FROM MICROFOSSILS TO MEGAFAUNA: AN OVERVIEW OF THE TAXONOMIC DIVERSITY OF NATIONAL PARK SERVICE FOSSILS

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Abstract—The vast taxonomic breadth of the National Park Service (NPS)'s fossil record has never been systematically examined until now. Paleontological resources have been documented within 277 NPS units and affiliated areas as of the date of submission of this publication (Summer 2020). The paleontological records of these units include fossils from dozens of high-level taxonomic divisions of plants, invertebrates, and vertebrates, as well as many types of ichnofossils and microfossils. Using data and archives developed for the NPS Paleontology Synthesis Project (PSP) that began in 2012, it is possible to examine and depict the broad taxonomic diversity of these paleontological resources. The breadth of the NPS fossil record ranges from Proterozoic microfossils and stromatolites to Quaternary plants, mollusks, and mammals. The most diverse taxonomic records have been found in parks in the western United States and Alaska, which are generally recognized for their long geologic records. Conifers, angiosperms, corals, brachiopods, bivalves, gastropods, artiodactyls, invertebrate burrows, and foraminiferans are among the most frequently reported fossil groups. Small to microscopic fossils such as pollen, spores, the bones of small vertebrates, and the tests of marine plankton are underrepresented because of their size and the specialized equipment and techniques needed to study them. The improved capacity to rapidly analyze the fossil record of NPS units granted by the PSP is valuable for pursuing resource management goals, and for making the wealth of NPS paleontological resources more available for scientific, educational, and interpretive purposes.

INTRODUCTION

The National Park Service includes some of the most notable fossil localities and fossiliferous strata in the United States, with a record extending back in time from the Quaternary well into the Mesoproterozoic. A great deal of information exists for this fossil record, as scientific publications, internal memos, informal communications, researchers' notes, museum records, photographs, newspaper articles, and other documentation. Beginning in 2012, the NPS Paleontology Program began an ambitious project to organize this information (Paleontology Synthesis Project, or PSP) and archive it (NPS Paleontology Archives and Library), as documented in Santucci et al. (2018). These data have greatly improved the capacity of the NPS Paleontology Program to assess the paleontological resources of each park, make comparisons between park units, respond to queries from NPS staff and others, support research, and prepare reports on park resources. The PSP format also provides a framework for adding new information on paleontological resources in parks, and has helped to identify deficiencies in the knowledge base and areas of high potential for future discoveries.

As part of the organization of the PSP, several thematic files were created, collating information pertaining to specific categories including: the servicewide occurrence of fossils over geologic time; holotype specimens from NPS areas (Tweet et al., 2016); museum repositories holding NPS fossils; and the subject of this report, the taxonomic diversity of NPS fossils. The taxonomic diversity of the fossils found in National Park Service units has never been systematically investigated, and there was no framework for investigating this topic before the initiation of the PSP. The assembled data presented here provide a picture of the breadth and depth of taxonomic diversity within the NPS.

Acronyms for Park Designations: NHP, National Historical Park; NHS, National Historic Site; NMEM, National Memorial; NM, National Monument; NM&PRES, National Monument and Preserve; NP, National Park; NP&PRES, National Park and Preserve; NRA, National Recreation Area; **NPRES**, National Preserve; **NS**, National Seashore; **NST**, National Scenic Trail; other, less frequently used designations will be written in full in the text.

METHODS

The immediate sources for the PSP were paleontological resource summaries prepared for the 32 NPS Inventory & Monitoring networks (I&M networks) and a small number of park-specific inventories and thematic inventories. These sources were in turn based on decades of research and data compilations involving NPS fossils, beginning in the mid-1980s. Paleontological resource inventories are an important component of the NPS Paleontology Program. These fossil inventories provide critical baseline data on the scope, significance, distribution, and management issues related to park paleontological resources. This information is not only important scientifically and helps to inform park managers about the park-specific issues related to fossils, but paleontological resources inventories are identified and mandated within the Paleontological Resources Preservation Act (PRPA) of 2009 (16 U.S.C. § 470aaa 1-11). The importance of paleontological resource inventories is also addressed in the document Report to Congress by the Secretary of Interior: Assessment of Fossil Management on Federal & Indian Lands (Department of the Interior [DOI], 2000). The Report to Congress presents this recommendation: "Future actions should acknowledge the need for gathering and analyzing information about where fossils occur, in particular the critical role of inventory in the effective management of fossil resources" (DOI, 2000). This information also ensures that park interpretive programs on paleontology are accurate and reflect the most current knowledge of the fossils and their geological context. The NPS piloted a paleontological resource inventory strategy and methodology at Yellowstone NP during 1996 and 1997 (Santucci, 1998).

The initial paleontological resource inventories undertaken by the NPS were primarily coordinated by the NPS Geologic Resources Division. They were compiled via a combination of literature research, assessments of fossils in park and non-



FIGURE 1. Examples of four of the five major categories ("other" excluded as primarily microfossils) in NPS areas with recent or current projects. **A**, *Chesapecten madisonius*, a Pliocene bivalve from Colonial NHP. **B**, A standing partial petrified tree of Eocene age at Yellowstone NP. **C**, Cartilage and teeth of the shark *Glikmanius* located in a cave wall at Mammoth Cave NP. **D**, A Permian trackway documented at Grand Canyon NP. Photos are NPS, except for A, which is courtesy Mackenzie Chriscoe.

federal repository collections, and communication with park staff, external geoscientists who had worked in the parks and surrounding areas, and other people knowledgeable about the paleontology of a given park and its surroundings. Because of the expansion of baseline paleontological resource data for the parks, identification of fossils in a greater number of parks, and evolving methodologies and technologies, the summaries became more comprehensive and larger in scope over time. The gaps in coverage, combined with research and publications that had been produced after the earliest inventories and summaries had been completed, required supplementation of the original information with additional literature searches during the first collection of data for the PSP. This was conducted using GeoRef as a starting point and then expanding to other databases as necessary (see comments with taxonomic groups below for specific examples). Concurrent with the initiation of the PSP in 2012, the NPS Paleontology Program has shifted from network-level reports to park-specific paleontological resource inventory reports, which are now deeply intertwined with PSP records as park projects inform the PSP and vice-versa. Files have been updated as necessary since 2012 to take into account new information and research, previously overlooked information, and the establishment of new park units that contain fossil resources.

The base PSP files are 32 documents representing the 32 I&M networks. A given network document contains information for the parks that are formally included in that network, as well as units that are geographically within that network but not

formally part of the I&M program. Each park is documented using a summary table that is organized stratigraphically, including information on age and fossils known from the various stratigraphic units in that park. The tables are followed by additional notes that collect information that was either published or otherwise brought to light after the completion of a network summary or park-specific inventory report. The taxonomic information from these network files has been used to assemble a master taxonomic spreadsheet. This spreadsheet allows rapid parsing of information that can then be expanded upon using the more detailed information in the network documents. For example, this system has made it much simpler to create thematic inventories of various groups (Cenozoic vertebrate tracks, Santucci et al., 2014; Mesozoic mammals and relatives, Tweet et al., 2015; trilobites, Norr et al., 2016; non-avian dinosaurs, Tweet and Santucci, 2018; proboscideans, Mead et al., 2020; belemnites, Schraer et al., in press).

Documenting park paleontological resources requires some practical considerations. The NPS administers, advises, recognizes, or is affiliated with a large number of sites, from the core official list (419 units as of July 2020), to a variety of national rivers and trails, to the National Natural Landmark (NNL) and National Historic Landmark (NHL) programs, to National Heritage Areas, to the National Register of Historic Places (NHRP). The PSP is primarily concerned with the core official units. Incomplete records exist for some of the other categories of units; affiliated areas are best understood at this point because they are the most manageable in terms of geography (most occupy small areas) and overall numbers (24). Documenting paleontological resources in national rivers and trails not included in the 419 is hampered by the absence of traditional boundaries, although it is known that some trails are associated with historical occurrences of fossils. NNLs and NHLs with paleontological resources are currently being documented separately from the main PSP files.

In the official list of 419 units, some units are seemingly "double-counted" because in administrative terms they include two distinct areas (e.g., several units in Alaska that include both a National Park or Monument as well as a National Preserve). For the purposes of the PSP, these "double" units are considered one unit. In other cases, various related units may be organized under an umbrella. This is particularly true of units in the District of Columbia and immediate surroundings. The rule of thumb for the PSP was to count units separately if they are part of the 419. For example, Fort Washington Park (FOWA) is managed by National Capital Parks-East (NACE), but is considered a stand-alone unit. An exception to this general rule is Roosevelt-Vanderbilt National Historic Sites (ROVA), which includes three stand-alone units; our existing information does not allow us to distinguish which unit produced a report, so ROVA is used. Units under a larger unit that are not stand-alone have been counted under their managing unit, unless it is more useful for management purposes to consider them separately. For example, Meridian Hill Park (MEHI) is not part of the 419, so it is counted as part of Rock Creek Park (ROCR). Occasionally the PSP files need to be updated following changes in designation, such as White Sands National Monument becoming White Sands National Park in 2019.

