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MIDDLE HOLOCENE FLORA AND FAUNA FROM A RINGTAIL (*BASSARISCUS*, CARNIVORA) DEN, WESTERN GRAND CANYON, ARIZONA

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ABSTRACT

Dietary remains recovered from *Bassariscus* (ringtail) midden deposits of middle Holocene age in the Weeping Cliffs, lower Grand Canyon, Arizona, indicate a diverse ringtail diet of plants and small vertebrates. Remains of fruits and seeds predominated among the plant parts, especially of hackberry, several cacti, and groundcherry. Highly fragmented remains of small vertebrates included anurans, lizards, snakes, bats, and rodents. Only one recovered vertebrate specimen exceeded 5 mm in length, necessitating meticulous morphological comparisons for taxonomic identifications, which were usually limited to generic level. Two radioisotopic dates on the middens range from ca. 7300 to 7900 cal yr BP. Vertebrate remains from the middens provide the first Quaternary records of amphibians (including *Anaxyrus* and *Hyla*/*Dryophytes*) and a bat (*Nyctinomops macrotis*) from the Grand Canyon. Rare, fragmentary specimens provide one of only two fossil records of *Dipsosaurus* in Arizona.

INTRODUCTION

The North American ringtail (Carnivora; Procyonidae; *Bassariscus astutus*) is a small to medium-sized (~1 kg) carnivore living today in arid, forested, and rocky habitats from southwestern Oregon south and east throughout most of the Intermountain West to Missouri, Texas, and south throughout most of Mexico (Poglayen-Neuwall and Toweill, 1988). Another similar living species of ringtail, *B. sumichrasti* (cacomistle), occurs in Central America north into southernmost Mexico (Pino et al., 2016). Fossils attributed to *Bassariscus* first appear in the Middle Miocene (Barstovian North American Land Mammal Age; Bever, 2003; Baskin, 2004; but see discussion in Koepfli et al., 2007) with additional early Neogene species from Washington and Oregon to Kansas and into the Southwest (Czaplewski, 1990; Bever, 2003; Gustafson, 2015; among others). Although the fossil history and skeleton of this small nocturnal carnivore have been assessed, its record of predation and consumption of the local biota is less well understood.

Quaternary-age vertebrates attributed to the collecting behavior of *Bassariscus astutus* are known from many caves including those in California (Mead et al., 2006; Stegner, 2015), Texas (Harris and Hearst, 2012), Arizona, New Mexico (Harris, 1985, 2013), Nevada (Emslie and Mead, 2023), and northern Mexico (White et al., 2010). In larger fossil cave deposits, the collecting behavior of the ringtail may be masked by other taphonomic scenarios such as at Papago Springs Cave, Arizona (Skinner, 1942; Czaplewski et al., 1999). Remains described as the extinct *B. sonoitensis* from Late Pleistocene deposits in Papago Springs Cave, southeastern Arizona, have been synonymized with the extant *B. astutus* (Skinner, 1942; Harris, 1990).

The Quaternary environmental history of the Grand Canyon has been reviewed showing that fossils of this age are typically found in caves (encompassing multiple taphonomic scenarios) and in isolated woodrat (packrat, *Neotoma*) middens within dry rock crevices (Phillips and Van Devender, 1974; Van Devender et al., 1977; Mead et al., 2003; Tweet et al., 2012; Mead et al., 2021). What has received much less attention has been the various deposits of vertebrates and plants that can be attributed to the ringtail. Large accumulations of Late Pleistocene fossils from the Grand Canyon are known from Rampart and Stanton Caves, localities where prior research has typically accented larger mammals and their dung (Mead, 1981), and a den comprising an accumulation of ringtail dung (coprolite debris accumulation; “latrinites” of Hunt and Lucas, 2012, 2021; here termed “ringtail midden”) was analyzed from Vulture Cave dating to the late Holocene (Mead and Van Devender, 1981). Here we report on the vertebrate and plant contents of a ringtail midden from a small crevice-cave positioned immediately above the alluvial terrace of the Colorado River, westernmost Grand Canyon. The Weeping Cliffs locality provides access to a riparian environment not previously sampled or preserved in other Grand Canyon cave deposits, and is one of the few direct dietary evidence records, thus making these finds noteworthy.

WEEPING CLIFFS, GRAND CANYON

The Weeping Cliffs (western Grand Canyon) are formed in the Muav Limestone, an exposure of cliffs along the Lower Granite Gorge of the Colorado River close to where the river exits the Grand Wash Cliffs of the Colorado Plateau (Fig. 1). Situated at 426 m elevation, the Weeping Cliffs contain small caves, overhangs, small shelters, and crevices. Prior to the development of Lake Mead reservoir in the 1930s, the position of the outcrop provided close access to sandy

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floodplain and riparian environments along the Colorado River and to rocky talus slope and side-canyon habitats now with desert biota above the cliffs. The alluvial floodplain biotic community along the Colorado River became submerged and locally extirpated until approximately 2002 with the retreat of Lake Mead from the Grand Canyon (Fig. 1). Based upon the geomorphology of the river corridor, an enduring floodplain and associated habitat had previously bordered the Colorado River, possibly as far upriver as River Mile 237 (40 river miles [65 river km] from its exit at River Mile 277; L. E. Stevens personal communication, December 2023).

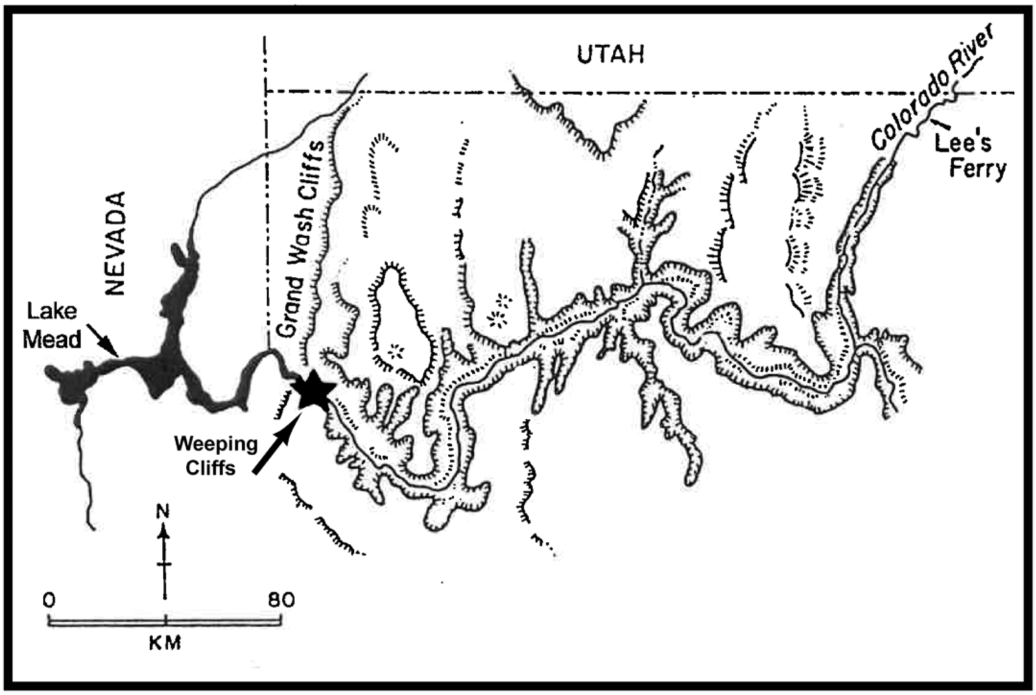

Figure 1. Map of Grand Canyon with location of Weeping Cliffs at the western, most down river location along the Colorado River. Other known cave sites with Late Pleistocene faunas nearby Weeping Cliffs (star) include Rampart, Muav, and Vulture Caves.

