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Chapter 11. 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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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 discussion 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 et al. 1997; Anderson et al. 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 Geology and Stratigraphy chapter in this report 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. 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 et al. (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 et al. 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 et al. 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 et al. 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 et al. 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 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 et al. 2018), with individual sinkholes tied to multiple springs. Springs on either side of the Colorado River have distinct flow patterns (Tobin et al. 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 et al. 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 11-1) (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 11-2).

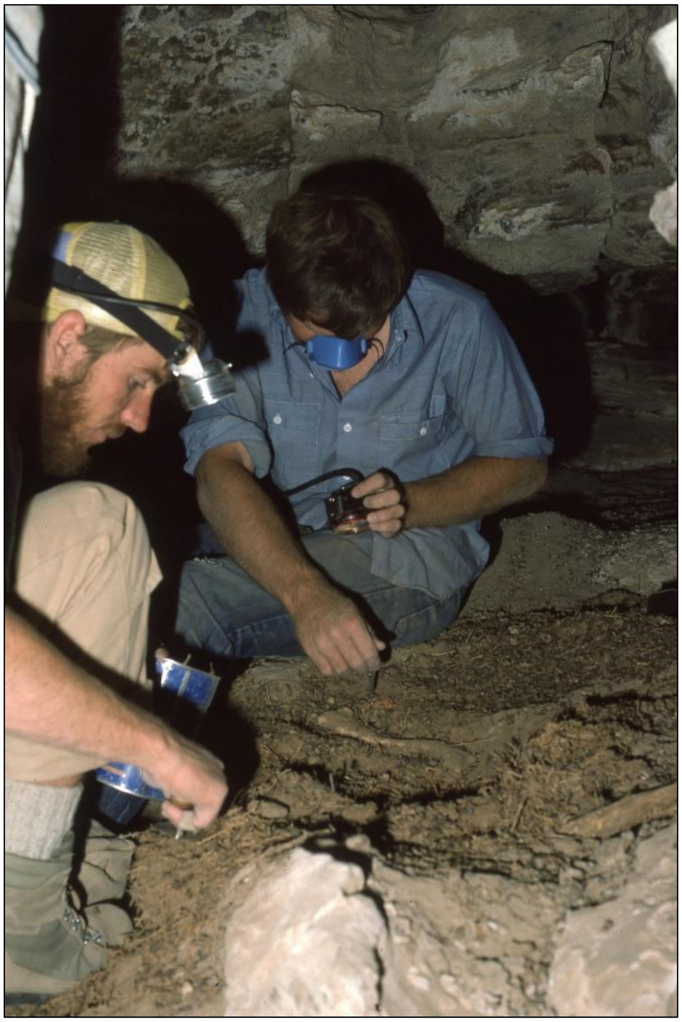

Figure 11-1. Steve Emslie (right) and Larry Coats (left) excavating a condor (*Gymnogyps*) nest and skeletal remains reclaimed by a packrat and made into a midden, Sandblast Cave, 1984 (EMILEE MEAD).

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 such as Stanton's Cave (Dryer 1994), Little Nankoweap Canyon (Mead et al. 2003), Chuar (Cole 1982, 1990), Hance Canyon and Horseshoe Mesa (Cole 1982, 1990), and Rampart Cave, Vulture Cave, and surrounding canyons (Phillips and Van Devender 1974; Mead and Phillips 1981; Phillips 1984; Spaulding 1990).

Figure 11-2. A juvenile extinct Harrington's mountain goat (*Oreamnos harringtoni*) skull in a packrat midden, Stevens Cave, 1984 (EMILEE MEAD).

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 et al. 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 11-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 typically underrepresenting the graze species such as the grasses. Although equally as well-preserved as the macrobotanical fossil, pollen remains from the region have been less frequently utilized for paleoenvironmental reconstructions.

Martin et al. (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 et al. 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 et al. (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 et al. 2002). The record of Pleistocene arthropods is restricted to those fossils recovered from dry-preserved packrat midden and cave sediment localities (Elias et al. 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 et al. 1992).

Vertebrates

The recovery and study of vertebrates from the GC is much more voluminous and well understood than the invertebrates. Appendix 11-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 11-3). 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 et al. 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.

Figure 11-3. A mummified myotid bat at its last perch among the gypsum crystals in Double Bopper Cave (NPS/SHAWN THOMAS).

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 11-4). 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 et al. 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).

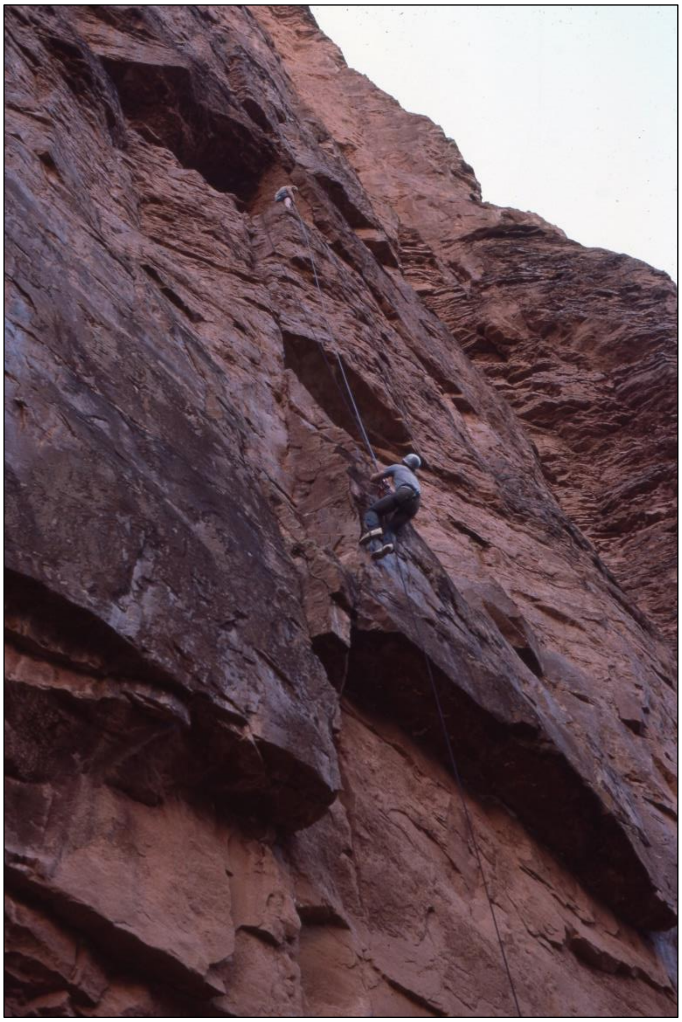

Figure 11-4. Ascending into Skylight Cave, 1984 (EMILEE MEAD).

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 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 et al. 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 et al. 1986; 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.; drift wood at the base of the sediments dated to > 35,000 years old (Robbins et al. 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 11-5) which is a grouping of crevices and tunnels (Emslie 1988). Excavations produced important data about the condor (*Gymnogyps californianus*, including a preserved nest; Figure 11-1) 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 et al. 2003). Other caves with fossils in the corridor stretch include Skylight (Figure 11-4) 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 et al. 2003).

Figure 11-5. Close-up of the entrance to Sandblast Cave showing the series of openings, 1984 (EMILEE MEAD).

Little Nankoweap

The Little Nankoweap drainage is known to have countless caves, many containing important archaeological and paleontological remains (Emslie et al. 1987; Mead and Lawler 1994; Emslie et al. 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 11-6) 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 et al. 2008) and faunal remains (Carpenter and Mead 2000; Mead et al. 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 11-7), 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 et al. 2003).

Figure 11-6. Stevens Cave entrance located high on the cliff face of the Redwall Limestone, 1984 (EMILEE MEAD).

Figure 11-7. 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).

Hance Canyon and Horseshoe Mesa

A series of packrat middens from Bida Cave were described by Cole (1981, 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 et al. 1986; Mead, Martin et al. 1986; Mead and Lawler 1994). The cave is extensive, with the lower 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 1981). *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 et al. 1986).

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 (1981, 1990) 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".

Only Kaetan Cave ("prayer stick cave"; Figure 11-8) in this area is fairly well studied; it is a small cavern with abundant archaeological material in the entrance chamber (Schwartz et al. 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 figures, Schwartz et al. (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).

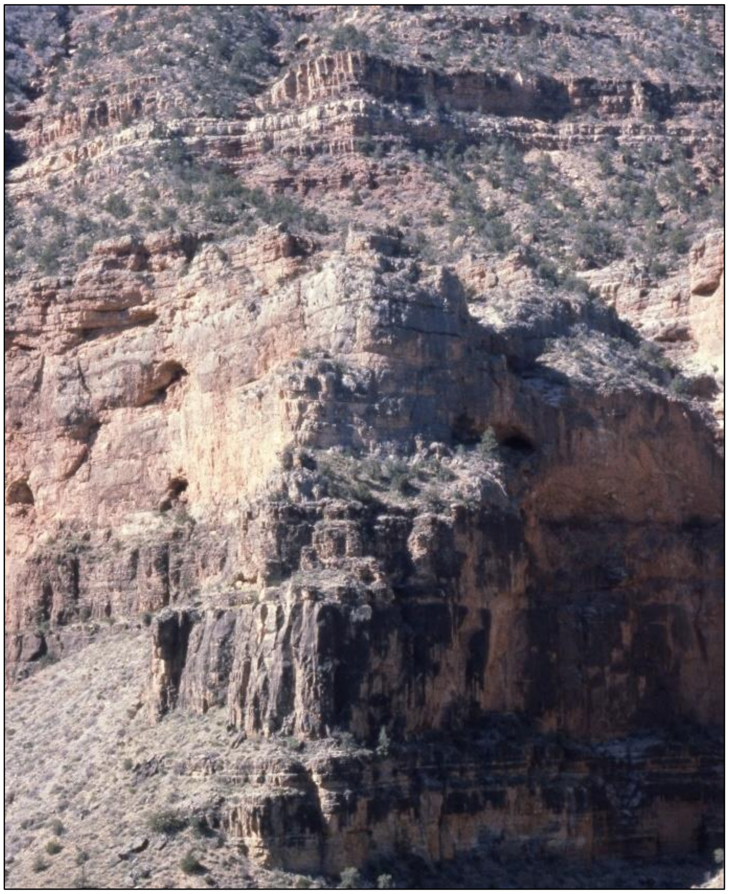

Figure 11-8. Entrance to Kaetan Cave, 1980 (JIM MEAD).

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 11-9). Difficult to access and largely hidden from view, the 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 et al. 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.

Figure 11-9. The two main entrances to Double Bopper Cave. Only the best of climbers and fliers can enter the cave via these entrances. Note that the green dot below the right entrance is a person entering the cave (NPS/SHAWN THOMAS).

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 11-3).

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 11-10) but have not been radiocarbon dated yet. Other skeletonized specimens have yet to be fully assessed, including one gray fox (*Urocyon cinereoargenteus*; Figure 11-11). Inventory and carbon dating continue for paleontological resources in Double Bopper Cave.

Figure 11-10. 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 11-11. An articulated gray fox skeleton (not radiocarbon dated) from Double Bopper Cave (NPS/SHAWN THOMAS).

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 during 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 11-12). 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). Martin et al. (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 et al. 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 (2004). 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 et al. 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 been published at this time (Mead et al. 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).