Fossil occurrences have been distinguished in terms of five modes or contexts: in situ, reworked, museum, cultural, and building stone. The first, and most common, is in situ, which in practical terms also includes float from formations which are exposed in a park. Next are reworked fossils, eroded from their original stratum and deposited in another. Both in situ and reworked fossils can be considered naturally occurring. A museum mode was invoked for specimens in taxonomic groups not yet reported as naturally occurring within a given park, but present in that park's fossil collections. This occurs in cases where park collections include specimens from outside of that park. Cultural specimens are those fossils found with a cultural context. This mode includes a wide variety of fossils and occurrences (Kenworthy and Santucci, 2006). Cultural specimens may fall under the museum mode as well. The provenance of cultural specimens often cannot be established, but in many cases such specimens were brought from somewhere else, because they are not known from the rocks found in the park. Cultural records are often missed when searching within the geological literature, requiring supplementation through archeological venues; this also sometimes captures Quaternary ecological records not found elsewhere. Finally, fossils have been found in building stone (Santucci et al., in press), which can be considered a subset of cultural fossils. The classic example is marine invertebrates in limestone used for a monument or memorial, as seen at the Lincoln Memorial and the Washington Monument. In other cases, fossiliferous building stone was utilized as a structural material in what is now a historic resource, such as in the coquina walls of the namesake fort of Castilla de San Marcos NM (CASA). Human utilization of fossils and fossiliferous materials is an aspect of human dimensions of paleontological resources, as discussed in Santucci et al. (2016).

Taxonomic sorting began with five primary taxonomic categories: plants, invertebrates, vertebrates, ichnofossils (here including eggshells), and other forms (primarily microfossils) (Fig. 1). A number of subcategories were then defined within each primary category. The primary categories and subcategories provide an approximation of high-level diversity, but do not show, for example, families or species. A park like John Day Fossil Beds NM (JODA), with many angiosperm taxa, or Florissant Fossil Beds NM (FLFO), with its hundreds of insect species, has a significant part of its diversity hidden by this approach. The great majority of parks do not have such exceptional records, so using higher-level taxonomic categories is more appropriate. Categorization has been revised on occasion to improve utility, usually to introduce a new category. Every mode of occurrence and taxonomic category can be further modified as "possible," which in practice usually indicates that it is unclear whether a record comes from within or outside a park, or the specimen's identification is equivocal.

FOSSIL CATEGORIES

Fossil Plants

Fossil plants are unusual among the five primary categories because they are almost invariably seen in the fossil record as constituent structures that often cannot be reconstructed into whole organisms. Wood or stems, foliage, flowers, embryonic forms (seeds, nuts, and so on), and plant palynomorphs (spores and pollen) are commonly found and described separately. Because of this factor, the categorization not only includes taxonomic categories, but several separate categories for unclassified remains of common structures rather than a single lumped "unidentified" group: unclassified wood, unclassified foliage, phytoliths, and spores and pollen, as well as a general category (Table 1). These latter categories are not taxonomic and are not treated as such, but do have other utility. For example, palynomorphs and phytoliths are frequently used in paleoenvironmental studies, so it is useful to keep track of their occurrences.

"Fossil Plants" as a category is restricted to modern understanding of Kingdom Plantae. Various groups of organisms sometimes assigned to Kingdom Plantae in the past, such as fungi, seaweeds, and many forms of "algae," are instead included with "Other." The only algae retained with plants are chlorophytes and charophytes. There are probably some misclassifications among early plants, because of changes in classification since the original description. "Seed ferns" are a particular area of concern. Extinct groups of plants are well-represented in the Paleozoic

440 TABLE 1. Organization of plant categories.

TAXONOMIC	STRUCTURAL
Chlorophytes	Unclassified wood
Charophytes	Unclassified foliage
Mosses	Unclassified/unspecified general
Liverworts and hornworts	Spores and pollen
Lycophytes	Phytoliths
Equisetopsids	
Ferns (minus equisetopsids)	
"Seed ferns"	
Cycads	
Cycadeoids	
Ginkgoes	
Conifers	
Gnetophytes	
Angiosperms	
Other plants	

and lower Mesozoic rocks of a handful of parks, including Big South Fork National River and Recreation Area (BISO), Canyon de Chelly NM (CACH), Dinosaur NM (DINO), Gates of the Arctic NP&PRES (GAAR), Grand Canyon NP (GRCA), Little River Canyon NPRES (LIRI), New River Gorge National River (NERI), Petrified Forest NP (PEFO), Upper Delaware Scenic and Recreational River (UPDE), and Yukon-Charley Rivers NPRES (YUCH). Therefore, the fossil plants from these parks are most likely to be recorded under outdated classifications.

Quaternary paleoecological studies are not always captured by GeoRef coverage, which is a particular issue for documenting Quaternary records of plants, invertebrates, and various microfossils. Alternative sources have been employed to address this gap, such as the NOAA National Climatic Data Center (https://www.ncdc.noaa.gov/data-access/paleoclimatologydata) and the Neotoma Paleoecology Database (https://www. neotomadb.org/), but relevant references and localities were no doubt missed.

Fossil Invertebrates

The fossil invertebrate taxonomic category is restricted to members of Kingdom Animalia outside of Vertebrata. Singlecelled heterotrophs such as foraminiferans are included as "Other" instead. Because the exact placement of conodonts in relation to Vertebrata is uncertain, they are included here as "Fossil Invertebrates." Generally, invertebrate fossil coverage is extensive and very accessible through GeoRef and similar channels, but, similar to plants, some reports may have been missed by being published in ecological or mollusk-focused journals that do not overlap with GeoRef's coverage. Fossil invertebrates can be divided into a number of groups (Table 2). Large divisions used here include sponges, corals, bryozoans, brachiopods, mollusks, annelids, arthropods, echinoderms, graptolites, and conodonts. Several of these are further subdivided. One consideration for categorizing invertebrates is the existence of a variety of extinct groups with controversial relationships to extant groups. Many of these problematic groups are only known from a small number of records and have been grouped together for convenience, with more details provided in the network files. In the future, some of these taxonomic groups may be split out or subdivided.

Fossil Vertebrates

As noted above, "Fossil Vertebrates" is limited to Vertebrata. Within this are several large radiations of fishes, and broad groups of amphibians, reptiles, birds, and mammals, which are subdivided further into a number of categories (Table 3). Reptiles and mammals have the most extensive fossil records and are generally of the greatest interest, so have been divided more finely than the other groups.

Although vertebrate fossils receive a great deal of attention, some journals that include publications on fossil vertebrates are not completely covered by GeoRef, because they are focused on the modern. Examples include Copeia, which publishes on ichthyology and herpetology, and the Journal of Mammalogy. Quaternary records of extant animals are sometimes missed by GeoRef, but records of extinct Quaternary mammals are usually found. Even if they are not in GeoRef, it is usually possible to find these records in other venues. There are numerous inventories focused on Quaternary mammals, although they are often decades old (e.g., O.P. Hay's compilations). Simple search engine queries can be productive, because fossils of large recently extinct mammals (mammoths, etc.) are often a matter of local interest and pride. Late Quaternary records may also cross over with archeological records and thus be considered cultural as well.

Ichnofossils

The ichnofossil category unites fossils that record biological activity and are not the physical structures of the organisms themselves. For the purposes of the PSP, "ichnofossil" is defined broadly, encompassing not only fossils such as burrows and tracks but also sedimentary structures induced by biological activity (e.g., stromatolites), root traces, coprolites, animal middens (e.g., packrat middens), and eggs and egg cases. Some specimens may represent both body and trace fossils, such as bored shells, bored or gnawed wood, and tooth-marked bones, and some ichnofossil occurrences may include multiple types of traces, such as coprolites that show burrows and trails.

Ichnofossils differ from the other primary categories because they are categorized morphologically as well as taxonomically (Table 4). Although most categories are self-explanatory, some require additional explanation. "Bioturbation" is the general disruption of sediment by organisms; other kinds of more narrowly identifiable ichnofossils such as invertebrate burrows or root traces may be associated. Locomotory trace fossils of invertebrates and vertebrates are divided into continuous traces (enclosed burrows and continuous surficial trails) and discontinuous traces (single prints and longer trackways).

Trace fossils are often mentioned in passing in the description of something else. One fruitful method to search the literature for common trace fossils in a park is to look for publications describing the stratigraphy and/or sedimentology of rocks from somewhere within that park. This method also holds for other common fossils, such as plant debris, wood, common mollusks and echinoderms, scrap bones and teeth, and some microfossils.