Today the local biotic community around the Weeping Cliffs contains plants and animals aligned with the Mojave and Sonoran deserts—many at the northern limits of their distributions. Well-known Late Pleistocene faunal localities near the Weeping Cliffs include Rampart Cave and Muav Caves (Wilson, 1942; Long and Martin, 1974; Van Devender et al., 1977), along with the more remote Vulture Cave (Mead and Phillips, 1981). Previous studies (Phillips, 1984; Phillips and Van Devender, 1974; Spaulding, 1990) provide details about the vegetation changes during the full and late Wisconsinan Glacial through the Holocene to today of this lower Grand Canyon region.

METHODS AND RESULTS

The Weeping Cliffs ringtail middens were found on a crevice-bearing ledge under an overhang about 65 m west of the Muav Caves. The moist alcove is unusual in that the northeast facing cliffs above provide shade and the name "Weeping Cliffs" suggests groundwater seepage, although none was observed at the time of collection. The alcove is further shaded by large trees of netleaf hackberry (*Celtis reticulata*) that occupy sites of groundwater seepage in this area (Phillips et al., 1987).

Limestone crevices and caves in the Grand Canyon, including the Weeping Cliffs with their horizontal and vertical crevices, have provided long-lasting shelters, protecting organic deposits such as the omnipresent packrat middens (organic debris piles dominated by plant remains) for thousands of years (chapters in Betancourt et al., 1990). Our report details the faunal and plant remains representing the diet of ringtails recovered from two ringtail middens that merge into a single unit within a crevice.

The Weeping Cliffs ringtail deposits are an accumulation of plant remains along with abundant, highly broken skeletal remnants. Most of the accumulation was cemented together presumably with the urine of the ringtail, analogous to the way that packrats solidify their middens with urine (amberat). We conducted no analysis to verify that ringtails cement their dung accumulations via continued urination, which may be more of a scent marking action (Barja and List, 2006). We have noted that packrat urine cement odor is distinctly different than that found in ringtail den accumulations. Multiple gallon-sized-bag masses of hardened ringtail midden were removed for our project. These middens were water-sieved through 0.5 mm mesh to remove the urine cement and then sorted by SLS for fossils using a 10x microscope. Plant macrofossils were identified by KLC, bat remains were identified by NJC, and other vertebrates were identified by JIM.

Due to their small size, the abundant plant fossils were not immediately evident during our crevice exploration. The collecting habits of packrats cause these rodents to construct their middens with abundant large plant macrofossils, many over 1 cm or more in length. In contrast, most of the plant macrofossils identified from the Weeping Cliffs ringtail middens were less than 2 mm in length. Many of these plant and vertebrate remains are damaged in such a way as to suggest that they may have passed through the digestive system of the ringtail, although we have no direct experimental evidence of the effects of ringtail mastication and digestion on plants. Significantly, modern ringtail dung accumulations and the Weeping Cliff middens also lack the voluminous remains of packrat dung pellets found in packrat middens; only the broken and fragmented remains of ringtail coprolites were observed.

All vertebrate remains are highly broken and sometimes etched. The extreme fragmentation suggests that the remains represent prey that was chewed by a small carnivore and do not exhibit the characteristics of raptor ingestion (e.g. , owl pellet). Only those skeletal remains that, although fragmented, exhibit diagnostic characters are identified and presented here. Identification to species typically was not conducted on these remains either due to the fragmented nature of the elements or because known characters providing specific rank identifications were not available.

To radiocarbon date the organics we used the Accelerator Mass Spectrometry (AMS) facility at the National Ocean Sciences AMS Facility, Woods Hole Oceanographic Institution; calibrations of the dates (cal yr BP) were assessed with OxCal 4.4, IntCal20. For the Weeping Cliffs 3a deposit, a single seed of *Opuntia* cf. *chlorotica* (prickly pear cactus) was dated to a median age 7,781 cal yr BP (95% confidence limits range: 7,925–7,666 cal yr BP; 6,950±65 radiocarbon yr BP, OS-33861). Weeping Cliffs 2 deposit was dated on plant debris mixed in with the ringtail dung to median age 7,460 cal BP (95% confidence limits range: 7,565–7,326 cal yr BP; 6,550±65 radiocarbon yr BP, OS-33862). Both dates indicate a middle Holocene age for the accumulation of the midden remains.

Plant Remains

The plant macrofossils identified from the middens (Table 1) all occur in the area today. The locality within 15 m of the fossils is in the shade of the netleaf hackberry trees, which were estimated to cover 70% of the immediate surrounding. Hackberry was by far the most common fossil in the ringtail midden. All the other plant macrofossils are of desert shrubs, herbs, and grasses that are now found just outside of this shaded refuge (Phillips et al., 1987). The predominant plant macrofossils recovered are the most fleshy, edible berries of these desert plants, suggesting that they had been collected as food. In contrast, packrat middens often contain more abundant thorns and spines, possibly collected to discourage predators, harvested but uneaten food plant foliage, and many other nonedible plant parts collected to make a shelter over the nesting area that contributes to security and thermoregulation of the packrat (Olsen, 1973; Vaughan, 1980).

Faunal Remains

All fossil remains are curated by the National Park Service, Grand Canyon National Park (GRCA), Arizona. In the taxonomic accounts below, the skeletal element listing is followed by parentheses that contain the specimen number for the GRCA archive along with the quantity of identifiable specimens. Abbreviations include: WP-2, Weeping Cliffs deposit sample 2; WP-3a, Weeping Cliffs deposit sample 3a. Given the Holocene age for the specimens, modern geographic distributions of locally extant amphibian and reptilian species played heavily into the identifications, although in select cases, other taxa well outside the modern range were considered. Terminology and characters used to describe the anuran (frog and toad) remains follows Bailon (1999) and Holman (2003). Descriptive terminology for the lizard remains usually follows Evans (2008). See text for the terminology and characters used to describe snake vertebrae, but typically follow Auffenberg (1963), Van Devender and Mead (1978), and LaDuke (1991).

