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Author(s): Jim I. Mead, Thomas W. McGinnis, Jon E. Keeley
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A Mid-Holocene Fauna from Bear Den Cave, Sequoia National Park, California

Jim I. Mead[1], Thomas W. McGinnis[2], and Jon E. Keeley[2]

[1]*Department of Geology and Quaternary Sciences Program, Laboratory of Quaternary Paleontology, Northern Arizona University, Flagstaff, AZ 86011, James.Mead@nau.edu*
[2]*USGS-Biological Resources Discipline, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271-9700*

Abstract.—Test excavation of floor fill deposits in the first room in Bear Den Cave, Sequoia National Park, produced fossiliferous sediments down to at least 40 cm depth. Radiocarbon analysis of charcoal from this layer indicates an early-middle Holocene age of 7220 CAL BP. The fossil accumulation represents prey recovered from generations of ringtail (*Bassariscus astutus*) dung. Microvertebrate remains include salamanders, lizards, snakes, and mammals. The recovery of *Aneides ferreus/vagrans* from early-middle Holocene deposits in Bear Den Cave is a first for this species group. Equally interesting is the recovery of *Plethodon* sp. Neither taxa live in the Sierra Nevada today. The fossil-rich deposits of Bear Den Cave indicate that future paleoecological studies will be productive in Sequoia National Park.

The National Park Service (NPS) is currently inventorying and monitoring its biological resources in an attempt to document the observed changes, understand if they are natural or human-caused, and understand the driving mechanisms. The most logical way that the NPS can determine how much change is acceptable is to compare the rate of change today with that of the rest of the Holocene (the most recent 11,000 years), including that period just prior to the arrival of Anglo-Americans. These data exist in caves that have preserved the environmental changes over several thousand years.

''The limestone caves of California have been the object of much fruitful investigation[s]. . . In purely paleontologic studies the cave faunas are of unusual importance, representing as they do an aspect or zone of [amphibian, reptilian, and] mammalian life not preserved in the more common lacustrine, fluviatile and alluvial accumulations'' (Stock 1918:462). Few late Pleistocene fossil localities were known in 1918, with the vast majority such as the tar seeps of Rancho La Brea and Carpinteria (among others) located in southern California. Faunas from caves were equally as rare and included Samwel, Potter Creek, and Hawver caves. Stock's statement above is still true today. Additional caves have been investigated since the time of Stock. Although important, most of these are located in the arid, lower elevations of San Bernardino County, southern California (e.g., Schuiling Cave [Downs et al. 1959; Jefferson 1983] and Kokoweef Cave [Goodwin and Reynolds 1989; Bell and Jass 2004]). Only a few cave faunas have been described from mountainous California, such as Eagle Feather Cave, Fresno County (Cole 1983; Mead et al. 1985).

A wealth of pollen and macrobotanical data has been recovered from woodrat middens (*Neotoma* nesting debris piles) and sediment cores extracted from meadows and lake bottoms from a multitude of locations within the Sierra Nevada Range (Anderson and Smith 1994; Woolfenden 1996; Anderson et al. 1997). From these studies a reconstruction is emerging of climate and vegetation changes during the late Pleistocene and through the Holocene. What have yet to be adequately examined are the changes in vertebrate communities, and of particular interest is how they responded to climate and vegetation changes. Here we report on the small microvertebrate fauna of early-middle Holocene age recently recovered from Bear Den Cave, Sequoia National Park, Tulare County. Bear Den Cave was selected for assessment because it was known to be a repository of skeletal remains and likely would record vertebrate changes through time.

Methods

Bear Den Cave is in a marble formation within the steep watershed of Yucca Creek, part of a western drainage (North Fork Kaweah River) of the Sierra Nevada Mountains, Sequoia National Park (Figure 1). The cave is at 1460 m (4790 ft) elevation with a north-northwest exposure about 30 m above the current streambed (approximately 36° 35′N, 118° 49′W). Entrance to this small cave of two rooms is via a short crawlway. The first room measures about 7 by 12 m with 3–4 m ceilings and is the site of our Test Pit A (approximately 17 m from the entrance). The excavation near the cave wall by TWM (NPS permit SEKI-2002-SCI-37) measured 0.5 by 0.5 m with 5 cm levels and was taken to a maximum depth of 40 cm. Although skeletal elements were found throughout the levels, we used the abundant remains from the 25–30 and 35–40 cm levels in this preliminary study. All sediments were wet sieved through 180 μm mesh screens, dried, and picked of all bone material under 10x magnification.

Results

The fauna of amphibians, reptiles, and mammals recovered from Bear Den Cave is presented in Table 1, with emphasis being placed on the amphibians and reptiles. The characters used to identify each taxon will not be discussed except for the geographically unusual or taxonomically confusing species. All specimens are curated by Sequoia-Kings Canyon National Parks (SEKI). Charcoal fragments were removed from the 35–40 cm depth in Test Pit A. Standard C14 analysis and C13/C12 ratio analysis (−24.0‰) on sample Beta-188747 produced a conventional radiocarbon age of 6260 ± 100 BP. The intercept of the age with the calibration curve produces a calibrated (corrected) age of CAL 7220 BP (one sigma calibration date range: CAL 7410 to 6900 BP).

