia? sp.	–	Y	–	McKee and Gutschick, 1969b
	Penniretepora sp.	–	Y	–	McKee and Gutschick, 1969b

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Bryozoa (continued)	*Polypora* sp.	–	Y	–	Schuchert, 1918b; McKee and Gutschick, 1969b
	Polypora? sp.	–	Y	–	McKee and Gutschick, 1969b
	Fenestellidae undetermined	–	Y	–	McKee and Gutschick, 1969b
	Undetermined “rhomboporoid”?	–	Y	–	McKee and Gutschick, 1969b
	Encrusting forms	–	–	Y	Beus, 1999
	Fenestrate forms	–	–	Y	Beus, 1999; Billingsley and Beus, 1999a
	Ramose forms	–	–	Y	Beus, 1999; Billingsley and Beus, 1999a
	Bryozoa undetermined	–	Y	Y	McKee and Gutschick, 1969a; Billingsley and Beus, 1985, 1999a; Hodnett and Elliott, 2018
Invertebrates: Brachiopoda	**Overall Brachiopoda**	**Y**	**Y**	**Y**	**–**
	Anthracospirifer bifurcatus	–	–	Y	Gordon E&R, 1973/1/3
	Anthracospirifer curvilateralis	–	–	Y	Beus, 1999
	Anthracospirifer aff. *A. curvilateralis*	–	–	Y	Billingsley and McKee, 1982
	Anthracospirifer cf. *A. curvilateralis*	–	–	Y	Gordon E&R, 1979/1/23
	Anthracospirifer sp. A	–	–	Y	Gordon E&R, 1979/1/23; Billingsley and McKee, 1982
	Beecheria cf. *B. arkansanum*	–	–	Y	Beus, 1999
	Beecheria sp.	–	–	Y	Billingsley and McKee, 1982
	Brachythyris subcardiiformis	–	–	Y	Gordon E&R, 1973/1/3
	Camarotoechia sp.	–	Y	–	Noble, 1922
	Camarotoechia? n. sp.	–	Y	–	Noble, 1922
	Camarotoechia? sp.	–	Y	–	Noble, 1922
	Cleiothyridina sp.	–	–	Y	Beus, 1999
	Composita gibbosa	–	–	Y	Billingsley and McKee, 1982
	Composita laevis	–	–	Y	Beus, 1999
	Composita ovata	–	–	Y	Billingsley and McKee, 1982
	Composita subquadrata	–	–	Y	Beus, 1999
	Composita sp.	–	Y	Y	Gordon E&R, 1979/1/23; GCM
	Composita? sp.	–	Y	–	Noble, 1922
	Cranaena sp.	–	–	Y	Gordon E&R, 1979/1/23
	Dielasma sp.	–	Y	–	Carter and others, 2014
	Eumetria sp.	–	–	Y	Beus, 1999

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Brachiopoda (continued)	*Flexaria* sp.	–	–	Y	Beus, 1999
	Floweria chemungensis	–	Y	–	Noble, 1922
	Inflatia aff. *I. clydensis*	–	–	Y	Gordon E&R, 1979/1/23; Billingsley and McKee, 1982
	Inflatia sp.	–	–	Y	Gordon E&R, 1979/1/23
	Inflatia? sp.	–	–	Y	Gordon E&R, 1973/1/3
	Inflatia sp. or *Sandia* sp.	–	–	Y	Billingsley and McKee, 1982
	Leiorhynchoidea carbonifera	–	–	Y	Beus, 1999
	Leiorhynchoidea sp.	–	–	Y	Gordon E&R, 1979/1/23
	Leptagonia sp.	–	Y	–	McKee and Gutschick, 1969c
	?*Macropotamorhynchus* cf. *M. purduei*	–	–	Y	Beus, 1999
	Mirifusella cf. *M. fortunata*	–	Y	–	Carter and others, 2014
	Neospirifer striatus	–	Y	–	Frech, 1893
	Orthotetes sp.	–	–	Y	Beus, 1999
	Ovatia sp.	–	–	Y	Gordon E&R, 1979/1/23; Beus, 1999
	Ovatia sp. (small)	–	–	Y	Billingsley and McKee, 1982
	Prospira sp. B.	–	Y	–	Carter and others, 2014
	Pugnoides sp.	–	Y	Y	Billingsley and McKee, 1982
	Rhipidomella nevadensis	–	–	Y	Beus, 1999
	Rhipidomella sp.	–	Y	–	Noble, 1922
	Rotaia neogenes	–	–	Y	Beus, 1999
	Schizophoria sp.	–	–	Y	Billingsley and McKee, 1982
	Spirifer centronatus	–	Y	–	Schuchert, 1918b; Noble, 1922
	Spirifer redwallensis	–	?	–	Carter and others, 2014
	Spirifer aff. *S. incertus*	–	Y	–	Noble, 1922
	Spirifer cf. *S. occidentalis*	–	Y	–	Grant E&R, 1963/10/16; Bonde and others, 2018
	Spirifer sp.	–	Y	–	Grant E&R, 1963/10/16; McKee and Gutschick, 1969b
	Spirifer sp. smaller	–	Y	–	Grant E&R, 1963/10/16
	Finely striated *Spirifer*	–	Y	–	Schuchert, 1918b
	Syringothyris? sp.	–	Y	–	Noble, 1922; Grant E&R, 1963/10/16; Bonde and others, 2018
	Tomiproductus gallatinensis	–	?	–	Carter and others, 2014

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Brachiopoda (continued)	*Torynifer setiger*?	–	–	Y	Billingsley and McKee, 1982
	Torynifer sp.	–	–	Y	Beus, 1999
	Unispirifer minnewankensis	–	Y	–	Carter and others, 2014
	Wellerella osagensis	–	Y	–	GCM
	Orthotetoidea undetermined	–	–	Y	Billingsley and McKee, 1982
	Small productoids	–	–	Y	Beus, 1999
	Productida undetermined	–	Y	Y	McKee and Gutschick, 1969b, 1969c; Billingsley and Beus, 1999a
	Rhynchonellida undetermined	–	Y	–	McKee and Gutschick, 1969c
	Punctate spiriferid	–	–	Y	Beus, 1999
	Spiriferida undetermined	–	Y	Y	Grant E&R, 1963/10/16; Billingsley and Beus, 1999a; Bonde and others, 2018
	Strophomenida undetermined	–	Y	–	McKee and Gutschick, 1969a
	Terebratulida undetermined	–	Y	–	McKee and Gutschick, 1969b; McKee and Gutschick, 1969c
	"Smooth-shelled brachiopod"	–	–	Y	Billingsley and Beus, 1999a
	Brachiopoda undetermined	Y	Y	Y	Walcott, 1883; Stoyanow, 1936; Grant E&R, 1963/10/16; McKee and Gutschick, 1969b, 1969c; Billingsley and McKee, 1982; Billingsley and Beus, 1985, 1999a; Hodnett and Elliott, 2018
Invertebrates: Mollusca	**Overall Mollusca**	**Y**	**Y**	**Y**	**–**
	Mollusca undetermined	–	–	?	Billingsley and Beus, 1985
	Mollusca undetermined?	–	Y	–	GCM
Invertebrates: Mollusca: Bivalvia	*Aviculopecten* sp.	–	–	Y	Gordon E&R, 1979/1/23; Beus, 1999
	?*Edmondia* sp.	–	–	Y	Beus, 1999
	Septimyalina sp.	–	–	Y	Beus, 1999
	Septimyalina? sp.	–	–	Y	Gordon E&R, 1979/1/23
	Schizodus sp.	–	–	Y	Billingsley and McKee, 1982
	Pectinida undetermined	–	–	Y	Billingsley and McKee, 1982
	Bivalvia undetermined	–	–	Y	Billingsley and McKee, 1982; Billingsley and Beus, 1999a
Invertebrates: Mollusca: Cephalopoda: Nautiloidea	*Rayonnoceras* sp.	–	Y	–	Breed, 1969; Billingsley and Breed, 1976
	Coiled nautiloid	–	Y	–	Billingsley and Breed, 1976
	Overall Gastropoda (snails)	**Y**	**Y**	**Y**	**–**

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Mollusca: Gastropoda	?*Bellazona* sp.	–	–	Y	Beus, 1999
	Bellerophon sp.	–	Y	–	Noble, 1922
	Bellerophon (*Bellerophon*) sp.	–	–	Y	Gordon E&R, 1979/1/23; Billingsley and McKee, 1982
	?*Bellerophon* spp.	–	–	Y	Beus, 1999
	Euconospira montezuma	–	Y	–	Bonde and others, 2018
	Euomphalus sp.	–	–	Y	Gordon E&R, 1979/1/23; Beus, 1999
	Euomphalus? sp.	–	Y	–	Noble, 1922
	cf. *Euphemites* sp.	–	Y	–	Bonde and others, 2018
	Glabrocingulum sp.	–	–	Y	Beus, 1999
	?*Loxonema* sp.	–	–	Y	Beus, 1999
	Straparollus (*Straparollus*?) sp.	–	–	Y	Billingsley and McKee, 1982
	High-spired gastropod	–	–	Y	Billingsley and Beus, 1999a
	Low-spired gastropod	–	Y	–	McKee and Gutschick, 1969b
	Bellerophontoidea undetermined	–	Y	–	Yochelson, 1969
	Euomphaloidea undetermined	–	Y	–	Yochelson, 1969
	Murchisoniacea undetermined	–	Y	–	Yochelson, 1969
	Gastropoda undetermined	Y	–	–	Walcott, 1883
Invertebrates: Arthropoda	**Overall Arthropoda**	**–**	**Y**	**Y**	**–**
Invertebrates: Arthropoda: Trilobita	*Aprathia* sp.	–	Y	–	McKee and Gutschick, 1969b, 1969d; Brezinski, 2017
	Breviphillipsia n. sp.	–	Y	–	Cisne, 1971
	Paladin cf. *P. chesterensis*	–	–	Y	Beus, 1999
	Paladin sp.	–	–	Y	Gordon E&R, 1979/1/23; Beus, 1999
	Phillipsia peroccidens	–	Y	–	GCM
	Trilobita undetermined	–	–	Y	Billingsley and Beus, 1999a
Invertebrates: Arthropoda: Ostracoda	Ostracoda undetermined	–	–	Y	Billingsley and Beus, 1999a
Invertebrates: Echinodermata	**Overall Echinodermata**	**–**	**Y**	**Y**	**–**
	Pelmatozoan debris	–	–	Y	Billingsley and McKee, 1982
	Echinodermata undetermined	–	–	?	Billingsley and Beus, 1985, 1999a