SYSTEMATICS

Amphibia

Anura

Remains: WP-2: various highly fragmented postcranial bones of anurans were recovered but were not identifiable to a lower taxonomic level (125701).

Bufonidae

Anaxyrus (formerly *Bufo*) sp. (toad)

Remains: WP-2: frontoparietal (125702; 1).

Discussion: One fragment (3.5 mm long) of a left frontoparietal having a portion of the thickened medial ridge rugose and pitted on the dorsal side. This bone is thin and smooth on *Scaphiopus* and *Spea* (spadefoot toads); smooth and narrow on *Hyla* (*Dryophytes*) *arenicolor* (canyon tree frog) and *Pseudacris* (chorus frog). *Anaxyrus borealis* (western toad) and *A. debilis* (Chihuahuan green toad) have a predominantly smooth dorsal surface to the frontoparietal, but there is slight rugosity along the medial ridge; this is more pronounced on *A. woodhousii* (Woodhouse's toad) but still a ridge. *Anaxyrus cognatus* (Great Plains toad) has a heavily rugose medial ridge as found on the fossil. We did not compare the fossil with the extant *A. microscaphus* (Arizona toad), *A. retiformis* (Sonoran green toad), or *A. punctatus* (red-spotted toad, which occurs throughout the Grand Canyon corridor; Miller et al., 1982). Without more of the single fragmented bone, we are reluctant to identify the fossil to species, but given the morphological similarity, it is most similar to that of the Great Plains toad. Today, *A. cognatus* does not occur in the Grand Canyon or along this southwestern portion of the Colorado Plateau, whereas *A. woodhousii* does (Murphy, 2018). The fossils from the Weeping Cliffs represent the first Quaternary *Anaxyrus*, or of any amphibian, from the Grand Canyon (Olsen and Olsen, 1984; Mead, 2005).

Hylidae

Hyla sp. (treefrog)

Remains: WP-2: maxilla (125703; 6).

Discussion: All maxillae were highly fragmented with the largest specimen 2.5 mm long. Teeth are pedicellate, relatively narrow, and 0.5 mm high as found on *Hyla* (*Dryophytes*) *arenicolor* and *H. wrightorum*. These are the only tree frogs in this genus living in the Grand Canyon and elsewhere nearby today. We did not compare in detail with *Smilisca fodiens* or *Acris blanchardi*, which are other tree frogs found in Arizona but not within the Grand Canyon region today (Murphy, 2018). Teeth on the spadefoot toads (*Spea* and *Scaphiopus*) are typically wide at the base and short unlike those from the Weeping Cliffs. *Hyla arenicolor* was found living in wet canyons and springs near Weeping Cliffs (JIM field notes) and throughout the Grand Canyon corridor (Miller et al., 1982). These fossils from the Weeping Cliffs represent the first Quaternary *Hyla*/*Dryophytes* from the Grand Canyon (Olsen and Olsen, 1984; Mead, 2005)

Reptilia

Sauria

Lizards

Families and Genera Indeterminate

Remains: WP-2: dentaries, maxillae, vertebrae (125704, 20), premaxilla (125705, 1); WP-3a: dentaries, maxillae, vertebrae (125706, 15).

Discussion: These skeletal elements were too highly fragmented and etched by digestive acids to permit identifications.

Iguanidae

Dipsosaurus sp. (Desert Iguana)

Remains: WP-2: dentary (125707; 1 left), maxilla (125708; 1 left).

Discussion: The fragmented left dentary (125707) is 2.7 mm long, preserving the mandibular symphysis and one complete tooth, with space for an additional three teeth. The single preserved tooth flares up from the base to the apex, which encompasses 4, possibly 5 cusps; it has no single main cusp. The left maxilla fragment (125708) has a preserved tooth row length of 1.4 mm with two teeth. Both teeth flare from the base to the apex and are mediolaterally flattened. There is one central cusp with two lateral cusps and an incipient additional lateral cusp posteriorly (Fig. 2A).

Maxillary and dentary teeth of iguanine lizards are described by Edmund (1969) and in detail by de Queiroz (1987). For many iguanines, the maximum number of cusps per tooth is 4, comprising 1 large apical (median), up to 2 anterior cusps, and 1 posterior cusp. Tooth crowns become progressively more laterally compressed posteriorly in the tooth row. Greater cuspation on a tooth occurs on some other iguanines (much larger individuals than *Dipsosaurus*) such as *Ctenosaura* (spiny iguana), *Cyclura* (rock iguana), and *Sauromalus* (chuckwalla), with 5 to 10 cusps; *Iguana* (iguana) can have the greatest cuspation to the point that the teeth are serrated (see de Queiroz, 1987: Fig. 30; Avery and Tanner, 1971).

Today, the northern extent of this hot, xeric-adapted lizard appears to coincide with the distribution of *Larrea divaricata* (creosote bush) and with substrate conditions of loose sand and patches of firm ground with scattered rocks (Hulse, 1992). *Dipsosaurus* is not known from the Grand Canyon in historic times (Miller et al., 1982; Hulse, 1992; Holycross et al., 2022). There does not appear to have been any published, detailed survey of the sandy, desert flood plain area adjacent to the Colorado River in the Grand Canyon prior to its flooding with Lake Mead reservoir water in the 1930s. Given the present habitat requirements of *Dipsosaurus*, the recently flooded, now exposed riparian floodplain would have been the only suitable area for the species' prior existence in the lower Grand Canyon.

Fossils of *Dipsosaurus* are not common. The living *D. dorsalis* is known from the late Pliocene (Blancan North American Land Mammal Age) deposits in the Anza-Borrego Desert, California (Norell, 1989) and is reviewed in Mead and Self (manuscript). This desert lizard is recently recorded in the Late Pleistocene deposits in La Tetera Cave outside of Tucson, Arizona (Czaplewski et al., in press). The *Dipsosaurus* from Weeping Cliffs represents one of two Quaternary records in Arizona and the only record from within the Grand Canyon where it does not live today (Miller et al., 1982; Mead, 2005; Murphy, 2018).

Phrynosomatidae

Uta/*Cophosaurus*/*Holbrookia* indeterminate

Remains: WP-3a: dentary (125709; 1).

Discussion: The fragmented left dentary extends from near the mandibular symphysis to a length of 3.1 mm with 12 teeth. The Meckelian fossa is fused from just short of the symphysis, but the suture line is visible the entire length of the ventral side of the dentary. Teeth are parallel sided in medial view and end in a single blunt cusp. Some teeth have an incipient cusplet on both sides of the main cusp. Apices of teeth show a slight lateral flattening; anterior teeth are blunt pointed.