Salamanders (Amphibia, Caudata)

Identifications of salamander fossils are based on morphologic and phenetic characters observed on vertebrae (in the modern comparative collection at the Laboratory of Quaternary Paleontology, Northern Arizona University) and the characters reported in Wake (1963, 1966). Modern comparative skeletal specimens of salamander used to compare to those from Bear Den Cave are listed in Appendix I. We feel that the morphology of plethodontid vertebrae is not understood well enough at present to conduct an apomorphic approach to identifications.

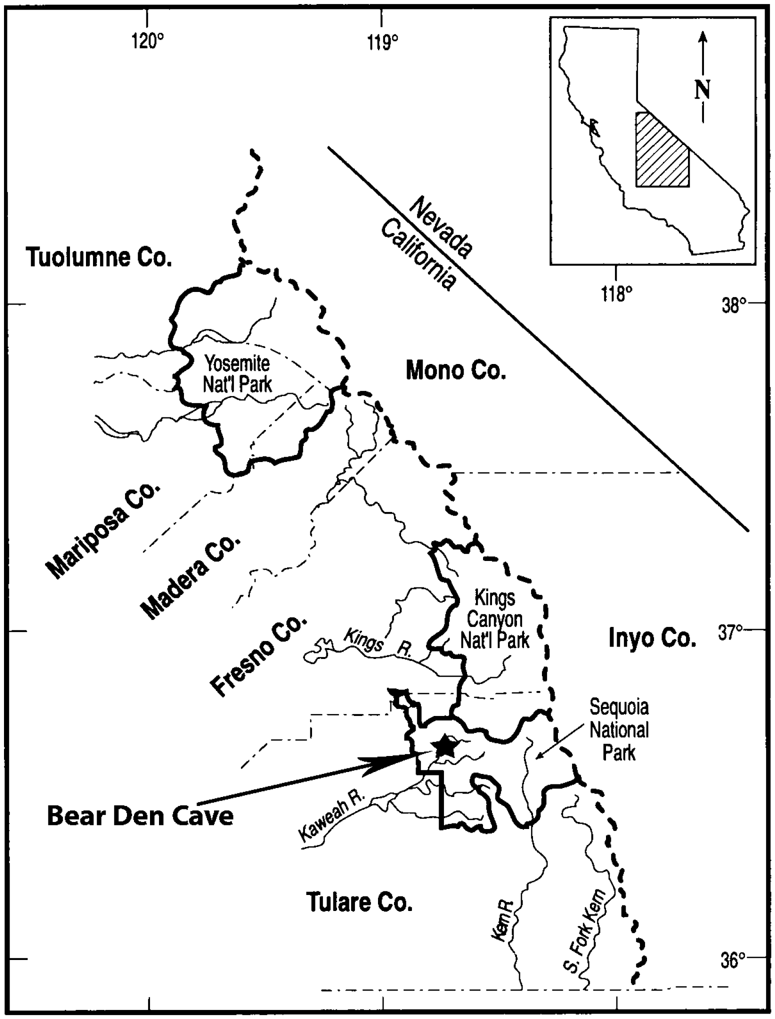

Fig. 1. Map of the southern Sierra Nevada Range of California locating Bear Den Cave in Sequoia National Park. Other nearby parks contain additional late Pleistocene and Holocene biotic remains related to those recovered from Bear Den Cave. Crest of mountain range denoted by dashed line. Adapted from Anderson and Smith (1994).

Because of our phenetic approach, our identifications should be viewed as a best-fit recognition, one that provides a direction for future morphological studies and biogeographical modeling.

One trunk vertebra (SEKI-20167; Figure 2A, B) is identified as cf. *Aneides ferreus/vagrans* (Plethodontidae). *A. ferreus* (clouded salamander) traditionally is known to occur today in coastal forests of northern California and Oregon (Wake 1974, Petranka 1998). Jackman (1998) used molecular data to show that the Oregon populations are *A. ferreus,* and that they are distinct from the California form which Wake and Jackman (1998) place into a different species, *A. vagrans* (wandering salamander). A detailed comparison of the vertebrae has not been conducted, yet Wake and Jackman (1998:1579) note that *A. vagrans* ''is similar to *A. ferreus* in general morphology and osteology.'' Here we will not make a distinction of the two species until further detailed morphological comparisons are conducted.

SEKI-20167 is nearly complete, missing only a portion of the posterior neural arch rise and the lateral extensions of the transverse processes. SEKI-20167 is from an adult individual based on the development of the thickness of the neural arch wall. Because of this and the overall size of the vertebra (see below) SEKI-20167 does not belong to *Ambystoma* (mole salamanders, Ambystomatidae) or *Diacamptodon* (giant salamanders, Dicamptodontidae [Dicamptodontinae of Frost et al. 2006]), which are much larger at adult growth.

The centrum length of SEKI-20167 is 2.2mm and the posterior centrum diameter is 0.9 mm, establishing a centrum ratio (**cr**) of 2.44. The various species of *Aneides* have a range of the **cr** from 1.8 to 2.4. Another plethodontid, *Ensatina,* has a stout vertebra with a **cr** of 2.5. The **cr** of other plethodontids is greater, illustrating their long, slender vertebrae: *Plethodon* (2.9–3.4), *Hydromantes* (3.0–3.9), *Batrachoseps* (3.0–3.5) (**cr** data from Wake 1966).