Table C-2. Continued

Category	Taxon Observed	Dtb	Mr	Msc	References
Invertebrates: Echinodermata: Asteroidea	Uractinida undetermined	–	–	Y	Beus, 1999
Invertebrates: Echinodermata: Blastoidea	*Pentremites* n. sp.	–	–	Y	Beus, 1999
	Pentremites sp.	–	Y	–	McKee and Gutschick, 1969b; Macurda, 1969
	Blastoidea undetermined	–	–	Y	Billingsley and Beus, 1999a
Invertebrates: Echinodermata: Crinoidea	*Cymbiocrinus* n. sp.	–	–	Y	Beus, 1999
	Long crinoid columnals	–	Y	–	McKee and Gutschick, 1969b
	Crinoidea undetermined	–	Y	Y	Frech, 1893; Schuchert, 1918b; Noble, 1922; McKee and Gutschick, 1969a, 1969c; McKee E&R, 1978/5/25; Beus, 1987; Billingsley and Beus, 1999a ; Hodnett and Elliott, 2018
	Crinoidea undetermined?	–	Y	–	GCM
Invertebrates: Echinodermata: Echinoidea	Echinoidea undetermined	–	–	Y	Billingsley and Beus, 1999a
Invertebrates: Conodonta	**Overall Conodonta**	**Y**	**–**	**Y**	**–**
	Adetognathus unicornis	–	–	Y	Martin and Barrick, 1999
	Adetognathus sp.	–	–	Y	Martin and Barrick, 1999
	Adetognathus/*Cavusgnathus* sp.	–	–	Y	Martin and Barrick, 1999
	Cavusgnathus naviculus	–	–	Y	Martin and Barrick, 1999
	Cavusgnathus unicornis	–	–	Y	Martin and Barrick, 1999
	Gnathodus bilineatus	–	–	Y	Martin and Barrick, 1999
	Gnathodus girtyi simplex	–	–	Y	Martin and Barrick, 1999
	Gnathodus sp.	–	–	Y	Martin and Barrick, 1999
	Icriodus cf. *I. subterminus*	Y	–	–	Beus, 1990b
	Kladognathus sp.	–	–	Y	Martin and Barrick, 1999
	Pandorinella insita	Y	–	–	Beus, 1990b
	Polygnathus pennatus	Y	–	–	Beus, 1990b
	Polygnathus xylus	Y	–	–	Beus, 1990b
	Polygnathus cf. *P. angustidiscus*	Y	–	–	Beus, 1990b
	“Spathagnotus” cf. *S. gradatus*	Y	–	–	Beus, 1990b
	Ramiforms	–	–	Y	Martin and Barrick, 1999

Table C-2. Continued

Category	Taxon Observed	Dtb	Mr	Msc	References
	Conodonta undetermined	–	–	Y	Hodnett and Elliott, 2018
Invertebrates: Other Invertebrates	Spicules	–	–	Y	Billingsley and Beus, 1999a
	Unspecified invertebrate fossils	–	–	Y	Billingsley and Beus, 1985; Beus, 1995
Vertebrates	**Overall Vertebrates**	**Y**	**Y**	**Y**	**–**
Vertebrates: Placodermi	*Bothriolepis coloradoensis* or *B. leidyi*	Y	–	–	Schuchert, 1918b; Noble, 1922; Denison, 1951; Elliott and Blakey, 2005
Vertebrates: Chondrichthyes	**Overall Chondrichthyes**	**–**	**Y**	**Y**	**–**
	Amaradontus santuccii	–	–	Y	Hodnett and Elliott, 2018
	Cladodus cf. *C. marginatus*	–	–	Y	Hodnett and Elliott, 2018
	Cochliodus cf. *C. contortus*	–	–	Y	Hodnett and Elliott, 2018
	Cooleyella platera	–	–	Y	Hodnett and Elliott, 2018
	Deltodus cf. *D. angularis*	–	–	Y	Hodnett and Elliott, 2018
	Deltodus cf. *D. cingulatus*	–	–	Y	Hodnett and Elliott, 2018
	Deltodus sp.	–	–	Y	Hodnett and Elliott, 2018
	Helodus sp.	–	Y	–	McKee and Gutschick, 1969b, 1969d; Elliott and Blakey, 2005
	Helodus? sp.	–	–	Y	Hodnett and Elliott, 2018
	cf. *Helodus* (*Psephodus*) *didymus*	–	Y	–	Hodnett and Elliott, this volume
	Heteropetalus sp.	–	–	Y	Hodnett and Elliott, 2018
	Microklomax carrieae	–	–	Y	Hodnett and Elliott, 2018
	Physonemus sp.	–	Y	–	Elliott and Blakey, 2005
	Orodontidae indet.	–	–	Y	Hodnett and Elliott, 2018
	Undetermined shark teeth	–	–	Y	Billingsley and Beus, 1999a
Vertebrates: Sarcopterygii	*Holoptychius* sp.	Y	–	–	Schuchert, 1918b; Elliott and Blakey, 2005
Vertebrates: Miscellaneous Fish	“Placoganoid” fish plates	Y	–	–	Walcott, 1883
	Indeterminate fish plates and scales	Y	–	–	Noble, 1922; Stoyanow, 1936
	Fish teeth	–	Y	Y	McKee and Gutschick, 1969b, 1969d; Gordon E&R, 1979/1/23
Vertebrates: Other Vertebrates	Undetermined vertebrate remains	–	–	Y	Billingsley and Beus, 1999a; Hodnett and Elliott, 2018
Ichnofossils	**Overall Ichnofossils**	**Y**	**Y**	**Y**	**–**
	Oncolites	–	–	Y	Beus, 1990a; Billingsley and Beus, 1999a

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Ichnofossils: Microbial Trace Fossils	Stromatolites	–	–	Y	Billingsley and Beus, 1985, 1999a
Ichnofossils: Invertebrate Trace Fossils	?*Conostichnus* isp.	–	–	Y	Billingsley and others, 1999
	Cruziana isp.	–	–	Y	Billingsley and others, 1999
	"Fucoids" (including "seaweeds")	–	Y	–	Noble, 1922
	Invertebrate borings and burrows	Y	–	Y	Beus, 1973; Billingsley and Beus, 1999a
	Worm borings and trails	Y	Y	Y	Schuchert, 1918b; Stoyanow, 1936; McKee E&R, 1978/5/25; GCM
	Undetermined invertebrate trace fossils	–	Y	–	GCM
Ichnofossils: Other Trace Fossils	"Algal" laminations	–	–	Y	Billingsley and Beus, 1999a
	General bioturbation	–	–	Y	Billingsley and Beus, 1999a
	Unspecified trace fossils	–	–	Y	Billingsley and Beus, 1999a
Other Fossils	**Overall Other Fossils**	**Y**	**Y**	**Y**	**–**
Other Fossils: Foraminifera	**Overall Foraminifera**	**–**	**Y**	**Y**	**–**
	Earlandia sp.	–	Y	–	McKee and Gutschick, 1969b
	Endothyra kleina?	–	Y	–	McKee and Gutschick, 1969b
	Endothyra tantala	–	Y	–	McKee and Gutschick, 1969b
	Endothyra trachida	–	Y	–	McKee and Gutschick, 1969b
	Endothyra trachida?	–	Y	–	McKee and Gutschick, 1969b
	Endothyra sp.	–	Y	–	McKee and Gutschick, 1969b
	Endothyra aff. *E. excellens*	–	Y	–	McKee and Gutschick, 1969b
	Endothyra aff. *E. gutschicki*	–	Y	–	McKee and Gutschick, 1969b
	Endothyra aff. *E. tantala*	–	Y	–	McKee and Gutschick, 1969b
	Eoendothyranopsis spiroides	–	Y	–	McKee and Gutschick, 1969b
	Eoendothyranopsis spiroides?	–	Y	–	McKee and Gutschick, 1969b
	Eoendothyranopsis aff. *E. spiroides*	–	Y	–	McKee and Gutschick, 1969b
	Eoendothyranopsis cf. *E. spiroides*	–	Y	–	McKee and Gutschick, 1969b
	Globoendothyra baileyi	–	Y	–	McKee and Gutschick, 1969b
	Globoendothyra baileyi poloumera	–	Y	–	McKee and Gutschick, 1969b; Skipp, 1969
	Globoendothyra baileyi?	–	Y	–	McKee and Gutschick, 1969b

Table C-2. *Continued*

Category	Taxon Observed	Dtb	Mr	Msc	References
Other Fossils: Foraminifera (continued)	*Inflatoendothyra eospiroides*	–	Y	–	McKee and Gutschick, 1969b
	Paracaligella? sp.	–	Y	–	McKee and Gutschick, 1969b
	Paramillerella? sp.	–	Y	–	McKee and Gutschick, 1969b
	Pohlia henbesti	–	Y	–	Skipp and others, 1966; McKee and Gutschick, 1969b
	Pohlia henbesti?	–	Y	–	McKee and Gutschick, 1969b
	Septabrunsiina parakrainica	–	Y	–	McKee and Gutschick, 1969b
	Septabrunsiina sp.	–	Y	–	McKee and Gutschick, 1969b
	Septabrunsiina sp.?	–	Y	–	McKee and Gutschick, 1969b
	Septaglomospiranella chernoussovensis	–	Y	–	Skipp and others, 1966; McKee and Gutschick, 1969b
	Septaglomospiranella rossi	–	Y	–	McKee and Gutschick, 1969b; Skipp, 1969
	Septaglomospiranella sp.	–	Y	–	McKee and Gutschick, 1969b
	Septatournayella? sp.	–	Y	–	McKee and Gutschick, 1969b
	Spinobrunsiina torquida	–	Y	–	McKee and Gutschick, 1969b
	Spinobrunsiina torquida?	–	Y	–	McKee and Gutschick, 1969b
	Spinoendothyra spinosa	–	Y	–	McKee and Gutschick, 1969b
	Spinoendothyra spinosa?	–	Y	–	McKee and Gutschick, 1969b
	Spiroplectamminoides cf. *S. parva*	–	Y	–	McKee and Gutschick, 1969b
	Tournayella sp.	–	Y	–	McKee and Gutschick, 1969b
	Tournayella? sp.	–	Y	–	McKee and Gutschick, 1969b
	Tuberendothyra paratumula	–	Y	–	McKee and Gutschick, 1969b
	Tuberendothyra tuberculata	–	Y	–	McKee and Gutschick, 1969b
	Tuberendothyra sp.	–	Y	–	McKee and Gutschick, 1969b
	Tuberendothyra sp.?	–	Y	–	McKee and Gutschick, 1969b
	Foraminifera undetermined	–	–	Y	Gordon E&R, 1979/1/23
Other Fossils: Miscellaneous	**Overall Miscellaneous**	**Y**	**Y**	**Y**	**–**
	“Algae”	–	Y	–	White, 1927, 1928
	“Algal” concretions	–	–	Y	Billingsley and Beus, 1999a
	Calcisphaera sp.	–	Y	–	McKee and Gutschick, 1969b
	Undetermined calcispheres	–	Y	–	McKee and Gutschick, 1969b
	Flaring vertical structures	–	–	Y	Billingsley and Beus, 1999a

Table C-2. Continued

Category	Taxon Observed	Dtb	Mr	Msc	References
Other Fossils: Miscellaneous	Reworked Redwall Limestone fossils	–	–	Y	Billingsley and Beus, 1999a
	Twig-like fossils	–	–	Y	Billingsley and Beus, 1999a
	Trace fossils or stromatoporoid sponges	Y	–	–	Beus, 1973, 1990b
	Unspecified or unidentifiable fossils	Y	Y	Y	McKee, 1969; McKee and Gutschick, 1969a, 1969c; Billingsley and Beus, 1999a

Devonian–Mississippian Taxonomic Notes

Fossils reported as Chesterian at Bright Angel Trail in McKee and Gutschick (1969a) are actually Meramecian and from the Horseshoe Mesa Member of the Redwall Limestone (Billingsley and Beus, 1999b).