Teeth of *Callisaurus* (zebra-tailed lizard) are overall larger and thus omitted from consideration. *Petrosaurus* (banded rock lizard) has distinctly wide teeth with a triangular medial cusp and two adjacent smaller cusps, unlike the fossil. Teeth of *Urosaurus* (both *U. ornatus* [tree lizard] and *U. graciosus* [long-tailed brush lizard]) have relatively longer teeth

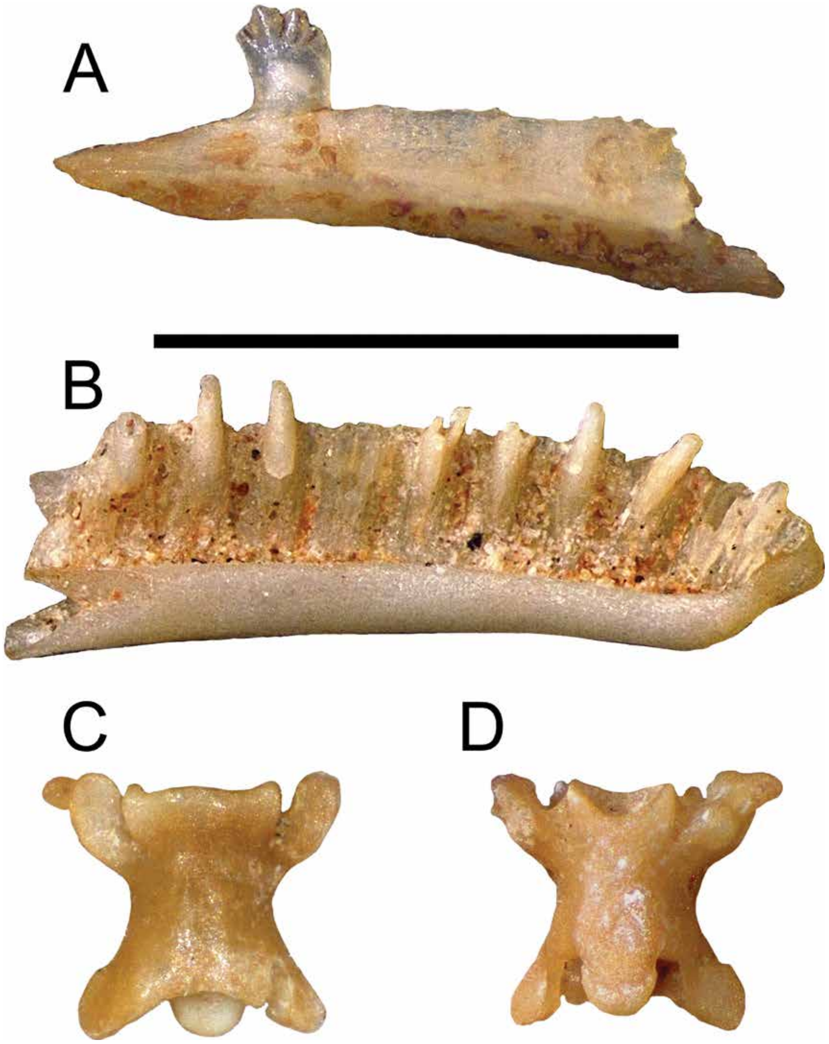

Figure 2. Selected reptile bones from the Weeping Cliffs ringtail midden locality. (A) fragmented dentary (GRCA 125707) belonging to *Dipsosaurus* (desert iguana). Although highly broken due to chewing by *Bassariscus*, the diagnostic tricuspate to multicuspate (shown here) pattern is preserved allowing identification, see text. (B) lingual view of the fragmented dentary (GRCA 125716) of *Coleonyx* (gecko). Vertebra of the scolecophidian snake, *Rena* (GRCA 125720) showing dorsal (C) and ventral (D) views, anterior is up. Note the extremely small adult size and the lack of a neural spine or hemal keel. Vertebra shown is the largest of several recovered vertebrae. Scale bar = 2 mm.

that culminate in a longer pointed apex cusp, unlike the fossil. Teeth of *Cophosaurus* (greater earless lizard), *Holbrookia* spp. (lesser earless lizard), and *Uta* (side-blotched lizard) all have tooth and Meckelian suture morphology similar to that on the fossil; however, because the fossil is fragmented, we are unable to make a more definitive identification. Other sand lizards, *Uma* spp., are not considered due to their modern distributions, dissimilar habitats, and age of the fossil deposit.

Urosaurus and *Uta* are extant today throughout the Grand Canyon. *Callisaurus* is recorded from a single location at the Colorado River at the confluence of Diamond Creek, which may have been its access route. *Cophosaurus* and *Holbrookia* are not recorded from the Grand Canyon in historic times, although the latter lizard can be found on the Colorado Plateau around the Canyon (Miller et al., 1982; Murphy, 2018).

Sceloporus sp. (spiny lizard)

Remains: WP-2: dentary (125710, 1).

Discussion: A left dentary fragment 7 mm long from symphysis to distal break. The Meckelian fossa is open ventrally at the symphysis, then becomes oriented lingually to close at the seventh tooth. Fourteen teeth have highly dissolved lingual faces, but one apex shows an indication of a tricuspate apex. The size of the dentary is similar to the range of sizes in extant *Sceloporus* species having a snout-vent length greater than 55 mm (i.e. , not the small species of desert spiny lizards). Morphology appears most similar to a form of *Sceloporus* such as *S. occidentalis* or *S. magister* and others that live in and around the Grand Canyon (Murphy, 2018). Late Pleistocene records of *Sceloporus* are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

Crotaphytidae

Crotaphytus sp. (collared lizard)

Remains: WP-3a: dentary (125711, 3).

Discussion: Three dentary fragments are highly broken, but all contain teeth. The largest fragment is 1.6 mm long with three tricuspate teeth. The largest tooth is 0.5 mm wide at the base and only 1.0 mm tall. There is one distinct medial cusp and two less distinct lateral cusps. The size and robustness of the teeth suggest that the dentary belongs to *Crotaphytus*; no teeth show the curvature or pointed apex as appears on the related genus *Gambelia* (leopard lizard). Both *C. bicinctores* (Great Basin collared lizard) and *C. collaris* (eastern collared lizard), as well as *G. wislizenii* (long-nosed leopard lizard), are known today in and around the Grand Canyon (Miller et al., 1982; Murphy, 2018) and elsewhere in arid Arizona (Holycross et al., 2022). Late Pleistocene records of *Crotaphytus* are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

Gekkonidae

Coleonyx sp. (banded gecko)

Remains: WP-2: dentary (125716; 8, 4 left, 4 right), maxilla (125713; 2 right), premaxilla (125714; 2), frontal (125715; 1); WP-3a: dentary (125712; 3, 2 left, 1 right), maxilla (125717; 1 right).