Although the transverse processes are incomplete on SEKI-20167, they are preserved at the proximal end showing that the diapophysis and parapophysis are likely joined. This is difficult to unequivocally determine as on one side the diapophysis and parapophysis seem not to be joined (i.e., separate processes) and on the other side there is an indication that they may be joined. A complete separation of these processes occurs with *Ensatina,* some species of *Aneides,* most species of *Plethodon,* and *Hydromantes.* If we conclude that SEKI-20167 has a connection at least at the proximal end, then the vertebra does not belong to *Ensatina, Hydromantes,* or some species of *Aneides* or *Plethodon.* There is a complete joining of the processes (proximal end to tip) on some species of *Plethodon* (e.g., *P. elongatus,* Del Norte salamander) and *Aneides flavipunctatus* (black salamander). There is only a proximal joining between these processes on some *Plethodon* and *Aneides ferreus/vagrans.*

The parapophysis is offset caudally from the diapophysis on SEKI-20167. These two processes are directly above each other on *Hydromantes* and *Batrachoseps,* indicating that SEKI-20167 is not either of these two genera. There is no alar expansion to the transverse processes on SEKI-20167, as is found on *Aneides lugubris* (arboreal salamander), *A. flavipuntatus* (to a lesser extent), and *Taricha* (newts, Salamandridae).

The **cr** indicate that the robust SEKI-20167 is likely a member of the genus *Aneides,* and not of the more slender *Plethodon, Hydromantes, Batrachoseps* (possibly including *B. robustus*), or the stout *Ensatina.* The conclusion that the diapophysis and parapophysis processes are joining implies that SEKI-20167 could belong to *Aneides ferreus/vagrans* or some species within *Plethodon.* The combination of the above phenetic characteristics implies that SEKI-20167 is probably *Aneides* and most likely *A. ferreus/vagrans.*

A second trunk vertebra (SEKI-20166) is identified as *Plethodon* sp. (Figure C,D). This vertebra is about 80% complete, missing the haemel arch, posterior cotyle, and left transverse process. The relative thickness of the bone implies a mature individual, or at least not a juvenile. The right transverse process is complete and extends beyond the zygapophysial lateral margin. This process begins straight then smoothly bends to the posterior (not the abrupt bend observed on

Table 1. Fauna (number of identifiable specimens) from Bear Den Cave in Sequoia National Park, California, recorded from sediment layers at 25–30cm depth and 35–40cm depth. Also indicated is whether or not that species, or related species, are known from the current fauna in the Park: x, present; —, not present. Note that the living anurans (frogs and toads), birds, and turtles are not listed below, and only the orders of living (Mod, modern) salamanders, squamates, and mammals that are also recovered in the cave are listed.

Taxon	Mod	25–30	35–40
AMPHIBIA, CAUDATA			
Plethodontidae			
cf. *Aneides ferreus/vagrans*	—	—	1
Batrachoseps gregarius, gregarious slender salamander	x	—	—
B. kawia, Sequoia slender salamander	x	—	—
B. regius, Kings River slender salamander	x	—	—
B. relictus, relictual slender salamander	x	—	—
B. simatus, Kern Canyon slender salamander	x	—	—
Ensatina eschscholtzi, ensatina	x	—	—
Hydromantes platycephalus, Mt. Lyell salamander	x	—	—
Plethodon sp., lungless salamander	—	—	1
Plethodontidae genus et species unidentified	—	—	1
Salamandridae			
Taricha torosa, California newt	x	—	—
REPTILIA, SQUAMATA			
Phrynosomatidae			
Phrynosoma coronatum, coastal horned lizard	x	—	—
Sceloporus graciosus, sagebrush lizard	x	—	—
S. occidentalis, western fence lizard	x	—	—
Uta stansburiana, side-blotched lizard	x	—	—
Scincidae			
Eumeces gilberti, Gilbert's skink	x	—	—
E. skiltonianus, western skink	x	—	—
Teiidae			
Cnemidophorus tigris, western whiptail	x	—	—
Cnemidophorus sp., whiptail	—	—	1
Anguidae			
Anniella pulchra, California legless lizard	x	—	—
Elgaria coerulea, northern alligator lizard	x	—	—
E. multicarinata, southern alligator lizard	x	—	—
cf. *Elgaria* sp., alligator lizard	—	2	—
Boidae			
Charina bottae, rubber boa	x	—	—
Charina sp., boa	—	—	1
Colubridae			
Colubridae genus et species unidentified	—	5	9
Coluber constrictor, racer	x	—	—
Contia tenuis, sharp-tailed snake	x	—	—
Diadophis punctatus, ring-necked snake	x	—	—
Diadophis/Tantilla	—	1	—
Hypsiglena torquata, night snake	x	—	—
Lampropeltis getula, common kingsnake	x	—	—
L. zonata, California mountain kingsnake	x	—	—
Masticophis lateralis, striped racer	x	—	—
Pituophis melanoleucus, gopher snake	x	—	—

Table 1. Continued.