- Bellerophontaceae = Bellerophontoidea
- *Bothriolepis nitidens* of Schuchert (1918b) and Noble (1922) accepted as *B. coloradoensis* or *B. leidyi* (Denison, 1951)
- *Caninophyllum incrassatum* = *Vesiculophyllum incrassatum*
- *Endothyra baileyi* = *Globoendothyra baileyi*
- *Endothyra baileyi poloumera* = *Globoendothyra baileyi poloumera*
- *Endothyra eospiroides* = *Inflatoendothyra eospiroides*
- *Endothyra spinosa* = *Spinoendothyra spinosa*
- *Endothyra torquida* = *Spinobrunsiina torquida*
- *Eomillerella spiroides* = *Eoendothyranopsis spiroides*
- *Lithostrotion* (*Diphyphyllum*) *inconstans* = *Dorlodotia inconstans*
- *Monilipora*? sp. = *Cladochonus* sp.
- *Phillipsia sampsoni* = *Aprathia* sp.
- *Phillipsia tuberculata* = *Phillipsia peroccidens*
- *Pugnoides osagensis* = *Wellerella osagensis*
- *Schuchertella chemungensis* = *Floweria chemungensis*
- *Septaglomospiranella primaeva* = *Septaglomospiranella chernoussovensis*
- *Septatournayella henbesti* = *Pohlia henbesti*
- *Spirifer striatus* = *Neospirifer striatus*
- *Straparollus* (*Euomphalus*) = *Euomphalus*
- *Triplophyllites* (*Homalophyllites*) *paucicinctus* = *Homalophyllites paucicinctus*

Table C-3. *Supai Group fossil taxa. IPswa = Watahomigi Formation, IPsm = Manakacha Formation, IPswe = Wescogame Formation, and Pse = Esplanade Sandstone. (continued on following page)*

Category	Taxon Observed	IPswa	IPsm	IPswe	Pse	References
Plants	**Overall Plants**	**Y**	**Y**	**Y**	**Y**	**–**
Plants: Equisetopsida	*Calamites* sp.	Y	–	–	–	White, 1929
Plants: Polypodiopsida	Polypodiopsida undetermined	–	Y	–	–	McKee, 1982a, 1982b
Plants: "Seed Ferns"	*Neuropteris* sp.	Y	–	–	–	White, 1929
Plants: Pinopsida	*Cordaites* sp.	Y	–	–	–	White, 1929
	Walchia sp.	Y	–	–	Y	White, 1929; McKee, 1982a, 1982b
	?*Walchia* sp. stems	Y	–	–	–	McKee, 1982a
Plants: Other Plants	*Taeniopteris* sp.	Y	–	–	–	White, 1929
	"Fern or cycadofilice" fragments	–	–	Y	–	Schuchert, 1918b; McKee, 1982b (record possibly from Esplanade instead)
	Plant stems	–	–	–	Y	McKee, 1982a, 1982b
	Undetermined plants	Y	Y	–	Y	McKee, 1982a, 1982b
Invertebrates	**Overall Invertebrates**	**Y**	**Y**	**Y**	**Y**	**–**
Invertebrates: Cnidaria: Anthozoa	Coral bioclasts	–	–	–	Y	McKee, 1982b
	Anthozoa undetermined	Y	–	–	–	McKee, 1982a
Invertebrates: Cnidaria: Anthozoa: Tabulata	*Michelinia* sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
Invertebrates: Cnidaria?: Conulariida	Conulariida undetermined	Y	–	–	–	McKee, 1982b; Gordon, 1982
Invertebrates: Bryozoa	**Overall Bryozoa**	**Y**	**Y**	**Y**	**Y**	**–**
	Cystiodictya? sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Fenestella sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Encrusting fistuliporoid	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Encrusting stenoporoid	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Ramose trepostome	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Indeterminate rhomboporoid	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Bryozoan bioclasts	Y	Y	Y	Y	McKee, 1982b
	Bryozoa undetermined	Y	–	–	–	McKee, 1982a; Billingsley and Beus, 1999a
	Overall Brachiopoda	**Y**	**–**	**–**	**–**	**–**

Table C-3. *Continued*

Category	Taxon Observed	IPswa	IPsm	IPswe	Pse	References
Invertebrates: Brachiopoda	*Anthracospirifer newberryi*	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Anthracospirifer tanoensis	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Composita ovata	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Composita subtilita	Y	–	–	–	McKee, 1938, 1982b; Gordon, 1982
	Composita sp.	Y	–	–	–	McKee, 1982a, 1982b; Gordon, 1982
	Rhynchonelloid cf. *Cupularostrum* sp.	Y	–	–	–	Gordon, 1982
	Derbyia sp. cf. *D. robusta*	Y	–	–	–	Gordon, 1982
	Derbyia sp.	Y	–	–	–	McKee, 1982a, 1982b
	Lingula sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Lingula sp.?	Y	–	–	–	McKee, 1982a
	Orbiculoidea meekana	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Orbiculoidea meekana?	Y	–	–	–	Gordon, 1982
	Orbiculoidea sp.	Y	–	–	–	McKee, 1982a
	Orbiculoidea sp.?	Y	–	–	–	GCM
	Orthotetes sp. A	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Punctospirifer transversus	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Reticulariina gonionota	Y	–	–	–	McKee, 1982b
	?*Reticulariina gonionota*	Y	–	–	–	Gordon, 1982
	Schizophoria altirostris	Y	–	–	–	McKee, 1982b
	Schizophoria altirostris?	Y	–	–	–	Gordon, 1982
	?*Schizophoria altirostris*	Y	–	–	–	Gordon, 1982
	Spirifer sp.	Y	–	–	–	McKee, 1982a
	Spiriferina sp.	Y	–	–	–	McKee, 1982a
	Productida undetermined	Y	–	–	–	McKee, 1982a, 1982b
	Brachiopoda undetermined	Y	–	–	–	Billingsley and Beus, 1999a
Invertebrates: Mollusca	**Overall Mollusca**	**Y**	**–**	**–**	**–**	**–**
Invertebrates: Bivalvia	**Overall Bivalvia**	**Y**	**–**	**–**	**–**	**–**
	Aviculopecten gravidus	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Aviculopecten gravidus?	Y	–	–	–	Gordon, 1982
	Aviculopecten sp. A	Y	–	–	–	Gordon, 1982
	Aviculopecten sp.	Y	–	–	–	McKee, 1982b

Table C-3. *Continued*

Category	Taxon Observed	IPswa	IPsm	IPswe	Pse	References
Invertebrates: Bivalvia (continued)	*Leptodesma* sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Myalina cuneiformis	Y	–	–	–	GCM
	Myalina perattenuata	Y	–	–	–	GCM
	Myalina permiana	Y	–	–	–	GCM
	Myalina sp.	Y	–	–	–	McKee, 1982b
	Myalina (*Myalina*) sp. B	Y	–	–	–	Gordon, 1982
	Oriocrassatella sp.	Y	–	–	–	Gordon, 1982
	Permophorus sp.	Y	–	–	–	McKee, 1982b
	Promytilus sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Schizodus sp. A	Y	–	–	–	Gordon, 1982
	Myalinidae undetermined	Y	–	–	–	McKee, 1982b; Gordon, 1982
Invertebrates: Mollusca: Gastropoda	*Euomphalus* sp.	Y	–	–	–	Gordon, 1982
	Straparollus sp.	Y	–	–	–	McKee, 1982b
	High spired gastropod	Y	–	–	–	Gordon, 1982; Billingsley and Beus, 1999a
	Bellerophontoidea undetermined	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Pleurotomarioidea undetermined	Y	–	–	–	McKee, 1982b
	Gastropoda undetermined	Y	–	–	–	McKee, 1982a
Invertebrates: Arthropoda: Trilobita	*Paladin* sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
	Paladin? sp.	Y	–	–	–	Gordon, 1982
	Trilobite free cheeks (librogenae)	Y	–	–	–	McKee, 1982b; Gordon, 1982
Invertebrates: Arthropoda: Ostracoda	Ostracode bioclasts	–	Y	–	–	McKee, 1982b
Invertebrates: Echinodermata	Pelmatozoan (stalked echinoderm) bioclasts	Y	Y	Y	Y	McKee, 1982b
Invertebrates: Echinodermata: Echinoidea	Echinoidea undetermined	Y	–	–	–	Gordon, 1982
Invertebrates: Conodonta (continued)	*Adetognathus lautus*	Y	–	–	–	Martin and Barrick, 1999
	Adetognathus spathus	Y	–	–	–	Martin and Barrick, 1999
	Adetognathus sp.	Y	–	–	–	Martin and Barrick, 1999
	Gnathodus sp.	Y	–	–	–	Martin and Barrick, 1999
	Rhachistognathus muricatus	Y	–	–	–	Martin and Barrick, 1999

