VERTEBRATE COPROLITES AND OTHER BROMALITES IN NATIONAL PARK SERVICE AREAS

ADRIAN P. HUNT[1], VINCENT L. SANTUCCI[2], JUSTIN S. TWEET[3] AND SPENCER G. LUCAS[4]

[1] Flying Heritage Collection, 3407 109th St SW, Everett, WA 98204, e-mail: adrianhu@flyingheritage.com;
[2] National Park Service, Geologic Resources Division, 1201 Eye Street NW, Washington, DC 20005, e-mail: vincent_santucci@nps.gov;
[3] Tweet Paleo-Consulting, 9149 79th Street South, Cottage Grove, MN 55016-2214, e-mail: jtweet.nps.paleo@gmail.com;
[4] New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104, e-mail: spencer.lucas@state.nm.us

Abstract—There are occurrences of coprolites and other bromalites at 47 National Park Service (NPS) areas: (1) Arches National Park; (2) Badlands National Park; (3) Bandelier National Monument; (4) Big Bend National Park; (5) Bighorn Canyon National Recreation Area; (6) Canyon de Chelly National Monument; (7) Canyonlands National Park; (8) Capitol Reef National Park; (9) Carlsbad Caverns National Park; (10) Chaco Culture National Historic Park; (11) Channel Islands National Park; (12) City of Rocks National Reserve; (13) Colorado National Monument; (14) Craters of the Moon National Monument; (15) Curecanti National Recreation Area and Preserve; (16) Denali National Park; (17) Death Valley National Park; (18) Dinosaur National Monument; (19) El Malpais National Monument; (20) Fossil Butte National Monument; (21) Gila Cliff Dwellings National Monument; (22) Glen Canyon National Recreation Area; (23) Golden Spike National Historic Site; (24) Great Basin National Park; (25) Grand Canyon National Park; (26) Guadalupe Mountains National Park; (27) Hagerman Fossil Beds National Monument; (28) Hubbell Trading Post National Historic Site; (29); Jewel Cave National Monument; (30) John Day Fossil Beds National Monument; (31) Joshua Tree National Park; (32) Lava Beds National Monument; (33) Lake Mead National Recreation Area; (34) Mammoth Cave National Park National Park; (35) Mesa Verde National Park; (36) Mojave National Preserve; (37) Natural Bridges National Monument; (38) Navajo National Monument National Monument; (39) Organ Pipe Cactus National Monument; (40) Petrified Forest National Park; (41) Grand Canyon-Parashant National Monument; (42) Pipe Spring National Monument National Park; (43) Saguaro National Park; (44) Sequoia and Kings Canyon National Park; (45) Timpanogos Cave National Monument; (46) Wupatki National Monument; and (47) Yellowstone National Park. The majority of the occurrences are vertebrate coprolites or paleomiddens, but there are also invertebrate coprolites from Big Bend National Park and fish cololites from Fossil Butte National Monument. The three most important coprolite assemblages in the NPS are at Petrified Forest National Park (PEFO), Badlands National Park (BADL) and Grand Canyon National Park (GRCA). These coprolite assemblages have been central to recent work on paleoecology and biochronology and represent three of the acme zones for vertebrate coprolites in North America: Late Triassic at PEFO (Chinle Group), Eocene-Oligocene at BADL (White River Group) and Pleistocene at GRCA (cave deposits). Coproassemblages from NPS units represent a significant paleontological resource that has been pivotal to recent advances in the study of coprolites. Resource management needs to be sensitive to the preservation and interpretation of vertebrate coprolites. Coprolites typically do not require any specific NPS management action, with the exception of some of the Pleistocene or Holocene coprolites that occur in caves. The partial destruction of sloth coprolite deposits by park visitors at Rampart Cave illustrates the need for park management action and implementation of preservation strategies to protect rare and sensitive paleontological resources.

INTRODUCTION

The cumulative fossil record preserved in units of the National Park Service (NPS) is very significant, as is apparent from focused inventories of discrete fossil types (Santucci et al., 1998, 2001, 2006; Hunt et al., 2006) and inventories of individual parks and monuments (Santucci, 1998, 2000; Nyborg and Santucci, 1999; Santucci et al., 1999, 2009; Santucci and Santucci, 1999; Koch et al., 2004; Swanson et al., 2005; DeBlieux et al., 2006; Visaggi et al., 2009; Clites and Santucci, 2010; Santucci and Kirkland, 2010). Vertebrate coprolites are an understudied resource in many National Park Service areas. Hunt et al. (2009) reported on fossil vertebrate coprolites from 12 national parks and monuments; here, we provide details on occurrences of coprolites and other bromalites from 47 NPS areas (Fig. 1). The majority of the occurrences are vertebrate coprolites or paleomiddens (*sensu* Hunt and Lucas, 2012), but there are also invertebrate coprolites from Big Bend National Park and fish cololites from Fossil Butte National Monument.