Taxon	Mod	25–30	35–40
cf. *Pituophis* sp., gopher snake	—	—	3
Rhinochelius lecontei, long-nosed snake	x	—	—
Tantilla hobartsmithi, black-headed snake	x	—	—
Thamnophis couchii, Couch's garter snake	x	—	—
T. elegans, western terrestrial garter snake	x	—	—
T. sirtalis, common garter snake	x	—	—
Viperidae			
Crotalus viridis, western rattlesnake	x	—	—
Crotalus sp., rattlesnake	—	1	—
MAMMALIA			
CHIROPTERA			
Verspertilionidae			
Antrozous pallidus, pallid bat	x	—	—
Corynorthinus townsendii, Townsend's big-ear bat	x	—	—
Eptesicus fuscus, big brown bat	x	—	—
Euderma maculatum, spotted bat	x	—	—
Lasionycteris noctivagans, silver-haired bat	x	—	—
Lasiurus blossevillii, western red bat	x	—	—
L. cinereus, hoary bat	x	—	—
Myotis spp. (seven species	x	—	—
Myotis sp.	—	—	1
Pipistrellus hesperus, western pipistrelle	x	—	—
Molossidae			
Eumops perotis, western mastiff bat	x	—	—
Tadarida brasiliensis, Brazilian free-tailed bat	x	—	—
RODENTIA			
Aplodontidae			
Aplodontia rufa, mountain beaver	?	—	1
Sciuridae			
Glaucomys sabrinus, northern flying squirrel	x	—	—
Marmota flaviventris, yellow-bellied marmot	x	—	—
Sciurus griseus, western gray squirrel	x	—	—
Sciurus sp.	—	—	1
Spermophilus beecheyi, California ground squirrel	x	—	—
S. beldingi, Belding's ground squirrel	x	—	—
S. lateralis, golden-mantled ground squirrel	x	—	—
Tamis alpinus, alpine chipmunk	x	—	—
T. amoenus, yellow-pine chipmunk	x	—	—
T. merriami, Merriam's chipmunk	x	—	—
T. minimus, least chipmunk	x	—	—
T. quadrimaculatus, long-eared chipmunk	x	—	—
T. senex, Allen's chipmunk	x	—	—
T. speciosus, lodgepole chipmunk	x	—	—
T. umbrinus, Uinta chipmunk	x	—	—
Tamiasciurus douglasii, douglas' squirrel	x	—	—
Sciuridae genus et species unidentified	—	6	9
Geomyidae			
Thomomys bottae, Botta's pocket gopher	x	—	—
T. monticola, mountain pocket gopher	x	—	—
Thomomys sp., pocket gopher	—	2	1
Heteromyidae			
Chaetodipus californicus, California pocket mouse	x	—	—
Chaetodipus sp., pocket mouse	—	2	2
Dipodomys heermanii, Heermann's kangaroo rat	x	—	—

Table 1. Continued.

Taxon	Mod	25–30	35–40
Castoridae			
Castor canadensis, beaver	x	—	—
Muridae			
Neotoma cinerea, bushy-tailed woodrat	x	—	—
N. fuscipes, dusky-footed woodrat	x	—	—
N. lepida, desert woodrat	x	—	—
Neotoma spp., woodrats	—	37	33
Peromyscus boylii, brush mouse	x	—	—
P. californicus, California mouse	x	—	—
P. maniculatus, deer mouse	x	—	—
P. truei, pinyon mouse	x	—	—
Reithrodontomys megalotis, western harvest mouse	x	—	—
Peromyscus/Reithrodontomys	—	19	27
Microtus californicus, California vole	x	—	—
M. longicaudus, long-tailed vole	x	—	—
M. montanus, montane vole	x	—	—
Microtus sp., meadow vole	—	6	8
Ondatra zibethicus, muskrat	x	—	—
Phenacomys intermedius, heather vole	x	—	—
Dipodidae (Zapodidae)			
Zapus princes, western jumping mouse	x	—	—
Erethizontidae			
Erethizon dorsatum, porcupine	x	—	—
CARNIVORA			
Canidae			
Canis latrans, coyote	x	—	—
Urocyon cinereoargenteus, gray fox	x	—	—
Vulpes vulpes, red fox	x	—	—
Ursidae			
Ursus americanus, black bear	x	*	*
U. arctos, brown bear	x	—	—
Procyonidae			
Bassariscus astutus, ringtail	x	—	—
Procycon lotor, raccoon	x	—	—
Mustelidae			
Gulo gulo, wolverine	x	—	—
Lontra canadensis, river otter	x	—	—
Martes americanus, marten	x	—	—
M. pennanti, fisher	x	—	—
Mephitis mephitis, striped skunk	x	—	—
Mustela erminea, ermine	x	—	—
M. frenata, long-tailed weasel	x	—	—
M. vison, mink	x	—	—
Spilogale putorius, spotted skunk	x	—	—
Taxidea taxus, badger	x	—	—
Felidae			
Puma concolor, mountain lion	x	—	—
Lynx rufus, bobcat	x	—	—

* = found elsewhere in the cave but not in the stratigraphic sections presented here.