Discussion: The dentaries of modern *Coleonyx* and the GRCA fossils have a fused (closed) Meckelian fossa and a wide dental shelf (gutter). Fragment lengths are from 1.2 to 2.0 mm for 125715, with the largest of eight in 125716 (Fig. 2B) being 4.3 mm as measured from the closed symphysis. Teeth of *Coleonyx* and the fossils are relatively tall and narrow on a wide dental shelf versus the condition observed on dentaries of *Xantusia* (night lizards). The fragmented maxillae (125717, 125713) (most complete is 3.2 mm long) have only a lateral orientation of the frontal process as in *Coleonyx* versus the condition in minute phrynosomatines in which the lateral orientation curves around more anteriorly to connect to the premaxilla process (e.g., *Urosaurus*, tree lizard). The Weeping Cliffs fossils lack the wide aspect of the premaxillary process and the longer more robust teeth of *Xantusia*. The fossil frontal (125715) has the midline fusion of the crista cranii forming a single covered frontal in palatal view, as found on modern *Coleonyx*. This contrasts with the open and paired characteristics to the frontals of *Xantusia*.

Today *C. variegatus* is a secretive, nocturnal lizard that lives in the hotter deserts of the Southwest, including throughout the Colorado River gorge of the Grand Canyon (Miller et al., 1982) and elsewhere in arid Arizona (Holycross et al., 2022). Although not a rare fossil in the Southwest, *Coleonyx* has been recovered in the Grand Canyon in deposits dating to the late Holocene and late Rancholabrean (Van Devender et al., 1977; Cole and Mead, 1981; Mead and Phillips, 1981; Mead and Van Devender, 1981; Mead, 2005). Its fossil record is typically found only in packrat middens and ringtail midden scats, although Norell (1986) recovered two specimens (of undefined age assignment) from accumulations in Kokoweef Cave, southern California.

Teiidae

Aspidoscelis sp. (whiptail lizard)

Remains: WP-2: dentary (125718, 1), frontal (125719, 1).

Discussion: The dentary (125718) fragment is 4.2 mm long with a closed Meckelian fossa closed on the ventral side of the bone. Six of the 10 teeth are bicuspate, which permits the identification as *Aspidoscelis* (formerly *Cnemidophorus*). The frontal fragment (125719) has an open groove at the cranial cristii in ventral view versus a shallow to no depression in the various sceloporine lizards. The dorsal surface on the fossil is fused but shows a suture line fusion for the two bones. There is some rugosity to the dorsal surface, and it lacks the distinct depression near the parietal suture found on *Sceloporus* (scaly lizards). The frontal is thin, smooth on the dorsal surface, and bowed on the various sand lizards, unlike the fossil. *Petrosaurus* has a frontal that is larger and more robust than the fossil. *Dipsosaurus* has a frontal about the same size as the fossil, but it is smoother and has a shallow groove between the cranial cristii, unlike the fossil. Anguid lizards such as *Elgaria kingii* (Arizona alligator lizard) has a frontal that is less diverging along the parietal/frontal suture, a deep groove between the cranial cristii that are highly expanded, and a more robust and textured dorsal surface than found on the fossil. Given these differences, we identify the frontal as that of a species of *Aspidoscelis*. We know of no characters of the frontal that permit identification of the species of this teiid, but it probably belonged to one of the many small species of the genus. At least twelve species are known to live in Arizona today, three of which occur in and around the Grand Canyon (Murphy, 2018). Late Pleistocene records of *Aspidoscelis* (recorded as *Cnemidophorus*) are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

Snakes

Leptotyphlopidae

Rena (Formerly *Leptotyphlops*; Threadsnake)

Remains: WP-2: vertebra (125720, 10).

Discussion: Ten vertebrae (two articulated) may represent a single individual. All are unique and readily identifiable as those of *Rena* in lacking the neural spine and the hypapophysis/hemal keel, and all are of an extremely small adult size (Fig. 2C and D; Mead, 2013).

Today *Rena humilis* (western thread snake, blind snake, or desert worm snake) is common in Arizona yet uncommon in the Grand Canyon (Fowlie, 1965; Miller et al., 1982; Wallach and Mitchell, 2020b). A second species, *Rena dissecta* (New Mexico thread snake) is known in southeastern Arizona and adjacent New Mexico (Wallach and Mitchell, 2020a). The occurrence of *Rena* in the Grand Canyon is not well understood, due likely to its secretive habits, but it is probably restricted to the desert environs of the river corridor similar to that previously discussed for the desert iguana. North American fossils of this tiny snake are rare and have been recovered only in Arizona (packrat middens) and New Mexico (owl roost and packrat midden; Van Devender and Worthington, 1977; Van Devender and Mead, 1978). The remains from Weeping Cliffs ringtail midden represent the first fossils for the Grand Canyon. We know of no vertebral characters that permit the identification to species, extant or fossil (Mead, 2013).

Colubridae

Sonora sp. (ground snake)

Remains: WP-2: vertebrae (125721, 3).

Discussion: Several small colubrid snakes have vertebrae that are similar to those of *Sonora*, including *Chilomeniscus* (sand snake), *Chionactis* (shovel-nosed snake), and *Hypsiglena* (night snake). The taxonomy of *Sonora* has been recently reinvestigated but does not seem to be fully resolved. Cox et al. (2018) place *Chionactis* and *Chilomeniscus* in the genus *Sonora*, which, according to these authors, now has at least 15 species. Here we will treat these genera as separate forms when examining the vertebrae and the vertebral characteristics.

Three vertebrae were recovered from the ringtail midden, 2 mid-trunk and 1 more cervical in position. Although all appear morphologically similar, only the characteristics of the largest are presented here. The large mid-trunk vertebra has a condyle length (cl) of 1.9 mm and a neural arch (na) width (naw) of 1.5 mm, thus a cl/naw ratio of 0.79. The na is slightly vaulted to not vaulted. The neural spine (ns) length is 1.3 mm, but its height cannot be determined due to breakage. Another of the vertebrae has its ns broken in part but shows enough to indicate that it was low. The zygosphene (z) is crenate as viewed from above and convex in anterior view. The accessory processes (ap) are directed laterally and are short and blunt pointed. There is no epizygapophyseal spine. The cotyle (ct) is round with a flat base (ventral). Two minute paracotylar foramina exist along with the paracotylar notches, but no ventrolateral cotylar processes occur. The hemal keel (hk) is a thin blade (gladiate; other vertebrae have an oblanceolate hk). The parapophysis is distinct from the diapophysis. The parapophysis is short, not protruding ventral to the ct. There are deep subcentral grooves alongside distinct subcentral ridges.