Packrat (*Neotoma*) middens (neotomalites of Hunt and Lucas, 2012) are very common in NPS units, and their distribution is reviewed in detail by Tweet et al. (2012). Hunt and Lucas (2012) have introduced a comprehensive classification of bromalites. They recognized Findley's (1990, p. 28) term paleomidden to refer to a fossil midden and furthermore they introduced the term neotomalite for paleomiddens of *Neotoma* spp. (packrats). Older paleomiddens are usually cemented by amberat (crystallized urine). The ring-tailed cat (*Bassariscus astutus*) and porcupine (*Erethizon dorsatum*) form similar, but much less common, accumulations.

In rare cases, excretory fossils have been attributed to birds. Indirect evidence for owl pellets (or other predatory birds) is based on analysis of microvertebrate accumulations (e.g., Mellet, 1974; Mayhew, 1977; Kusmer, 1990). There is strong evidence that some cave microvertebrate accumulations, particularly of bats and lizards, resulted from accumulated regurgitations of owls (e.g., Williams, 1952; Andrews, 1990; Morgan, 1994). We believe that fossil bat guano

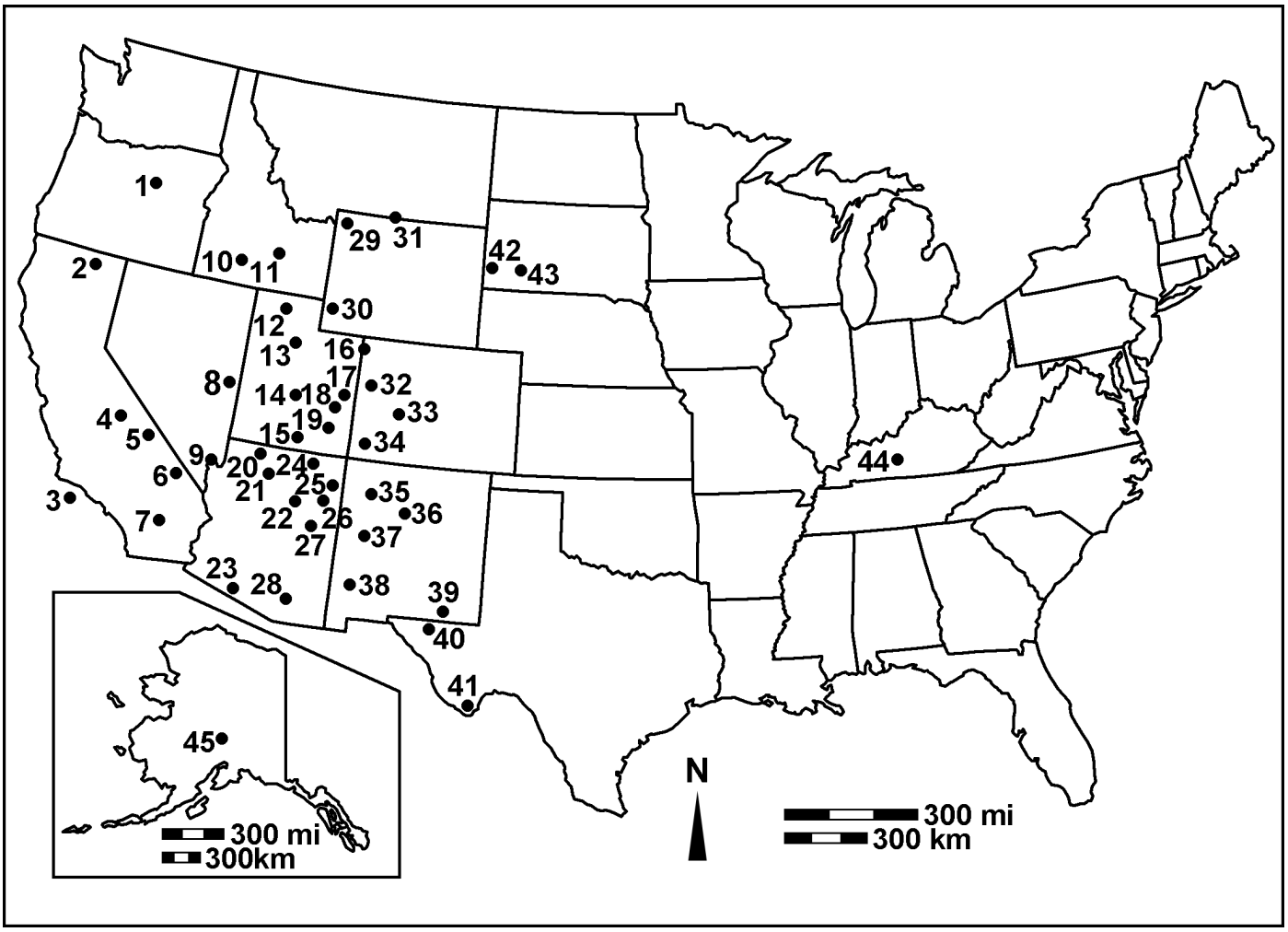

FIGURE 1. National Park Service units with bromalites. Localities are: **1**, JODA (John Day Fossil Beds NM); **2**, LABE (Lava Beds NM); **3**, CHIS (Channel Islands NP); **4**, SEKI (Sequoia and Kings Canyon NP); **5**, DEVA (Death Valley NP); **6**, MOJA (Mojave N Preserve); **7**, JOTR (Joshua Tree NP); **8**, GRBA (Great Basin NP); **9**, LAME (Lake Mead NRA); **10**, HAFO (Hagerman Fossil Beds NM); **11**, CRMO (Craters of the Moon NM and Preserve); **12**, GOSP (Golden Spike NHS); **13**, TICA (Timpanogos Cave NM); **14**, CARE (Capitol Reef NP); **15**, GLCA (Glen Canyon NRA); **16**, DINO (Dinosaur NM); **17**, ARCH (Arches NP); **18**, CANY (Canyonlands NP); **19**, NABR (Natural Bridges NM); **20**, PISP (Pipe Spring NM); **21**, GRCA (Grand Canyon NP); **22**, WUPA (Wupatki NM); **23**, ORPI (Organ Pipe Cactus NM); **24**, NAVA (Navajo NM); **25**, CACH (Canyon de Chelly NM); **26**, HUTR (Hubbell Trading Post NHS); **27**, PEFO (Petrified Forest NP); **28**, SAGU (Saguaro NP); **29**, YELL (Yellowstone NP); **30**, FOBU (Fossil Butte NM); **31**, BICA (Bighorn Canyon NRA); **32**, COLM (Colorado NM); **33**, CURE (Curecanti NRA); **34**, MEVE (Mesa Verde NP); **35**, CHCU (Chaco Culture NHP); **36**, BAND (Bandelier NM); **37**, ELMA (El Malpais NM); **38**, GICL (Gila Cliff Dwellings NM); **39**, CAVE (Carlsbad Caverns NP); **40**, GUMO (Guadalupe Mountains NP); **41**, BIBE (Big Bend NP); **42**, BADL (Badlands NP); **43**, JECA (Jewel Cave NM); **44**, MACA (Mammoth Cave NP); **45**, DENA (Denali NP and Preserve).

(chiropteraguanolite of Hunt and Lucas, 2012) is under-reported in NPS areas, so our listings of this important trace fossil are incomplete.

All NPS units have a four letter designation based on their name, which is used in this paper (e.g., Petrified Forest National Park is PEFO). USNM refers to the United States National Museum, Washington, DC.

ARCHES NATIONAL PARK (ARCH)

More than a dozen packrat paleomiddens (neotomalites) have been described from Bison Alcove at Arches National Park, Utah, and have been utilized in a number of studies related to vegetational history and radioisotopic dating (Tweet et al., 2012). A packrat paleomidden exhibit is on display in the Arches National Park Visitor Center.

BADLANDS NATIONAL PARK (BADL)

The White River Group (Eocene-Oligocene), extensively exposed at Badlands National Park, South Dakota, has yielded the most-studied Tertiary coprolites in North America (Sinclair, 1921; Wanless, 1923; Abel, 1926, 1935; Stovall and Strain, 1936; Vogeltanz, 1965, 1967; Clark et al., 1967; Häntzschel et al., 1968; Lemley, 1971; Edwards, 1973a, b; Edwards and Yatkola, 1974; Retallack, 1983; LaGarry, 1997, 2004; Dibenedetto, 2002; Hembree and Hasiotis, 2004, 2007; Meehan, 2007; Hunt and Lucas, 2007). The coprolites occur in the Chadron and Brule formations (middle Chadronian through upper Orellan) and represent mammalian herbivores and carnivores. Some of them preserve delicate features such as plant phytoliths and casts or molds of hair (Vogeltanz, 1965, 1967; LaGarry, 1997, 2004; Dibenedetto, 2002; Meehan, 2007). LaGarry (1997, 2004) suggested that Orellan coprolites were produced by a carnivore similar in size and feeding habits to the coyote (*Canis latrans*), likely the amphicyonid *Daphoenus vetus*.