Figure 11-12. Rampart Cave in the 1930s. **A.** Photograph by the CCC (Civilian Conservation Corp) of the Shasta 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 sloth skeleton from the dung deposit in the 1930s.

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 to the recovery of the details. Any cave or shelter with the occurrence of split-twig figures (e.g., Farmer and deSaussure 1955; Emslie et al. 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 figures 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 (1986), and Janetski et al. 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 et al. (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 et al. 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 et al. 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 11-13 shows diagrammatically the inferred elevational distribution of plant communities in and adjacent to the GC 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 et al. 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 et al. 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.

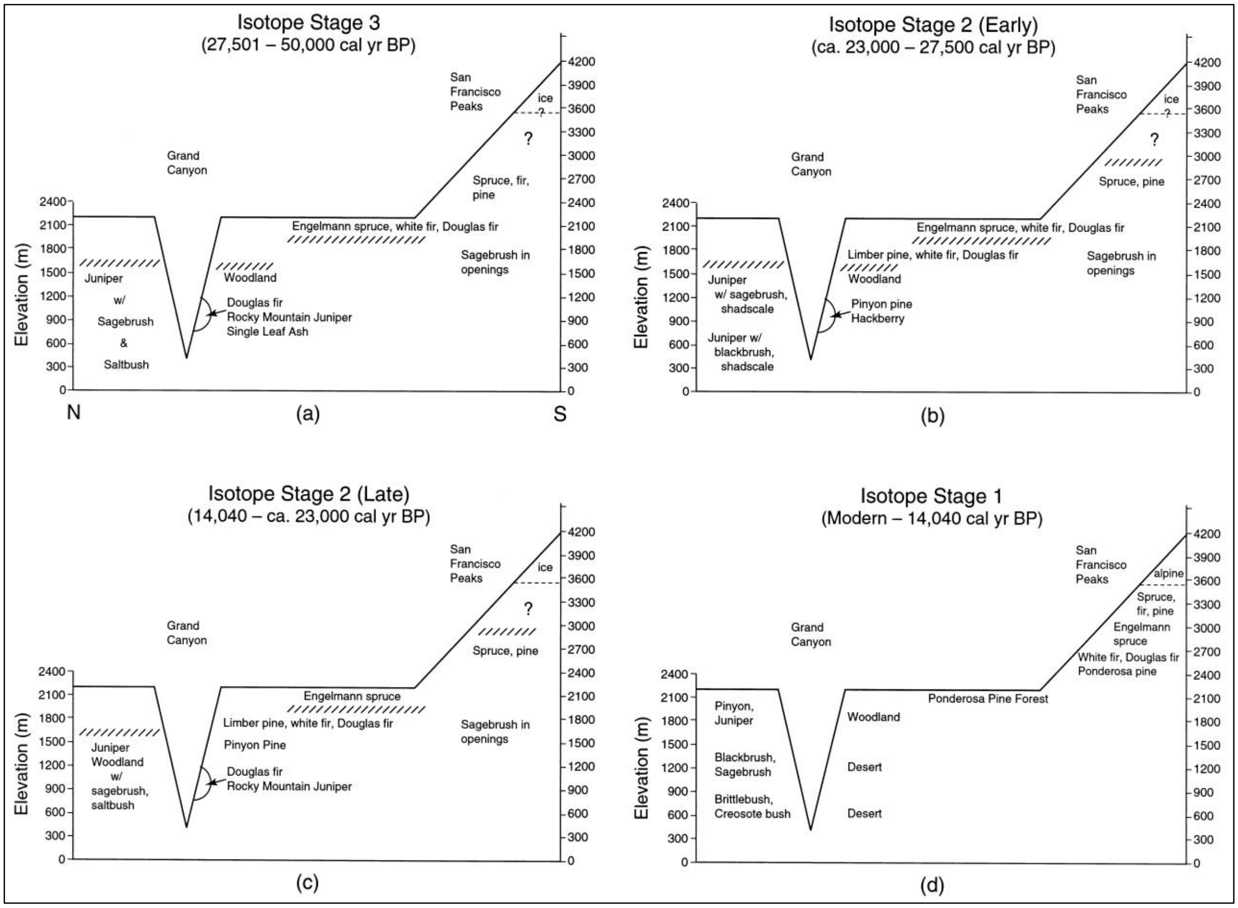

Figure 11-13. Inferred elevational distribution of plant communities within and adjacent to the Grand Canyon during the most recent 50,000 years. Cross-section is a line oriented from the San Francisco Peaks north through the Grand Canyon to the North Rim region (Anderson et al. 2000: Figure 8).

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Appendix 11-A. Grand Canyon Ice Age Taxa

The following tables list plants and animals reported from various Ice Age localities in the greater Grand Canyon (GC), Arizona. Almost all reports are of localities within Grand Canyon National Park (GRCA) itself, although a few localities are just outside of the park (e.g., some mollusks from Kaufman et al. 1992). The tables are set up taxonomically and refer to the publication(s) that discuss each taxon. The publications are included in “Literature Cited”. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Plants

Ice Age plant taxa reported from the Grand Canyon are listed in Appendix Table 11-A-1.

Appendix Table 11-A-1. Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Polypodiopsida	Equisetaceae	*Equisetum* sp	Hansen 1978, Robbins et al. 1984
	Pteridaceae	*Adiantum capillus-veneris*	Laudermilk and Munz 1938
	Pteridaceae	*Adiantum* sp	Hansen 1978, Robbins et al. 1984
Gnetophyta	Ephedraceae	*Ephedra nevadensis*	Laudermilk and Munz 1938, Hansen 1978
	Ephedraceae	*Ephedra nevadensis*/*viridis*	Cole 1985
	Ephedraceae	*Ephedra torreyana*	Robbins et al. 1984, Dryer 1994
	Ephedraceae	*Ephedra viridis*	Cole and Mead 1981
	Ephedraceae	*Ephedra* cf. *E. nevadensis*	Long et al. 1974, Phillips and Van Devender 1974
	Ephedraceae	*Ephedra* sp.	Euler 1978, Mead and Phillips 1981, Hevly 1984, Phillips 1984, Robbins et al. 1984, O’Rourke and Mead 1985, Cole 1990, Dryer 1994

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Pinophyta	Cupressaceae	*Juniperus communis*	Cole 1990, Coats 1997, Coats et al. 2008
	Cupressaceae	*Juniperus monosperma*	Coats et al. 2008
	Cupressaceae	*Juniperus monosperma* and/or *J. osteosperma*	Phillips and Van Devender 1974
	Cupressaceae	*Juniperus osteosperma*[1]	Hansen 1978, Cole and Mead 1981, Cole 1982, Cole 1990, Coats 1997, Coats et al. 2008, Cole et al. 2013
	Cupressaceae	*Juniperus scopulorum*	Dryer 1994, Coats 1997
	Cupressaceae	*Juniperus* cf. *J. monosperma*	Cole 1985, Cole 1990
	Cupressaceae	*Juniperus* cf. *J. osteosperma*	Cole 1985, O'Rourke and Mead 1985
	Cupressaceae	*Juniperus* sp.	Martin et al. 1961, Van Devender and Mead 1976, Van Devender et al. 1977, Euler 1978, Mead et al. 1978, Mead et al. 1986, Mead and Phillips 1981, Cole 1982, Ferguson 1984, Hevly 1984, Phillips 1984, O'Rourke and Mead 1985, Dryer 1994, Cole et al. 2013
	Cupressaceae	Cupressaceae undetermined	Hansen 1978
	Pinaceae	*Abies concolor*	Mead et al. 1978, Cole and Mead 1981, Cole 1985, Cole 1990, O'Rourke and Mead 1985, Cole et al. 2013
	Pinaceae	*Abies* sp	O'Rourke and Mead 1985, Mead et al. 1986, Dryer 1994
	Pinaceae	*Picea engelmannii*	Cole 1985
	Pinaceae	*Picea engelmannii/pungens*	Cole 1990
	Pinaceae	*Picea* cf. *P. pungens*	Dryer 1994
	Pinaceae	*Picea* sp.	Euler 1978, Cole and Mead 1981, Cole 1982, Hevly 1984, O'Rourke and Mead 1985, Mead et al. 1986
	Pinaceae	*Pinus* cf. *P. contorta*	O'Rourke and Mead 1985
	Pinaceae	*Pinus edulis*	Van Devender and Spaulding 1979, Cole and Mead 1981, Ferguson 1984, Cole 1990, Dryer 1994, Cole et al. 2013
	Pinaceae	*Pinus* cf. *P. edulis* (late Holocene)	O'Rourke and Mead 1985
	Pinaceae	*Pinus edulis* var. *fallax*	Cole et al. 2013

[1] *Juniperus californicus* var. *osteosperma* = *Juniperus osteosperma*

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Pinophyta (continued)	Pinaceae	*Pinus flexilis*	Cole and Mead 1981, Cole 1982, Cole 1985, Cole 1990, Van Devender et al. 1985, Coats 1997, Coats et al. 2008
	Pinaceae	*Pinus* cf. *P. flexilis*	O'Rourke and Mead 1985
	Pinaceae	*Pinus monophylla*	Van Devender and Spaulding 1979
	Pinaceae	*Pinus ponderosa*	Cole 1982, Cole 1985, Cole 1990, O'Rourke and Mead 1985
	Pinaceae	*Pinus* sp.	Euler 1978, Hevly 1984, O'Rourke and Mead 1985, Mead et al. 1986, Coats 1997
	Pinaceae	*Pseudotsuga menziesii*	Euler 1978, Mead et al. 1978, Cole and Mead 1981, Cole 1982, Cole 1985, Cole 1990, Ferguson 1984, O'Rourke and Mead 1985, Dryer 1994, Coats 1997, Coats et al. 2008
	Pinaceae	*Pseudotsuga* sp.	O'Rourke and Mead 1985, Mead et al. 1986
Magnoliophyta	Amaranthaceae	*Amaranthus* cf. *A. palmeri*	Coats 1997
	Amaranthaceae	*Amaranthus* sp.	Long et al. 1974
	Amaranthaceae	*Amaranthus* spp.	Hansen 1978
	Amaranthaceae	*Atriplex confertifolia*	Van Devender and Mead 1976, Van Devender et al. 1977, Van Devender and Spaulding 1979, Cole and Mead 1981, Mead and Phillips 1981, Cole 1982, Cole 1985, Cole 1990, Phillips 1984, Dryer 1994, Coats 1997
	Amaranthaceae	*Atriplex* cf. *A. confertifolia*	Long et al. 1974
	Amaranthaceae	*Atriplex* cf. *A. jonesi* (Holocene)	Robbins et al. 1984
	Amaranthaceae	*Atriplex* sp.	Laudermilk and Munz 1938, Robbins et al. 1984, Mead et al. 1986, Dryer 1994, Coats 1997
	Amaranthaceae	*Atriplex* spp.	Hansen 1978
	Amaranthaceae	*Chenopodium* sp. (Holocene only?)	Robbins et al. 1984
	Amaranthaceae	*Eurotia lanata*	Hansen 1978
	Amaranthaceae	*Tidestromia oblongifolia*	Long et al. 1974
	Amaranthaceae	*Tidestromia* spp.	Hansen 1978
	Amaranthaceae	Cheno-am pollen	Euler 1978, Hevly 1984, O'Rourke and Mead 1985, Mead et al. 1986
	Anacardiaceae	*Rhus trilobata*	Van Devender and Mead 1976, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, O'Rourke and Mead 1985, Coats 1997