Table C-3. *Continued*

Category	Taxon Observed	IPswa	IPsm	IPswe	Pse	References
Invertebrates: Conodonta (continued)	*Rhachistognathus websteri*	Y	–	–	–	Martin and Barrick, 1999
	Ramiforms	Y	–	–	–	Martin and Barrick, 1999
Invertebrates: Other Invertebrates	Bivalve or brachiopod bioclasts	Y	Y	Y	Y	McKee, 1982b
	Marine fossil clasts	–	–	Y	–	McKee, 1982b
	Unspecified invertebrate fossils	Y	Y	Y	Y	McKee, 1982a
Vertebrates	**Overall Vertebrates**	**Y**	**–**	**–**	**–**	**–**
Vertebrates: Chondrichthyes	*Deltodus mercurii*	Y	–	–	–	Gordon, 1982
	Deltodus sp.	Y	–	–	–	McKee, 1982b; Gordon, 1982
Vertebrates: Miscellaneous Fish	Fish teeth	Y	–	–	–	McKee, 1982a
Ichnofossils	**Overall Ichnofossils**	**Y**	**Y**	**Y**	**Y**	**–**
Ichnofossils: Microbial Trace Fossils	*Rivularites* (as microbially induced sedimentary structure, not taxon)	Y	Y	–	Y	White, 1929; MicKee, 1982a, 1982b
	Stromatolites	Y	Y	–	–	Rawson and Turner, 1974; McKee, 1982a, 1982b
	Possible stromatolitic laminations	Y	–	–	–	McKee, 1982a
Ichnofossils: Invertebrate Trace Fossils	*Diplichnites* isp.	–	–	Y	–	Gilmore, 1928 (identified in Miller and others, this volume)
	Helminthopsis isp.	–	–	Y	–	Gilmore, 1928 (identified in Miller and others, this volume)
	Horseshoe-crab-like invertebrate tracks	–	Y	–	–	McKee, 1982a
	Unnamed invertebrate tracks (two types)	–	–	Y	–	McKee, 1982b
	Worm borings and trails	Y	Y	Y	Y	McKee, 1982a, 1982b
Ichnofossils: Vertebrate Trace Fossils	cf. *Amphisauropus* isp.	–	–	Y	–	Gilmore, 1928; Haubold, 1971; McKee, 1982b; Santucci and Hunt, 1998; Marchetti and others, this volume
	Batrachichnus isp.	–	–	Y	–	Marchetti and others, this volume
	cf. *Limnopus* isp.	–	–	Y	–	Gilmore, 1927; Haubold, 1971; McKee, 1982b; Santucci and Hunt, 1998; Santucci and others, 1998; Marchetti and others, 2019; Marchetti and others, this volume
	Varanopus isp.	–	–	Y	–	Marchetti and others, this volume

__Table C-3.__ Continued

Category	Taxon Observed	IPswa	IPsm	IPswe	Pse	References
Ichnofossils: Vertebrate Trace Fossils (continued)	cf. *Varanopus* isp.	–	–	Y	–	Gilmore, 1927; Haubold, 1971; McKee, 1982b; Santucci and Hunt, 1998; Santucci and others, 1998; Marchetti and others, this volume
	Undetermined tetrapod tracks (“cf. *Chelichnus* isp.”)	–	Y	–	–	Rowland, 2017; Rowland and Caputo, 2018; Marchetti and others, this volume
	Undetermined vertebrate tracks	–	–	Y	–	Schuchert, 1918b; Gilmore, 1927; Haubold, 1971; McKee, 1982a, 1982b; Santucci and Hunt, 1998; Santucci and others, 1998; Marchetti and others, 2019; Marchetti and others, this volume
Ichnofossils: Other Trace Fossils	Unspecified trace fossils	–	–	–	Y	McKee, 1982a
Other Fossils	**Overall Other Fossils**	**Y**	**Y**	**Y**	**Y**	**–**
Other Fossils: Foraminifera	**Overall Subphylum Foraminifera**	**Y**	**Y**	**Y**	**Y**	**–**
	Endothyra media	–	Y	–	–	McKee, 1982b (record possibly from Wescogame instead)
	Endothyra teres	–	Y	–	–	McKee, 1982b (record possibly from Wescogame instead)
	Endothyra sp.	–	Y	–	–	McKee, 1982c
	Eoschubertella sp.	–	Y	–	–	McKee, 1982a, 1982b
	Fusulinella sp.	Y	Y	–	–	McKee, 1982a, 1982b
	Pseudostaffella sp.	Y	Y	–	–	McKee, 1982a, 1982b
	Schubertella sp.	–	–	–	Y	McKee, 1982b
	Fusulinida undetermined	–	Y	Y	–	McKee, 1982a, 1982c
	Foraminifera bioclasts	–	Y	Y	Y	McKee, 1982b
Other Fossils: Miscellaneous	**Overall Miscellaneous**	**Y**	**Y**	**Y**	**–**	**–**
	“Algal” laminations	Y	–	–	–	Billingsley and Beus, 1999a
	Miscellaneous “algae”	Y	–	Y	–	McKee, 1982b
	Probable “algal” limestone nodules	–	Y	–	–	McKee, 1982a
	Possible “algal” features	–	–	Y	–	White, 1927
	Calcisphere bioclasts	–	Y	–	–	McKee, 1982b
	Girvanella bioclasts	–	Y	–	–	McKee, 1982b
	Possible organic features	–	–	Y	–	McKee, 1982a
	Unspecified fossils	Y	–	–	–	McKee, 1982a; Billingsley and Beus, 1999a

Supai Group Taxonomic Notes

Undivided Supai: the only fossils not otherwise accounted for in Supai units are cup corals and brachiopods in a limestone bed (Schuchert, 1918b), thread-like algae in limestone of red shales of middle Supai (White, 1929), calcareous algae (Stoyanow, 1936), and the gastropod *Euomphalus* cf. *E. hollingsworthi* (Yochelson E&R, 1969/6/23).

[Genus] sp. and [Genus] sp. undet. as used in White (1929) are consolidated as [Genus] sp.

Pre-1982 records from the Supai Group have been distributed according to modern stratigraphic definitions if it was possible to determine the proper usage.

- *Ammobatrachus turbatans* = *Limnopus* isp. = undetermined tracks = cf. *Amphisauropus* isp.
- *Anomalopus sturdevanti* = *Limnopus* isp. = undetermined tracks
- Bellerophontaceae = Bellerophontoidea
- *Derbyia* may also be spelled *Derbya* in some references
- "Horse-hoof-like" features in Gilmore (1926) and McKee (1982b) are pseudofossils
- Pleurotomariaceae = Pleurotomarioidea
- *Stenichnus yakiensis* = *Batrachichnus delicatulus* = cf. *Varanopus* isp.
- *Straparollus* (*Euomphalus*) = *Euomphalus*
- *Tridentichnus supaiensis* = *Anomalopus* (*Tridentichnus*) *supaiensis* = *Limnopus* isp. = cf. *Limnopus* isp.

Table C-4. *Post-Supai Permian fossil taxa. Ph = Hermit Formation, Pc = Coconino Sandstone, Pt = Toroweap Formation, and Pk = Kaibab Formation. (continued on following page)*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Plants	**Overall Plants**	**Y**	**–**	**–**	**Y**	**–**
Plants: Ulvophyceae	Dasycladaceae undetermined	–	–	–	Y	GCM
Plants: Equisetopsida	*Sphenophyllum gilmorei*	Y	–	–	–	White, 1929
	Sphenophyllum gilmorei?	Y	–	–	–	GCM
	Sphenophyllum sp.	Y	–	–	–	GCM
	Equisetopsida undetermined	Y	–	–	–	GCM
Plants: “Seed Ferns”	**Overall “Seed ferns”**	**Y**	**–**	**–**	**–**	**–**
	Auritifolia anomala	Y	–	–	–	White, 1929
	Autunia conferta	Y	–	–	–	White, 1929
	Brongniartites sp.	Y	–	–	–	GCM
	Brongniartites? *aliena*	Y	–	–	–	White, 1929
	Brongniartites? *aliena*?	Y	–	–	–	GCM
	Brongniartites? *yakiensis*	Y	–	–	–	White, 1929
	Gracilopteris raymondii	Y	–	–	–	White, 1929
	Neuropteridium? sp.	Y	–	–	–	White, 1929
	Rhachiphyllum sp.	Y	–	–	–	White, 1929
	Rhachiphyllum sp.?	Y	–	–	–	GCM
	Rhachiphyllum? sp.	Y	–	–	–	White, 1929
	Supaia breviloba	Y	–	–	–	White, 1929
	Supaia compacta	Y	–	–	–	White, 1929
	Supaia linearifolia	Y	–	–	–	White, 1929
	Supaia merriami	Y	–	–	–	White, 1929
	Supaia merriami?	Y	–	–	–	GCM
	Supaia rigida	Y	–	–	–	White, 1929
	Supaia sturdevantii	Y	–	–	–	White, 1929
	Supaia subgoepperti	Y	–	–	–	White, 1929
	Supaia thinnfeldioides	Y	–	–	–	White, 1929
	Supaia sp.	Y	–	–	–	White, 1929

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Plants: "Seed Ferns" (continued)	*Supaia*? sp.	Y	–	–	–	White, 1929
	Yakia heterophylla	Y	–	–	–	White, 1929
	Yakia heterophylla?	Y	–	–	–	GCM
	Yakia sp.	Y	–	–	–	GCM
	Yakia sp.?	Y	–	–	–	GCM
	Seed-bearing pteridosperm frond	Y	–	–	–	White, 1929
	Undetermined seed ferns	Y	–	–	–	GCM
Plants: Ginkgoopsida	*Psygmophyllum*? sp.	Y	–	–	–	White, 1929
	Rhipidopsis sp.?	Y	–	–	–	GCM
Plants: Pinopsida	**Overall Pinopsida**	**Y**	**–**	**–**	**–**	**–**
	Brachyphyllum arizonicum	Y	–	–	–	White, 1929
	Brachyphyllum tenue	Y	–	–	–	White, 1929
	Feysia sp.	Y	–	–	–	White, 1929
	Hermitia dawsoni	Y	–	–	–	White, 1929
	Hermitia sp.	Y	–	–	–	White, 1929
	Otovicia hypnoides	Y	–	–	–	White, 1929
	Pagiophyllum dubium	Y	–	–	–	White, 1929
	Pagiophyllum sp.?	Y	–	–	–	GCM
	Paleotaxites praecursor	Y	–	–	–	White, 1929
	Paleotaxites sp.	Y	–	–	–	GCM
	Paleotaxites sp.?	Y	–	–	–	GCM
	Taxites? sp.	Y	–	–	–	White, 1929
	Voltzia dentiloba	Y	–	–	–	White, 1929
	Voltzia sp.	Y	–	–	–	White, 1929
	Walchia piniformis	Y	–	–	–	White, 1929
	Walchia sp.	Y	–	–	–	GCM
	Walchia sp.?	Y	–	–	–	GCM
	Walchiostrobus sp.	Y	–	–	–	GCM
	Pinopsida undetermined	Y	–	–	–	GCM
Plants: Other Plants	**Overall Other Plants**	**Y**	**–**	**–**	**–**	**–**
	Carpolithus sp.	Y	–	–	–	White, 1929