Other Fossils

There are many fossils outside of the plant, invertebrate, vertebrate, and ichnofossil categories above (Table 4). The great majority are microfossils from a variety of groups, usually represented by mineralized or resistant organic body structures such as tests. In the past, some of them would have been included with one of the other categories, but now these groups of "microbes," "algae," and so forth, are known to be distinct. Many of them have great utility for biostratigraphy and paleoenvironmental studies. Because of their microscopic sizes and the specialized equipment and techniques required to study them, these fossil groups are inevitably underreported, and would easily be the most abundant and diverse NPS fossils if

TABLE 2. Organization of invertebrate categories. TAXONOMIC CATEGORIES

Sponges		
Corals		
Bryozoans		
Brachiopods		
Hyoliths		
Mollusks	Chitons	
	Bivalves	
	Cephalopods	Ammonoids
	1 I	Coleoids
		Nautiloids
		Other/unspecified cephalopods
	Gastropods	
	Scaphopods	
	Other mollusks (helcionelloids, monoplacophorans, rostroconchs, <i>Scaevogyra</i>)	,
Annelids	Onspecified monusks	
Arthropods	Trilohites	
Thunopous	Cheliceratans	
	Myriapods	
	Crustaceans	Branchionods
		Barnacles
		Ostraçodes
		Malacostracans
		Other/unspecified crustaceans
	Insects	other/unspectified crustaceans
	Other/unerganified arthreneds	
Febinoderms	Asteroids	
Lennouenns	Orbiuroida	
	Plastoida	
	Crinoida	
	Echinoida	
	Echimolds Other askingdommes (avateida, admisectareida	
	eocrinoids, helicoplacoids, paracrinoids, stylophorans) Unspecified echinoderms	
Graptolites		
Conodonts		
Enigmatic or uncertain (chancellorids, conulariids, scenellids, small shelly fauna, tentaculitids)		
Other invertebrates		

Unspecified invertebrates

TAXONOMIC CATEGORIES (MINUS REPTILES AND MAMMALS)	REPTILE CATEGORIES	MAMMAL CATEGORIES
Jawless fish	Turtles	"Pelycosaurs" and "therapsids"
Placoderms	Ichthyosaurs	Early mammals and mammal relatives
Chondrichthyans	Plesiosaurs	Marsupials
Acanthodians	Sphenodontians	Xenarthrans
Ray-finned fish	Lizards	"Insectivores"
Sarcopterygians	Snakes	Rodents
Unspecified fish	Mosasaurs	Lagomorphs
Salamanders	Phytosaurs	Primatomorphs (minus Homo)
Anurans	Aetosaurs	Chiropterans
Other amphibians	Crocodylomorphs	Cimolestans
Unspecified amphibians	Dinosaurs	"Creodonts"
Waterfowl/seabirds/shorebirds	Pterosaurs	Carnivorans
Birds of prey	Other reptiles	"Condylarths"
Perching birds	Unspecified reptiles	Proboscideans
Other/unspecified birds		Sirenians and desmostylians
Other vertebrates		Perissodactyls
Unspecified vertebrates		Artiodactyls
		Cetaceans
		Other mammals
		Unspecified mammals

their true extent was known. How many parks have rocks that are essentially made of coccoliths, foraminiferans, radiolarians, or diatoms? Their size and abundance also make it difficult to create meaningful strategies for their management.

RESULTS

As of July 2020, 277 current NPS and affiliated units from all 12 unified DOI regions and all 32 I&M networks have been found to have some kind of fossil occurrence (Fig. 2). Their fossil resources range in scope from a single fossil specimen in a park's museum collection to some of the most significant fossil accumulations in the world. These NPS units and their acronyms are listed at the end under the recently adopted unified DOI regions (Appendix). It is thought that this number includes almost all of the official 419 parks with natural occurrences (in situ or reworked) of macroscopic paleontological resources, because the great majority of the remainder are either small urban cultural sites or have unfossiliferous metamorphic or igneous bedrock. Additionally, two other units may have fossil occurrences (Castle Mountains NM and San Juan NHS), and there is one abolished unit that is known to have been fossiliferous (Fossil Cycad NM), but they are not included here. Of the 277 parks that have some kind of paleontological occurrence, 235 have fossil resources which were found in situ or reworked. These will be the focus of the rest of the discussion.

Fossil Plants

In situ or reworked plant fossils have been documented at 163 NPS units. Fossil plants in general are probably somewhat underrepresented, for a variety of reasons. Many plant fossils, particularly undiagnostic remains, are rather humble specimens that may simply be overlooked in the field, particularly if someone is not looking for them. Other common plant fossils are microscopic and can only be found if someone is specifically looking for them. Spores, pollen, and phytoliths are certainly more widely distributed than presently known, and promise to be an important area for study in the next few decades because of their utility for land management. Finally, there are the methodological issues described previously.

Reports of fossil plants are dominated by those of conifers and angiosperms (Fig. 3), confirmed as reworked or in situ at 77 and 70 units, respectively. This is unsurprising given their combination of resistant macroscopic tissues (particularly wood and seeds) and long records of dominance. Conifers have existed since the Pennsylvanian and dominated Mesozoic floras, and angiosperms took over preeminence during the Cenozoic. Other groups are represented in much smaller numbers, with no other group exceeding 36 records (ferns). Depending on the group, this is either a function of poor fossilization potential (e.g., mosses and ferns) or extinction before the Cenozoic and therefore no benefit from the "pull of the recent" (e.g., "seed ferns" and cycadeoids). A deeper look shows that many of the groups that could be considered "unlikely fossils" are represented in large part by palynomorphs. For example, of the 18 moss records, 10 are of moss spores, and all records of liverworts and hornworts are of spores.

Given the high frequency of plants being found as fragments with limited diagnostic value, or simply being described as such in the literature (e.g., "wood" or "leaves"), it is useful to consider the reports of undetermined plant fossils. Eighty-one TABLE 4. Organization of ichnofossil and "other" categories.

ICHNOFOSSIL CATEGORIES	"OTHER" CATEGORIES
General bioturbation	Proterozoic microfossils
Stromatolites and similar structures	Ediacaran biota
Microbially induced sedimentary structures	Phanerozoic acritarchs
Root traces	Coccoliths
Invertebrate burrows and other continuous traces	Foraminiferans
Invertebrate tracks	Radiolarians
Invertebrate nests and reproductive traces	Diatoms
Invertebrate coprolites	Silicoflagellates
Unspecified invertebrate trace fossils	Dinoflagellates
Vertebrate burrows	Receptaculitids
Vertebrate tracks	Seaweeds
Reptile eggs	Coralline red algae
Bird eggs	Unspecified "algae"
Vertebrate coprolites	Fungi
Vertebrate regurgialites	Other
Packrat middens	Unspecified or unidentified fossils
Other middens	

Other trace fossil

Unspecified trace fossil

units have reports of in situ or reworked unidentified wood, generally described as petrified or silicified wood, and 108 units have reports of undefined plant fossils. Given the predominance of conifer and angiosperm records, it is likely that the great majority of undetermined fossil plant records belong to these two groups.

Including only natural occurrences (in situ or reworked) of the 15 taxonomic categories of fossil plants (Table 1), the NPS units with the most diverse higher-level paleobotanical records at this time are as follows:

- Petrified Forest NP (PEFO): 13
- Yellowstone NP (YÈLL): 12
- Grand Teton NP (GRTE): 11
- Big Bend NP (BIBE): 10
- Grand Canyon NP (GRCA): 10
- Dinosaur ŇM (DINO): 9
- Florissant Fossil Beds NM (FLFO): 8
- Yukon-Charley Rivers NPRES (YUCH): 8

These NPS units can be divided into two groups. Some parks are notable for extensive paleobotanical remains found in either a single formation or a group of related formations, such as at FLFO and PEFO. In other cases, there are multiple productive formations spread throughout geologic time, such as at DINO and GRCA. As is typical of NPS units with significant paleontological resources, almost all of the listed units are geographically large and geologically varied, and located either in Alaska or west of the Rockies. Chronologically, the floral assemblages of the parks on this list present a "tour" and summation of much of the paleobotanical record of North America. The Devonian and Mississippian are best represented by YUCH, the Pennsylvanian and Permian are represented by GRCA, the Late Triassic is represented by PEFO, the Late Jurassic is represented by DINO, the Late Cretaceous is represented by GRTE, the Late Cretaceous–Paleocene is represented by BIBE and YUCH, the Eocene is represented by BIBE, FLFO, and YELL, and the Quaternary is represented by GRCA. One unit not on this list that is otherwise noted for paleobotany is John Day Fossil Beds NM; in its case, diversity is great within a few of the broad fossil plant taxonomic categories, but is not known to encompass as many of the categories as the parks listed above.

Fossil Invertebrates

Fossil invertebrates are currently the best represented of the five general categories. At least 178 NPS units have records of either in situ or reworked invertebrate fossils. Marine invertebrates with hard parts are the most widespread and best represented (Fig. 4), because the combination of hard parts and living in depositional basins is most favorable for preservation. Within the larger subgroups, mollusks are mostly represented by bivalves, cephalopods, and gastropods. Arthropods are best represented by ostracode crustaceans, trilobites, and insects. The insect record is almost entirely of Quaternary age, although there are notable exceptions such as the Permian insects of GRCA and Eocene insects of FLFO. Echinoderms are primarily represented by crinoids and echinoids.