Coprolites are common at BADL and include latrinites (accumulations of coprolites *sensu* Hunt and Lucas, 2012) such as Last Stand that has yielded over 40 examples, and the Brian Maebius Site (Fig. 2D-F). The coprolites appear to be closely associated with carnivore denning activity (Rachel Benton, pers. commun., 2011) and as such would represent ethological latrinites that were produced by animal behavior

(Hunt and Lucas, 2012). A specimen of *Stibarus* at the Field Museum of Natural History (PM 49840) from the upper Peanut Peak Member of the Chadron Formation in South Dakota has been identified as a possible stigilite (fossil owl pellet: Hunt and Lucas, 2007, 2012).

Retallack (1984) reported on the occurrence of fossil dung beetle balls from the Scenic Member of the Brule Formation at BADL. The fossil dung beetle balls are preserved as nearly spherical internal molds of chambers. These trace fossils have been assigned to the ichnotaxon *Pallichnus dakotensis* (Fig. 2I-J).

BANDELIER NATIONAL MONUMENT (BAND)

There is an unpublished report that mentions a single packrat paleomidden in Frijoles Canyon at Bandelier National Monument, New Mexico (Tweet et al., 2012).

BIG BEND NATIONAL PARK (BIBE)

Baghai-Riding and DiBenedetto (2001) described a large vertebrate coprolite from the Upper Cretaceous Aguja Formation at Big Bend National Park, Texas. This specimen is attributed to an herbivorous dinosaur. Lehman and Wick collected small coprolites from a microvertebrate locality in the Aguja including a coiled one that they attributed to a shark (Don Corrick, pers. commun., 2012).

The overlying Javelina Formation contains fossil wood of the dicot *Javelinoxylon* (Wheeler et al., 1994). Some specimens of this wood are riddled with fossil termite borings that contain termite coprolites (frass) (Rohr et al., 1986a, b; Wheeler et al., 1994). The coprolites are oblong and weakly hexagonal in cross section, and their layered distribution in some galleries is consistent with termite colonization after the trees had fallen (Rohr et al., 1986a, b; Wheeler et al., 1994).

Standhardt (1995) reported that coprolites are common at the Dogie locality in the northwestern part of the park. This locality is in the Paleocene portion of the lower Tornillo Formation.

Big Bend National Park is one of the most prolific and most studied sources of packrat paleomiddens (neotomalites) within the NPS system, notably in the Rio Grande Village, Burro Mesa and Dagger Mountain areas (Tweet et al., 2012). The park's paleomiddens preserve a rich record of floral history, as well as yielding arthropod remains and vertebrate bones. The oldest paleomiddens date from more than 45,000 yr BP (Tweet et al., 2012).

BIGHORN CANYON NATIONAL RECREATION AREA (BICA)

Dozens of packrat paleomiddens have been documented at Bighorn Canyon National Recreation Area, Montana and Wyoming (Tweet et al., 2012).

CANYON DE CHELLY NATIONAL MONUMENT (CACH)

Antelope House, at Canyon De Chelly National Monument, Arizona, has yielded 16 human coprolites, one from the Pueblo I period and 15 from Pueblo II (Williams-Dean and Bryant, 1975; Fry and Hall, 1986; Williams-Dean, 1986; Brand, 1994). Stiger (1977) described other coprolites from the Pueblo III period at Antelope House. Three packrat paleomiddens from CACH have been extensively studied (Tweet et al., 2012).

CANYONLANDS NATIONAL PARK (CANY)

Vertebrate coprolites are reported from the lower part of the Chinle Group (Upper Triassic) at Canyonlands National Park, Utah (A. Hunt, personal observation, 1992). A number of packrat paleomiddens (neotomalites) are known from several areas within the park, including Salt Creek Canyon, Island-in-the-Sky, The Maze and White Rim (Tweet et al., 2012). The paleomiddens range widely in age and some include significant arthropod fossils (Tweet et al., 2012).

CAPITOL REEF NATIONAL PARK (CARE)

Twenty-two packrat paleomiddens have been described from Capitol Reef National Park, Utah (Tweet et al., 2012).

CARLSBAD CAVERNS NATIONAL PARK (CAVE)

Extensive deposits of chiropteraguanolite (bat guano *sensu* Hunt and Lucas, 2012) occur in Carlsbad Caverns. Sloth coprolites have also been reported from CAVE (Paul Martin, written commun., 2010).