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Plants: Other Plants (continued)	*Cyclocarpon angelicum*	Y	–	–	–	White, 1929
	Cyclocarpon sp.	Y	–	–	–	White, 1929
	Eltovaria bursiformis	Y	–	–	–	White, 1929
	Taeniopteris angelica	Y	–	–	–	White, 1929
	Taeniopteris coriacea	Y	–	–	–	White, 1929
	Taeniopteris eckhardti	Y	–	–	–	GCM
	Taeniopteris cf. *T. eckhardti*	Y	–	–	–	White, 1929
	"Gymnospermous ament"	Y	–	–	–	White, 1929
	Undetermined plants	Y	–	–	–	White, 1929
Invertebrates	**Overall Invertebrates**	**Y**	**–**	**Y**	**Y**	**–**
	Invertebrata undetermined	–	–	–	Y	GCM
Invertebrates: Porifera	*Actinocoelia maeandrina*	–	–	–	Y	Griffin, 1966
	Actinocoelia sp.	–	–	–	Y	Thompson, 1995; Thayer, 2009
	Hexactinellida undetermined	–	–	–	Y	GCM
	Porifera undetermined	–	–	–	Y	Schuchert, 1918b; McKee, 1938; Sorauf and Billingsley, 1991
	Porifera undetermined?	–	–	–	Y	GCM
Invertebrates: Cnidaria: Anthozoa	Anthozoa undetermined	–	–	–	Y	GCM
	Anthozoa undetermined?	–	–	–	Y	GCM
Invertebrates: Cnidaria: Anthozoa: Rugosa	*Lophophyllum* sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Lophophyllum sp.?	–	–	–	Y	GCM
	Undetermined horn corals	–	–	–	Y	McKee, 1938
Invertebrates: Cnidaria?: Conulariida	*Conularia kaibabensis*	–	–	–	Y	McKee, 1935; Sinclair, 1948; Spamer, 1984
Invertebrates: Bryozoa	**Overall Bryozoa**	**–**	**–**	**Y**	**Y**	**–**
	Bascomella subsphaerica	–	–	–	Y	Condra and Elias, 1944
	Bicorbis arizonica	–	–	–	Y	Condra and Elias, 1945a, 1945b; McKinney, 1983
	Chasmatopora sp.	–	–	–	Y	GCM
	Fistulipora n. sp.	–	–	–	Y	McKee, 1938
	Fistulipora sp.	–	–	–	Y	McKinney, 1983
	Girtypora maculata	–	–	–	Y	McKinney, 1983
	Meekopora parilis	–	–	–	Y	McKinney, 1983

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Bryozoa (continued)	*Meekopora* n. sp.	–	–	–	Y	McKee, 1938
	Meekopora sp.	–	–	–	Y	GCM
	Polypora spinulifera	–	–	–	Y	McKee, 1938
	Polypora spinulifera?	–	–	–	Y	GCM
	Polypora sp.	–	–	–	Y	GCM
	Rhabdomeson sp.	–	–	–	Y	McKinney, 1983
	Rhipidomella hessensis	–	–	–	Y	Condra and Elias, 1944
	Rhombopora lepidodendroides	–	–	–	Y	McKee, 1938
	Septopora biserialis	–	–	–	Y	McKee, 1938
	Septopora n. sp. #2	–	–	–	Y	McKee, 1938
	Septopora sp.	–	–	–	Y	GCM
	?*Stenodiscus* sp.	–	–	–	Y	McKinney, 1983
	Stenopora n. sp. #1	–	–	–	Y	McKee, 1938
	Stenopora n. sp. #2	–	–	–	Y	McKee, 1938
	Stenopora sp.	–	–	–	Y	GCM
	Streblotrypa sp.	–	–	–	Y	McKinney, 1983
	Undetermined fenestellid	–	–	–	Y	McKinney, 1983
	Bryozoa undetermined	–	–	Y	Y	McKee, 1938; Sorauf and Billingsley, 1991; Thompson, 1995
Invertebrates: Brachiopoda	**Overall Brachiopoda**	**–**	**–**	**Y**	**Y**	**–**
	Anomaloria sp., *Neophricadothyris* sp., or *Squamularia* sp.	–	–	–	Y	GCM
	Avonia sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Bathymyonia nevadensis	–	–	–	Y	McKee, 1938
	Camarophoria sp.	–	–	–	Y	GCM
	Camarotoechia sp.	–	–	–	Y	GCM
	Chonetes sp.	–	–	–	Y	McKee, 1938
	Chonetes sp.?	–	–	–	Y	GCM
	Composita arizonica	–	–	–	Y	McKee, 1938
	Composita arizonica var.	–	–	–	Y	GCM
	Composita cf. *C. ovata*	–	–	–	Y	GCM
	Composita subtilita	–	–	–	Y	McKee, 1938, 1982b; Gordon, 1982

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Brachiopoda (continued)	*Composita* sp.	–	–	Y	Y	McKee, 1938; Sorauf and Billingsley, 1991
	cf. *Composita* sp.	–	–	–	Y	McKee, 1938
	Derbyia arizonensis	–	–	–	Y	McKee, 1938, 1941
	Derbyia multistriata	–	–	–	Y	GCM
	Derbyia nasuta	–	–	–	Y	McKee, 1938
	Derbyia sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991; Thayer, 2009
	Derbyia sp.?	–	–	–	Y	GCM
	Dielasma phosphoriensis	–	–	–	Y	McKee, 1938
	Dielasma sp.	–	–	–	Y	GCM
	Dyoros aff. *D. hillanus*	–	–	–	Y	GCM
	Dyoros kaibabensis	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Dyoros subliratus	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Dyoros tetragonus	–	–	–	Y	King, 1931; Cooper and Grant, 1975
	Echinauris dorsoconcava	–	–	–	Y	McKee, 1938
	Echinauris subhorrida?	–	–	–	Y	GCM
	Echinauris newberryi	–	–	–	Y	McKee, 1938
	Echinauris sp.	–	–	–	Y	Thompson, 1995
	Hustedia meekana	–	–	–	Y	McKee, 1938
	Hustedia sp.	–	–	–	Y	Thompson, 1995
	Kozlowskia sp.	–	–	–	Y	Thompson, 1995
	Kutorginella meridionalis	–	–	–	Y	McKee, 1938
	Liosotella popei	–	–	–	Y	McKee, 1938
	Marginifera sp.	–	–	–	Y	McKee, 1938
	Meekella occidentalis	–	–	–	Y	GCM
	Meekella pyramidalis	–	–	–	Y	Schuchert, 1918b; McKee, 1938
	Meekella sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991; Thompson, 1995; Thayer, 2009
	Neophricadothyris sp.	–	–	–	Y	Thompson, 1995
	Neophricadothyris sp., or *Rugatia occidentalis*, or *Rugatia paraindicus*	–	–	–	Y	GCM
	Orbiculoidea sp.	–	–	–	Y	GCM

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Brachiopoda (continued)	*Orthotetes* sp.	–	–	–	Y	GCM
	Peniculauris bassi	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Peniculauris bassi or *Reticulatia* sp.	–	–	–	Y	GCM
	Peniculauris ivesi	–	–	Y	Y	Schuchert, 1918b; McKee, 1938
	Peniculauris sp.	–	–	–	Y	Thompson, 1995; Thayer, 2009
	Phrenophoria pinguis	–	–	–	Y	McKee, 1938
	Phricodothyris guadalupensis	–	–	–	Y	McKee, 1938
	Productus sp.	–	–	–	Y	GCM
	Pugnax sp.	–	–	–	Y	GCM
	Pugnoides sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Punctospirifer? sp.	–	–	–	Y	McKee, 1938
	Rhipidomella transversa	–	–	–	Y	McKee, 1938
	Rhynchonella sp.	–	–	–	Y	GCM
	Rugatia occidentalis	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Rugatia paraindicus	–	–	–	Y	McKee, 1938
	Rugatia sp.	–	–	–	Y	Thompson, 1995
	Spirifer sp.	–	–	–	Y	GCM
	Spiriferellina hilli	–	–	–	Y	McKee, 1938
	Spiriferina sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Squamularia sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Waagenoconcha irginae	–	–	–	Y	GCM
	Waagenoconcha sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Wellerella osagensis	–	–	–	Y	GCM
	Productida undetermined	–	–	–	Y	Thompson, 1995
	Brachiopoda undetermined	–	–	–	Y	McKee, 1938; Thompson, 1995
	Brachiopoda undetermined?	–	–	–	Y	GCM
Invertebrates: Mollusca	**Overall Mollusca**	**–**	**–**	**Y**	**Y**	**–**
	Mollusca undetermined	–	–	Y	Y	McKee, 1938; Thompson, 1995
Invertebrates: Mollusca: Bivalvia	**Overall Bivalvia**	**–**	**–**	**Y**	**Y**	**–**
	Acanthopecten coloradoensis	–	–	–	Y	Newell, 1937
	Allorisma capax	–	–	–	Y	GCM

Table C-4. Continued

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Mollusca: Bivalvia (continued)	*Allorisma* sp.	–	–	Y	–	McKee, 1938
	Astartella gurleyi	–	–	–	Y	Shimer, 1919; McKee, 1938
	Astartella sp.	–	–	–	Y	GCM
	Aviculopecten sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Bakewellia parva	–	–	–	Y	Shimer, 1919; McKee, 1938
	Deltopecten coreyanus	–	–	–	Y	GCM
	Deltopecten coreyanus var.	–	–	–	Y	GCM
	Deltopecten sp.	–	–	Y	Y	GCM
	Edmondia sp.	–	–	Y	–	McKee, 1938
	Modiomorpha sp.	–	–	–	Y	GCM
	Nuculana? sp.	–	–	Y	Y	McKee, 1938; GCM
	Pecten sp.	–	–	–	Y	GCM
	Permophorus sp.	–	–	Y	Y	McKee, 1938; GCM
	Pseudomonotis sp.	–	–	–	Y	GCM
	Pteria sp.	–	–	Y	Y	McKee, 1938; GCM
	Pterinopecten sp.	–	–	–	Y	GCM
	Schizodus canalis	–	–	–	Y	GCM
	Schizodus sp.	–	–	Y	Y	McKee, 1938; GCM
	Schizodus? sp.	–	–	Y	Y	McKee, 1938
	Schizodus sp.?	–	–	–	Y	GCM
	Solenomya naenia	–	–	–	Y	GCM
	Solenomya trapezoides	–	–	–	Y	GCM
	Solenomya trapezoides?	–	–	–	Y	GCM
	Solenomya sp.	–	–	Y	Y	McKee, 1938; GCM
	Bivalvia undetermined	–	–	Y	Y	McKee, 1938
Invertebrates: Mollusca: Cephalopoda	Cephalopoda undetermined	–	–	–	Y	GCM
Invertebrates: Mollusca: Cephalopoda: Nautiloidea	**Overall Nautiloidea**	**–**	**–**	**Y**	**Y**	**–**
	Domatoceras bradyi	–	–	–	Y	Miller and Unklesbay, 1942; Miller and Youngquist, 1949
	Domatoceras simplex	–	–	–	Y	McKee, 1938
	Domatoceras? sp.	–	–	Y	–	McKee, 1938