The two groups that have been most frequently reported in situ or reworked are bivalves (116) and gastropods (112) (Figs. 4 and 5), both exceeding any other category, invertebrate or not. This reflects a combination of long fossil records (both groups have been at least minor constituents of faunas since the Cambrian), durable remains that are also frequently recognizable to even inexperienced observers, and spreading from marine environments into freshwater (and onto land for gastropods). They are followed by corals (75 reports) and brachiopods (72),



FIGURE 2. A map of NPS units with paleontological resources.

and then bryozoans (59), crinoids (56), and ostracodes (52) (Fig. 5). These seven groups are typical constituents of the shallow marine formations deposited during the Paleozoic in many areas of North America. Twenty-two units share all seven of these groups, and another 11 share six of them. Trilobite records also are strongly correlated with this assortment of seven groups; 21 of the 22 units with the other seven groups also have trilobites, as well as six of the 11 units that have six of seven. This accounts for two-thirds of the 39 units with in situ or reworked trilobites. Several of these groups (bryozoans, brachiopods, and crinoids) are largely confined to the Paleozoic, due to a combination of declining abundance after the end-Permian extinctions and relative understudy of Mesozoic and Cenozoic examples.

Fossil invertebrate groups that are primarily or entirely represented by microscopic remains are certainly underrepresented. This includes sponges known from spicules, annelids known from scolecodont elements, branchiopod crustaceans, ostracodes, and conodonts. Existing invertebrate microfossil records are generally focused on a certain group of interest for paleoecological reasons (particularly ostracodes and cladoceran branchiopods) or biostratigraphic reasons (conodonts). Those microfossils without some wider application, such as sponge spicules, are presumably the least represented, because they will only be recorded in passing.

Unlike the other major subcategories of invertebrates, the arthropod record is biased to the Cenozoic, and to the Quaternary within the Cenozoic. With the notable exceptions of trilobites and to a lesser extent ostracodes, NPS records of the delicate remains of most arthropods are headlined by cave assemblages and the fine-grained rocks of FLFO. Arthropods are much better represented in deep time by their tracks, trails, burrows, and other trace fossils.

Including only natural occurrences (in situ or reworked) of the 34 taxonomic categories (Table 2: all but "unspecified cephalopods," "unspecified mollusks," "unspecified/unidentified echinoderms," and "unspecified invertebrates"), the NPS units with the most diverse higher-level invertebrate records at this time are as follows:

- Grand Canyon NP (GRCA): 24
- Yukon-Charley Rivers NPRES (YUCH): 21
- Death Valley NP (DEVA): 20
- Wrangell-St. Elias NP&PRES (WRST): 20
- Yellowstone NP (YELL): 20
- Mississippi National River and Recreation Area (MISS): 18
- Mojave NPRES (MOJA): 18
- Delaware Water Gap NRA (DEWA): 17
- Dinosaur NM (DINO): 17

Unlike the park units with diverse paleobotanical records, almost all of the above parks attained high diversity through multiple productive formations; the only listed park with narrowly confined diversity is MISS, which derives almost all of its invertebrate diversity from two Upper Ordovician formations. Otherwise, the listed parks have a number of marine formations representing numerous geological periods, and many of them also have Quaternary terrestrial and/or freshwater records as well.

Fossil Vertebrates

In situ or reworked vertebrate fossils are documented in 127 NPS units. Large fossil vertebrates are probably the best documented of any type of NPS fossil. The bones of large vertebrates are among the most likely kinds of fossil to be



FIGURE 3. Park records (in situ and reworked) of plant categories. Parks with both in situ and reworked records for a given category are only counted once.



FIGURE 4. Park records (in situ and reworked) of invertebrate categories. Parks with both in situ and reworked records for a given category are only counted once.



FIGURE 5. The most frequently reported invertebrate categories.

reported by the general public, if for no other reason than these specimens are frequently large and unusual in appearance. The general public is also more familiar with large extinct tetrapods such as dinosaurs and mammoths than any other kind of fossil organism, increasing awareness. In addition, although other types of fossils are more abundant, identifiable large vertebrate remains are more likely to receive scientific attention.

Small vertebrates, represented by microvertebrate fossils, are another matter entirely. Definitions of microvertebrate fossils vary, but are understood to include any isolated skeletal elements (bones, teeth, scutes, scales, etc.) smaller than a particular size, such as 0.5 inches (about 12.5 mm). Because of their size, they are easily overlooked by both the public and by researchers who are not prepared to collect and study them. Microvertebrate fossils represent a wide range of small fish, amphibians, reptiles, birds, and mammals, as well as teeth and small bones of larger animals. Microvertebrate paleontological studies are of recent vintage in NPS units; Big Bend NP (BIBE), Bryce Canyon NP (BRCA), Dinosaur NM (DINO), Hagerman Fossil Beds NM (HAFO), and Petrified Forest NP (PEFO) are among parks that have had significant investigation of microvertebrates. Further microvertebrate fossil studies should fill out the diversity of small vertebrates in parks otherwise known for large vertebrates.

Because the fossil vertebrates have been divided into more and finer sub-categories than the other primary taxonomic categories, many of the sub-categories have small sample populations; 24 have fewer than 10 records. Artiodactyls are the most frequently reported group of vertebrates (67 parks, in situ or reworked) (Figs. 6 and 7). They are followed by carnivorans (52), rodents (48), proboscideans (42), ray-finned fish (41), and chondrichthyans (40). A park with one of the common mammal categories frequently has others. For example, 38 have artiodactyls, carnivorans, and rodents, and 14 have two of the three. Only two parks have carnivorans but not artiodactyls, and only six parks have rodents but not artiodactyls. Of reptiles, turtles are the most frequently reported group (37), followed by snakes (30) and lizards (27). The turtle record is helped by the shell, while snakes and lizards are probably undercounted due to their small, delicate bones. Many of their records come from paleoecological studies of Quaternary finds, such as caves and packrat middens. Lizards and snakes are frequently found at the same parks; 23 parks have both. Nineteen of these 23 parks also have records of turtles.

Mammals are the best-documented taxonomic group of fossil vertebrates, for several reasons: mammal teeth are durable, compact, and informative, making them appealing for study; they are biostratigraphically informative and have been used as model organisms for large-scale studies of evolution (e.g., horses); they are found in Cenozoic terrestrial formations and deposits, which improves the chances of discovery compared to Mesozoic and Paleozoic vertebrates; and there is a natural human bias toward mammals. Historically, the other groups have had niche interest, because of the perceived relative rarity of good remains (birds), because they were not regarded as worthwhile objects of serious study (dinosaurs and other large extinct reptiles, turtles, and crocodilians), or both (fish, amphibians, and small reptiles). Changes in vertebrate paleontology over the last few decades of the 20^{th} century and into the 21^{st} century (the expansion of vertebrate paleontology as a field; reassessments of the value of non-mammalian groups; increasing interest in microfossils outside of mammals) have broadened the knowledge base, but some groups still lag.

Including only natural occurrences (in situ or reworked) of the 47 taxonomic categories (Table 3: omitting "unspecified amphibians," "unspecified reptiles," "unspecified mammals," and "unclassified bones/teeth"), the NPS units with the most diverse higher-level fossil vertebrate records at this time are as follows:

- Big Bend NP (BIBE): 27
- Grand Canyon NP (GRCA): 23
- Glen Canyon NRA (GLCA): 21
- Chaco Culture NHP (CHCU): 19
- Petrified Forest NP (PEFO): 19
- Potomac Heritage NST (POHE): 19
- Santa Monica Mountains NRA (SAMO): 19
- Channel Islands NP (CHIS): 18
- Fossil Butte NM (FOBU): 18
- Guadalupe Mountains NP (GUMO): 18
- Wind Cave NP (WICA): 18
- Badlands NP (BADL): 17

Most of these parks have multiple formations that have produced vertebrates, but there are a few whose records are derived almost entirely from one or two formations (e.g., FOBU) or Quaternary occurrences (CHIS, GRCA, GUMO, and POHE). A few of the most famous vertebrate-producing parks are not on this list, because their record is dominated by one subgroup, for example reptiles (Dinosaur NM) or mammals (Hagerman Fossil Beds NM, John Day Fossil Beds NM, and Valley Forge NHP). Unlike plants, invertebrates, and "other" fossils, no Alaska parks are in this list, a reflection of their relatively poor Cenozoic terrestrial records. Instead, the units are almost entirely located in the Colorado Plateau, Trans-Pecos Texas, southern California, or the Black Hills–Badlands.

Using the 13 reptile taxonomic categories ("unspecified reptiles" omitted), the most diverse higher-level fossil reptile records are found at the following:

- Petrified Forest NP (PEFO): 9
- Big Bend NP (BIBE): 8
- Dinosaur NM (DINO): 7
- Glen Canyon NRA (GLCA): 6
- Badlands NP (BADL): 5
- Chaco Culture NHP (CHCU): 5

The first three of the listed units are among the most famous fossil reptile sites in North America, while the other three may



FIGURE 6. Park records (in situ and reworked) of vertebrate categories. Parks with both in situ and reworked records for a given category are only counted once.



FIGURE 7. The most frequently reported vertebrate categories.

come as surprises. GLCA has a strong Mesozoic record, including both marine and terrestrial reptiles. Reptiles, particularly turtles, are a significant but sometimes overlooked part of the White River Group fauna of BADL. CHCU is the least known of these, but recent inventorying there has uncovered significant vertebrate fossils in marine and terrestrial rocks (Varela et al., 2019).