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Anacardiaceae	*Rhus* sp.	O'Rourke and Mead 1985, Mead et al. 1986, Emslie et al. 1987, Cole 1990, Dryer 1994, Coats 1997
	Apiaceae	*Caucalis microcarpa*	Phillips 1984
	Apiaceae	*Cymopterus* sp.	Mead et al. 1986
	Apiaceae	*Lomatium* sp.	Dryer 1994
	Apiaceae	Apiaceae (or "Umbelliferae") undetermined (pollen)	Mead et al. 1986
	Apocynaceae	*Amsonia eastwoodiana*	Van Devender et al. 1977
	Apocynaceae	*Amsonia tormentosa*	Phillips 1984
	Apocynaceae	*Amsonia* sp.	Mead and Phillips 1981
	Asparagaceae	*Agave utahensis*	Van Devender and Mead 1976, Mead et al. 1978, Cole and Mead 1981, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, Cole 1985, Cole 1990, O'Rourke and Mead 1985, Van Devender et al. 1985, Cole et al. 2013
	Asparagaceae	*Agave* cf. *A. utahensis*	Long et al. 1974
	Asparagaceae	*Agave* sp.	Mead et al. 1978, Robbins et al. 1984, Dryer 1994, Coats 1997, Coats et al. 2008
	Asparagaceae	*Agave* spp.	Hansen 1978
	Asparagaceae	*Nolina microcarpa*	Van Devender et al. 1977, Hansen 1978, Mead et al. 1978, Van Devender and Spaulding 1979, Mead and Phillips 1981, Phillips 1984
	Asparagaceae	*Nolina* cf. *N. parryi*	Phillips and Van Devender 1974
	Asparagaceae	*Nolina* sp.	Laudermilk and Munz 1938, Long et al. 1974, Van Devender and Mead 1976
	Asparagaceae	*Yucca angustissima*	Robbins et al. 1984, Cole 1990, Dryer 1994
	Asparagaceae	*Yucca baccata*	Van Devender and Mead 1976, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, Coats 1997
	Asparagaceae	*Yucca brevifolia*	Van Devender et al. 1977
	Asparagaceae	*Yucca mohavensis*	Laudermilk and Munz 1938
	Asparagaceae	*Yucca schidigera*	Mead and Phillips 1981
	Asparagaceae	*Yucca* cf. *Y. newberryi*	Long et al. 1974
	Asparagaceae	*Yucca* sp.	Mead et al. 1978, 1986, Hevly 1984, Robbins et al. 1984, Coats 1997
	Asparagaceae	*Yucca* spp.	Hansen 1978
	Asparagaceae	*Agave* and *Yucca* undifferentiated	Hevly 1984

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Asteraceae	*Ambrosia* sp.	O'Rourke and Mead 1985, Dryer 1994
	Asteraceae	cf. *Ambrosia* (pollen)	O'Rourke and Mead 1985, Mead et al. 1986
	Asteraceae	*Artemisia ludoviciana*	Cole 1990
	Asteraceae	*Artemisia tridentata*	Hansen 1978, Robbins et al. 1984, Cole 1985, Cole 1990, Coats 1997, Coats et al. 2008
	Asteraceae	*Artemisia* cf. *A. ludoviciana*	Van Devender and Mead 1976
	Asteraceae	*Artemisia* sp.	Euler 1978, Cole 1982, Hevly 1984, O'Rourke and Mead 1985, Mead et al. 1986
	Asteraceae	*Artemisia* spp.	Dryer 1994
	Asteraceae	*Aster* sp.	Robbins et al. 1984
	Asteraceae	*Aster* spp.	Hansen 1978
	Asteraceae	*Baccharis sergiloides*	Robbins et al. 1984
	Asteraceae	*Baccharis* sp.	Dryer 1994
	Asteraceae	*Bahia* sp.	Coats 1997
	Asteraceae	*Bahia* spp.	Hansen 1978
	Asteraceae	*Brickellia atractyloides*	Coats 1997
	Asteraceae	*Brickellia* cf. *B. scabra*	Coats 1997
	Asteraceae	*Brickellia* sp.	Mead and Phillips 1981, Hevly 1984, Robbins et al. 1984, Dryer 1994, Coats 1997
	Asteraceae	*Chrysopsis* cf. *C. hispida*	Robbins et al. 1984
	Asteraceae	*Chrysothamnus nauseosus*	Hansen 1978
	Asteraceae	*Chrysothamnus* cf. *C. viscidiflorus*	Coats 1997, Coats et al. 2008
	Asteraceae	*Chrysothamnus* sp.	Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, Dryer 1994, Coats 1997
	Asteraceae	*Cirsium* sp.	Mead and Phillips 1981, Phillips 1984
	Asteraceae	*Cirsium* spp.	Dryer 1994
	Asteraceae	cf. *Cirsium* (pollen)	Mead et al. 1986
	Asteraceae	*Coreopsis* sp.	Dryer 1994
	Asteraceae	*Dyssodia pentachaeta*	Robbins et al. 1984
	Asteraceae	*Dyssodia* sp.	Robbins et al. 1984
	Asteraceae	*Encelia farinosa*	Van Devender and Mead 1976, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, Cole 1990
	Asteraceae	*Encelia* sp.	O'Rourke and Mead 1985
	Asteraceae	*Encelia* spp.	Hansen 1978

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Asteraceae	*Erigeron* sp.	Mead and Phillips 1981
	Asteraceae	*Franseria confertifolia*	Phillips 1984
	Asteraceae	*Gutierrezia lucida*	Phillips and Van Devender 1974, Van Devender et al. 1977, Hansen 1978, Mead and Phillips 1981
	Asteraceae	*Gutierrezia microcephala*	Phillips 1984
	Asteraceae	*Gutierrezia* sp.	Long et al. 1974, Robbins et al. 1984, Dryer 1994
	Asteraceae	*Haplopappus* sp. (Holocene)[2]	Robbins et al. 1984
	Asteraceae	cf. *Helianthus* (pollen)	Mead et al. 1986
	Asteraceae	*Hofmeisteria pluriseta*	Hansen 1978
	Asteraceae	*Hofmeisteria* sp.	Long et al. 1974
	Asteraceae	*Laphamia congesta*	Robbins et al. 1984
	Asteraceae	*Lygodesmia exigua*	Robbins et al. 1984
	Asteraceae	*Peucephyllum schottii*	Hansen 1978
	Asteraceae	*Solidago* sp.	Robbins et al. 1984
	Asteraceae	*Tetradymia canescens*?	Robbins et al. 1984
	Asteraceae	cf. *Brickellia* and *Cirsium*	Hevly 1984
	Asteraceae	Asteraceae (or "Compositae") undetermined (pollen)	Euler 1978, Hevly 1984, O'Rourke and Mead 1985, Mead et al. 1986
	Berberidaceae	*Berberis repens* (Holocene)	Robbins et al. 1984
	Berberidaceae	*Berberis* sp.	O'Rourke and Mead 1985, Dryer 1994
	Betulaceae	*Alnus* sp. (pollen)	Euler 1978, Hevly 1984
	Betulaceae	*Betula* sp. (pollen)	Euler 1978, Hevly 1984
	Betulaceae	*Ostrya knowltoni*	Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, O'Rourke and Mead 1985, Cole 1990, Coats 1997
	Betulaceae	*Ostrya* sp. (pollen)	O'Rourke and Mead 1985, Mead et al. 1986
	Boraginaceae	*Amsinckia intermedia*	Hansen 1978, Mead and Phillips 1981
	Boraginaceae	*Amsinckia* sp.	Van Devender and Mead 1976
	Boraginaceae	*Coldenia hispidissima*	Robbins et al. 1984
	Boraginaceae	*Coldenia* sp.	Robbins et al. 1984
	Boraginaceae	Cryptantha pterocarya	Mead and Phillips 1981
	Boraginaceae	*Cryptantha virginensis*	Mead and Phillips 1981, Phillips 1984
	Boraginaceae	*Cryptantha* cf. *C. confertiflora*	Coats 1997

[2] *Aplopappus = Haplopappus*

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Boraginaceae	*Cryptantha* cf. *C. recurvata*	Dryer 1994
	Boraginaceae	*Cryptantha* cf. *C. torreyana*	Coats 1997
	Boraginaceae	*Cryptantha* cf. *C. virginensis*	Coats 1997
	Boraginaceae	*Cryptantha* sp.	Robbins et al. 1984, Mead et al. 1986, Dryer 1994, Coats 1997
	Boraginaceae	*Cryptantha* spp.	Hansen 1978
	Boraginaceae	*Lappula occidentalis*	Dryer 1994, Coats 1997
	Boraginaceae	*Lappula redowskii*	Van Devender and Mead 1976
	Boraginaceae	*Lithospermum incisum*	Coats 1997, Coats et al. 2008
	Boraginaceae	*Pectocarya* spp.	Hansen 1978
	Boraginaceae	*Phacelia crenulata*	Mead and Phillips 1981, Phillips 1984
	Boraginaceae	*Phacelia* sp.	Long et al. 1974
	Boraginaceae	*Phacelia* spp.	Hansen 1978
	Boraginaceae	*Tiquilia* sp.	Coats 1997
	Boraginaceae	cf. *Trixis* (pollen)	Mead et al. 1986
	Boraginaceae	*Coldenia–Cryptantha*	Robbins et al. 1984
	Brassicaceae	*Descurainia pinnata*	Hansen 1978
	Brassicaceae	*Draba cuneifolia*	Hansen 1978
	Brassicaceae	*Lepidium* sp.	Long et al. 1974, Mead and Phillips 1981, Phillips 1984, Dryer 1994, Coats 1997
	Brassicaceae	*Lepidium* spp.	Hansen 1978
	Brassicaceae	*Lesquerella* sp.	Robbins et al. 1984, Mead et al. 1986
	Brassicaceae	cf. *Lesquerella* (pollen)	Mead et al. 1986
	Brassicaceae	*Streptanthella longirostris*	Dryer 1994
	Brassicaceae	*Thysanocarpus amplectens*	Phillips 1984
	Brassicaceae	Brassicaceae (or “Cruciferae”) undetermined	Hevly 1984, Mead et al. 1986
	Cactaceae	*Cylindropuntia* sp.	Dryer 1994, Coats 1997
	Cactaceae	*Echinocactus polycephalus*	Phillips and Van Devender 1974, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984
	Cactaceae	*Echinocactus* sp.	Martin et al. 1961, Phillips 1984
	Cactaceae	*Echinocereus* sp.	Mead and Phillips 1981, Coats 1997
	Cactaceae	*Ferocactus acanthodes*	Van Devender and Mead 1976, Mead and Phillips 1981, Phillips 1984
	Cactaceae	*Ferocactus wislizeni*	Coats 1997
	Cactaceae	*Opuntia basilaris*	Phillips and Van Devender 1974, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, Cole 1990