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Mollusca: Cephalopoda: Nautiloidea (continued)	*Orthoceras* sp.	–	–	–	Y	McKee, 1938
	Stearoceras rotundatum?	–	–	–	Y	Miller and Unklesbay, 1942; Miller and Youngquist, 1949
	Stearoceras sanandreasense?	–	–	–	Y	Miller and Unklesbay, 1942; Miller and Youngquist, 1949
	Stearoceras sp.	–	–	–	Y	GCM
	Stearoceras sp.?	–	–	–	Y	GCM
Invertebrates: Mollusca: Gastropoda	**Overall Gastropoda**	**–**	**–**	**Y**	**Y**	**–**
	Aclisina sp.	–	–	Y	–	McKee, 1938
	Bellerophon majusculus	–	–	–	Y	McKee, 1938
	Bellerophon sp.	–	–	Y	–	McKee, 1938
	Euomphalus kaibabensis	–	–	–	Y	GCM
	Euomphalus sp.	–	–	Y	Y	McKee, 1938; GCM
	Euomphalus sp.?	–	–	–	Y	GCM
	Euphemites sp.	–	–	Y	Y	McKee, 1938
	Euphemites cf. *E. carbonarius*	–	–	–	Y	Shimer, 1919; McKee, 1938
	Goniospira sp.	–	–	Y	Y	McKee, 1938
	Murchisonia? cf. *M terebra*	–	–	–	Y	Shimer, 1919; McKee, 1938
	Naticopsis sp.	–	–	Y	Y	McKee, 1938
	Pleurotomaria sp.	–	–	–	Y	McKee, 1938
	Gastropoda undetermined	–	–	Y	Y	McKee, 1938
	Gastropoda undetermined?	–	–	–	Y	GCM
Invertebrates: Mollusca: Scaphopoda	*Dentalium* sp.	–	–	Y	Y	GCM
	Plagioglypta sp.	–	–	–	Y	GCM
	Prodentalium canna	–	–	–	Y	Shimer, 1919; McKee, 1938
	Scaphopoda undetermined	–	–	–	Y	GCM
Invertebrates: Arthropoda	**Overall Arthropoda**	**Y**	**–**	**Y**	**Y**	**–**
Invertebrates: Arthropoda: Trilobita	*Ameura* sp.	–	–	–	Y	GCM
	Delaria sevilloidia	–	–	–	Y	Cisne, 1971
	Delaria snowi	–	–	–	Y	Cisne, 1971
	Ditomopyge scitulus	–	–	–	Y	GCM
	Ditomopyge sp.	–	–	–	Y	McKee, 1938; Sorauf and Billingsley, 1991; Thayer, 2009

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Invertebrates: Arthropoda: Trilobita (continued)	*Novoameura mckeei*	–	–	–	Y	Cisne, 1971
	Trilobita undetermined	–	–	–	Y	McKee, 1938; Snow, 1945; Sorauf and Billingsley, 1991
	Trilobita undetermined?	–	–	–	Y	GCM
Invertebrates: Arthropoda: Eurypterida	*Hastimima* sp.?	Y	–	–	–	White, 1929
Invertebrata: Arthropoda: Ostracoda	Ostracoda undetermined	–	–	Y	–	McKee, 1938
Invertebrates: Arthropoda: Insecta	*Tupus gilmorei*	Y	–	–	–	Carpenter, 1927; White, 1929
	Tupus whitei	Y	–	–	–	Carpenter, 1928; White, 1929
	Blattodea undetermined	Y	–	–	–	Carpenter, 1928; Spamer, 1984
	Odonata undetermined	Y	–	–	–	Carpenter, 1928
Invertebrates: Echinodermata	**Overall Echinodermata**	**–**	**–**	**Y**	**Y**	**–**
	Echinodermata undetermined	–	–	–	Y	GCM
	Echinodermata undetermined?	–	–	–	Y	GCM
Invertebrates: Echinodermata: Crinoidea	Crinoidea undetermined (star-shape plates)	–	–	–	Y	GCM
	Crinoidea undetermined	–	–	Y	Y	Shimer, 1919; McKee, 1938; Sorauf and Billingsley, 1991; Thompson, 1995; Thayer, 2009
Invertebrates: Echinodermata: Echinoidea	*Archaeocidaris ornatus*	–	–	–	Y	GCM
	Archaeocidaris sp.	–	–	Y	Y	McKee, 1938; Sorauf and Billingsley, 1991
	Echinoidea undetermined	–	–	–	Y	GCM
Invertebrates: Conodonta	*Hindeodus excavatus*	–	–	–	Y	Thompson, 1995
	Neostreptognathus newelli	–	–	–	Y	Thompson, 1995
	Neostreptognathus prayi	–	–	–	Y	Thompson, 1995
	Neostreptognathus ruzhencevi	–	–	–	Y	Thompson, 1995
	Neostreptognathus cf *N. tschuvashovi*	–	–	–	Y	Thompson, 1995
	Sweetia festiva	–	–	–	Y	Thompson, 1995
Vertebrates	**Overall Vertebrates**	**–**	**–**	**–**	**Y**	**–**
Vertebrates: Chondrichthyes	**Overall Chondrichthyes**	**–**	**–**	**–**	**Y**	**–**
	Cooleyella typicalis	–	–	–	Y	Thompson, 1995
	Cooperella striatula	–	–	–	Y	Thompson, 1995

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Vertebrates: Chondrichthyes (continued)	*Deltodus mercurii*	–	–	–	?	David, 1944; Gass, 1963
	Hybodus sp.	–	–	–	Y	Gass, 1963; GCM
	Kirkella typicalis	–	–	–	Y	Thompson, 1995
	Megactenopetalus kaibabanus	–	–	–	Y	David, 1944; Gass, 1963; Ossian, 1976
	Mooreyella typicalis	–	–	–	Y	Thompson, 1995
	Petrodus sp.	–	–	–	Y	Thompson, 1995
	Psephodus sp. A	–	–	–	Y	Gass, 1963
	Sturgeonella quinqueloba	–	–	–	Y	Thompson, 1995
	Symmorium cf. *S. reniforme*	–	–	–	Y	Thompson, 1995
	Symmoriid mucus membrane denticle	–	–	–	Y	Thompson, 1995
	Undescribed ctenacanthoid	–	–	–	Y	Thompson, 1995
	Undescribed hybodontoid	–	–	–	Y	Thompson, 1995
	Hybodontiformes undetermined	–	–	–	Y	Thompson, 1995
	Undetermined dermal denticle	–	–	–	Y	Thompson, 1995
	Undetermined shark tooth	–	–	–	Y	McKee, 1938
Vertebrates: Actinopterygii	Palaeoniscidae undetermined	–	–	–	Y	Thompson, 1995
	Undetermined phyllodont	–	–	–	Y	Johnson and Zidek, 1981; Thompson, 1995
Vertebrates: Miscellaneous Fish	Fish teeth	–	–	–	Y	McKee, 1938; Thompson, 1995
Ichnofossils	**Overall Ichnofossils**	**Y**	**Y**	**Y**	**Y**	**–**
Ichnofossils: Microbial Trace Fossils	*Rivularites* (as microbially induced sedimentary structure, not taxon)	Y	–	–	–	White, 1929
	Stromatolites	–	–	Y	–	Rawson and Turner, 1974; McKee, 1982a, 1982b
Ichnofossils: Invertebrate Trace Fossils	**Overall Invertebrate Trace Fossils**	**Y**	**Y**	**–**	**Y**	**–**
	Diplopodichnus isp.	–	Y	–	–	Miller and others, this volume
	Octopodichnus didactylus	–	Y	–	–	Gilmore, 1927
	Paleohelcura benjamini	–	Y	–	–	Gilmore, 1927
	Paleohelcura tridactyla	–	Y	–	–	Gilmore, 1926, 1927
	Scoyenia gracilis	Y	–	–	–	White, 1929
	Sphaerapus larvalis	Y	–	–	–	White, 1929; Lucas and others, 2013

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Ichnofossils: Invertebrate Trace Fossils (continued)	*Taenidium serpentinum*	–	–	–	Y	DeCourten, 1978
	Unisulcus sinuosus	–	Y	–	–	Gilmore, 1927
	“Fucoids”	–	–	–	Y	McKee, 1932, 1938
	Gastropod trail	–	–	–	Y	GCM
	?*Teichichnus*-derived heavy bioturbation	–	–	–	Y	Thompson, 1995
	Trilobite trails	–	–	–	Y	McKee, 1938; GCM
	Worm borings and trails	Y	Y	–	Y	White, 1929; McKee, 1933, 1938, 1982a; GCM
	Unspecified invertebrate traces	–	Y	–	Y	McKee, 1933; Thompson, 1995
Ichnofossils: Vertebrate Trace Fossils	**Overall Vertebrate Trace Fossils**	**Y**	**Y**	**–**	**–**	**–**
	Amphisauropus kablikae	Y	–	–	–	Marchetti and others, this volume
	cf. *Amphisauropus* isp.	Y	Y	–	–	Marchetti and others, this volume
	Batrachichnus salamandroides	Y	–	–	–	Marchetti and others, this volume
	cf. *Batrachichnus* isp.	Y	–	–	–	Marchetti and others, this volume
	Dimetropus isp.	Y	–	–	–	Marchetti and others, this volume
	Cf. *Dimetropus* isp.	Y	–	–	–	Marchetti and others, this volume
	Dromopus lacertoides	Y	–	–	–	Marchetti and others, this volume
	cf. *Dromopus* isp.	–	Y	–	–	Marchetti and others, 2019
	Erpetopus isp.	Y	Y	–	–	Marchetti and others, this volume
	cf. *Erpetopus* isp.	Y	Y	–	–	Marchetti and others, this volume
	Hyloidichnus bifurcatus	Y	–	–	–	Marchetti and others, this volume
	cf. *Hyloidichnus* isp.	Y	–	–	–	Marchetti and others, this volume
	Ichniotherium cottae	Y	–	–	–	Marchetti and others, this volume
	Ichniotherium gilmorei	Y	–	–	–	Haubold, 1971
	Ichniotherium sphaerodactylum	–	Y	–	–	Marchetti and others, this volume
	cf. *Ichniotherium* isp.	–	Y	–	–	Marchetti and others, this volume
	cf. *Tambachichnium* isp.	–	Y	–	–	Marchetti and others, this volume
	Varanopus curvidactylus	–	Y	–	–	Marchetti and others, this volume
	cf. *Varanopus* isp.	–	Y	–	–	Marchetti and others, this volume
	Mud-puppy-like traces	Y	–	–	–	White, 1929
	Undescribed vertebrate track 1	–	Y	–	–	Hunt and Santucci, 2001

Table C-4. *Continued*

Category	Taxon Observed	Ph	Pc	Pt	Pk	References
Ichnofossils: Vertebrate Trace Fossils (continued)	Undescribed vertebrate track 2	–	Y	–	–	Santucci and others, 2006
	Undetermined vertebrate traces	Y	Y	–	–	Beus and Billingsley, 1989; Marchetti and others, this volume
Ichnofossils: Other Trace Fossils	Undetermined trace fossils	Y	Y	–	–	GCM
Other Fossils	Possible “algal” features	Y	–	–	–	White, 1927
	Unspecified fossils	Y	–	Y	Y	Reeside and Bassler, 1922; McKee, 1938; Rawson and Turner, 1974; GCM

Post-Supai Permian Taxonomic notes

[Genus] sp. and [Genus] sp. undet. as used in White (1929) are consolidated as [Genus] sp.