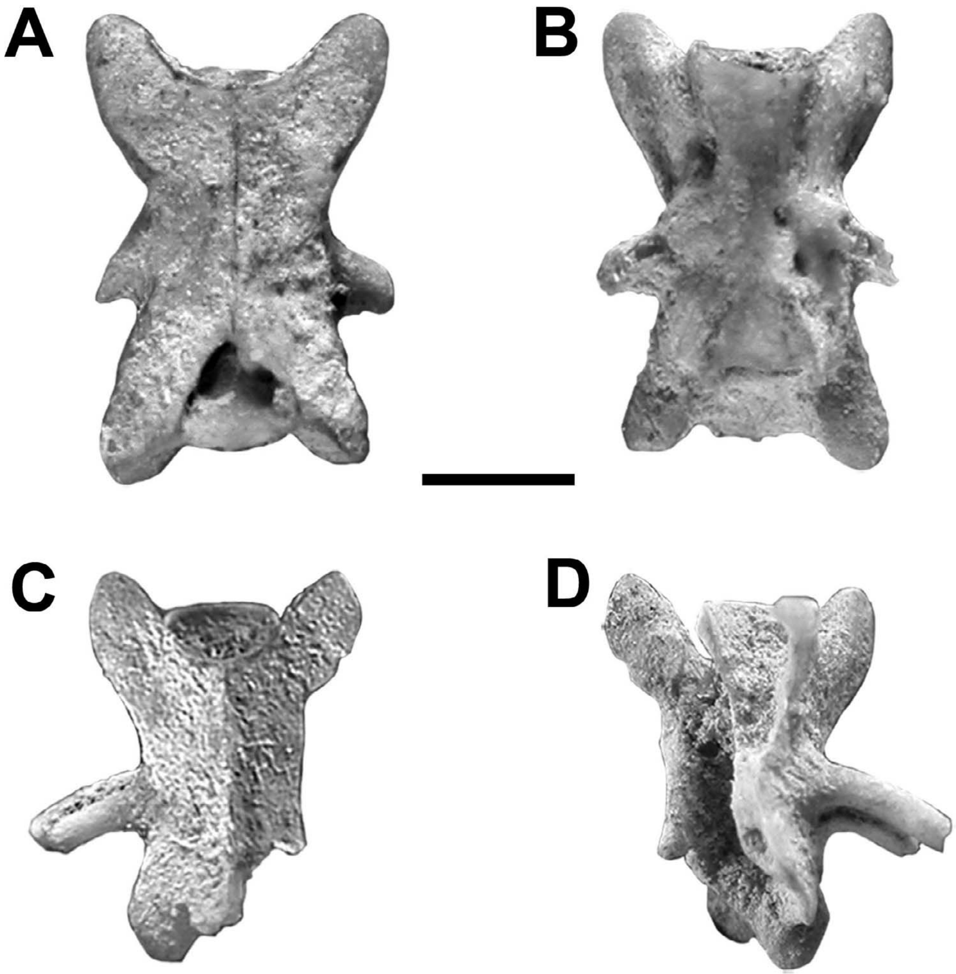

Fig. 2. Photograph of salamander trunk vertebrae from Bear Den Cave. A, dorsal and B, ventral of cf. *Aneides ferreus/vagrans,* SEKI-20167. C, dorsal and D, ventral of *Plethodon* sp., SEKI-20166. Photographs by Sandra L. Swift. Scale equals 1 mm.

Batrachoseps). The diapophysis and parapophysis are connected to the tip, indicating that SEKI-20166 does not belong to *Ensatina, Aneides ferreus/vagrans, Hydromantes,* or some species of *Plethodon.* The parapophysis is offset slightly from the diapophysis indicating that SEKI-20166 is not *Hydromantes* or *Batrachoseps.* Based on this character, SEKI-20166 could belong to some species of *Plethodon* or *Aneides flavipuntatus.* There is no alar expansion, which indicates that SEKI-20166 does not belong to *Taricha* spp., *Aneides lugubris,* or *A. flavipuntatus.* Given these characteristics, SEKI-20166 seems best to belong to a form of *Plethodon,* although which species cannot be determined at this time.

A fragmented sacral vertebra (SEKI-20165) is identified as Plethodontidae genus et species indeterminate. The specimen is only about 50% represented, preserving most of the posterior half, left transverse process and some of the right process. The hyperapophysis is well expanded, which is typical of the sacral vertebra, but SEKI-20165 has a larger-than-usual flaring. *Taricha* species do not have a hyperapophysis. The hyperapophysis is minute on *Rhyacotriton* spp. (torrent salamanders; Rhyacotritonidae), and its neural arch is markedly flattened, completely unlike that area on SEKI-20165. The diapophysis and parapophysis are not divided, indicating that SEKI-20165 is not *Ensatina.* There is no alar expansion, indicating SEKI-20165 is not *Aneides lugubris* or *A. flavipunctatus.* There is not enough of SEKI-20165 to provide an unequivocal identity. It does have similarities with *Aneides ferreus/vagrans* and *Plethodon elongatus.* The proximal end of the diapophysis of SEKI-20165 is more expanded than observed on *Ensatina* and more like *Aneides ferreus/vagrans* and *Plethodon elongatus.*

Lizards and Snakes (Reptilia, Squamata)

As with the salamander vertebrae, most of the lizard bones (SEKI-20172, 20183, 20185) from Bear Den Cave are fragmented due to chewing by a predator; there is no evidence of etching. A fragmented right quadrate and fragmented left dentary are identified as cf. *Elgaria* (Anguidae, alligator lizard). The quadrate (from a large lizard; SEKI-20184a) has the posterior crest only slightly curved, as in *Elgaria,* and not heavily curved as found on *Eumeces* (skinks). The dorsal end of the medial crest is a wider flange as found on *Elgaria* and not the near absence observed on *Eumeces.* All morphological characters observed on the fossil quadrate are distinct from those found on the robust *Phrynosoma coronatum* (coast horned lizard) or large, robust *Sceloporus* (spiny lizard). The dentary of SEKI-20184b is from a large, robust individual; in living *Eumeces* and *Elgaria* this dentary would be from individuals with snout-vent lengths greater than 125 mm. Seven teeth (and placement for an eight) occur along the 5.5 mm fragment. The teeth have a single apex in the middle of the cone, with a slight posterior orientation. This apex on *Elgaria* is also posteriorly oriented whereas it is lingual on *Eumeces.* Teeth on SEKI-20184b are long and slender with parallel sides, and not similar to the blunt-coned, tapering teeth on many phrynosomatids such as *Phrynosoma* or *Sceloporus.* The Mecklian groove on SEKI-20184b is on the ventral surface, as found on *Elgaria* and *Eumeces,* yet unlike that of phrynosomatids. The symphysis is rounded and not pointed as found on *Cnemidophorus* (Teiidae).