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Cactaceae	*Opuntia chorotica*	Van Devender and Mead 1976
	Cactaceae	*Opuntia erinacea*	Mead and Phillips 1981, Phillips 1984, Cole 1985, Cole 1990
	Cactaceae	*Opuntia macrorhiza*	Mead and Phillips 1981
	Cactaceae	*Opuntia phaeacantha*	Van Devender and Mead 1976, Cole 1990
	Cactaceae	*Opuntia whipplei*	Phillips and Van Devender 1974, Van Devender and Mead 1976, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, Dryer 1994
	Cactaceae	*Opuntia* cf. *O. whipplei*	Mead et al. 1978
	Cactaceae	*Opuntia* (*Platyopuntia*) sp.[3]	Coats 1997
	Cactaceae	*Opuntia* sp.	Laudermilk and Munz 1938, Long et al. 1974, Mead and Phillips 1981, Hevly 1984, Cole 1985, Cole 1990, O'Rourke and Mead 1985, Dryer 1994, Coats 1997, Coats et al. 2008
	Cactaceae	Cactaceae undetermined	Hansen 1978, Dryer 1994, Coats 1997
	Cannabaceae	*Celtis reticulata*	Van Devender and Mead 1976, Hansen 1978, Mead and Phillips 1981, O'Rourke and Mead 1985, Dryer 1994
	Cannabaceae	*Celtis* sp. (Holocene)	Hevly 1984
	Caprifoliaceae	*Lonicera* sp.	Mead et al. 1986
	Caprifoliaceae	*Symphoricarpos* sp.	Van Devender et al. 1977, Van Devender and Spaulding 1979, Mead and Phillips 1981, Phillips 1984, Mead et al. 1986, Cole 1990, Dryer 1994, Coats 1997, Coats et al. 2008
	Caryophyllaceae	*Arenaria fendleri*	Robbins et al. 1984
	Caryophyllaceae	*Arenaria* sp.	Robbins et al. 1984
	Caryophyllaceae	Caryophyllaceae undetermined (pollen)	O'Rourke and Mead 1985, Mead et al. 1986
	Celastraceae	*Mortonia scabrella*	Phillips and Van Devender 1974, Van Devender et al. 1977, Mead et al. 1978, Mead and Phillips 1981
	Celastraceae	*Mortonia scabrella* var. *utahensis*	Phillips 1984
	Celastraceae	*Pachystima myrsinites*	Cole 1990

[3] *Platypuntia* of Coats 1997 accepted as *Opuntia* (*Platyopuntia*)

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Convolvulacea	*Convolvulus* sp.	Robbins et al. 1984
	Crossosomaceae	*Crossosoma bigelovii*	Hansen 1978, Mead and Phillips 1981, Phillips 1984
	Crossosomaceae	*Crossosoma* sp.	Long et al. 1974
	Crossosomaceae	*Glossopetalon nevadense*	Hansen 1978
	Crossosomaceae	*Glossopetalon* sp.	Mead et al. 1986
	Cucurbitaceae	*Cucurbita* sp.	Van Devender and Mead 1976
	Cyperaceae	*Carex* sp.	Long et al. 1974, Robbins et al. 1984, Mead et al. 1986
	Cyperaceae	*Eleocharis* sp.	Robbins et al. 1984
	Cyperaceae	Cyperaceae undetermined	Hansen 1978
	Elaeagnaceae	*Shepherdia* sp.	Hevly 1984
	Elaeagnaceae	*Shepherdia* spp.	Hansen 1978
	Euphorbiaceae	*Argythamnia* sp.	Dryer 1994
	Euphorbiaceae	*Euphorbia* cf. *E. fendleri*	Coats 1997
	Euphorbiaceae	*Euphorbia sp.*	Van Devender and Mead 1976, Robbins et al. 1984, Dryer 1994
	Euphorbiaceae	*Tragia* sp.	Robbins et al. 1984
	Fabaceae	*Acacia greggii*	Long et al. 1974, Hansen 1978, Mead and Phillips 1981, Phillips 1984
	Fabaceae	*Acacia* sp.	Mead et al. 1986
	Fabaceae	*Astragalus nutallianus*	Phillips 1984
	Fabaceae	*Astragalus* sp.	Hansen 1978, Robbins et al. 1984, O’Rourke and Mead 1985, Dryer 1994
	Fabaceae	*Astragalus*-type pollen	Mead et al. 1986
	Fabaceae	*Cassia* sp.	Laudermilk and Munz 1938
	Fabaceae	*Cercis occidentalis*	O’Rourke and Mead 1985, Cole 1990
	Fabaceae	*Lotus* spp.	Hansen 1978
	Fabaceae	*Prosopis juliflora*	Long et al. 1974, Hansen 1978, Cole 1990
	Fabaceae	Fabaceae (or “Leguminosae”) undetermined (pollen)	Mead et al. 1986
	Fabaceae	Fabaceae undetermined (driftwood)	Ferguson 1984
	Fabaceae	“Legume a and b”	Hevly 1984
	Fagaceae	*Quercus turbinella*	Mead and Phillips 1981, Cole 1982, Cole 1985, Cole 1990
	Fagaceae	*Quercus* sp.	Euler 1978, Hansen 1978, Hevly 1984, O’Rourke and Mead 1985, Mead et al. 1986

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Grossulariaceae	*Ribes montigenum*	Van Devender et al. 1977, Van Devender and Spaulding 1979, Mead and Phillips 1981, O'Rourke and Mead 1985
	Grossulariaceae	*Ribes pinetorum*	Coats et al. 2008
	Grossulariaceae	*Ribes* cf. *R. pinetorum*	Coats 1997
	Grossulariaceae	*Ribes* sp.	Cole 1985, Cole 1990, Coats 1997
	Grossulariaceae	cf. *Ribes* sp.	Dryer 1994
	Hydrangeaceae	*Fendlera rupicola*	Cole 1990
	Juglandaceae	*Juglans* sp. (Holocene body fossils)	Hevly 1984
	Juglandaceae	*Juglans* sp. (pollen)	Euler 1978, Hevly 1984
	Krameriaceae	*Krameria parvifolia*	Hansen 1978
	Lamiaceae	*Hedeoma diffusum*	Robbins et al. 1984
	Lamiaceae	*Hedeoma* sp.	Robbins et al. 1984
	Lamiaceae	*Salvia dorrii*	Mead and Phillips 1981, Phillips 1984
	Lamiaceae	Lamiaceae (or "Labiatae") undetermined (pollen)	Mead et al. 1986
	Liliaceae	Liliaceae undetermined (pollen)	Mead et al. 1986
	Linaceae	*Linum* sp. (pollen)	Mead et al. 1986
	Loasaceae	*Eucnide urens*	Hansen 1978
	Loasaceae	*Mentzelia puberula*	Mead and Phillips 1981
	Loasaceae	*Mentzelia* sp.	Phillips 1984, Robbins et al. 1984, Dryer 1994
	Malpighiaceae	*Janusia gracilis*	Van Devender and Mead 1976
	Malpighiaceae	*Janusia* sp.	Hansen 1978
	Malvaceae	*Malvastrum rotundifolium*	Hansen 1978
	Malvaceae	*Sida* sp.	Mead et al. 1986
	Malvaceae	*Sphaeralcea ambigua*	Laudermilk and Munz 1938, Van Devender et al. 1977, Hansen 1978
	Malvaceae	*Sphaeralcea* cf. *S. laxa*	Long et al. 1974
	Malvaceae	*Sphaeralcea* sp.	Martin et al. 1961, Van Devender and Mead 1976, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984, O'Rourke and Mead 1985, Mead et al. 1986, Dryer 1994
	Nyctaginaceae	*Abronia* sp.	Hansen 1978
	Nyctaginaceae	*Allionia incarnata*	Hansen 1978, Phillips 1984
	Nyctaginaceae	*Allionia* sp.	Long et al. 1974
	Nyctaginaceae	*Boerhavia coulteri*	Mead and Phillips 1981
	Nyctaginaceae	*Boerhavia* sp.	Van Devender and Mead 1976
	Nyctaginaceae	*Mirabilis multiflora*	Coats 1997

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Nyctaginaceae	*Oxybaphus* sp.	O'Rourke and Mead 1985
	Oleaceae	*Fraxinus anomala*	Long et al. 1974, Phillips and Van Devender 1974, Van Devender and Mead 1976, Van Devender et al. 1977, Hansen 1978, Mead et al. 1978, Van Devender and Spaulding 1979, Mead and Phillips 1981, Cole 1982, Cole 1985, Cole 1990, Phillips 1984, O'Rourke and Mead 1985, Coats 1997, Coats et al. 2008
	Oleaceae	*Fraxinus* cf. *F. anomala*	Dryer 1994
	Oleaceae	*Fraxinus* sp.	Laudermilk and Munz 1938
	Oleaceae	*Fraxinus* spp.	Hansen 1978
	Onagraceae	*Oenothera cavernae*	Phillips 1984
	Onagraceae	*Oenothera* sp.	Robbins et al. 1984, Mead et al. 1986
	Onagraceae	*Oenothera* spp.	Hansen 1978
	Orobanchaceae	*Castilleja* cf. *C. miniata*	Coats 1997
	Orobanchaceae	*Castilleja* sp.	Coats 1997
	Orobanchaceae	*Castilleja* spp.	Hansen 1978
	Orobanchaceae	*Castilleja* or *Orthocarpus*	Van Devender and Mead 1976
	Papaveraceae	*Argemone* sp.	Mead and Phillips 1981, Phillips 1984, O'Rourke and Mead 1985, Dryer 1994, Coats 1997
	Phrymaceae	*Mimulus* sp.	Robbins et al. 1984
	Plantaginaceae	*Penstemon eatonii*	Phillips 1984
	Plantaginaceae	*Penstemon* sp.	Van Devender and Mead 1976, Mead and Phillips 1981
	Plantaginaceae	*Plantago* sp.	Dryer 1994
	Poaceae	*Agropyron* sp.	Robbins et al. 1984, Mead et al. 1986
	Poaceae	*Agropyron* spp.	Hansen 1978
	Poaceae	*Andropogon* sp.	Robbins et al. 1984
	Poaceae	*Aristida glauca*	Robbins et al. 1984
	Poaceae	*Aristida longiseta*	Robbins et al. 1984
	Poaceae	*Aristida* sp.	Laudermilk and Munz 1938, Long et al. 1974, Robbins et al. 1984, Mead et al. 1986, Dryer 1994
	Poaceae	*Aristida* spp.	Hansen 1978
	Poaceae	*Bouteloua eripoda* (Holocene)	Robbins et al. 1984
	Poaceae	*Bouteloua gracilis*	Robbins et al. 1984
	Poaceae	*Bouteloua simplex*	Robbins et al. 1984
	Poaceae	*Bouteloua trifida*	Robbins et al. 1984
	Poaceae	*Bouteloua* sp.	Robbins et al. 1984, Mead et al. 1986
	Poaceae	*Bouteloua* spp.	Hansen 1978