CHACO CULTURE NATIONAL HISTORICAL PARK SITE (CHCU)

Thirty-five human coprolites of the Pueblo II period have been recovered from Chaco Canyon, 23 from Pueblo Alto and 13 from Pueblo Bonito within Chaco Culture National Historical Park, New Mexico (Clary, 1984). There are more than 300 packrat middens at CHCU. Study of these specimens has helped elucidate the human occupational history of the area (Tweet et al., 2012).

CHANNEL ISLANDS NATIONAL PARK (CHIS)

Ornithoguanolite (bird guano *sensu* Hunt and Lucas, 2012) and strigilites (owl pellets *sensu* Hunt and Lucas, 2012) have been reported from sites on two of the islands protected within Channel Islands National Park, California. Ornithoguanolite was found interspersed with Early Holocene shell midden material within Daisy Cave, an archaeological and paleontological site on San Miguel Island. The associated shell cumulate deposits (*sensu* Hunt and Lucas, 2012) are dated to between ca. 9900 and 8500 cal yr BP (Erlandson et al., 1996). On Santa Rosa Island, deposits of a long-term barn-owl roost have been found near the mouth of Arlington Canyon. Strigilites (owl pellets) from this site included the bones of Pacific rattlesnakes (*Crotalus oreganus*), ornate shrews (*Sorex ornatus*), and the extinct giant deer mouse (*Peromyscus nesodytes*). The base of the deposit is at least 28,240 ± 940 radiocarbon yr BP (34,620–31,160 calendar yr BP) in age, and the top is dated to 10,240 ± 180 radiocarbon yr BP (12,450–11,330 calendar yr BP) (Guthrie, 1998). The abundant *Peromyscus nesodytes* bones are the result of prehistoric owl pellets decomposing at the edge of an ancient bog and it has been possible to delimit the shape of strigilites in the clay soil matrix (John Johnson, pers. commun., 2012).

CITY OF ROCKS NATIONAL RESERVE (CIRO)

Recent fieldwork found a packrat paleomidden dating back to at least the Pleistocene/Holocene boundary. The paleomidden record of this Idaho reserve is being used in conjunction with charcoal to detail its Holocene climate and fire history (Tweet et al., 2012).

COLORADO NATIONAL MONUMENT (COLM)

There are numerous packrat paleomiddens (neotomalites) at Colorado National Monument, Colorado, but they are largely unstudied (Tweet et al., 2012).

CRATERS OF THE MOON NATIONAL MONUMENT AND PRESERVE (CRMO)

Packrat paleomiddens occur within lava tubes at Craters of the Moon National Monument, Idaho (Tweet et al., 2012).

CURECANTI NATIONAL RECREATION AREA (CURE)

Packrat paleomiddens (neotomalites) are known from the area of Curecanti National Recreation Area, Colorado, but it is not certain if any of them occur within the boundaries of the NPS unit (Tweet et al., 2012).