Using the 19 mammal taxonomic categories ("unspecified mammals" omitted), the most diverse higher-level fossil

mammal records are found at the following:

- Big Bend NP (BIBE): 12
- Fossil Butte NM (FOBU): 11
- John Day Fossil Beds NM (JODA): 11
- Santa Monica Mountains NRA (SAMO): 11

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- Glen Canyon NRA (GLCA): 9
- Grand Canyon NP (GRCA): 9
- Potomac Heritage NST (POHE): 9
- Badlands NP (BADL): 8
- Carlsbad Caverns NP (CAVE): 8
- Channel Islands NP (CHIS): 8
- Guadalupe Mountains NP (GUMO): 8
- Hagerman Fossil Beds NM (HAFO): 8
- Niobrara National Scenic River (NIOB): 8
- Valley Forge NHP (VAFO): 8
- Wind Cave NP (WICA): 8

Many of these units are notable in the history of fossil mammal studies, such as BADL, HAFO, JODA, and NIOB. Others have diverse Quaternary cave records, such as CAVE, GLCA, GRCA, GUMO, POHE, WICA, and VAFO. While BIBE may not immediately come to mind when thinking of NPS units with mammal fossils, it has a stratigraphic record from the Upper Cretaceous to the Quaternary, capturing many stages in mammalian evolution. Exemplars of several North American land mammal ages (NALMAs) can be found at BADL (the Chadronian, Orellan, and Whitneyan NALMAs are based on the mammals of the White River Badlands) and AGFO ("Agate being most typical locality" of the Arikareean; Wood et al., 1941, p. 11).

Ichnofossils

In situ or reworked ichnofossils are documented in 143 NPS areas. Among this group are 9 units in the Washington, D.C. area whose only record is reworked Cambrian quartzite cobbles with *Skolithos* burrows, which seem to be ubiquitous in areas near the Potomac River. Ichnofossils are doubtless underreported, because many ichnofossils are inconspicuous and

not necessarily identifiable, even when observed. Some of them, though, are instantly obvious and are among the iconic fossils of the National Park Service; parks of the desert Southwest would not be the same without their dinosaur tracks, for example. Ichnofossils are particularly useful for educational purposes, because as examples of the activities of living organisms they can evoke the past for visitors in ways that most body fossils cannot.

By far the most frequently reported type of ichnofossil is invertebrate burrows and trails (101, in situ and reworked) (Fig. 8). Next are packrat middens (37), stromatolites and similar microbial trace fossils (33), vertebrate tracks (33), root traces (30), and "other ichnofossils" (30). Because of the broad definition of ichnofossils used here, "other ichnofossils" is a diverse assortment that captures types of traces such as plant molds and various invertebrate and vertebrate feeding traces.

Including only natural occurrences (in situ or reworked) of the 17 morphological categories (Table 4: "unspecified invertebrate trace fossils" and "unspecified trace fossils" are omitted), the NPS units with the most diverse ichnofossil records at this time are as follows:

- Grand Canyon NP (GRCA): 12
- Glen Canyon NRA (GLCA): 10
- Arches NP (ARCH): 9
- Badlands NP (BADL): 9
- Dinosaur NM (DINO): 9
- Big Bend NP (BIBE): 8
- Canyonlands NP (CÁNY): 8
- Death Valley NP (DEVA): 8
- Lake Mead NRA (LAKE): 8
- Yellowstone NP (YELL): 8

Aside from BADL, BIBE, and YELL, these parks are

located in a narrow corridor from northwestern Colorado to eastern California, and the Colorado River or Green River pass through almost all of them. These other seven parks share Paleozoic marine ichnofossils and late Quaternary terrestrial ichnofossils, and most also have terrestrial ichnofossils from the vast Pennsylvanian–Jurassic interior deserts. With sites and assemblages such as the Coconino Sandstone tracks of GRCA, the Copper Canyon beds of DEVA, Lower Jurassic dinosaur tracks from DINO to GLCA, and the dung caves of GLCA and GRCA, the ichnofossils at these parks are among the most significant in North America.

Other Fossils

There are reports of "other" fossils (in situ or reworked) at 115 parks (Fig. 9), although, as mentioned, this figure should be considered an undercount of the actual prevalence. Foraminiferans are by far the most frequently reported (64), surpassing the combined total of the next two groups (diatoms with 33 reports and miscellaneous "algae" with 28).

Including only natural occurrences (in situ or reworked) of the 15 taxonomic categories (Table 5: "unspecified fossils" omitted), the NPS units with the most diverse higher-level records of "other" fossils at this time are as follows:

- Death Valley NP (DEVA): 9
- Channel Islands NP (CHIS): 8
- Yellowstone NP (YELL): 8
- Santa Monica Mountains NRA (SAMO): 7
- Big Bend NP (BIBE): 6
- Everglades NP (EVER): 6
- Grand Canyon NP (GRCA): 6

Most of these NPS units share the presence of multiple productive marine formations and scientific interest in



FIGURE 8. Park records (in situ and reworked) of ichnofossil categories. Parks with both in situ and reworked records for a given category are only counted once.

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FIGURE 9. Park records (in situ and reworked) of "other" categories. Parks with both in situ and reworked records for a given category are only counted once.

microfossils.

Servicewide Taxonomic Summary

As mentioned previously, 235 units have at least one report of in situ or reworked fossils. Approximately a quarter of this total (64, or 27.2%) have records of only one or two types of fossils, which shows that the great majority of parks with natural occurrences of fossils have representatives of at least three groups (the average is 12.5 and the median is 8) (Table 5). Parks with occurrences of invertebrate or vertebrate body fossils tended to have more groups represented than plants, ichnofossils, or "other" fossils. In part, this can be attributed to the greater number of subdivisions for invertebrate and vertebrate body fossils. However, it is interesting to note that although plants, ichnofossils, and "other" fossils share a similar number of counted categories (15 for plants and "other," 17 for ichnofossils), approximately 72% of parks with "other" fossils recorded only one or two groups, while approximately 66% of parks with plant records and approximately 64% of parks with ichnofossils had similarly low diversity (Table 5). This is another indication of the relatively minimal exploration and reporting of "other" fossils, which are mostly microfossils.

A simple way of assessing the taxonomic richness of paleontological resources in NPS units is to observe which units have natural occurrences of fossils (in situ or reworked) from all five primary categories. Sixty-four units qualify under this metric. In the interest of space, these parks are denoted with underlines in the Appendix rather than listed. As a firstorder approximation, this includes many of the most notable fossiliferous units of the NPS, but some are omitted. For example, a park with mostly terrestrial rocks or cave paleontological resources may lack examples of the "other" primary category (e.g., Agate Fossil Beds NM, Tule Springs Fossil Beds NM, or Valley Forge NHP), while a park with mostly marine units or Paleozoic units may have a paucity of plants or vertebrates (e.g., Chesapeake & Ohio Canal NHP or Vicksburg National Military Park). On the other hand, some of the parks that are included may have only one instance of one or more primary categories, and therefore may not be as productive as their presence in the list might imply. For example, El Malpais NM and Montezuma

Castle NM both have occurrences of all five primary categories, but only have seven groups each.

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Another way to look at the question is to combine category tallies. Of course, strictly speaking the categories under the primary categories are not directly comparable. The vertebrates are divided at lower taxonomic levels than plants, invertebrates, or "other," and the ichnofossils are of necessity split using different criteria than the four primary categories of body fossils, producing categories which are not strictly "taxonomic." However, as before, this exercise makes for useful general observations. Combining all 128 of the subcategories used in the tallies above, the NPS units with the most diverse fossil records found as natural occurrences (in situ or reworked) at this time are as follows (Fig. 10):

- Grand Canyon NP (GRCA): 75
- Big Bend NP (BIBE): 66
- Yellowstone NP (YELL): 64 .
- Death Valley NP (DEVA): 57
- Channel Islands NP (CHIS): 54
- Glen Canyon NRA (GLCA): 53 •
- Dinosaur NM (DINO): 52 .
- Petrified Forest NP (PEFO): 52
- Santa Monica Mountains NRA (SAMO): 46
- Guadalupe Mountains NP (GUMO): 43
- Yukon-Charley Rivers NPRES (YÚCH): 43
- Grand Teton NP (GRTE): 41 .
- . Great Basin NP (GRBA): 40
- Lake Mead NRA (LAKE): 40
- Denali NP&PRES (DENA): 36 •
- Badlands NP (BADL): 35
- Mojave NPRÈS (MOJA): 35
- Wrangell-St. Elias NP&PRES (WRST): 35
- Arches NP (ARCH): 33
- Capitol Reef NP (CARE): 32
- Carlsbad Caverns NP (CAVE): 32
- . Chaco Culture NHP (CHCU): 32
- Golden Gate NRA (GOGA): 32
- Potomac Heritage NST (POHE): 32 •

TABLE 5. Summary of record distribution in the five primary taxonomic categories of NPS paleontological resources.