A right dentary (SEKI-20171) with bi-conate teeth, pointed symphysis, and lingually-bent bone is diagnostic to a form of *Cnemidophorus.*

One vertebra of the boid snake, *Charina* sp., was recovered from the 35–40 cm level (SEKI-20169). Discussion about the fossil history of *Charina* (including Eagle Feather Cave, Kings Canyon NP) and characters used to identify their vertebrae are provided in Bell and Mead (1996). Although *C. bottae* lives in the region of Bear Den Cave today, and the fossil specimen likely represents this species, we refrain from making a species-level identification until a detailed examination of ontogenetic and serial vertebral variation of all living and extinct forms of *Charina* is completed.

Fourteen colubrid snake vertebrae were recovered (Table 1; SEKI-20170, 20182), that represent both small and large individuals. Three vertebrae (SEKI-20168) were identified as cf. *Pituophis* (gopher snake). Terminology and identifying characters used here are from observations on specimens in the comparative collection in the Laboratory of Quaternary Paleontology, NAU, and from LaDuke

(1991). A small vertebra is identified as *Diadophis/Tantilla* (SEKI-20181). *Diadophis* and *Tantilla* vertebrae are similar, but there are some subtle differences. SEKI-20181 and *Diadophis* have an acute posterior notch of the neural arch (versus obtuse for *Tantilla*). The postzygapophysis on SEKI-20181 and *Diadophis* is only slightly longer than wide (versus distinctly longer than wide for *Tantilla*). The haemel keel is broad, has sloping edges, and flattened ventrally on SEKI-20181 and *Tantilla.* The centrum length of SEKI-20181 is 1.8 mm and the neural arch width is 1.1 mm, providing a ratio of 1.6; this overlaps with both *Tantilla* and *Diadophis.* Additional vertebrae are needed to determine which taxon is represented in the cave, although both species can be found in the region today (Table 1). A single vertebra of the rattlesnake, *Crotalus* was recovered (SEKI-20180), but not identified to species. Today only *C. viridis* is known from the region.

Mammals (Mammalia)

One complete, isolate M3 of a bat was recovered (SEKI-20188). Based on the width of the tooth, SEKI-20188 belongs to the genus *Myotis* and not a genus with a highly antero-posterior compressed M3 (e.g., *Eptesicus* and *Antrozous*). The species is indeterminable. Bats are known to use Bear Den Cave.

A single, distinctive cheek tooth of a mountain beaver (*Aplodontia rufa*) was recovered from the 35–40 cm depth (SEKI-20173). Although this taxon is known to occur today in the Sierra Nevada, it is thought not to live in the immediate area of the cave.

One fairly-complete skull (occipital region missing; M1–2 preserved) of a squirrel (SEKI-20174b) was recovered at the 30–35 cm level. Based on the overall large size, the specimen does not belong to any of the small ground or tree squirrels, but it is not as large or robust as *Marmota* (marmot) or *Cynomys* (prairie dog). The alveolus for the P3 indicates that the tooth was developed, but near vestigial. This feature and the overall size imply the specimen is not *Spermophilus variegatus* (rock squirrel) and thus appears to belong to *Sciurus* (but not *S. arizonensis*; Arizona gray squirrel which lacks the P3). This specimen could not be differentiated from *S. aberti* (Abert's squirrel) or *S. griseus* (western gray tree squirrel), both which have two upper premolars. *S. griseus* is the only tree squirrel to live in the Sierra Nevada today.

Isolated and fragmented squirrel teeth were numerous in both levels of the deposit (Table 1); these were not identified (SEKI-20174a, 20186). Fifteen species live in the region today, including the chipmunks (*Tamias* spp.), ground squirrels (*Spermophilus* spp.), *Sciurus griseus,* flying squirrel (*Glaucomys sabrinus*), and the large *Marmota flaviventris.* A number of the teeth were small and may represent one or more of the *Tamias.* The larger teeth could be from the larger species of *Spermophilus* or *Sciurus. Marmota,* with its conspicuous large teeth, was not recovered from the cave.

Two species of geomyid pocket gophers live in the region today, *Thomomys bottae* and *T. monticola.* Three isolate teeth (SEKI-20179, 20192) were recovered representing this genus. Four teeth (SEKI-20176, 20189) were recovered representing a small heteromyid, either *Chaetodipus* or *Perognathus* (pocket mouse). *Chaetodipus* and the larger, *Dipodomys* (kangaroo rat) are known from the park today.

Teeth of *Neotoma* are the most abundant identifiable fossils from the deposit

(SEKI-20178, 20191; Table 1). *Neotoma cinerea, N. fuscipes,* and *N. lepida* live in the region today. We feel at this time that there are inadequate characters of the dentition to unequivocally identify isolated teeth; therefore, we have not identified the fossils to species. The pattern to the occlusal surface varies from lophs and re-entrant angles that are rounded and obtuse to those that are acute and sharp, which implies that at least two species are represented in Bear Den Cave.

Peromyscine teeth (SEKI-20175, 20187) were also abundant and not identified beyond *Peromyscus/Reithrodontomys* (Table 1). Today four species of *Peromyscus* and one species of *Reithrodontomys* live in the region of the cave.