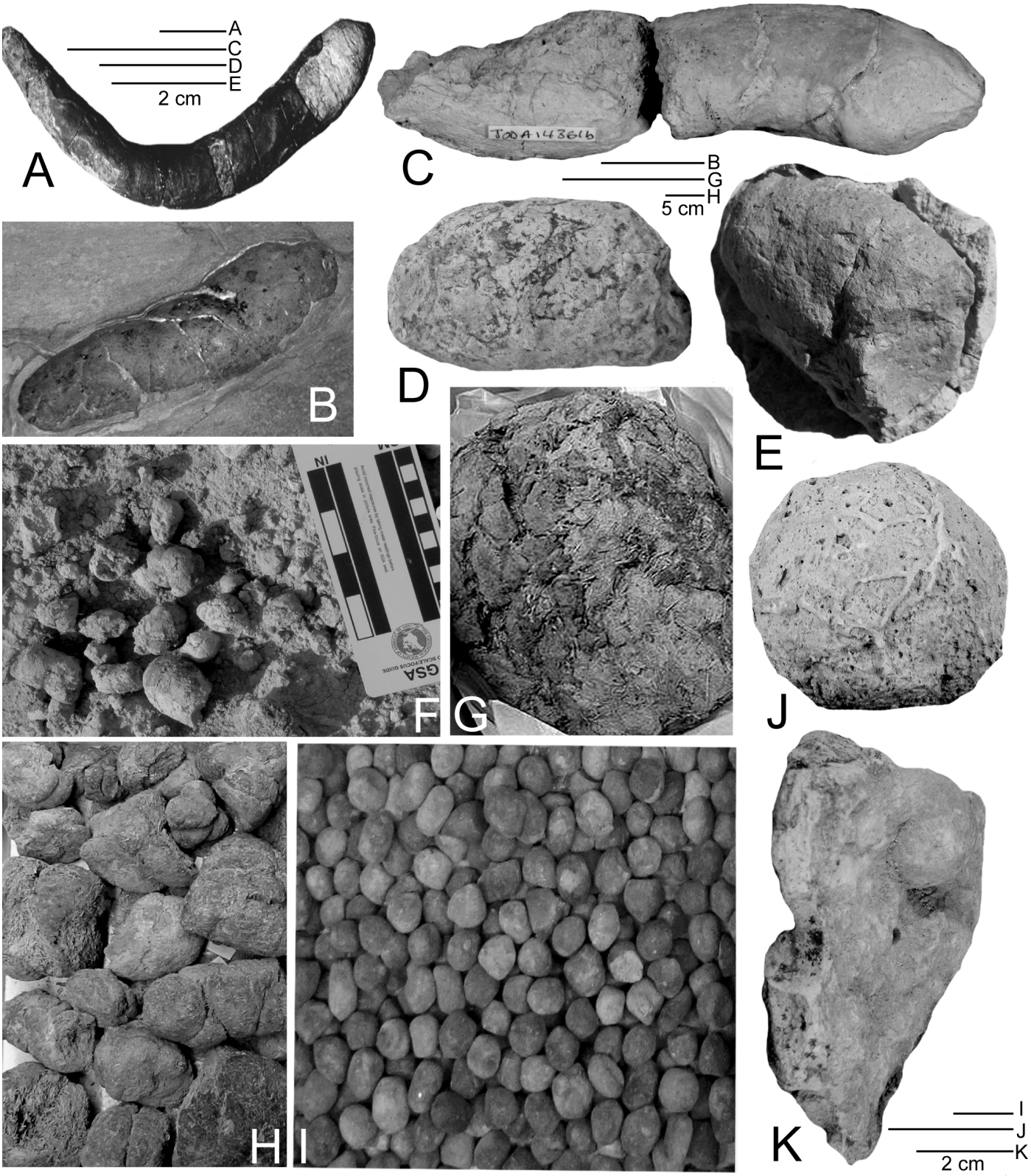

FIGURE 2. Coprolites from National Park service units. **A**, *Falcatocoprus oxfordensis* from PEFO (Petrified Forest National Park). **B**, Coprolite (crocodilian?) from FOBU (Fossil Butte National Monument). **C**, Carnivore coprolite from JODA (John Day Fossil Beds National Monument). **D**, Typical coprolite from BADL (Badlands National Park). **E**, Atypical coprolite from BADL (Badlands National Park) of tan color. **F**, Last Stand latrinite locality at BADL (Badlands National Park). **G**, Mammoth coprolite from Bechan Cave at GCNP (Glen Canyon National Park). **H**, Shasta Ground Sloth coprolites (*Nothrotheriops shastensis*) from Rampart Cave at GRCA (Grand Canyon National Park) in the collections of USNM. **I**, Harrington's Mountain Goat (*Oreamnos harringtoni*) coprolites from Rampart Cave at GRCA (Grand Canyon National Park) in the collections of USNM. **J-K**, *Pallichnus dakotensis* from BADL (Badlands National Park); **J**, individual specimen; **K**, specimen in matrix.

DEATH VALLEY NATIONAL PARK (DEVA)

A large number of packrat paleomiddens have been described from Death Valley National Park, California (Tweet et al., 2012).

DENALI NATIONAL PARK AND PRESERVE (DENA)

Two coprolites are known from the lower part of the Upper Cretaceous Cantwell Formation (Anonymous, 2008, unnumbered fig. on p. 2; Phil Brease, personal comm., 2009).

DINOSAUR NATIONAL MONUMENT (DINO)

Lockley et al. (1992) first noted that abundant coprolites occur in the upper part of the Bell Springs Formation (Chinle Group; Upper Triassic). The probable fish coprolites occur in the uppermost portion of the formation over a wide area in northeastern Utah and northwestern Colorado, in and around the boundaries of Dinosaur National Monument, Colorado and Utah (Hunt et al., 1993). This is one of several instances where a coprolite acme zone can be used for biostratigraphic correlation (Johnson, 1934).

Five packrat paleomiddens (neotomalites) have been described from the Colorado portion of DINO (Tweet et al., 2012).

EL MALPAIS NATIONAL MONUMENT (ELMA)

There are multiple packrat paleomiddens at El Malpais National Monument, New Mexico, but they are unstudied (Tweet et al., 2012).