Van Devender et al. (1991a) determined that vertebrae of *Chionactis palarostris* (Sonoran shovel-nosed snake) differ, albeit slightly, from those of *C. occidentalis* (Mohave shovel-nosed snake; Van Devender and Mead, 1978). We feel that more data are needed about vertebral characteristics and potential variations between these two species along with a third Arizona shovel-nosed snake, *C. annulata* (resplendent shovel-nosed snake), as well as for all the species of *Sonora*, sensu lato.

Diadophis (ring-necked snake) has a long depressed na (cl=2.2 mm; naw=1.3; cl/naw=1.69; our data; see also LaDuke, 1991); thus, this snake is omitted from the fossil identification. Another small snake is *Tantilla* (black-headed snake) with vertebral characteristics similar to those for *Diadophis* (although smaller) and with long, thin, pointed ap (LaDuke, 1991), thus also differing from the fossil. *Hypsiglena* has a short, wide vertebra (cl=2.0 mm; naw=1.8 mm; cl/naw=1.11; our data; 1.18–1.3 from Van Devender and Mead, 1978). The prezygapophyseal facet shape and ap characters are not like those observed in the fossil (additional characters in Mead et al., 1984; Van Devender et al., 1991b). Thus, the fossil does not belong to *Hypsiglena*.

The vertebral characteristics of *Chilomeniscus* are not well represented in the literature; we present select data from both *C. cinctus* (banded sand snake; Arizona) and *C. stramineus* (of Baja California). The mid-trunk vertebra has the following characteristics: cl=1.4 mm, naw=1.0, and cl/naw=1.4. The z is crenate from above. The ap are directed laterally, are long, and robust. The ns is thin as on *Chionactis*. The hk is spatulate. The parapophyses drop below the ventral level of the ct, which is orbicular in shape. Vertebral characteristics for *Chionactis* from (Van Devender and Mead, 1978) are: ns is low, z is convex to crenate, ap are blunt pointed.

Given the characteristics of the mid-trunk vertebrae, as provided above from the literature and our data here, the fossils are most similar to *Chionactis* and *Sonora* and likely not *Chilomeniscus* or the other clearly different small snake vertebrae. Granted that molecular evidence argues for the synonymizing of *Chionactis* and *Chilomeniscus* with *Sonora* in the Sonorini (Grismer et al., 2002; Cox et al., 2018), our necessarily morphological approach suggests that the fossil is some form of *Sonora* (sensu lato) or of either *Chionactis* or *Sonora* (sensu stricto).

Three species of *Chionactis* live in Arizona today, *C. annulata* (resplendent shovel-nosed snake; Wood and Holycross, 2020a), *C. occipitalis* (Mohave shovel-nosed snake; Wood and Holycross, 2020b), and *C. palarostris* (Sonoran shovel-nosed snake; Wood and Holycross, 2020c; see also Fowlie, 1965; Rosen, 2007). None live in, around, or near the Grand Canyon today. However, *Sonora semiannulata* does occur in various locations in and around the Grand Canyon (Cox et al., 2020). As noted above, these authors recognize 15 species in the genus *Sonora*, that are distributed from central Mexico to the northwestern USA. It is doubtful that there will be definitive characteristics of the vertebrae that will permit the identification of isolated vertebrae to species or species-groups.

Late Pleistocene and Holocene *Chionactis* and *Sonora* vertebrae were recovered from packrat middens in southern Arizona in a reconstructed plant community containing *Larrea-Ambrosia* desert scrub intermixed with *Pinus* and *Juniperus* woodland species dating from 8,000 to 12,000 yr BP (Van Devender and Mead, 1978). Today *Chionactis* do not live within a woodland habitat but may live on the lower altitudinal edge of such a community (Miller et al., 1982; Mahrdt et al., 2001). It lives today in habitats similar to those occupied by *Dipsosaurus*. *Sonora* is found as a fossil in only a few places in the Grand Canyon (Mead, 1981) (now including the Weeping Cliffs record) and rarely elsewhere in Arizona (Mead, 2005). *Sonora semiannulata* lives today in open habitats, semiarid to arid environments, riparian zones, mixed *Juniper* to desert grasslands, and paloverde-saguaro habitats (Cox et al., 2020).

Mammalia

Vespertilionidae

Myotis sp. (bat)

Remains: WP-2 (125722): right upper first molar (M1).

Discussion: The tooth is in near-perfect condition, relatively easy to assign to genus *Myotis*, but alone it is not identifiable to species because of dental similarities across numerous species of the genus. Eight species of *Myotis* have been reported in the modern fauna within the Grand Canyon, *M. californicus, M. ciliolabrum, M. evotis, M. occultus, M. thysanodes, M. velifer, M. volans,* and *M. yumanensis* (Ruffner et al., 1978; Suttkus et al., 1978; Hoffmeister, 1986; Harvey et al., 2011). Generic characters that allow assignation to *Myotis* (following Gunnell et al., 2017) are: upper molars with very weak paraloph, short sloping postprotocrista, anteroposteriorly broad protofossa, and two narrow but distinct ectoflexi. The M1 measures 1.25 mm in anteroposterior length and 1.40 mm in transverse width.

There are few records of *Myotis* of Quaternary age from Grand Canyon deposits; the genus is recorded only in cave deposits of the eastern region (Olsen and Olsen, 1984; Emslie, 1988; Mead et al., 2021). In historic times, at least three species of bats (*Myotis* and *Tadarida*) have inhabited Bat Cave in the western Grand Canyon; ringtails also frequent this cave and are known to prey on the bats exiting the cave (Pape, 2014).

Molossidae

Nyctinomops macrotis (big freetail bat)

Remains: WP-2 (125723): Eleven isolated teeth, right C1, right P4, M1, M2, and M3, left M1, M2, and M3, right m1 and m3, left m2.

Discussion: Because there are no redundant teeth from this single sample, we assume that these 11 teeth represent a single individual bat that was consumed. Many teeth exhibit missing enamel likely through digestion, however, diagnostic characters are still discernible in remnants of enamel and in the underlying dentin. Most important for assigning the specimens to *N. macrotis* include the upper molar morphology; the upper molars show very long paralophs and metalophs extending from the bases of paracones and metacones all the way to the protocone apices on the upper M1s and M2s. These structures are shared derived features unique to the genus *Nyctinomops* (Czaplewski, 1997; Czaplewski et al., 2003). The lower teeth are also consistent with the morphology of *N. macrotis*. The large size of the teeth from Weeping Cliffs is that of *N. macrotis*, which is approximately twice the body mass of *N. femorosacca* (25–30 g for *N. macrotis* versus 10–14 g for *N. femorosacca*; Harvey et al., 2011), the only species of *Nyctinomops* so far reported from Grand Canyon cave deposits (Mead et al., 2021). However, living *N. macrotis* has been radio-tracked across parts of northern Arizona, including Marble Canyon and Kanab Canyon (Corbett et al., 2005), and almost certainly also occurs today in the lower Grand Canyon, including the Weeping Cliffs area. The only other molossids known in Grand Canyon and adjacent region are the common, smaller *Tadarida brasiliensis* and the even larger (than *N. macrotis*) *Eumops* sp. , both reported as fossils by Carpenter (2003) and Mead et al. (2021), or as part of the modern bat fauna by Hoffmeister (1971, 1986), Hoffmeister and Durham (1971), Ruffner et al. (1978), Suttkus et al. (1978), Rabe et al. (1998), Drost et al. (2000), and Pape (2014).