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Poaceae	*Bromus* sp.	Long et al. 1974, Robbins et al. 1984, Mead et al. 1986
	Poaceae	*Bromus* spp.	Hansen 1978
	Poaceae	*Enneapogon desvauxii*	Robbins et al. 1984
	Poaceae	*Festuca arizonica*	Hansen 1978
	Poaceae	*Festuca* sp.	Robbins et al. 1984, Mead et al. 1986
	Poaceae	*Hilaria rigida*	Hansen 1978
	Poaceae	*Lycurus phleoides* (Holocene)	Robbins et al. 1984
	Poaceae	*Muhlenbergia* sp.	Long et al. 1974, Hansen 1978
	Poaceae	*Panicum huachucae*	Robbins et al. 1984
	Poaceae	*Oryzopsis hymenoides*	Mead and Phillips 1981, O'Rourke and Mead 1985, Coats 1997, Coats et al. 2008
	Poaceae	*Oryzopsis* sp.	Hansen 1978, Mead et al. 1986
	Poaceae	*Phragmites communis*	Laudermilk and Munz 1938, Hansen 1978
	Poaceae	*Phragmites* sp.	Long et al. 1974, Robbins et al. 1984
	Poaceae	*Poa* sp.	Mead et al. 1986
	Poaceae	*Poa* spp.	Hansen 1978
	Poaceae	*Schedonnardus paniculatus*	Robbins et al. 1984
	Poaceae	*Schizachyrium scoparium*	Dryer 1994
	Poaceae	*Sporobolus flexuosus*	Robbins et al. 1984
	Poaceae	*Sporobolus texanus*	Robbins et al. 1984
	Poaceae	*Sporobolus* cf. *S. cryptandrus*	Robbins et al. 1984
	Poaceae	*Sporobolus* sp.	Robbins et al. 1984, Mead et al. 1986
	Poaceae	*Sporobolus* spp.	Hansen 1978
	Poaceae	*Stipa arida*	Robbins et al. 1984
	Poaceae	*Stipa hymenoides*	Dryer 1994
	Poaceae	*Stipa* cf. *neomexicana*	Dryer 1994
	Poaceae	*Stipa* sp.	Long et al. 1974, Mead et al. 1986
	Poaceae	*Stipa* spp.	Hansen 1978
	Poaceae	*Tridens pulchellus*	Robbins et al. 1984
	Poaceae	*Tridens* sp	Long et al. 1974, Hansen 1978
	Poaceae	*Tridens* spp.	Hansen 1978
	Poaceae	*Zea mays* (late Holocene)	Cole 1982
	Poaceae	Gramineae A	Robbins et al. 1984
	Poaceae	Poaceae (or "Gramineae") undetermined	Euler 1978, Hevly 1984, Robbins et al. 1984, O'Rourke and Mead 1985, Mead et al. 1986
	Polemoniaceae	*Gilia* sp.	Hevly 1984
	Polemoniaceae	cf. *Leptodactylon* (pollen)	Mead et al. 1986
	Polemoniaceae	*Linanthus demissus*	Hansen 1978
	Polemoniaceae	*Phlox* sp. (pollen)	Mead et al. 1986
	Polemoniaceae	*Phlox*/*Leptodactylon*	Mead et al. 1986
	Polemoniaceae	Polemoniaceae undetermined (pollen)	O'Rourke and Mead 1985

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Polygonaceae	*Eriogonum deflexum*	Robbins et al. 1984
	Polygonaceae	*Eriogonum* sp.	Robbins et al. 1984, Mead et al. 1986
	Polygonaceae	*Eriogonum* spp.	Hansen 1978
	Polygonaceae	*Polygonum* sp.	Dryer 1994
	Polygonaceae	*Rumex* sp.	Dryer 1994
	Polygonaceae	Polygonaceae undetermined (pollen)	O'Rourke and Mead 1985, Mead et al. 1986
	Ranunculaceae	*Anemone tuberosa*	Hansen 1978, Phillips 1984
	Ranunculaceae	*Anemone* sp.	Van Devender and Mead 1976
	Ranunculaceae	*Aquilegia chrysantha*	Hansen 1978
	Ranunculaceae	*Caltha* sp. (pollen)	Mead et al. 1986
	Ranunculaceae	*Clematis ligusticifolia*	Robbins et al. 1984
	Ranunculaceae	*Ranunculus* sp.	Dryer 1994
	Ranunculaceae	Ranunculaceae undetermined (pollen)	O'Rourke and Mead 1985, Mead et al. 1986
	Rhamnaceae	*Rhamnus betulaefolia*	Phillips 1984
	Rhamnaceae	*Rhamnus* sp. (late Holocene)	O'Rourke and Mead 1985
	Rhamnaceae	Rhamnaceae undetermined (pollen)	O'Rourke and Mead 1985
	Rosaceae	*Amelanchier* sp.	Hevly 1984, Robbins et al. 1984, Coats 1997
	Rosaceae	*Cercocarpus intricatus*	Van Devender et al. 1977, Van Devender and Spaulding 1979, Phillips 1984, Robbins et al. 1984, O'Rourke and Mead 1985, Cole 1990, Coats 1997, Coats et al. 2008
	Rosaceae	*Cercocarpus montanus*	Hansen 1978
	Rosaceae	*Cercocarpus* sp. (pollen)	Mead et al. 1986
	Rosaceae	cf. *Cercocarpus* (pollen)	O'Rourke and Mead 1985
	Rosaceae	*Chamaebatiaria millefolium*	Cole 1990, Coats 1997, Coats et al. 2008
	Rosaceae	*Coleogyne ramosissima*	Phillips and Van Devender 1974, Van Devender et al. 1977, Mead and Phillips 1981, Phillips 1984, O'Rourke and Mead 1985, Cole 1990, Coats 1997, Coats et al. 2008
	Rosaceae	*Cowania mexicana*	O'Rourke and Mead 1985, Cole 1990, Coats 1997
	Rosaceae	*Fallugia paradoxa*	Van Devender and Mead 1976, Robbins et al. 1984
	Rosaceae	*Geum* spp.	Hansen 1978
	Rosaceae	*Holodiscus dumosus*	Cole 1990, Coats 1997
	Rosaceae	*Potentilla* spp.	Hansen 1978
	Rosaceae	*Prunus fasciculata*	Phillips and Van Devender 1974, Van Devender et al. 1977, Hansen 1978, Mead et al. 1978, Phillips 1984, Robbins et al. 1984, Cole 1990

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Rosaceae	*Prunus virginiana*	Dryer 1994, Coats 1997
	Rosaceae	*Prunus* sp.	Laudermilk and Munz 1938, Long et al. 1974, Mead et al. 1986
	Rosaceae	*Purshia mexicana*	Dryer 1994
	Rosaceae	*Purshia* sp.	Hevly 1984
	Rosaceae	*Rosa* cf. *R. arizonica*	O'Rourke and Mead 1985
	Rosaceae	*Rosa stellata*	Coats et al. 2008
	Rosaceae	*Rosa* cf. *R. stellata*	Cole 1985, Cole 1990, Dryer 1994, Coats 1997
	Rosaceae	*Rosa* sp.	O'Rourke and Mead 1985, Dryer 1994, Coats 1997
	Rosaceae	*Rubus* sp.	Cole 1990, Dryer 1994, Coats 1997
	Rosaceae	Rosaceae undetermined (pollen)	Mead et al. 1986
	Rubiaceae	*Galium* sp.	Van Devender and Mead 1976, Mead and Phillips 1981, Phillips 1984, Robbins et al. 1984
	Rubiaceae	*Galium* spp.	Hansen 1978
	Rutaceae	*Ptelea trifoliata*	Coats 1997, Coats et al. 2008
	Rutaceae	*Ptelea trifoliata* var. *pallida*	Cole 1985, Cole 1990, O'Rourke and Mead 1985
	Rutaceae	*Thamnosma montana*	Dryer 1994
	Rutaceae	*Thamnosma* sp.	Mead and Phillips 1981, Hevly 1984
	Salicaceae	*Populus fremontii*	Hansen 1978
	Salicaceae	*Populus fremontii*?	Euler 1978
	Salicaceae	*Populus* sp.	Laudermilk and Munz 1938, Ferguson 1984, Mead et al. 1986
	Salicaceae	*Salix* sp. (pollen)	Euler 1978, Hevly 1984, Mead et al. 1986
	Salicaceae	*Populus* and *Salix* (Holocene body fossils)	Hevly 1984
	Santalaceae	*Phoradendron californicum*	Phillips 1984
	Santalaceae	*Phoradendron* sp.	Long et al. 1974, Hansen 1978, Mead and Phillips 1981, Robbins et al. 1984
	Sapindaceae	*Acer glabrum*	Coats 1997, Coats et al. 2008
	Sapindaceae	*Acer* sp. (pollen)	Euler 1978, Hevly 1984
	Sarcobataceae	*Sarcobatus vermiculatus*	Robbins et al. 1984
	Sarcobataceae	*Sarcobatus* sp. (pollen)	Euler 1978, Hevly 1984
	Saxifragaceae	*Mitella* sp.	Dryer 1994
	Saxifragaceae	cf. *Saxifraga* (pollen)	Mead et al. 1986
	Saxifragaceae	Saxifragaceae undetermined (pollen)	O'Rourke and Mead 1985
	Solanaceae	*Datura metaloides* (GRCA: Holocene)	Van Devender and Mead 1976, Robbins et al. 1984
	Solanaceae	*Lycium andersonii*	Phillips 1984
	Solanaceae	*Lycium* sp.	Dryer 1994
	Solanaceae	cf. *Lycium* (pollen)	Mead et al. 1986

Appendix Table 11-A-1 (continued). Ice Age plant taxa reported from the Grand Canyon. Those records that are pollen-only are reported as such; otherwise, records may be macrofossil-only or mixed macrofossil and palynomorph.

Category	Family	Taxa Observed	Sources
Magnoliophyta (continued)	Solanaceae	*Physalis fendleri*	Robbins et al. 1984
	Solanaceae	*Physalis* sp.	Laudermilk and Munz 1938, Van Devender and Mead 1976, Mead and Phillips 1981, Phillips 1984
	Solanaceae	Solanaceae undetermined (pollen)	Mead et al. 1986
	Urticaceae	*Urtica* sp.	Robbins et al. 1984
	Verbenaceae	*Aloysia wrightii*	Robbins et al. 1984, Cole 1990
	Verbenaceae	*Verbena* sp.	Van Devender and Mead 1976
	Vitaceae	*Vitis arizonica*	Mead and Phillips 1981, Phillips 1984
	Vitaceae	*Vitis* sp.	Mead et al. 1978
	Zygophyllaceae	*Kallstroemia* sp.	Van Devender and Mead 1976
	Zygophyllaceae	*Larrea divaricata*	Laudermilk and Munz 1938
	Zygophyllaceae	*Larrea tridentata*	Martin et al. 1961, Hansen 1978, Mead and Phillips 1981, Phillips 1984
	Zygophyllaceae	*Ceanothus*/*Cercocarpus*	Mead et al. 1986
	Zygophyllaceae	Undetermined wood	Emslie 1988, Dryer 1994, Kaufman et al. 2002
	Zygophyllaceae	Undetermined plants	Phillips and Van Devender 1974, Mead et al. 1978, Mead et al. 1986, Hevly 1984, Emslie et al. 1987, Emslie 1988, Kaufman et al. 2002

Invertebrates

Ice Age invertebrate taxa reported from the Grand Canyon are listed in Appendix Table 11-A-2.