FOSSIL BUTTE NATIONAL MONUMENT (FOBU)

Vertebrate coprolites are locally common in the Eocene Green River Formation of Utah, Wyoming and Colorado, particularly in paleoenvironments that preserve complete fish (e.g., Grande, 1980; Wilson, 1987; Wells et al., 1993). Most are presumed to have been produced by fish, although Wilson (1987) argued that birds are likely predators to produce coprolites with bones. Fossil Butte National Monument, Wyoming, has fish and "crocodile" coprolites in their museum collections, and a large "crocodile" coprolite is on display at the visitor center (Fig. 2). A large 18-cm-long coprolite from FOBU has been ascribed to a crocodile, primarily based on size (Fig. 2B).

In addition, many fossil fish from FOBU preserve cololites (digestive tract contents). Cololites are more commonly preserved in fish as compared to tetrapods throughout the geological record. Indeed, they are relatively common in the Green River Formation (e.g., Grande, 1980). Nonmarine terrestrial cololites have rarely been described from the Cenozoic of North America.

Regurgitalites are poorly studied. Fish regurgitalites have been recognized for about 50 years (Zangerl and Richardson, 1963). They usually can be distinguished from coprolites by a lack of groundmass, discrete shape and possible bone damage (Wilson, 1987). Such specimens occur in the Green River Formation in and around FOBU and elsewhere (Wilson, 1987).

GILA CLIFF DWELLINGS NATIONAL MONUMENT (GICL)

There are unstudied packrat paleomiddens in alcoves at Gila Cliff Dwellings National Monument, New Mexico (Tweet et al., 2012).

GLEN CANYON NATIONAL RECREATION AREA (GLCA)

Vertebrate coprolites have been observed in intraformational conglomerates of the Upper Triassic Rock Point Formation (Chinle Group) at Glen Canyon National Recreation Area, Arizona and Utah. However, GLCA's best-known coprolite assemblage consists of Quaternary coprolites preserved in caves and rock shelters.

Bechan Cave is a large, west-facing shelter formed in the Lower Jurassic Navajo Sandstone, and it is an important Pleistocene paleontological locality (Mead et al., 1986a; Santucci et al., 2001). The cave contains a large organic deposit, with a volume of approximately 300 cubic meters, that is dominated by coprolites (Davis et al., 1984, 1985; Mead et al., 1984, 1986b; Agenbroad and Mead, 1987, 1989). The name "Bechan" comes from the Navajo word for "big feces" (Mead et al., 1986a). Some very complete coprolites from Bechan Cave have been utilized for paleoenvironmental analyses (Davis et al., 1984). The majority of the coprolites in the cave have been identified as mammoth (probably *Mammuthus columbi*), based on similarities to modern African elephant dung and differences from *Nothrotheriops shastensis* (Shatsa ground sloth) coprolites. Other coprolites discovered in the cave represent dung from rabbits, rodents, mountain sheep or deer (*Ovis canadensis* or *Odocoileus* sp.), Shasta ground sloth, and a large, unidentified artiodactyl (Mead et al., 1984). Six samples of mammoth coprolites and a number of plant fossils from the coprolites were radiocarbon dated, producing an age of occupation ranging from about 14,665 to 11,070 years B.P. (Mead et al., 1986c; Mead and Agenbroad, 1992). Packrat activity has produced paleomiddens in the cave, and it appears that packrats have been active at the site for about 12,000 years (Davis et al., 1984).

Another locality known as BF Alcove contains numerous coprolites, which were dated as follows: *Mammuthus* (28,290 and 26,140 years B.P.); *Bison* (15,270 B.P.); and ?*Euceratherium* (shrubox) (20,930 and 18,320 B.P.). The ?*Euceratherium* coprolites exhibit a morphology similar to that of *Ovibos moschatus* (living muskox) and *Symbos* (extinct muskox) (Mead and Agenbroad, 1992).

Hooper's Hollow is a wide alcove with packrat paleomiddens (dated radioisotopically to 13,110, 12,010, and 10,630 B.P.), and *Bison* coprolites (18,840 B.P.) (Mead and Agenbroad, 1992). Mammoth Alcove is a medium-sized shelter that contains dated coprolites of *Mammuthus* (dated at 16,630 B.P.), *Bison*, and cf. *Ovis* (Mead and Agenbroad, 1992). Oak Haven is a small shelter that preserves a stratified sequence of sediments including coprolites of *Mammuthus*, *Bison*, and *Euceratherium* (Mead and Agenbroad, 1992).

Oakleaf Alcove, now submerged under Lake Powell, produced human coprolites and one other coprolite, tentatively identified as pertaining to *Equus*, which was radiometrically dated to approximately 24,600 years B.P. (Mead and Agenbroad,1992).