The taxonomic histories of the vertebrate ichnotaxa of the Hermit Formation and Coconino Sandstone are extremely convoluted, and the names currently in use (Marchetti and others, this volume) are almost entirely different from the names introduced in the 1910s and 1920s. Because of this, Marchetti and others, this volume is listed as the reference for all such ichnotaxa. The histories of the ichnotaxa can be traced through a number of documents (Lull, 1918; Noble, 1922; Gilmore, 1926, 1927, 1928; Haubold, 1971; McKeever and Haubold, 1996; Hunt and Santucci, 1998; Santucci and Hunt, 1998; Santucci and others, 1998; Francischini and others, 2018; Marchetti and others, 2019). Chains of synonyms are included below.

- *Agostopus matheri* = *Chelichnus duncani* = cf. *Amphisauropus* isp.
- *Agostopus medius* = *Chelichnus duncani* = undetermined tracks
- *Allopus*? *arizonae* = *Baropezia arizonae* = *Chelichnus duncani* = undetermined tracks
- *Amblyopus pachypodus* = *Chelichnus gigas* = undetermined tracks
- *Anisopyge mckeei* = *Novoameura mckeei*
- *Avonia dorsoconcava* = *Echinauris dorsoconcava*
- *Avonia subhorrida newberryi* = *Echinauris newberryi*
- *Baropezia eakini* = *Chelichnus duncani* = *Ichniotherium sphaerodactylum*
- *Baropus coconinoensis* = *Chelichnus gigas* = *Ichniotherium sphaerodactylum*
- *Barypodus metszeri* = *Chelichnus duncani* = cf. *Tambachichnium* isp.
- *Barypodus palmatus* = *Chelichnus gigas* = undetermined tracks
- *Barypodus tridactylus* = cf. *Tambachichnium* isp.
- *Batrachichnus obscurus* = *Batrachichnus delicatulus* = cf. *Batrachichnus* isp.
- *Bicorbula arizonica* = *Bicorbis arizonica*
- *Callipteris arizonae* = *Rhachiphyllum* sp.
- *Callipteris conferta* = *Autunia conferta*
- *Callipteris raymondii* = *Gracilopteris raymondii*
- *Callipteris* sp. = *Rhachiphyllum* sp.
- *Chonetes* (*Lissochonetes*) *subliratus* = *Dyoros subliratus*
- *Chonetes hillanus* = *Dyoros hillanus*
- *Chonetes kaibabensis* = *Quadrochonetes kaibabensis* = *Dyoros kaibabensis*
- *Chonetes quadratus* = *Dyoros tetragonus*
- Coconino Sandstone "fucoidal coprolites" of McKee (1933) = invertebrate burrows (*Scolecocoprus*)
- *Collettosaurus pentadactylus* = *Gilmoreichnus hermitanus* = cf. *Dimetropus* isp.
- *Cursipes* sp. = *Gilmoreichnus hermitanus* = cf. *Hyloidichnus* isp.
- *Delaria macclintocki* = *Delaria sevilloidia*
- *Dentalium canna* = *Plagioglypta canna* = *Prodentalium canna*
- *Derbyia* may also be spelled *Derbya* in some references
- *Derbyia regularis* = *Derbyia arizonensis*
- *Dolichopodus tetradactylus* = *Chelichnus bucklandi* = undetermined tracks
- *Dromillopus parvus* = *Batrachichnus delicatulus* = *Batrachichnus salamandroides*
- *Echinocrinus* = *Archaeocidaris* (suppressed for *Archaeocidaris*)
- *Endothyra spinosa* = *Spinoendothyra spinosa*
- *Endothyra torquida* = *Spinobrunsiina torquida*
- *Euphemus* = *Euphemites*
- *Exocampe*? *delicatula* = *Batrachichnus delicatula* = *Nanipes delicatulus* = *Batrachichnus delicatulus* = *Batrachichnus salamandroides*
- *Gilmoreichnus hermitanus* = cf. *Hyloidichnus* isp.
- *Griffithides scitulus* = *Ditomoyge scitulus*
- Hermit Formation "coprolites" in GCM = *Sphaerapus larvalis* (via *Walpia hermitensis*)
- *Hyloidichnus whitei* = *Hyloidichnus bifurcatus*

- *Hylopus hermitanus* = *Palaeosauropus hermitanus* = *Gilmoreichnus hermitanus* = cf. *Hyloidichnus* isp.
- *Laoporus coloradoensis* = *Chelichnus bucklandi* = cf. *Varanopus* isp.
- *Laoporus noblei* of Gilmore (1926) (in part) = *Chelichnus duncani* = cf. *Varanopus* isp.
- *Laoporus noblei* of Lull (1918) = *Chelichnus bucklandi* = cf. *Varanopus* isp.
- *Laoporus schucherti* = *Chelichnus bucklandi* = cf. *Varanopus* isp.
- *Leda* sp. and *Nucula* sp. of McKee (1938) = *Nuculana*? sp.
- *Marginifera meridionalis* = *Kozlowskia meridionalis* = *Kutorginella meridionalis*
- *Marginifera popei* = *Liosotella popei*
- *Megapezia*? *coloradensis* = *Parabaropus coloradensis* = cf. *Amphisauropus* isp. and *Dimetropus* isp.
- *Mesichnium benjamini* = *Paleohelcura benjamini*
- *Nanopus maximus* = *Chelichnus duncani* = undetermined tracks = cf. *Tambachichnium* isp.
- *Nanopus merriami* = *Chelichnus bucklandi* = cf. *Erpetopus* isp.
- *Palaeopus regularis* = *Chelichnus duncani* = undetermined tracks
- *Pleurophorus* = *Permophorus*
- Pleurotomariaceae = Pleurotomarioidea
- *Productus* (*Dictyoclostus*) *bassi* = *Peniculauris bassi*
- *Productus* (*Dictyoclostus*) *ivesi* = *Dictyoclostus ivesi* = *Peniculauris ivesi*
- *Productus* (*Dictyoclostus*) *occidentalis* = *Dictyoclostus occidentalis* = *Rugatia occidentalis*
- *Productus* (*Dictyoclostus*) *paraindicus* = *Rugatia paraindicus*
- *Productus irginae* = *Waagenoconcha irginae*
- *Productus montpelierensis* = *Waagenoconcha montpelieriensis* = *Bathymyonia nevadensis*
- *Productus subhorridus* = *Avonia subhorrida* = *Echinauris subhorrida*
- *Pugnax osagensis* = *Wellerella osagensis*
- *Pugnoides pinguis* = *Wellerella pinguis* = *Phrenophoria pinguis*
- *Retzia meekana* = *Hustedia meekana*
- *Scolecocoprus cameronensis* = *Taenidium serpentinum*
- *Spiriferina hilli* = *Spiriferellina hilli*
- *Squamularia guadalupensis* = *Phricodothyris guadalupensis*
- *Straparollus* (*Euomphalus*) = *Euomphalus*
- *Titanoceras rotundatum* = *Stearoceras rotundatum*
- *Titanoceras sanandreasense* = *Stearoceras sanandreasense*
- *Triavestigia niningeri* = *Paleohelcura tridactyla*
- *Typus gilmorei* = *Tupus gilmorei*
- *Typus whitei* = *Tupus whitei*
- *Ullmannia frumentaria* = *Feysia* sp.
- *Walchia dawsoni* = *Hermitia dawsoni*
- *Walchia gracillima* = *Hermitia* sp.
- *Walchia hypnoides* = *Otovicia hypnoides*
- *Walpia hermitensis* = *Sphaerapus larvalis*

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Grand Canyon National Park Paleontological Supplemental Information: Part D Paleontological Resource Law and Policy

Complied by Vincent L. Santucci and Justin S. Tweet

General Resource Management Considerations

Paleontological resources are non-renewable remains of past life preserved in a geologic context. Fossils possess scientific and educational values and are of great interest to the public; therefore, it is exceedingly important that appropriate management attention be placed on protecting, monitoring, collecting, and curating of these paleontological specimens from federal lands. In 2009, the Paleontological Resources Preservation Act (PRPA) was signed into law as part of the Omnibus Public Land Management Act of 2009. The new paleontology-focused legislation includes provisions related to inventory, monitoring, public education, research and collecting permits, curation, and criminal/civil prosecution associated with fossils from designated DOI lands. Paleontological resource protection training is available for NPS staff through the NPS Geologic Resources Division (GRD). GRD is also available to provide support in paleontological resource theft or vandalism investigations.

National Park Service management policies state

> *…management actions will be taken to prevent illegal collecting [of fossil resources] and may be taken to prevent damage from natural processes such as erosion. Protection may include construction of shelters over specimens for interpretation in situ, stabilization in the field [which can include reburial] or collection, preparation, and placement of specimens in museum collections. The locality and geologic data associated with a specimen will be adequately documented at the time of specimen collection. Protection may also include, where necessary, the salvage collection of threatened specimens that are scientifically significant*.

Effective paleontological resource management serves to protect fossil resources by implementing strategies that mitigate, reduce, or eliminate loss of fossilized materials and their relevant data. Because fossils are representatives of adaptation, evolution, and diversity of life through deep time, they have intrinsic scientific value beyond that of the physical objects themselves. Their geological and geospatial contexts provide additional critical data concerning paleoenvironmental, paleogeographic, paleoecologic, and a number of other conditions that together allow for a more complete interpretation of the physical and biological history of the earth. Therefore, paleontological resource management must act to protect not only the fossils themselves, but to collect and maintain the ancillary data as well.

In general, losses of paleontological resources result from naturally occurring physical processes, by direct or indirect human activities, or by a combination of both. The greatest loss of ancillary data occurs when fossils are removed from their original geological context. Thus, when a fossil weathers and erodes from its surrounding sediments and geologic context, it begins to lose significant ancillary data until, at some point, it becomes more a scientific curiosity than a useful piece of scientific data. A piece of loose fossil “float” can still be of scientific value; however, when a fossil has been completely removed from its original context, such as an unlabeled personal souvenir or a specimen with no provenance information in a collection, it is of very limited scientific utility. Similarly, fossils inadvertently exhumed during roadway construction or a building excavation may result in the loss or impairment of the scientific and educational values associated with those fossils. It is not necessary to list here all of the natural and anthropogenic factors that can lead to the loss of paleontological resources; rather it is sufficient to acknowledge that anything which disturbs native sediment or original bedrock has potential to result in the loss of the paleontological resources that occur there, or the loss of the associated paleontological resource data.