	PLANTS	INVERTEBRATES	VERTEBRATES	ICHNOFOSSILS	OTHER	OVERALL
# of parks	164	178	128	143	115	235
Counted groups	15	34	47	17	15	128
Average count	2.68	5.96	6.29	2.65	2.21	12.5
Median count	2	4	4	2	2	8
1 or 2 records	108	68	46	91	83	64
% 1 or 2	65.80%	38.20%	36.20%	63.60%	72.20%	27.20%

FIGURE 10. A map of the NPS units that have yielded the most diverse fossil records at high taxonomic levels. **1**, Arches NP (ARCH), Utah; **2**, Badlands NP, South Dakota; **3**, Big Bend NP (BIBE), Texas; **4**, Capitol Reef NP (CARE), Utah; **5**, Carlsbad Caverns NP (CAVE), New Mexico; **6**, Chaco Culture NHP (CHCU), New Mexico; **7**, Channel Islands NP (CHIS), California; **8**, Death Valley NP (DEVA), California–Nevada; **9**, Denali NP&PRES (DENA), Alaska; **10**, Dinosaur NM (DINO), Colorado–Utah; **11**, Glen Canyon NRA (GLCA), Arizona–Utah; **12**, Golden Gate NRA (GOGA), California; **13**, Grand Canyon NP (GRCA), Arizona; **14**, Grand Teton NP (GRTE), Wyoming; **15**, Great Basin NP (GRBA), Nevada; **16**, Guadalupe Mountains NP (GUMO), Texas; **17**, Lake Mead NRA (LAKE), Arizona–Nevada; **18**, Mojave NPRES (MOJA), California; **19**, Petrified Forest NP (PEFO), Arizona; **20**, Potomac Heritage NST (POHE), District of Columbia–Maryland–Pennsylvania–Virginia; **21**, Santa Monica Mountains NRA (SAMO), California; **22**, Wrangell-St. Elias NP&PRES (WRST), Alaska; **23**, Yellowstone NP (YELL), Idaho–Montana–Wyoming; and **24**, Yukon-Charley Rivers NPRES (YUCH).

This list includes all units with 32 or more categories, or at least one-quarter of the total. Again, a few notable fossil parks missed the cut, such as AGFO (18), FLFO (25), and HAFO (21). In some of these cases, significant diversity is found at lower taxonomic levels (within angiosperms and arthropods for FLFO), while in others the fossil record consists of great numbers of relatively few taxa (AGFO and HAFO).

All of these parks are located west of the Mississippi River except for POHE, and almost all of them are located, at least partially, in Alaska, Arizona, California, Texas, Utah, or Wyoming (Fig. 10). The most diverse records east of the Mississippi River, using these categories, are at POHE (32), Mississippi National River and Recreation Area (30) (if some latitude is permitted for crossing the Mississippi), Delaware Water Gap NRA (26), Cape Cod NS (25, with substantially more if cultural records are included), Mammoth Cave NP (25), and affiliated New Jersey Pinelands National Reserve (25).

The distribution of parks with notably diverse records reflects park size, diversity of sedimentary rocks and deposits, the presence of significant areas of exposed outcrops, and the focus of a park's purpose. Eastern parks have disadvantages in all of these factors. First, they are usually substantially smaller than western parks, because they often have to fit into a setting that has already been developed, and/or because they often commemorate discrete historical or cultural subjects instead of preserving large undeveloped tracts. Second, eastern geology is not as conducive to great diversity. The land between the Mississippi River and the Appalachians and from Tennessee north to the Canadian border has few formations of Mesozoic or pre-Quaternary Cenozoic age, and the Paleozoic rocks are predominantly marine, which eliminates much of the potential for diverse terrestrial plants and vertebrates outside of the Quaternary. A significant part of the bedrock of the Appalachian region is either heavily metamorphosed or igneous, so even though there are some large parks in the mountains (e.g., Great Smoky Mountains NP and Shenandoah NP), their fossiliferous potential is limited by their bedrock. Third, rocks in parks in the eastern half of the United States are frequently obscured by vegetation, surficial deposits, and/or historic/cultural resources (often the same resources that a park was created to protect or

recognize). Finally, as noted, many eastern parks are focused on historical/cultural subjects, so natural resources have received less attention. It is all but assured that more thorough exploration of available exposures would uncover additional occurrences and diversity, particularly where Paleozoic marine rocks are present.

Almost all of the 24 listed parks have lengthy geologic records, with three notable exceptions: the bedrock of CAVE and GUMO is limited to Permian rocks, and the bedrock of PEFO is almost entirely composed of various members of the Upper Triassic Chinle Formation. Diversity at CAVE and GUMO results from a combination of abundantly fossiliferous bedrock and productive Quaternary cave sites, while the Chinle Formation of PEFO contains practically as close to a complete terrestrial ecosystem as could be reasonably expected.

The most frequently reported groups (omitting "unspecified" categories) are dominated by invertebrates, primarily from marine settings (Fig. 11). Five of the 10 most frequently reported groups are groups of invertebrates represented by hard shells or other resistant body structures, while another is composed of trace fossils produced by invertebrates (invertebrate burrows), and yet another has frequently been lumped with fossil invertebrates (foraminiferans). These results are in accordance with the general wisdom that a combination of a marine environment and durable body structures that are not too large to be readily buried are best for producing fossils. Indeed, the other three groups (conifers, angiosperms, and artiodactyls) are almost always found as substantially incomplete specimens, such as pieces of wood, seeds, or teeth.

CONCLUSIONS

The development of the PSP has provided an opportunity

FIGURE 11. The most frequently reported fossil groups (in situ and reworked). Letters in parentheses represent the primary category: I=invertebrate body fossil, T=ichnofossil, P=plant, V=vertebrate body fossil, O=other fossil.

to synoptically assess the richness and distribution of NPS paleontological resources within and between parks. The PSP files, supplemented with the NPS Paleontology Archives & Library, allow rapid assessment of park records servicewide and make detailed analysis of specific topics much easier, as in thematic inventories. At least 277 official NPS units and affiliated areas have some kind of paleontological resources, and of that group 235 have confirmed in situ or reworked resources representing the history of life from the Proterozoic to the Quaternary. A wide variety of fossil organisms are represented at these parks, from abundant and well-represented groups such as bivalves and gastropods, to groups that are uncommon or very rare, such as sea stars (found at five parks) and brown algae (a single record, at SAMO, which is among the oldest known definite records of this group).

This exercise also offers some ideas for future investigations. For example, parks with "unidentified" resources are candidates for further exploration. Parks in the eastern half of the country also appear to be relatively understudied, as do occurrences of plants, ichnofossils, and microfossils. These three groups may not be as "charismatic" as large fossil vertebrates, or as easily studied as the fossils of marine invertebrates, but they are key elements to understanding ancient life and paleoenvironments as a whole. Microscopic fossils such as pollen and spores, phytoliths, ostracode shells, and the tests of various groups of protists are also of interest for reconstructing the recent past at parks, and thus can be very useful for park management of other resources. With the PSP framework for incorporating new discoveries, the numbers presented above can be expected to increase with additional research.

Despite biases as described above, in what is known and what has been collected and studied, the fossil record of the NPS encompasses a significant cross-section of North American paleontology. Furthermore, the public visibility of the NPS makes it an excellent venue for educating the public about paleontology. Tools like the PSP improve our ability to gather and find relevant information, which can then be used to improve paleontological resource management, support scientific investigation, and share with the public, fulfilling our operational mandates.

ACKNOWLEDGMENTS

Our data set is a monument to the innumerable contributions, large and small, of generations of geoscientists, park staff, and interested members of the public. Every piece has its place in the vast mosaic that is the history of past life associated with National Park Service lands and the world as a whole, of which this report is barely a thumbnail icon. In lieu of attempting to individually account for everyone who could be mentioned, we would like to acknowledge our frequent collaborators since 2012, the year the PSP was initiated: Arvid Aase, Larry Agenbroad, Mike Antonioni, Madison Armstrong, Ben Becker, Gorden Bell, Rachel Benton, Kim Besom, Chuck Bitting, Robert Blodgett, Bobby Boessenecker, Dave Bohaska, Aubrey Bonde, Diana Boudreau, Clint Boyd, Mike Bozek, David Bustos, Denny Capps, Mary Carpenter, Jennifer Cavin, Mackenzie Chriscoe, Erica Clites, Ronnie Colvin, Tim Connors, Don Corrick, Ted Daeschler, Don DeBlieux, John Dennis, Kara Deutsch, Jeff Eaton, Erin Eichenberg, Will Elder, Dave Elliott, Emmett Evanoff, Nick Famoso, Matt Ferlicchi, Ron Fields, Tony Fiorillo, Terry Fisk, John Foster, David Fox, Bert Frost, Dorothy Geyer, Dave Gillette, Janet Gillette, Stephen Godfrey, William Harrison, David Hays, Robyn Henderek, James Hill, Ann Hitchcock, J. P. Hodnett, Jonathan Hoffman, John Hoganson, Kathy Hollis, Rod Horrocks, Jeff Hungerford, Robert Hunt, Adrian Hunt, ReBecca Hunt-Foster, Colleen Hyde, Beth Johnson, Jason Kenworthy, Ron Kerbo, Jim Kirkland, Cassie Knight, Amnesty Kochanowski, Aliera Konett, Alysia Korn,