At least 11 genera of bats are known from Grand Canyon fossil deposits listed in Mead et al. (2021), but *Nyctinomops* is not among them. Although this bat lives in the region today, the report from Weeping Cliffs represents its first record as a fossil in Grand Canyon.

Rodentia

Cricetidae

Neotoma sp. (packrat, woodrat)

Remains: WP-2 (125724): M1 (1), M2 (3), M3 (1), m1 (1), m2 (3), m3 (1); WP-3a (125725): M2 (2), M3 (1), m1 (1), m2 (1), m3 (3).

Discussion: Many species of packrats live in and around the Grand Canyon today including (*Neotoma albigula* [white-throated woodrat], *N. cinerea* [bushytailed woodrat], *N. lepida* [desert woodrat], *N. mexicana* [Mexican woodrat], *N. stephensi* [Stephens' woodrat] (Hoffmeister, 1971, 1986). The identification of isolated woodrat teeth to species was not attempted due to the diversity of known occlusal patterns, inter- and intraspecies variability and overlap in dental characters, and the availability of complete toothrows for statistical significance (e.g., Harris, 1984, 2013).

Peromyscus/*Reithrodontomys* (deer mouse/mouse)

Remains: WP-2 (125726): isolated molars (67); WP-3a (125727): isolated molars (11).

Discussion: Six or seven species of *Peromyscus* and one of *Reithrodontomys* occur in and near GRCA in the modern fauna (Kays and Wilson, 2002). All have teeth that are morphologically similar qualitatively and overlap quantitatively. Although there have been attempts to distinguish some of them dentally (e.g., Hooper, 1957), their systematics and taxonomy have changed in the 76 years since that study, and its applicability today is thus compromised. The same caveats apply to teeth of these mice as mentioned above for *Neotoma*. We are unaware of dental characteristics to consistently identify isolated molars for all species within *Peromyscus/Reithrodontomys*.

Heteromyidae

Perognathus/*Chaetodipus*. (pocket mouse)

Remains: WP-2 (125728–125731): isolated cheek teeth (28); WP-3a (125732): isolated cheek teeth (15).

Discussion: About five species of *Perognathus* and two of *Chaetodipus* are known in the modern fauna of the GRCA area (Hoffmeister, 1986). Their teeth are qualitatively similar to one another, and the same caveats apply to teeth of these mice as mentioned above for *Neotoma*. We are unaware of dental characteristics to consistently identify isolated molars to species within *Perognathus* and *Chaetodipus*.

Table 1. Plant macrofossil contents from Weeping Cliffs ringtail middens lower Grand Canyon, Arizona. Radiocarbon dates are calibrated median age, see text.

Genus	Species	Family	Common Name	Fossil type and number of specimens
		WP-2 **7,460 cal BP**		
Celtis	*laevigata* var. *reticulata*	Ulmaceae	Netleaf hackberry	152 testa pieces; 30 exocarp pieces; 25 pedicels
Opuntia	*chlorotica*	Cactaceae	Pancake prickly pear	55 seed coats; 2 seeds
Echinocactus	*polycephalus*	Cactaceae	Cottontop cactus	40 seed pieces
Echinocereus	sp.	Cactaceae	Claretcup cactus	8 seeds
Ferocactus	*cylindraceus* var. *lecontei*	Cactaceae	California barrel cactus	5 seeds, 1 spine
Physalis	sp.	Solanaceae	Groundcherry	38 seeds
Cryptantha	*pterocarya*	Boraginaceae	Wingnut cryptantha	18 seeds
Dasyochloa	*pulchella*	Poaceae	Fluffgrass	6 florets
Bouteloua	sp.	Poaceae	Grama grass	1 floret
Senegalia (*Acacia*)	*greggii*	Fabaceae	Catclaw acacia	2 leaves
Phacelia	sp.	Hydrophyllaceae	Scorpionweed	2 seeds
Allionia	*incarnata*	Nyctaginaceae	Trailing allionia	1 seed coat piece
Astragalus	sp.	Fabaceae	Locoweed	1 seed
		WP-3a **7,781 cal yr BP**		
Celtis	*laevigata* var. *reticulata*	Ulmaceae	Netleaf hackberry	3 twigs; 2 berries; 103 exocarp pieces; 20 pedicels
Echinocereus	sp.	Cactaceae	Claretcup cactus	12 seed pieces
Physalis	sp.	Solanaceae	Groundcherry	8 seeds
Senegalia (*Acacia*)	*greggii*	Fabaceae	Catclaw acacia	2 spines
Allionia	*incarnata*	Nyctaginaceae	Trailing allionia	2 seed coat pieces
Dasyochloa	*pulchella*	Poaceae	Fluffgrass	2 florets
Astragalus	sp.	Fabaceae	Locoweed	1 seed
Sphaeralcea	sp.	Malvaceae	Globemallow	1 seed coat piece

DISCUSSION AND CONCLUSIONS

Studies of the feces of extant *Bassariscus* from southern Mexico, islands in Baja California, northern California, Oregon, Utah, New Mexico, Texas, and elsewhere have shown that the ringtail is consistently an omnivore (Trapp, 1978; Poglayen-Neuwall and Toweill, 1988; Rodríguez-Estrella et al., 2000; among others). This nocturnal, small carnivore varies its diet from season to season, habitat to habitat, and includes a diverse array of food comprised of plants, arthropods, mammals, birds, herps, and scavenged carcasses (Alexander et al., 1994; Allen, 2013; among others). Single scats often include a variety of contents from plants to animals suggesting a smorgasbord approach to nightly eating. Ringtails also inhabit a variety of denning settings from bushes, trees, downed logs, caves, rock crevices, stumps, abandoned human-built structures (Gundermann et al., 2023), and including the active historic Desert Laboratory on Tumamoc Hill (Tucson, Arizona). Denning areas never seem to be occupied for a long time but are frequented often as latrines and scent marking areas (e.g., Barja and List, 2006; Harrison, 2012). Frequented latrines (here we call them ringtail middens) are accumulations of scats representing multiple eating episodes over time, and possibly over a number of seasons. The analysis of more ancient diets of ringtails is less well understood than modern (e.g., Alexander et al., 1994) but still supports an omnivorous diet as climate has changed through time (e.g., Mead and Van Devender, 1981).