Appendix Table 11-A-2. Ice Age invertebrate taxa reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Phylum	Class	Order	Family	Taxon Observed	Sources
Mollusca	Bivalvia	Sphaeriida	Sphaeriidae	*Pisidium* cf. *P. casertanum*	Kaufman et al. 2002
	Bivalvia	Sphaeriida	Sphaeriidae	*Pisidium* cf. *P. nitidum*	Kaufman et al. 2002
	Bivalvia	Sphaeriida	Sphaeriidae	*Pisidium* cf. *P. subtruncatum*	Kaufman et al. 2002
	Bivalvia	Sphaeriida	Sphaeriidae	*Pisidium* cf. *P. walkeri*	Kaufman et al. 2002
	Bivalvia	Sphaeriida	Sphaeriidae	*Pisidium* sp.	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Succineidae	*Catinella* cf. *C. vermeta*[4]	Spamer 1993, Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Succineidae	*Catinella* sp.	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Cionellidae	*Cionella lubrica*[5]	Spamer 1993, Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Lymnaeidae	*Fossaria dalli*	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Lymnaeidae	*Fossaria* sp.	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Planorbidae	*Gyraulus parvus*	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Oreohelicidae	*Oreohelix yavapai*[6]	Spamer and Bogan 1993, Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Succineidae	*Oxyloma* cf. *O. haydeni kanabensis*	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Succineidae	*Oxyloma* sp.	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Physidae	*Physella* cf. *P. humerosa*	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Physidae	*Physella* cf. *P. virgata*	Kaufman et al. 2002
	Gastropoda	“Pulmonata”	Xanthonychidae	cf. *Sonorella* sp.	Cole and Mead 1981

[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 rolled into *Oreohelix yavapai*

Appendix Table 11-A-2 (continued). Ice Age invertebrate taxa reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Phylum	Class	Order	Family	Taxon Observed	Sources
Mollusca (continued)	Gastropoda	"Pulmonata"	Vertiginidae	*Vertigo ovata*	Kaufman et al. 2002
	–	–	–	Mollusca undetermined	Hevly 1984
Nematoda	–	–	–	*Agamofilaria oxyura**	Schmidt et al. 1992
	–	–	–	*Strongyloides shastensis**	Schmidt et al. 1992
	–	–	–	Nematoda unspecified	Laudermilk and Munz 1938
Arthropoda	Arachnida	Ixodida	Ixodidae	*Dermacentor andersoni*	Elias et al. 1992
	Arachnida	Ixodida	Ixodidae	*Dermacentor* sp.	Elias et al. 1992
	Arachnida	Scorpiones	Buthidae	*Centruroides* sp.	Elias et al. 1992
	Diplopoda	–	–	Diplopoda undetermined	Elias et al. 1992
	Insecta	Coleoptera	Carabidae	*Agonum* (*Rhadine*) *perlevis* (late Holocene)	Elias et al. 1992
	Insecta	Coleoptera	Carabidae	*Agonum (Rhadine*) sp.	Elias et al. 1992
	Insecta	Coleoptera	Carabidae	*Calosoma* cf. *C. scrutator* (late Holocene)	Elias et al. 1992
	Insecta	Coleoptera	Chrysomelidae	*Chaetocnema* sp. (late Holocene)	Elias et al. 1992
	Insecta	Coleoptera	Chrysomelidae	*Lema trilinea*	Elias et al. 1992
	Insecta	Coleoptera	Chrysomelidae	Chrysomelidae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Cleridae	*Acanthoscelides* sp.	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Apleurus angularis*	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Cleonidus trivittatus* or *C. quadrilineatus*	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Ophryastes* sp.	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Orimodema protracta* (late Holocene)	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Sapotes* sp.	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	*Scyphophorus acupunctatus*	Elias et al. 1992
	Insecta	Coleoptera	Curculionidae	Cleridae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Dermestidae	Dermestidae undetermined	Elias et al. 1992

Appendix Table 11-A-2 (continued). Ice Age invertebrate taxa reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Phylum	Class	Order	Family	Taxon Observed	Sources
Arthropoda (continued)	Insecta	Coleoptera	Elateridae	Elateridae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Histeridae	Histeridae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Melandryidae	*Anaspis rufa*	Elias et al. 1992
	Insecta	Coleoptera	Meloidae	Meloidae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Nitidulidae	Nitidulidae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Ptinidae	*Niptus* cf. *N. ventriculus*	Elias et al. 1992
	Insecta	Coleoptera	Ptinidae	*Ptinis* sp.	Elias et al. 1992
	Insecta	Coleoptera	Ptinidae	Ptinidae undetermined	Cole and Mead 1981
	Insecta	Coleoptera	Scarabaeidae	*Aphodius* near *A. ruficlarus*	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Aphodius* near *A. ruficlarus*	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Aphodius* sp.	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Diplotaxis* sp.	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Onthophagus* sp.	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Phyllophaga* sp.	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	*Serica* sp.	Elias et al. 1992
	Insecta	Coleoptera	Scarabaeidae	Scarabaeidae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Scotylidae	Scotylidae undetermined	Elias et al. 1992
	Insecta	Coleoptera	Silphidae	*Thanatophilus truncatus* (late Holocene)	Elias et al. 1992
	Insecta	Coleoptera	Tenebrionidae	*Coniontis* sp.	Elias et al. 1992
	Insecta	Coleoptera	Tenebrionidae	*Eleodes* cf. *E. nigrina*	Elias et al. 1992
	Insecta	Coleoptera	Tenebrionidae	*Eleodes* spp.	Elias et al. 1992
	Insecta	Coleoptera	Tenebrionidae	Tenebrionidae undetermined	Hevly 1984
	Insecta	Diptera	–	Diptera undetermined	Elias et al. 1992
	Insecta	Hemiptera	–	Hemiptera undetermined	Elias et al. 1992
	Insecta	Homoptera	Cicadidae	Cicadidae undetermined	Elias et al. 1992
	Insecta	Hymenoptera	Superfamily Apoidea	Apoidea undetermined	Elias et al. 1992

Appendix Table 11-A-2 (continued). Ice Age invertebrate taxa reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Phylum	Class	Order	Family	Taxon Observed	Sources
Arthropoda (continued)	Insecta	Lepidoptera	–	Lepidoptera undetermined	Elias et al. 1992
	Insecta	Neuroptera	Myrmelodontidae	Myrmelodontidae undetermined	Elias et al. 1992
	Insecta	Orthoptera	Acrididae	Acrididae undetermined	Elias et al. 1992
	Insecta	–	–	Insecta undetermined	Cole and Mead 1981, Mead and Phillips 1981
	Ostracoda	Podocopida	Candonidae	*Candona* sp. (late Holocene)	Kaufman et al. 2002
	Ostracoda	Podocopida	Cyprididae	*Cypridopsis okeechobei*	Kaufman et al. 2002
	Ostracoda	Podocopida	Cyprididae	*Cypridopsis vidua*	Kaufman et al. 2002
	Ostracoda	Podocopida	Darwinulidae	*Darwinula stevensoni*	Kaufman et al. 2002
	Ostracoda	Podocopida	Cyprididae	*Heterocypris incongruens*	Kaufman et al. 2002
	Ostracoda	Podocopida	Cyprididae	*Ilyocypris bradyi*	Kaufman et al. 2002
	Ostracoda	Podocopida	Cyprididae	*Strandesia meadensis*	Kaufman et al. 2002
	–	–	–	Arthropoda undetermined	Mead and Van Devender 1981, Hevly 1984

Vertebrates

Ice Age vertebrate taxa reported from the Grand Canyon are listed in Appendix Table 11-A-3.

Appendix Table 11-A-3. Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
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
Amphibia	Anura	*Bufo* sp.	Spamer 1988
	Anura	*Hyla* sp.	Spamer 1988
	Anura	*Scaphiopus* sp.	GCM
	Urodela	*Ambystoma tigrinum* (late Holocene)	Mead 2005
Reptilia	Testudines	*Gopherus agassizii*	Wilson 1942, Van Devender et al. 1977, Mead 1981, Mead 2005, Hunt et al. 2018
	Testudines	*Gopherus morafkai*	Hunt et al. 2018
	Squamata	*Cnemidophorus tigris*	Mead 2005
	Squamata	*Cnemidophorus* cf. *C. tigris*	Van Devender et al. 1977, Mead 1981
	Squamata	*Cnemidophorus* sp.	Cole and Van Devender 1976, Van Devender et al. 1977, Cole and Mead 1981
	Squamata	*Coleonyx variegatus*	Van Devender et al. 1977, Mead 1981, Mead 2005
	Squamata	*Crotaphytus collaris*	Van Devender et al. 1977, Mead 1981, Mead 2005, Mead and Phillips 1981
	Squamata	*Crotaphytus* cf. *C. collaris*	Cole and Mead 1981
	Squamata	*Crotaphytus* sp.	Cole and Van Devender 1976
	Squamata	*Heloderma suspectum* (uncertain age)	Mead 2005
	Squamata	*Phrynosoma hernandesi*	Mead et al. 2003, Mead 2005
	Squamata	cf. *Phrynosoma*	Mead et al. 2003
	Squamata	*Sauromalus ater*[7]	Wilson 1942, Van Devender et al. 1977, Mead 1981, Mead 2005, Hunt et al. 2018
	Squamata	*Sceloporus magister*	Hunt et al. 2018

[7] *Sauromalus obesus = Sauromalus ater*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Reptilia (continued)	Squamata	*Sceloporus tristichus*	Hunt et al. 2018
	Squamata	*Sceloporus undulatus*	Mead 2005
	Squamata	*Sceloporus* cf. *S. magister*	Van Devender et al. 1977, Mead 1981, Mead and Phillips 1981
	Squamata	*Sceloporus* cf. *S. undulatus*	Van Devender et al. 1977, Cole and Mead 1981, Mead 1981, Mead and Phillips 1981, Hunt et al. 2018
	Squamata	*Sceloporus* sp.	Van Devender et al. 1977, Cole and Mead 1981
	Squamata	*Sceloporus* spp.	Cole and Van Devender 1976
	Squamata	*Uta stansburiana*	Van Devender et al. 1977, Mead 1981, Mead 2005, Mead and Phillips 1981
	Squamata	Undetermined lizard	Emslie 1988, Dryer 1994, Emslie et al. 1995
	Suborder Serpentes	*Coluber* or *Masticophis* (late Holocene)	Mead and Phillips 1981
	Suborder Serpentes	*Crotalus mitchelli* or *C. viridis*	Van Devender et al. 1977, Mead 1981, Mead 2005, Mead and Phillips 1981
	Suborder Serpentes	*Crotalus* sp.	Van Devender et al. 1977
	Suborder Serpentes	*Diadophis punctatus*	Mead et al. 2003, Mead 2005
	Suborder Serpentes	*Hypsiglena torquata*	Van Devender et al. 1977, Mead 1981, Mead 2005, Mead and Phillips 1981
	Suborder Serpentes	*Lampropeltis getula*[8]	Van Devender et al. 1977, Mead 1981, Mead 2005, Mead and Phillips 1981, Olsen and Olsen 1984, Hunt et al. 2018
	Suborder Serpentes	*Lampropeltis pyromelana*	Mead 1981, Mead 2005, Mead and Phillips 1981
	Suborder Serpentes	*Lampropeltis triangulum* (late Holocene)	Mead and Phillips 1981, Mead 2005
	Suborder Serpentes	cf. *Lampropeltis*	Mead et al. 2003
	Suborder Serpentes	*Pituophis catenifer*	Hunt et al. 2018
	Suborder Serpentes	*Pituophis melanoleucus*	Van Devender et al. 1977; Mead 1981, 2005
	Suborder Serpentes	*Rhinocheilus lecontei*	Van Devender et al. 1977; Mead 1981, Mead 2005, Mead and Phillips 1981; Hunt et al. 2018
	Suborder Serpentes	*Salvadora* cf. *S. hexalepis* (late Holocene)	Mead and Phillips 1981