Isolated, rootless teeth of arvicoline rodents were identified as *Microtus* (SEKI-20177, 20190), but not to species. Today both *Microtus* (three species) and *Phenacomys intermedius* (with rooted teeth) can be found in SEKI (Table 1).

Discussion and Conclusions

Test excavation of floor fill in the first room in Bear Den Cave produced fossiliferous sediments down to at least 40 cm depth. Radiocarbon analysis of charcoal indicates an early-middle Holocene age of 7220 CAL BP. Microvertebrate remains, including salamanders, lizards, snakes, and mammals, were recovered from layers at 25–30 and 35–40 cm depth (Table 1). No skeletal remains of anurans (frogs and toads), birds, large mammals, or carnivores were recovered from the test pit. The cave is occasionally used today by *Ursus americanus* (black bear; Ursidae; skeletal remains were recovered from elsewhere in the cave) as well as *Bassariscus astutus* (ringtail; Procyonidae). The skeletal remains presented here could have been brought into the cave via the collecting behavior of *Neotoma,* which could include the scavenging of raptor (hawk, eagle, owl) stomach pellets. No owl or diurnal raptor roost is known in or near the cave, although several owls and hawks live in the region.

Taphonomy

Most of the bones from the test pit in Bear Den Cave are slightly to highly fragmented, sharp-edged, and show little to no etching due to stomach acid. Diurnal raptors typically will break bones, and their strong stomach acid characteristically etches, dissolves, and polishes the prey skeletal elements. Skeletal elements from owl pellets typically show little to no etching and most of the bones are unbroken (see Andrews 1990). The recovered skeletal elements from Bear Den Cave do not appear to represent remains from any form of raptor. Ringtails are small carnivores that hunt at night, selecting medium to small-sized nocturnal and crepuscular prey within its home range of <600 ha. (Grinnell et al. 1937). The recovery of a fauna composed of only small species and skeletal remains showing broken bones with sharp edges and without significant etching, polishing, or dissolutioning is consistent with prey remains from ringtail dung (Mead and Van Devender 1981). The accumulation in Bear Den Cave appears to represent, at least in part, generations of ringtail dung deposition. Most of the recovered taxa represent only locally procured species, in contrast to the prey species recovered from raptor stomach pellets.

Environments

Today the Sierra Nevada has a Mediterranean-climate with hot arid summers and cool humid winters (Major 1988). Forest occurs above 1200 m elevation with oak woodland grading into ponderosa and ultimately mixed conifer forests above 1600 m. The vegetation today in the watershed surrounding Bear Den Cave (1460 m elevation) includes ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), canyon live oak (*Quercus chrysolepis*), incense cedar (*Calocedrus decurrens*), California bay (*Umbellularia californica*), California nutmeg (*Torreya californica*), big-leaf maple (*Acer macrophyllum*), wood fern (*Dryopteris arguta*) and others on the north-facing, more mesic, slope where the cave is situated. A riparian community occurs in the canyon bottom.

Aplodontia today are uncommon in Sierra Nevada and SEKI, and significantly, are not near the cave today. This medium-sized rodent is more commonly found in humid, densely vegetation areas. Limits to distribution are associated with rainfall and edaphic conditions that promote succulent vegetation and relatively high humidity within its burrows (Voth 1968, Feldhamer and Rochelle 1982, Carraway and Verts 1993). The current climate regime does not permit such an environment to persist near the cave today.

All of the mammals and most of the amphibians and reptiles from Test Pit A are thought to occur today within the hunting distance of a ringtail except for *Aplodontia, Aneides,* and *Plethodon.* The occurrences of cf. *Aneides ferreus/vagrans* and *Plethodon* sp. are an intrigue and puzzle. The characters used in the identifications seem secure enough to determine that the two vertebrae do not belong to any of the salamanders known from Sequoia National Park or nearby region today (Table 1). Indeed, only one species of *Aneides* (*A. lugubris*) is even known from the Sierra Nevada Range (Petranka 1998). *A. lugubris* lives in the northern Sierra Nevada and to the west of the region (Lynch and Wake 1974; Jennings 1996); *A. ferreus/vagrans* lives along the coastal region of northern California and north (Jackman 1998), as does *A. flavipunctatus* (Lynch 1974). Today *A. ferreus/vagrans* is a forest species, typically associated with large logs and talus slopes, and is one of the most arboreal salamanders in North America. Although fossil and subfossil remains of *Aneides* are known (Tihen and Wake 1981; Clark 1985), *A. ferreus* and *A. vagrans* are known only from the modern record. Their recovery from early-middle Holocene deposits in Bear Den Cave is a first for this species group. Equally interesting is the recovery of a vertebra of *Plethodon* sp. No species of *Plethodon* live today in the Sierra Nevada (Petranka 1998).

The salamanders living today in the Sequoia National Park region are either a plethodontid (*Batrachoseps, Ensatina,* and *Hydromantes*) or salamandrid (*Taricha*). Some of these (e.g., *B. gregarius*) can live in areas of intense summer heat and drought (Jockusch et al. 1998). *Ensatina* normally lives in mesic microhabitats; in arid regions, it typically lives only on north-facing slopes. *Hydromantes platycephalus* likely does not currently live in the immediate vicinity of the cave because it requires greater mesic habitats (Adams 1942). *Taricha torosa* can live in mesic forests and in the drier habitats with oak forests, chaparral, rolling grasslands, and the more arid gray pine-blue oak communities of the Sierra Nevada and likely does occur in the vicinity of the cave (Petranka 1998). Although it is not understood specifically which salamanders live today in the immediate vicinity of Bear Den Cave, the vegetation community would imply that the more mesic areas would harbor some *Batrachoseps, Ensatina,* and *Taricha.* Because of the present taxa in the area, we wonder what environment and climate is needed to allow *Aneides ferreus/vagrans* and at least one *Plethodon* species to inhabit the presently somewhat marginal mesic-arid habitat adjacent to Bear Den Cave.