The value of the study of scats and diet of extant *Bassariscus* is not only a better understanding of its modern ecology and habitat usage (Poglayen-Neuwall and Toweill, 1988; Gundermann et al., 2023), but as with the plant-collecting behavior of the packrat (Betancourt et al., 1990), provides a partial and detailed assessment of the local biota. Feces of the ringtail become a desirable resource for the reconstruction of past biotic communities, one where the biased fossil record is often not as all-inclusive as with modern studies. Fossils preserved in select locations are biased towards the taphonomic scenarios of that setting. Assessment of these fossil locations and the resulting reconstructions also can be biased by the analysis procedures of the researchers (such as a bias towards size of sieving of matrix or a taxonomic bias).

Ringtail middens are an unusual and neglected resource of micro-vertebrate and plant fossils, and the added value is that this carnivore selects a diverse set of prey that is typically nocturnal and small in size. Analysis of this resource mandates wet sieving through at least 500 µm mesh and sorting for skeletal and plant elements under low power microscope. For example, the minute vertebrae of an adult thread snake would have been lost using the often-used 1.0 mm or larger 1/16-inch (1.6 mm) screen.

Here we report on the scat contents (plant and vertebrate remains) based on the analysis of a ringtail midden from the lower Grand Canyon at the Weeping Cliffs and reconstruct the middle Holocene local biota of the area. Reconstructed Late Pleistocene and Holocene environments of this region have been based on many packrat middens that have produced a detailed, chronologically controlled succession of plant communities (Phillips and Van Devender, 1974; Phillips, 1984; Cole, 1990). Although packrat middens often contain micro-vertebrate remains (species that were either commensals in the packrat nest or that represent contents from raptor pellets or carnivore dung; Van Devender et al., 1977; Mead, 2005), packrat midden locations (dry shelters and caves) are typically situated well above the Colorado River riparian and floodplain environments.

The sandy, desert floodplain environment adjacent to the Colorado River extended up-canyon only a short distance (see above). This unusual habitat in the Grand Canyon was flooded and destroyed by the Lake Mead reservoir before being ecologically assessed in detail. The Weeping Cliffs ringtail midden locality is situated adjacent to this now-missing habitat. *Bassariscus* preyed on micro-vertebrates that inhabited this and other nearby communities and deposited these remains as scats in the dry cave crevices that have been preserved for many millennia. The Weeping Cliffs ringtail midden dates to the middle Holocene.

Plant remains are a common component in extant ringtail diets and include wood, leaves, moss, lichens, fruits, conifer scales, and seeds (Toweill and Teer, 1977; Alexander et al., 1994). The most common plant recovered from the Weeping Cliffs midden (Table 1) was the netleaf hackberry (*Celtis*), which grows at the locality today. Our study illustrates that the plant collecting habit of the ringtail is oriented towards just dietary needs (consumption) versus the catholic collection by the packrat. The ringtail can provide important data for reconstructing the local flora.

Today the anurans *Anxyrus*, *Hyla*, *Rana*, and *Scaphiopus* live adjacent to and in a variety of habitats throughout the Grand Canyon region along the river, active springs, and flowing side canyons (Miller et al., 1982). However, previous research failed to recover a fossil record of any anuran from the region. The Weeping Cliffs ringtail midden provides the first and only dated fossil anurans in the Grand Canyon (Mead, 1981). The nocturnal collecting habit of *Bassariscus* and the location of the Weeping Cliffs midden close to the river floodplain appears to have permitted the sampling of some anurans.

The Weeping Cliffs ringtail midden provides additional information about the existence of the gecko, *Coleonyx*, which is recorded in fossil packrat middens from the central Grand Canyon along with packrat middens near the Weeping Cliffs (Van Devender et al., 1977; Cole and Mead, 1981). The Weeping Cliffs ringtail midden provides the first evidence of the desert iguana (*Dipsosaurus*) in the Grand Canyon and one of the few for the arid Southwest (Mead and Self, in review). This lizard does not occur in the Grand Canyon today, although its habitat and the lizard likely occurred in the sandy floodplain a few miles upriver until it was inundated by the Lake Mead reservoir. The ringtail midden also provides evidence of the rare blind snake, *Rena*, from the Grand Canyon (Mead, 1981). Its fossil record is poor for the arid Southwest (Mead, 2005). The Weeping Cliffs ringtail midden also records the ground snake, Sonora. This snake was previously recorded from the nearby Vulture Cave,as well as in a few other Arizona localities (as Chionactis), but its late Quaternary distribution is still poorly understood (Van Devender et al., 1991a, b; Mead, 2005).

Ringtails are known to prey on a variety of amphibians, lizards, and snakes. In Oregon, *Bassariscus* rarely preyed on herp species (Alexander et al., 1994) but on Isla San José (Gulf of California), lizards, including the local *Dipsosaurus*, were a common food item (Rodríguez-Estrella et al., 2000). Small mammals, mainly rodents, are a typical prey item for *Bassariscus* for all dietary studies (Poglayen-Neuwall and Toweill, 1988), including the record from Weeping Cliffs. Winkler and Adams (1972) suggested that ringtail eating of bats might be limited to scavenging behavior. Certainly, the ringtail

Table 2. Vertebrate remains identified from the Weeping Cliffs ringtail middens, lower Grand Canyon, Arizona. Radiocarbon dates are calibrated median age, see text. Unkn, unidentifiable skeletal remains. Common names in text.

Taxon	WP-2: 7,460 cal BP	WP-3a: 7,781 cal yr BP
Unkn Anuran	X	-
Anaxyrus sp.	X	-
Hyla sp.	X	-
Unkn lizard	X	X
Dipsosaurus sp.	X	-
Uta/Cophosaurus/Holbrookia	-	X
Sceloporus sp.	X	-
Crotaphytus sp.	-	X
Coleonyx sp.	X	X
Aspidoscelis sp.	X	-
Rena sp.	X	-
Sonora sp.	X	-
Myotis sp.	X	-
Nyctinomops macrotis	X	-
Neotoma sp.	X	X
Peromyscus/Reithrodontomys	X	X
Perognathus/Chaetodipus	X	X

is known to scavenge carcasses such as the skunk, *Mephitis* (Allen, 2013). The two species of bats in the Weeping Cliffs ringtail midden are of interest as they include the first record of the big freetail bat (*Nyctinomops macrotis*) in the Grand Canyon. We do not know if the Weeping Cliffs ringtail captured the bat or if it scavenged a carcass, but ringtails are known to prey upon bats in the Grand Canyon (Pape, 2014) and elsewhere (Sparks et al., 2000). Bird remains and arthropods are common in the diet of modern ringtail (Poglayen-Neuwall and Toweill, 1988), however, the Weeping Cliffs ringtail midden does not record either of these groups as part of the sampled diet.

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