For management purposes, paleontological localities are evaluated for factors that could cause potential loss of paleontological resources. Their overall conditions are reported as good, fair, or poor based on the situations found at each individual locality. Risks and conditions that influence the degree of potential loss are categorized as Disturbance, Fragility, Abundance, and Site Access. “Disturbance” evaluates conditions that promote accelerated erosion or mass wasting resulting from human activities. “Fragility” evaluates natural conditions that may influence the degree to which fossil transportation is occurring, such as inherently soft rapidly eroding sediment or mass wasting on steep hillsides. “Abundance” judges both the natural condition and number of specimens actually preserved in the deposits as well as the risk of being easily recognized as a fossil-rich area which could lead to the possibility of unpermitted collecting. “Site Access” assesses the risk of a locality being visited by large numbers of visitors or the potential for easy removal of large quantities of fossils or fossil-bearing sediments as a result of proximity to public use areas or other access (along trails, at roadcuts, at beach or river access points, and so on). There is no simple formula for convenience, because it is influenced by each visitor’s appreciation of factors such as terrain, distance from the access point, the presence and types of potentially harmful plant and animal life, the weather, and the visitor’s capabilities, interest, and energy level. Generally speaking, any sedimentary exposures or accumulations of loose rock that are visible from a trail or other means of access and do not require significant climbing will attract geology enthusiasts, the curious, and the energetic.

Each of the factors noted above may be mitigated by management actions. Localities exhibiting a significant degree of disturbance may require either active intervention to slow accelerated erosion, periodic collection and documentation of fossil materials, or both. Localities developed on sediments of high fragility naturally erode at a relatively rapid rate and would require frequent visits to collect and document exposed fossils in order to prevent or reduce losses. Localities with abundant or rare fossils, or high rates of erosion, may be considered for periodic monitoring in order to assess the stability and condition of the locality and resources, in regard to both natural processes and human-related activities. Localities that are easily accessible by road or trail would benefit from the same management strategies as those with abundant fossils and by occasional unscheduled visits by park staff, documentation of in situ specimens, and/or frequent law enforcement patrols.

Cave localities are in a distinct class for management due to the close connection with archeological resources and unique issues affecting cave resources. See Santucci and others (2001) for additional discussion of paleontological resources in cave settings.

Management strategies to address any of these conditions and factors could also incorporate the assistance of qualified specialists to collect and document resources rather than relying solely on staff to accomplish such a large task at GRCA. Active recruitment of paleontological research scientists should also be used as a management strategy.

Management Actions

The following material is reproduced and adapted in large part from Henkel and others (2015):

In March 2009, the Paleontological Resources Preservation Act (PRPA) (16 USC 460aaa) was signed into law (Public Law 111–11). This act defines paleontological resources as

> *…any fossilized remains, traces, or imprints of organisms, preserved in or on the earth’s crust, that are of paleontological interest and that provide information about the history of life on earth.*

The law stipulates that the Secretary of the Interior should manage and protect paleontological resources using scientific principles. The Secretary should also develop plans for

> *…inventory, monitoring, and the scientific and educational use of paleontological resources.*

Paleontological resources are considered park resources and values that are subject to the “no impairment” standard in the National Park Service Organic Act (1916). In addition to the Organic Act, PRPA will serve as a primary authority for the management, protection and interpretation of paleontological resources. The proper management and preservation of these non-renewable resources should be considered by park resource managers whether or not fossil resources are specifically identified in the park’s enabling legislation.

The Paleontological Resources Management section of NPS Reference Manual 77 provides guidance on the implementation and continuation of paleontological resource management programs. Administrative options include those listed below and a park management program will probably incorporate multiple options depending on specific circumstances:

No action—no action would be taken to collect the fossils as they erode from the strata. The fossils would be left to erode naturally and over time crumble away, or possibly be vandalized by visitors, either intentionally or unintentionally.

Surveys—will be set up to document potential fossil localities. All sites will be documented with the use of GPS and will be entered into the park GIS database. Associated stratigraphic and depositional environment information will be collected for each locality. A preliminary faunal list will be developed. Any evidence of poaching activity will be recorded. Rates of erosion will be estimated for the site and a monitoring schedule will be developed based upon this information. An NPS Paleontological Locality Database Form will also be completed for each locality. A standard version of this form will be provided by the Paleontology Program of the Geologic Resources Division upon request and can be modified to account for local conditions and needs.

Monitoring—fossil-rich areas would be examined periodically to determine if conditions have changed to such an extent that additional management actions are warranted. Photographic records should be kept so that changes can be more easily ascertained.

Cyclic prospecting—areas of high erosion which also have a high potential for producing significant specimens would be examined periodically for new sites. The periodicity of such cyclic prospecting will depend on locality-specific characteristics such as rates of sediment erosion, abundance or rarity of fossils, and proximity to visitor use areas.

Stabilization and reburial—significant specimens which cannot be immediately collected may be stabilized using appropriate consolidants and reburied. Reburial slows down but does not stop the destruction of a fossil by erosion. Therefore, this method would be used only as an interim and temporary stop-gap measure. In some situations, stabilization of a locality may require the consideration of vegetation. For example, roots can destroy in situ fossils, but can also protect against slope erosion, while plant growth can effectively obscure localities, which can be positive or negative depending on how park staff want to manage a locality.

Shelter construction—it may be appropriate to exhibit certain fossil sites or specimens in situ, which would require the construction of protective shelters to protect them from the natural forces of erosion. The use of shelters draws attention to the fossils and increases the risk of vandalism or theft, but also provides opportunities for interpretation and education.

Excavation—partial or complete removal of any or all fossils present on the surface and potentially the removal of specimens still beneath the surface which have not been exposed by erosion.

Closure—the area containing fossils may be temporarily or permanently closed to the public to protect the fossil resources. Fossil-rich areas may be closed to the public unless accompanied by an interpretive ranger on a guided hike.

Patrols—may be increased in areas of known fossil resources. Patrols can prevent and/or reduce theft and vandalism. The scientific community and the public expect the NPS to protect its paleontological resources from vandalism and theft. In some situations a volunteer site stewardship program may be appropriate (for example the “Paleo Protectors” at Chesapeake & Ohio Canal National Historical Park).

Alarm systems/electronic surveillance—seismic monitoring systems can be installed to alert rangers of disturbances to sensitive paleontological sites. Once the alarm is engaged, a ranger can be dispatched to investigate. Motion-activated cameras may also be mounted to visually document human activity in areas of vulnerable paleontological sites.

National Park Service Management Policies (2006; Section 4.8.2.1) also require that paleontological resources, including both organic and mineralized remains in body or trace form, will be protected, preserved, and managed for public education, interpretation, and scientific research. In 2010, the National Park Service established National Fossil Day as a celebration and partnership organized to promote public awareness and stewardship of fossils, as well as to foster a greater appreciation of their scientific and educational value (https://www.nps.gov/subjects/fossilday/index.htm). National Fossil Day occurs annually on Wednesday of the second full week in each October in conjunction with Earth Science Week.

Related Laws, Legislation, and Management Guidelines

National Park Service Organic Act

The NPS Organic Act directs the NPS to manage units

> *...to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner as will leave them unimpaired for the enjoyment of future generations.* (16 U.S.C. § 1).

Congress reiterated this mandate in the Redwood National Park Expansion Act of 1978 by stating that the NPS must conduct its actions in a manner that will ensure no

> *...derogation of the values and purposes for which these various areas have been established, except as may have been or shall be directly and specifically provided by Congress.* (16 U.S.C. § 1 a-1).

The Organic Act prohibits actions that permanently impair park resources unless a law directly and specifically allows for the acts. An action constitutes an impairment when its impacts

> *...harm the integrity of park resources or values, including the opportunities that otherwise would be present for the enjoyment of those resources and values.* (Management Policies 2006 1.4.3).

Paleontological Resources Protection Act (P.L. 111-011, Omnibus Public Land Management Act of 2009, Subtitle D)

Section 6302 states

> *The Secretary (of the Interior) shall manage and protect paleontological resources on Federal land using scientific principles and expertise. The Secretary shall develop appropriate plans for inventory, monitoring, and the scientific and educational use of paleontological resources, in accordance with applicable agency laws, regulations, and policies. These plans shall emphasize interagency coordination and collaborative efforts where possible with non-Federal partners, the scientific community, and the general public.*

The Federal Cave Resources Protection Act of 1988 (16 USC 4301)

The law provides a legal authority for the protection of all cave resources on NPS and other federal lands. The definition for "Cave Resource" in Section 4302 states

> *Cave resources include any material or substance occurring naturally in caves on Federal lands, such as animal life, plant life, paleontological deposits, sediments, minerals, speleogens, and speleothems.*

NPS Management Policies 2006

NPS Management Policies 2006 include direction for preserving and protecting cultural resources, natural resources, processes, systems, and values (NPS, 2006). It is the goal of the NPS to avoid or minimize potential impacts to resources to the greatest extent practicable consistent with the management policies.

NPS Director's Order-77, Paleontological Resources Management

DO-77 describes fossils as non-renewable resources and identifies the two major types, body fossils and trace fossils. It describes the need for managers to identify potential paleontological resources using literature and collection surveys, identify areas with potential for significant paleontological resources, and conduct paleontological surveys (inventory). It also describes appropriate actions for managing paleontological resources including: no action, monitoring, cyclic prospecting, stabilization and reburial, construction of protective structures, excavation, area closures, patrols, and the need to maintain confidentiality of sensitive location information.

Excerpt from Clites and Santucci (2012):

Monitoring

An important aspect of paleontological resource management is establishing a long-term paleontological resource monitoring program. National Park Service paleontological resource monitoring strategies were developed by Santucci and others (2009). The park's monitoring program should incorporate the measurement and evaluation of the factors stated below.

Climatological Data Assessments

These assessments include measurements of factors such as annual and storm precipitation, freeze/thaw index (number of 24-hour periods per year where temperature fluctuates above and below 32 degrees Fahrenheit), relative humidity, and peak hourly wind speeds.

Rates of Erosion Studies

These studies require evaluation of lithology, slope degree, percent vegetation cover, and rates of denudation around established benchmarks. If a park does not have this information, there may be opportunities to set up joint projects, because erosion affects more than just paleontological resources.

Assessment of Human Activities, Behaviors, and Other Variables

These assessments involve determining access/proximity of paleontological resources to visitor use areas, annual visitor use, documented cases of theft/vandalism, commercial market value of the fossils, and amount of published material on the fossils.

Condition Assessment and Cyclic Prospecting

These monitoring methods entail visits to the locality to observe physical changes in the rocks and fossils, including the number of specimens lost and gained at the surface exposure. Paleontological prospecting would be especially beneficial during construction projects or road repair.

Periodic Photographic Monitoring

Maintaining photographic archives and continuing to photo-document fossil localities from established photo-points enables visual comparison of long-term changes in site variables.

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