[8] *Lampropeltis getulus* = *Lampropeltis getula*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Reptilia (continued)	Suborder Serpentes	*Sonora semiannulata*	Van Devender et al. 1977; Mead 1981, Mead 2005, Mead and Phillips 1981
	Suborder Serpentes	*Thamnophis* sp.	Mead 1981
	Suborder Serpentes	*Trimorphodon bisulcatus* (late Holocene)	Mead and Phillips 1981
	Suborder Serpentes	Serpentes undetermined	Emslie 1988, Dryer 1994, Mead et al. 2003
	–	Reptilia undetermined	Hevly 1984
Aves	Accipitriformes	*Accipiter striatus* (Holocene general)	Mead 1981, Hevly 1984
	Accipitriformes	*Aquila chrysaetos*	Hevly 1984, Carpenter 2003, Hunt et al. 2018
	Accipitriformes	*Buteo jamaicensis*	Hevly 1984, Hunt et al. 2018
	Accipitriformes	*Buteo regalis* (Holocene general)	Mead 1981
	Accipitriformes	*Buteo* sp.	Emslie 1988
	Accipitriformes	cf. *Buteo jamaicensis*	Carpenter 2003
	Accipitriformes	*Buteogallus anthracinus* (Holocene general)	Mead 1981, Hevly 1984
	Accipitriformes	*Circus cyaneus*	Emslie 1988
	Accipitriformes	cf. *Circus cyaneus* (Holocene general)	Hevly 1984
	Accipitriformes	Hawk similar to *Buteo jamaicensis*	Miller 1960
	Anseriformes	*Aix sponsa* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Anas acuta* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Anas americana*	Hevly 1984, Emslie 1988
	Anseriformes	*Anas clypeata*	Hevly 1984, Emslie 1988
	Anseriformes	*Anas crecca*	Emslie 1988
	Anseriformes	*Anas crecca carolinensis*?	Mead 1981
	Anseriformes	*Anas crecca* cf. *carolinensis* (Holocene general)	Hevly 1984
	Anseriformes	*Anas cyanoptera* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Anas discors*	Rea and Hargrave 1984
	Anseriformes	*Anas platyrhynchos*	Rea and Hargrave 1984, Emslie 1988
	Anseriformes	*Anas strepera* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Anas* sp.	Emslie 1988, Emslie et al. 1995
	Anseriformes	*Aythya americana* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Aythya affinis*	Hevly 1984, Emslie 1988
	Anseriformes	*Aythya marila* (Holocene general)	Mead 1981, Hevly 1984

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Aves (continued)	Anseriformes	*Aythya valisineria* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Aythya* sp.	Emslie 1988
	Anseriformes	*Aythya* sp.? (Holocene general)	Hevly 1984
	Anseriformes	*Branta canadensis* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Bucephala albeola* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Bucephala clangula* (Holocene general)	Mead 1981
	Anseriformes	*Chen caerulescens*	Hevly 1984, Emslie 1988
	Anseriformes	cf. *Clangula hyemalis* (Holocene general)	Hevly 1984
	Anseriformes	*Mergus cucullatus* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Mergus merganser* (Holocene general)	Mead 1981, Hevly 1984
	Anseriformes	*Olor columbianus* (Holocene general)	Mead 1981
	Anseriformes	cf. *Olor columbianus* (Holocene general)	Hevly 1984
	Anseriformes	*Oxyura jamaicensis* (Holocene general)	Mead 1981, Hevly 1984
	Apodiformes	*Aeronautes saxatalis*	Emslie 1988
	Cathartiformes	*Cathartes aura*	Mead 1981, Hevly 1984, Emslie 1988, Mead and Phillips 1981
	Cathartiformes	?*Cathartes aura*	Carpenter 2003
	Cathartiformes	*Coragyps atratus*	Carpenter 2003, Hunt et al. 2018
	Cathartiformes	*Coragyps occidentalis*	Hunt et al. 2018
	Cathartiformes	*Gymnogyps amplus*?	deSaussure 1956
	Cathartiformes	*Gymnogyps californianus*	*see text*
	Cathartiformes	*Gymnogyps* sp.	Rea and Hargrave 1984
	Cathartiformes	*Teratornis merriami*	Mead 1981, Rea and Hargrave 1984
	Cathartiformes	*Teratornis* cf. *T. merriami*	Dryer 1994
	Cathartiformes	*Teratornis* sp.	Lindsay and Tessman 1974
	Charadriiformes	*Actitis macularia*	Rea and Hargrave 1984
	Charadriiformes	*Calidris melanotos*	Rea and Hargrave 1984
	Charadriiformes	*Capella gallinago*	Mead 1981, Rea and Hargrave 1984
	Charadriiformes	*Larus pipixcan* (Holocene general)	Hevly 1984
	Charadriiformes	*Larus* sp.	Emslie 1988
	Charadriiformes	*Numenius americanus* (Holocene general)	Mead 1981, Hevly 1984
	Charadriiformes	*Phalaropus fulicarius*	Rea and Hargrave 1984

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Aves (continued)	Charadriiformes	*Phalaropus lobatus*	Rea and Hargrave 1984, Emslie 1988
	Charadriiformes	*Phalaropus* cf. *fulicarius*	Mead 1981
	Charadriiformes	*Recurvirostra americana*	Hevly 1984, Emslie 1988
	Charadriiformes	*Tringa semipalmata*[9]	Emslie et al. 1995
	Columbiformes	*Zenaida macroura*	Hevly 1984, Emslie 1988, Emslie et al. 1995
	Falconiformes	*Falco femoralis*	Miller 1960, Carpenter 2003, Hunt et al. 2018
	Falconiformes	*Falco mexicanus*	Hevly 1984, Emslie 1988
	Falconiformes	*Falco peregrinus*	Emslie 1988
	Falconiformes	*Falco sparverius*	Rea and Hargrave 1984, Emslie 1988, Emslie et al. 1995
	Galliformes	*Centrocercus urophasianus* (Holocene general)	Mead 1981, Hevly 1984
	Galliformes	cf. *Colinus virginianus*	Emslie 1988
	Galliformes	*Meleagris crassipes* (Holocene general)	Mead 1981, Hevly 1984
	Gruiformes	*Fulica americana*	Emslie 1988
	Gruiformes	*Gallinula chloropus* (Holocene general)	Mead 1981, Hevly 1984
	Gruiformes	cf. *Porzana carolina*	Emslie 1988
	Passeriformes	*Agelaius phoeniceus*	Emslie 1988
	Passeriformes	*Aphelocoma caerulescens* (Holocene general)	Mead 1981
	Passeriformes	cf. *Aphelocoma caerulescens* (Holocene general)	Hevly 1984
	Passeriformes	*Catherpes mexicanus* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Cinclus mexicanus*	Rea and Hargrave 1984
	Passeriformes	*Contopus sordidulus* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Corvus corax*	Hevly 1984, Emslie 1988
	Passeriformes	*Corvus corax sinuatus* (Holocene general)	Mead 1981
	Passeriformes	*Corvus* sp.	Emslie 1988, Emslie et al. 1995
	Passeriformes	*Dendroica coronata* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Empidonax* sp.? (Holocene general)	Hevly 1984
	Passeriformes	*Eremophila alpestris*	Mead 1981, Hevly 1984
	Passeriformes	*Hirundo* sp. (Holocene general)	Mead 1981

[9] *Catoptrophorus semipalmatus = Tringa semipalmata*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Aves (continued)	Passeriformes	*Hirundo* sp.? (Holocene general)	Hevly 1984
	Passeriformes	*Icterus galbula* (Holocene general)	Hevly 1984
	Passeriformes	*Icterus* sp. (Holocene general)	Mead 1981
	Passeriformes	*Junco hyemalis*	Mead 1981, Rea and Hargrave 1984
	Passeriformes	cf. *Junco* sp.	Emslie 1988
	Passeriformes	*Lanius excubitor* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Loxia* cf. *L. curvirostra*	Mead 1981
	Passeriformes	*Myadestes townsendi* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Passerella iliaca* (Holocene general)	Hevly 1984
	Passeriformes	*Passerina* sp. (Holocene general)	Hevly 1984
	Passeriformes	*Pica hudsonia* (Holocene general)[10]	Hevly 1984
	Passeriformes	*Salpinctes obsoletus* (Holocene general)	Hevly 1984
	Passeriformes	*Salpinctes obsoletus*?	Mead 1981
	Passeriformes	*Sayornis nigricans* (Holocene general)	Hevly 1984
	Passeriformes	*Sayornis saya* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Sialia currucoides* (Holocene general)	Mead 1981, Hevly 1984
	Passeriformes	*Turdus grayi* (Holocene general)	Hevly 1984
	Passeriformes	*Turdus migratorius* (Holocene general)	Hevly 1984
	Passeriformes	*Turdus migratorius*?	Mead 1981
	Passeriformes	*Turdus* sp.?	Mead 1981
	Passeriformes	*Zonotrichia* cf. *Z. leucophrys* (Holocene general)	Hevly 1984
	Passeriformes	cf. Fringillidae (late Holocene)	Mead and Van Devender 1981
	Passeriformes	Passeriformes undetermined	Emslie 1988, Dryer 1994, Emslie et al. 1995
	Pelecaniformes	*Ardea herodias* (Holocene general)	Mead 1981, Hevly 1984
	Pelecaniformes	*Nycticorax nycticorax*	Hunt et al. 2018
	Pelecaniformes	cf. *Nycticorax nycticorax*	Carpenter 2003

[10] *Pica pica hudsonica = Pica hudsonia*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Aves (continued)	Pelecaniformes	Ardeidae undetermined	Carpenter 2003
	Piciformes	*Colaptes auratus*	Emslie 1988
	Piciformes	*Sphyrapicus varius*	Emslie 1988
	Piciformes	Picidae undetermined	Emslie 1988
	Podicipediformes	*Aechmophorus occidentalis*	Hevly 1984, Emslie 1988
	Podicipediformes	*Podiceps auritus* (Holocene general)	Mead 1981
	Podicipediformes	*Podiceps nigricollis* (Holocene general)	Mead 1981, Hevly 1984
	Podicipediformes	cf. *Podiceps nigricollis*	Emslie 1988
	Podicipediformes	*Podilymbus podiceps*	Emslie 1988
	Strigiformes	*Bubo virginianus*	Mead 1981, Mead and Van Devender 1981, Rea and Hargrave 1984
	Strigiformes	*Otus asio* (Holocene general)	Mead 1981, Hevly 1984
	Strigiformes	*Tyto alba*	Miller 1960, Carpenter 2003, Hunt et al. 2018
	–	Aves undetermined	Cole and Mead 1981, Mead and Phillips 1981, Hevly 1984, Emslie 1988, Dryer 1994
Mammalia	Pilosa	*Nothrotheriops shastensis*[11]	*see text*
	Eulipotyphla	*Notiosorex crawfordi*	Mead 1981, Mead and Phillips 1981, Mead and Van Devender 1981, Emslie 1988
	Rodentia	*Ammospermophilus* cf. *A. leucurus* (late Holocene)	Mead and Van Devender 1981
	Rodentia	*Castor canadensis* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Rodentia	*Dipodomys* sp.	Lindsay and Tessman 1974, Mead 1981, Mead and Van Devender 1981, Hunt et al. 2018
	Rodentia	*Erethizon dorsatum*	Van Devender et al. 1977, Mead 1981, Mead and Phillips 1981, Hunt et al. 2018
	Rodentia	*Eutamias* sp.	Lindsay and Tessman 1974, Cole and Mead 1981, Hunt et al. 2018
	Rodentia	*Lemmiscus curtatus*	Mead et al. 2003
	Rodentia	*Marmota flaviventris*	Lange 1956, Van Devender et al. 1977, Hunt et al. 2018
	Rodentia	*Marmota flaviventris* cf. *M. f. engelhardti*	Wilson 1942
	Rodentia	*Marmota* cf. *M. flaviventris*	Mead 1981, Mead and Phillips 1981