Plethodontid salamanders lack aquatic larvae indicating that free-flowing streams are not a prerequisite in their reproductive strategy (as it is with salamandrids and ambystomatids). The closest locations of living *Plethodon* are along coastal northern California and the mountainous area bordering Oregon (*P. dunni, P. elongatus,* and *P. stormi*; Petranka 1998). *Plethodon elongatus* is usually found in rocky situations within forested areas and seems to be able to withstand somewhat more arid conditions than *P. dunni,* which requires a more humid environment (Leonard et al. 1993). *Plethodon stormi* is typically found in rocky, forested habitats (Leonard et al. 1993). Unless there are traits about the terrestrial ecology and habitat requirements that are not fully understood about these species of *Plethodon,* we speculate that they could possibly live in select mesic habitats of the Sierra Nevada region today. *Aneides ferreus/vagrans* are closely associated with wood decay of Douglas-fir forests (Lowe 1950; Leonard et al. 1993; Jackman 1998). Although it appears that the present climate and habitat around Bear Den Cave is not suitable for *A. ferreus/vagrans,* higher elevations with more moisture and forests could prove appropriate.

These salamanders are not currently found from the southern Sierra Nevada region and their distribution in the very lowest layer of Bear Den Cave suggests they have been missing for some time. Lowe (1950:96) hypothesized that "*Aneides* was a more or less continuously distributed series of populations in the Trans-continental Arcto-Tertiary Flora. . ." It is apparent from the report here that *Aneides ferreus/vagrans* were still present in the southern Sierra Nevada until the mid-Holocene. Approximately 90% of the last two million years in the Sierra Nevada have been wetter and cooler than the last 10,000 years that marks the Holocene (Woolfenden 1996).

The paleoecological record the Sierra Nevada suggests very different climate and vegetation changes throughout the region. Coastal areas of the Pacific slope appear to have been characterized by a marked shift to warmer and drier conditions. Associated with this change in climate was a shift from denser late Pleistocene forest canopies to more open forest and woodlands that were subject to wildfires, which in turn were responsible for even greater opening of the forest and drying of the forest floor habitat (Davis and Moratto 1988).

The west side of the Sierra Nevada 11,000–7,000 BP appears to have been considerably drier than at present (Davis et al. 1985; Davis and Moratto 1988; Anderson 1990; Anderson and Smith 1994, 1997). Early Holocene pollen assemblages are dominated by plants that grow in dry open exposure sites and forests were more open than today. Vegetation on the west side of the Sierra Nevada exhibited a marked Great Basin influence and was similar to contemporary vegetation at higher elevations on the east side of the Sierra crest. Thus, it appears that the early Holocene was drier and cooler than at present and the vegetation more open forest and scrub. Mid-Holocene (7,000–3,000 BP) pollen assemblages indicate a return to a warmer but moister climate and a lower tree line (Davis et al. 1984; Davis and Moratto 1988).

The early Holocene presence of *Aneides* and *Plethodon* in the Sierra Nevada, and subsequent mid-late Holocene disappearance are not easily understood. Today these taxa are distributed in cooler and more mesic forest types typical of the

Pacific Northwest. When placed in the context of our current understanding of the mid-Holocene paleoecology and paleoclimates of the Sierra Nevada, the presence of these salamanders appears to be somewhat anomalous. It would seem that today they are restricted to more mesic forest types than are present in the Sierra Nevada today, yet the present forests are more mesic than their early Holocene counterparts. However, the climate feature both the current coastal habitats of these salamanders have with the early Holocene Sierra Nevada habitats is that they were cooler than contemporary Sierra Nevada sites. Thus, it would appear that temperature is perhaps the critical factor determining the distribution of these taxa.

The fossil-rich deposits of Bear Den Cave indicate that future paleoecological studies will be productive in Sequoia National Park. As such, this park has a unique opportunity to study ecosystem changes over the past several thousand years. What are natural rates of ecosystem change on the Pacific slope of the Sierra Nevada? The answers are preserved in layers of fossils found in caves.

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Appendix

Modern comparative specimens of western USA salamanders used to compare with remains recovered from Bear Den Cave. Number of articulate or disarticulated specimens in parentheses.

Ambystomatidae: *Ambystoma tigrinum* (26).

Diacamptodontidae: *Dicamptodon ensatus* (2); *D. tenebrosus* (3).

Plethodontidae: *Batrachoseps attenuatus* (8); *Hydromantes platycephalus* (1; juvenile); *H. shastae* (2); *Aneides ferreus* (1) [based on locality]; *A. flavipunctatus* (4); *A. lugubris* (1); *Ensatina eschscholtzii* (24); *Plethodon dunni* (2); *P. elongatus* (7); *P. vehiculum* (1).

Rhyacotritonidae: *Rhyacotriton variegates* (2).

Salamandridae: *Taricha torosa* (5); *T. granulose* (8).