Scott Kottkamp, Bruce Lander, Lisa Leap, Seth Lerman, Elaine Leslie, Martin Lockley, Rowan Lockwood, Katie Loughney, Denise Louie, Spencer Lucas, Scott Madsen, Adam Marsh, Blake McCann, Lindsay McClelland, Greg McDonald, Eathan McIntyre, Jim Mead, Herb Meyer, Anne Miller, Matt Miller, Andrew Milner, Alison Mims, Ariana Miranda, Gary Morgan, Don Morris, Amy Muraca, Mark Nebel, Margot Nelson, Megan Norr, Torrey Nyborg, Noel Osborn, Darrin Pagnac, Bill Parker, Dave Parris, Lillian Pearson, Jeff Pigati, Kari Prassack, Chris Racay, Jeff Rasic, Maria Rodriguez, Nancy Russell, Charles Salcido, George San Miguel, Mark Sappington, Chris Schierup, Cindy Schraer, Eric Scott, Sally Shelton, Dennis Skidds, Matthew Smith, Dave Soller, Earle Spamer, John Spence, Melanie Spoo, Kathleen Springer, Nancy Stamm, Ellen Starck, Tim Sveum, Mark Szydlo, Emily Thorpe, Alaina Tocci, Rick Toomey, Phil Varela, George Veni, Christy Visaggi, Don Weeks, Robert Weems, Ed Welsh, Steve Wick, Klara Widrig, Patrick Wilson, Jack Wood, and Jim Wood. For Fig. 1, Mackenzie Chriscoe supplied the photo of Chesapecten and Rick Toomey supplied the shark photo.

REFERENCES

- Department of Interior, 2000, Report to Congress by the Secretary of Interior: Assessment of Fossil Management on Federal and Indian Lands: U.S. Government Printing Office, 50 p.
- Kenworthy, J.P., and Santucci, V.L., 2006, A preliminary investigation of National Park Service paleontological resources in cultural context: Part 1, general overview: New Mexico Museum of Natural History and Science, Bulletin 34, p. 70-76.
- Mead, J.I., Tweet, J.S., Santucci, V.L., Rasic, J.T., and Holte, S.E., 2020, Proboscideans from US National Park Service lands: Eastern Paleontologist 6, p. 1-48.
- Norr, M.R., Santucci, V.L., and J.S. Tweet, J.S., 2016, An inventory of trilobites from National Park Service areas: New Mexico Museum of Natural History and Science, Bulletin 74, p. 179-203.
- Santucci, B.A., Moneymaker, C., Lisco, J.F., and Santucci, V.L., in press, An overview of paleontological resources preserved within prehistoric and historic structures: New Mexico Museum of Natural History and Science, Bulletin 82..

- Santucci, V.L., 1998, The Yellowstone Paleontological Survey: Yellowstone Center for Resources, YCR-NR-98-1, 54 p.
- Santucci, V.L., Tweet, J., Bustos, D., Nyborg, T., and Hunt, A.P., 2014, An inventory of Cenozoic fossil vertebrate tracks and burrows in National Park Service areas: New Mexico Museum of Natural History and Science, Bulletin 62, p. 469-488.
- Santucci, V.L., Newman, P., and Taff, B.D., 2016. Toward a conceptual framework for assessing the human dimensions of paleontological resources: New Mexico Museum of Natural History and Science, Bulletin 74, p. 239-248.
- Santucci, V.L., Tweet, J.S., and Connors, T.B., 2018, The Paleontology Synthesis Project and establishing a framework for managing National Park Service paleontological resource archives and data: New Mexico Museum of Natural History and Science, Bulletin 79, p. 589-601.
- Schraer, C.D., Schraer, D.J., Tweet, J.S., Blodgett, R.B., and Santucci, V.L., in press, An inventory of belemnites documented in US National Parks in Alaska: New Mexico Museum of Natural History and Science, Bulletin 82.
- Tweet, J.S., and Santucci, V.L., 2015, An inventory of Mesozoic mammals and non-mammalian therapsids in National Park Service Areas: New Mexico Museum of Natural History and Science, Bulletin 68, p. 297-302.
- Tweet, J.S., and Santucci, V.L., 2018, An inventory of non-avian dinosaurs from National Park Service Areas: New Mexico Museum of Natural History and Science, Bulletin 80, p. 5-34.
- Tweet, J.S., Santucci, V.L., and McDonald, H.G., 2016, Name-bearing fossil type specimens and species named from National Park Service areas: New Mexico Museum of Natural History and Science, Bulletin 74, p. 277-288.
- Varela, P.J., Santucci, V.L., and Tweet, J.S., 2019, Chaco Culture National Historical Park: Paleontological resources inventory (non-sensitive version). National Park Service Natural Resource Report NPS/CHCU/NRR—2019/1915, 118 p.
- Wood, H.E., II, Chaney, R.W., Clark, J. Colbert, E.H., Jepsen, G.L., Reeside, J.B., Jr., and Stock, C., 1941, Nomenclature and correlation of the North American continental Tertiary: Bulletin of the Geological Society of America, v. 52, p. 1-48.

APPENDIX

List of 277 NPS units and affiliated units, organized by unified DOI regions, in which fossils occur in situ within a geologic context, in museum collections, and/or within a cultural resource context. Asterisks (*) identify the 18 NPS units that include paleontological resources in their enabling legislation or proclamation. Units marked with a dagger (†) are affiliated units. Underlined units have in situ or reworked occurrences of all five primary categories. A small number of parks cross regions; they are included in the region where their headquarters are located. The unified DOI regions were established in 2019 and supersede previous NPS regions.

Region 1a: North Atlantic – Appalachian (40)

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ABLI	Abraham Lincoln Birthplace National Historic Site
ACAD	Acadia National Park
ALPO	Allegheny Portage Railroad National Historic Site
APPA	Appalachian National Scenic Trail
ASIS	Assateague Island National Seashore
BLUE	Bluestone National Scenic River
BOHA	Boston Harbor Islands National Recreation Area
CACO	Cape Cod National Seashore
CANE	Camp Nelson National Monument
COLO	Colonial National Historical Park
CUGA	Cumberland Gap National Historical Park
DEWA	Delaware Water Gap National Recreation Area
FIIS	Fire Island National Seashore
FODO	Fort Donelson National Battlefield
FOMC	Fort McHenry National Monument & Historic Shrine
FOMR	Fort Monroe National Monument
FONE	Fort Necessity National Battlefield
FOST	Fort Stanwix National Monument
FRSP	Fredericksburg & Spotsylvania National Military Park
GARI	Gauley River National Recreation Area
GATE	Gateway National Recreation Area
GETT	Gettysburg National Military Park
GEWA	George Washington Birthplace National Monument
HATU	Harriet Tubman Underground Railroad National Monument
HOFU	Hopewell Furnace National Historic Site
INDE	Independence National Historical Park
KAWW	Katahdin Woods and Waters National Monument*
MABI	Marsh-Billings-Rockefeller National Historical Park
MACA	Mammoth Cave National Park
NERI	New River Gorge National River
PETE	Petersburg National Battlefield
PINE	New Jersey Pinelands National Reserve [†]
POHE	Potomac Heritage National Scenic Trail
RICH	Richmond National Battlefield Park
ROVA	Roosevelt-Vanderbilt National Historic Sites
SARA	Saratoga National Historical Park
SHEN	Shenandoah National Park
SPAR	Springfield Armory National Historic Park
EDIS	Thomas Edison National Historical Park
UPDE	Upper Delaware Scenic and Recreational River
VAFO	Valley Forge National Historical Park

Region 1b: National Capital (26)

ANAC	Anacostia Park
ANTI	Antietam National Battlefield
BAWA	Baltimore-Washington Parkway
CHOH	Chesapeake & Ohio Canal National Historical Park
FODU	Fort Dupont Park
FOFO	Fort Foote Park
FOWA	Fort Washington Park
FRDO	Frederick Douglas National Historic Site
GWMP	George Washington Memorial Parkway
GREE	Greenbelt Park
HAFE	Harpers Ferry National Historical Park
LINC	Lincoln Memorial
MANA	Manassas National Battlefield Park
MLKM	Martin Luther King, Jr. Memorial
MONO	Monocacy National Battlefield