[11] *Nothrotherium shastense* = *Nothrotheriops shastensis*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Mammalia (continued)	Rodentia	*Marmota* sp.	Lindsay and Tessman 1974, Emslie et al. 1995
	Rodentia	*Microtus* sp.	Cole and Mead 1981, Mead 1981, Mead and Phillips 1981, Emslie 1988, Mead et al. 2003
	Rodentia	*Neotoma cinerea*	Mead et al. 2003
	Rodentia	*Neotoma devia* or *N. lepida*	Hunt et al. 2018
	Rodentia	*Neotoma lepida*	Van Devender et al. 1977, Mead 1981, Hunt et al. 2018
	Rodentia	*Neotoma mexicana*	Mead 1981, Hunt et al. 2018
	Rodentia	*Neotoma stephensi*	Van Devender et al. 1977, Mead 1981, Hunt et al. 2018
	Rodentia	*Neotoma* cf. *N. cinerea*	Cole and Mead 1981
	Rodentia	*Neotoma* cf. *N. lepida*	Cole and Mead 1981
	Rodentia	*Neotoma* cf. *N. mexicana*	Van Devender et al. 1977
	Rodentia	*Neotoma* sp.	Lindsay and Tessman 1974, Van Devender et al. 1977, Cole and Mead 1981, Olsen and Olsen 1984, Emslie 1988, Dryer 1994, Mead et al. 2003
	Rodentia	*Neotoma* spp.	Mead 1981, Mead and Phillips 1981
	Rodentia	*Ondatra zibethicus* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Rodentia	*Perognathus* cf. *P. intermedius*	Mead 1981, Mead and Phillips 1981
	Rodentia	*Perognathus* sp.	Emslie 1988
	Rodentia	*Peromyscus* sp.	Van Devender et al. 1977, Cole and Mead 1981, Mead and Phillips 1981, Olsen and Olsen 1984, Emslie 1988, Dryer 1994, Mead et al. 2003, Hunt et al. 2018
	Rodentia	*Peromyscus* spp.	Mead 1981, Mead and Van Devender 1981
	Rodentia	cf. *Reithrodontomys*	Cole and Mead 1981
	Rodentia	*Sciurus* sp. (Holocene?)	Olsen and Olsen 1984
	Rodentia	cf. *Sciurus* sp.	Emslie 1988
	Rodentia	*Spermophilus variegatus*	Mead 1981, Mead and Phillips 1981
	Rodentia	*Spermophilus* sp.	Lindsay and Tessman 1974, Mead et al. 2003, Hunt et al. 2018
	Rodentia	*Tamias* sp.	Hunt et al. 2018
	Rodentia	*Thomomys* sp.	Lindsay and Tessman 1974, Cole and Mead 1981, Hunt et al. 2018
	Rodentia	Sciuridae undetermined	Emslie et al. 1995
	Rodentia	Rodentia undetermined	Hevly 1984
	Lagomorpha	*Lepus californicus*	Mead 1981, Olsen and Olsen 1984
	Lagomorpha	*Lepus* near *L. californicus*	Wilson 1942

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Mammalia (continued)	Lagomorpha	*Lepus* sp.	Lindsay and Tessman 1974, Emslie 1988, Emslie et al. 1995, Hunt et al. 2018
	Lagomorpha	*Sylvilagus* cf. *S. audubonii*	Olsen and Olsen 1984
	Lagomorpha	*Sylvilagus* sp.	Lindsay and Tessman 1974, Van Devender et al. 1977, Mead 1981, Emslie 1988, Emslie et al. 1995, Mead et al. 2003, Hunt et al. 2018
	Lagomorpha	Lagomorpha undetermined	Hevly 1984
	Chiroptera	*Antrozous pallidus*	Emslie 1988
	Chiroptera	*Desmodus stocki*	Ray et al. 1988, Carpenter 2003, Hunt et al. 2018
	Chiroptera	*Eptesicus* cf. *E. fuscus*	Olsen and Olsen 1984
	Chiroptera	*Euderma maculatum*	Mead and Mikesic 2005
	Chiroptera	*Eumops* sp.	Carpenter 2003, Hunt et al. 2018
	Chiroptera	*Lasiurus cinereus*	*see text*
	Chiroptera	*Lasionycteris noctivagens*	*see text*
	Chiroptera	*Myotis* sp. (possibly Holocene)	Olsen and Olsen 1984
	Chiroptera	cf. *Myotis* sp.	Emslie 1988
	Chiroptera	*Pipistrellus hesperus* [*Parastrellus*]	Emslie 1988
	Chiroptera	*Plecotus townsendi* [*Corynorhinus*]	Emslie 1988
	Chiroptera	*Tadarida brasiliensis*	Carpenter 2003, Hunt et al. 2018
	Chiroptera	Undetermined Chiroptera	Van Devender et al. 1977
	Carnivora	*Bassariscus astutus*	Wilson 1942, Mead 1981, Mead and Phillips 1981, Hunt et al. 2018
	Carnivora	*Bassariscus* sp.	Lindsay and Tessman 1974
	Carnivora	*Canis latrans* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Carnivora	*Canis* sp. (wolf)	Emslie 1988
	Carnivora	*Lontra canadensis*	Mead 1981, Olsen and Olsen 1984
	Carnivora	*Lynx rufus*	Mead 1981
	Carnivora	*Lynx* sp.	Wilson 1942, Hunt et al. 2018
	Carnivora	*Mustela* sp.	Lindsay and Tessman 1974, Hunt et al. 2018
	Carnivora	*Procyon lotor* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Carnivora	*Puma concolor*[12]	Mead 1981, Mead et al. 2003, Hunt et al. 2018
	Carnivora	*Puma concolor*?	Wilson 1942

[12] *Felis concolor = Puma concolor*

Appendix Table 11-A-3 (continued). Ice Age vertebrate taxa reported from the Grand Canyon.

Class	Order	Taxa Observed	Sources
Mammalia (continued)	Carnivora	*Spilogale putorius*	Emslie 1988
	Carnivora	*Spilogale gracilis* or *S. putorius*	Hunt et al. 2018
	Carnivora	*Spilogale* sp.	Lindsay and Tessman 1974
	Carnivora	*Urocyon cinereoargenteus* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Carnivora	*Vulpes vulpes*	Carpenter 2002
	Carnivora	Canidae undetermined	Carpenter and Mead 2000
	Proboscidea	*Mammuthus* sp.	Emslie 1987, Emslie 1988
	Perissodactyla	*Equus* sp. (*E. conversidens*?)	Harington 1984
	Perissodactyla	*Equus* sp.	Wilson 1942, Mead 1981, Emslie 1987, Emslie 1988, Carpenter 2003, Mead et al. 2003, Hunt et al. 2018
	Artiodactyla	*Antilocapra americana*	Mead 1981, Mead and Phillips 1981
	Artiodactyla	*Bison* sp.	Harington 1984, Emslie 1987, Emslie 1988, Mead et al. 2003, Martin 2014, Martin et al. 2017
	Artiodactyla	*Camelops hesternus*	Mead et al. 2003
	Artiodactyla	*Camelops* cf. *C. hesternus*	Mead 1981, Mead and Phillips 1981
	Artiodactyla	?*Camelops* sp.	Emslie 1987
	Artiodactyla	cf. *Camelops* sp.	Emslie 1988
	Artiodactyla	*Euceratherium collinum*	Mead et al. 2003, Kropf et al. 2007
	Artiodactyla	cf. *Euceratherium collinum*	Mead et al. 2003
	Artiodactyla	*Odocoileus hemionus* (Holocene general)	Mead 1981, Olsen and Olsen 1984
	Artiodactyla	*Odocoileus* sp.	Mead 1981, Mead and Phillips 1981
	Artiodactyla	*Oreamnos harringtoni*	*see text*
	Artiodactyla	*Oreamnos* sp. (probably Holocene)	Harington 1984
	Artiodactyla	*Oreamnos* or *Ovis*	Emslie 1988
	Artiodactyla	*Ovis canadensis*	Mead 1981, Mead and Phillips 1981, Olsen and Olsen 1984, Harington 1984, Carpenter 2003, Mead et al. 2003, Hunt et al. 2018
	Artiodactyla	*Ovis* sp.	Wilson 1942
	Artiodactyla	Bovidae undetermined	Carpenter 2003
	Artiodactyla	Artiodactyla undetermined	Cole and Mead 1981, Harington 1984, Dryer 1994, Carpenter 2003
	–	Undetermined large mammal	Emslie 1988, Emslie et al. 1995
	–	Mammalia undetermined	Hevly 1984
	–	Vertebrata undetermined	Hevly 1984

Ichnofossils and Reproductive Traces

Ice Age ichnofossils and reproductive traces reported from the Grand Canyon can be seen in Appendix Table 11-A-4.

Appendix Table 11-A-4. Ice Age ichnofossils and reproductive traces reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Category	Traces Observed	Sources
Invertebrates	Dipteran pupal case	Hevly 1984
	“Helminth” eggs	Schmidt et al. 1992
	Nematode eggs	Laudermilk and Munz 1938
Vertebrates	Artiodactyl dung	Mead and Swift 2012, Hunt et al. 2018
	Bassariscus astutus dung	Mead and Swift 2012, Hunt et al. 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 et al. 2018
	cf. *Lepus* sp. dung	Mead and Swift 2012, Hunt et al. 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 et al. 1984, O’Rourke and Mead 1985, Mead and Swift 2012, Hunt et al. 2018
	Peromyscus sp. dung	Emslie 1988
	Rabbit dung	Hevly 1984
	Rodent dung	Hevly 1984, Mead and Swift 2012, Hunt et al. 2018
	Sauromalus dung (age not stated)	Mead and Swift 2012
	cf. *Sylvilagus* sp. dung	Mead and Swift 2012, Hunt et al. 2018
	Bird regurgitation pellets	Emslie et al. 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

Other fossil Ice Age taxa reported from the Grand Canyon are listed in Appendix Table 11-A-5.

Appendix Table 11-A-5. Other Ice Age fossil taxa reported from the Grand Canyon. Taxa followed by an asterisk (*) were named from specimens found within GRCA.

Phylum	Class	Class or Subclass	Traces Observed	Sources
Apicomplexa	Conoidasida	Coccidia	*Archaeococcidia antiquus**	Schmidt et al. 1992
	Conoidasida	Coccidia	*Archaeococcidia nothrotheriopsae**	Schmidt et al. 1992
–	–	–	Fungal spores	Robbins et al. 1984, Schmidt et al. 1992