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	NAMA	National Mall & Memorial Parks
	OXHI	Oxon Cove Park/Oxon Hill Farm
	OXRU	Oxon Run Parkwav†
	PISC	Piscataway Park
	PRWI	Prince William Forest Park
	ROCR	Rock Creek Park
	SUIT	Suitland Parkway
	THIS	Theodore Roosevelt Island
	THIF	Thomas Jefferson Memorial
	WAMO	Washington Monument
	WHHO	White House – President's Park
	Region 2: South Atla	antic = Gulf(34)
	BICY	Big Cypress National Preserve
	BISC	Biscovne National Park
	BISO	Big South Fork National River and Recreation Area
	BIBI	Blue Ridge Parkway
		Buck Island Deef National Monument
	CANA	Canaveral National Seashore
	САНА	Cana Veral National Seashore
		Cape Lookout National Seashore
	CARI	Carl Sandherg Home National Historic Site
	CASA	Castilla de San Marcos National Monument
	СНСИ	Chickamauga & Chattanaaga National Military Park
	CONG	Congarae National Park
		Cumberland Island National Seashore
	DESO	De Soto National Memorial
	DESC	Dry Tortugas National Park
	EVED	Everalades National Dark
	EVER	Evelgiaues National Monument
	FORK	Fort Materica National Monument
	FORIA	Fort Pulaski National Monument
		Fort Palaigh National Historia Site
	FORA	Fort Sumter National Monument
	CDSM	Creat Smalty Mountaing National Dark
	CLUS	Culf Islands National Sooshare
		Little Diver Conven National Dresonue
	LINI	Magnag Craals National Dattlafield
	ODED	Obad Wild and Saamia Divan
	OCMU	Obed wild and Scenic River
		Duragell Cave National Monument
	KUCA CADI	Russen Cave National Monument
	SAKI	Salt Kiver National Historical Park & Ecological Preserve
	STIL	Stance Diver National Dattlefald
		Siones River National Dattieneru
		The second
		Virgin Islanda National Dark
	v 115	virgin Islands National Park

Region 3: Great Lakes (14)

APĪS	Apostle Islands National Lakeshore
CUVA	Cuyahoga Valley National Park
HOCU	Hopewell Culture National Historical Park
IATR	Ice Age National Scenic Trail/Scientific Reserve*
INDU	Indiana Dunes National Lakeshore
ISRO	Isle Royale National Park
LIBO	Lincoln Boyhood National Memorial
LIHO	Lincoln Home National Historic Site
MISS	Mississippi National River & Recreation Area
PEVI	Perry's Victory & International Peace Memorial
PIRO	Pictured Rocks National Lakeshore
SACN	Saint Croix National Scenic River
SLBE	Sleeping Bear Dunes National Lakeshore
VOYA	Voyageurs National Park

Region 4: Mississippi Basin (14)

BRCR	Brices Cross Roads National Battlefield Site
BUFF	Buffalo National River
EFMO	Effigy Mounds National Monument

Fort Smith National Historic Site
George Washington Carver National Monument
Herbert Hoover National Historic Site
Hot Springs National Park
Gateway Arch National Park
Natchez Trace Parkway
Ozark National Scenic Riverways
Pea Ridge National Military Park
Ulysses S Grant National Historic Site
Vicksburg National Military Park
Wilson's Creek National Battlefield

Region 5: Missouri Basin (16)

AGFO	Agate Fossil Beds National Monument*
BADL	Badlands National Park
CHRO	Chimney Rock National Historic Site [†]
FOLS	Fort Larned National Historic Site
FOSC	Fort Scott National Historic Site
FOUS	Fort Union Trading Post National Historic Site
JECA	Jewel Cave National Monument
KNRI	Knife River Indian Villages National Historic Site
LECL	Lewis & Clark National Historic Trail
LIBI	Little Bighorn Battlefield National Monument
MNRR	Missouri National Recreational River
NIOB	Niobrara National Scenic River
SCBL	Scotts Bluff National Monument
TAPR	Tallgrass Prairie National Preserve
THRO	Theodore Roosevelt National Park
WICA	Wind Cave National Park

Region 6: Arkansas – Rio Grande – Texas – Gulf (12)

Alibates Flint Quarry National Monument
Amistad National Recreation Area
Big Bend National Park
Big Thicket National Preserve
Chickasaw National Recreation Area
Guadalupe Mountains National Park
Lake Meredith National Recreation Area
Padre Island National Seashore
Palo Alto Battlefield National Historic Site
Rio Grande Wild and Scenic River
San Antonio Missions National Historical Park
Waco Mammoth National Monument*

Region 7: Upper Colorado Basin (43)

ARCH	Arches National Park
AZRU	Aztec Ruins National Monument
BAND	Bandelier National Monument
BEOL	Bent's Old Fort National Historic Site
BICA	Bighorn Canyon National Recreation Area
BLCA	Black Canyon of the Gunnison National Park
BRCA	Bryce Canyon National Park
CANY	Canyonlands National Park
CARE	Capitol Reef National Park
CAVE	Carlsbad Caverns National Park
CEBR	Cedar Breaks National Monument
CHCU	Chaco Culture National Historical Park
COLM	Colorado National Monument
CURE	Curecanti National Recreation Area
DETO	Devil's Tower National Monument
DINO	Dinosaur National Monument*
ELMA	El Malpais National Monument
ELMO	El Morrow National Monument
FLFO	Florissant Fossil Beds National Monument*
FOBU	Fossil Butte National Monument*
FOLA	Fort Laramie National Historic Site
GICL	Gila Cliff Dwellings National Monument
GOSP	Golden Spike National Historic Site

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GRSA	Great Sand Dunes National Park and Preserve
GRTE	Grand Teton National Park
HOVE	Hovenweep National Monument
JODR	John D. Rockefeller, Jr. Memorial Parkway
MEVE	Mesa Verde National Park
NABR	Natural Bridges National Monument
OREG	Oregon National Historic Trail
PECO	Pecos National Historical Park
PETR	Petroglyphs National Monument
PISP	Pipe Spring National Monument
RABR	Rainbow Bridge National Monument
ROMO	Rocky Mountain National Park
SAFE	Santa Fe National Historic Trail
SAPU	Salinas Pueblo Missions National Monument
TICA	Timpanogos Cave National Monument
VALL	Valles Caldera National Preserve
WHSA	White Sands National Park*
YELL	Yellowstone National Park
YUHO	Yucca House National Monument
ZION	Zion National Park*

Region 8: Lower Colorado Basin (28)

CABR	Cabrillo National Monument
CACH	Canyon de Chelly National Monument
CAGR	Casa Grande Ruins National Monument
CHIR	Chiricahua National Monument
CHIS	Channel Islands National Park*
CORO	Coronado National Memorial
FOBO	Fort Bowie National Historic Site
GLCA	Glen Canyon National Recreation Area
GRCA	Grand Canyon National Park
HUTR	Hubbell Trading Post National Historic Site
JOTR	Joshua Tree National Park*
LAKE	Lake Mead National Recreation Area
MANZ	Manzanar National Historic Site
MOCA	Montezuma Castle National Monument
MOJA	Mojave National Preserve
NAVA	Navajo National Monument
ORPI	Organ Pipe Cactus National Monument
PARA	Grand Canyon-Parashant National Monument*
PEFO	Petrified Forest National Park*
PIMA	Hohokam Pima National Monument
SAGU	Saguaro National Park
SAMO	Santa Monica Mountains National Recreation Area
TONT	Tonto National Monument
TUMA	Tumacacori National Historical Park
TUSK	Tule Springs Fossil Beds National Monument*
TUZI	Tuzigoot National Monument
WACA	Walnut Canyon National Monument
WUPA	Wupatki National Monument

Region 9: Columbia - Pacific Northwest (15) CIÃO City of Rocks National Reserve CRMO Craters of the Moon National Monument and Preserve Ebey's Landing National Historical Reserve EBLA Fort Vancouver National Historic Site FOVA **GLAC** Glacier National Park Hagerman Fossil Beds National Monument* HAFO John Day Fossil Beds National Monument* JODA LARO Lake Roosevelt National Recreation Area LEWI Lewis & Clark National Historical Park MORA Mount Rainier National Park Nez Perce National Historical Park NEPE NOCA North Cascades National Park OLYM **Olympic National Park** ORCA Oregon Caves National Monument SAJH San Juan Island National Historical Park

<u>Region 10: California – Great Basin (14)</u>

Crater Lake National Park
Death Valley National Park*
Golden Gate National Recreation Area
Great Basin National Park
John Muir National Historic Site
Lava Beds National Monument
Lassen Volcanic National Park
Pinnacles National Monument
Point Reyes National Seashore
Redwood National and State Parks
Sequoia and Kings Canyon National Parks
Whiskeytown National Recreation Area
Yosemite National Park

Region 11: Alaska (16)

ALEU	Aleutian World War II National Historic Area†
ANIA	Aniakchak National Monument and Preserve
BELA	Bering Land Bridge National Preserve*
CAKR	Cape Krusenstern National Monument
DENA	Denali National Park and Preserve
GAAR	Gates of the Arctic National Park and Preserve
GLBA	Glacier Bay National Park and Preserve
KATM	Katmai National Park and Preserve
KEFJ	Kenai Fjords National Park
KLGO	Klondike Gold Rush National Historical Park
KOVA	Kobuk Valley National Park
LACL	Lake Clark National Park and Preserve
NOAT	Noatak National Preserve
SITK	Sitka National Historical Park
WRST	Wrangell-St. Elias National Park and Preserve
YUCH	Yukon-Charley Rivers National Preserve*

Region 12: Pacific Islands (5)

HALE	Haleakala National Park
HAVO	Hawaii Volcanoes National Park
PUHO	Pu' Uhonua o Honaunau National Historic Park
VALR	Pearl Harbor National Memorial
WAPA	War in the Pacific National Historical Park