Several other caves and rock shelters at GLCA contain coprolites. Withers Wallow is a small sandstone shelter with coprolites of cf. *Ovis*, *Bison*, and *Mammuthus* (Mead and Agenbroad, 1992). Isolated coprolites assigned to *Euceratherium* from Cottonwood Alcove were dated to about 12,510 years B.P. Shrubox Cave contains coprolites assigned to *Euceratherium collinum*, *Bison*, *Oreamnos*, *Ovis*, and *Mammuthus* (Mead and Agenbroad, 1992).

Packrat paleomiddens occur at several localities within GLCA, and their plant material has been used for comparison with plant material from mammoth coprolites (Tweet et al., 2012).

GOLDEN SPIKE NATIONAL HISTORIC SITE (GOSP)

Two packrat paleomiddens have been described from Golden Spike National Historic Site, Utah (Tweet et al., 2012).

GRAND CANYON NATIONAL PARK (GRCA)

Grand Canyon National Park, Arizona, preserves some of the most extensive late Pleistocene coprolite deposits in the world, principally in some of the hundreds of caves developed in the Muav Limestone of the Tonto Group (Cambrian) and the Redwall Limestone (Mississippian) (Mead, 1981; Mead et al., 1986a; Santucci et al., 2001; Hunt et al., 2005). These paleontological deposits are the result of a unique set of circumstances (Hunt et al., 2005): (1) long and deep canyons; (2) exposure of a sequence of marine limestones; (3) development of hundreds of caves in these limestones; (4) dry, hot climate, which provides exceptional conditions for preservation; and (5) inaccessible location of many of these caves, which has limited disturbance. Because the Grand Can-

yon caves provide exceptional preservation and an abundance of fossils, providing a window into an ancient world, Hunt et al. (2005) recognized them as collectively comprising two forms of speleological Lagerstätte: a Konzentrat-Lagerstätte and a Konservat-Lagerstätte.

Many of the caves in Grand Canyon National Park preserve coprolites, including Vulture Cave, Rampart Cave, Muav Caves, Stanton's Cave, Tse'an Bida Cave, Tse'an Kaetan Cave, Steven's Cave, Sandblast Cave, Shrine's Cave, Hummingbird Cave, Crescendo Cave, Rebound Cave, Left Eye Cave, Five Windows Cave, White Cave, Disappearing Cave, CC:5:1 cave, CC:5:3 cave, CC:5:4 cave and CC:5:6 cave (Santucci et al., 2001; Mead et al., 2003; Hunt et al., 2005). The coprolites represent rodents (?*Peromyscus*, *Neotoma* spp.), carnivorans (*Bassariscus astutus*), Shasta Ground Sloth (*Nothrotheriops shastensis*), Harrington's Mountain Goat (*Oreamnos harringtoni*), Bighorn Sheep (*Ovis canadensis*) and raptors (Santucci et al., 2001; Mead et al., 2003). The coprolites occur in a variety of contexts, from isolated pellets to stratified latrinites (Santucci et al., 2001). Chiropteraguanolite (bat guano) is also common in caves in GRCA (e.g., Santucci et al., 2001), but its distribution has not been well documented. In addition, GRCA has yielded more than 150 described packrat paleomiddens, the largest number of paleomiddens within one single unit of the NPS system (Tweet et al., 2012).

Rampart Cave was one of the first caves to be studied in Grand Canyon National Park and it contained the most significant coprolite resources, notably extensive Shasta ground sloth dung (Fig. 2H; Martin et al., 1961; Santucci et al., 2001, figs. 9-12; McDonald, 2003, fig. 1.6: Hunt et al., 2005, fig. 5). Rampart Cave was originally within the boundaries of Lake Mead National Recreation Area, but was incorporated into Grand Canyon National Park in January 1975 (Hansen, 1978; Santucci et al., 2001). In 1936, Willis Evans, a Park Service employee, first entered Rampart Cave and discovered the extensive Shasta ground sloth coprolite deposit (Martin et al., 1961). Until 1976, when a fire destroyed much of the sample, Rampart Cave contained the thickest and largest stratified latrinite of *Nothrotheriops shastensis* coprolites (Long and Martin, 1974; Hansen, 1978; Santucci et al., 2001, figs. 10-11). Coprolites and latrinite samples have been radioisotopically dated, showing their production to have occurred between more than 40,000 years B.P. and approximately 10,035 years B.P. (Martin et al., 1961; Long and Martin, 1974; Mead and Agenbroad, 1992). Plant and pollen analyses of coprolites have been undertaken in order to reconstruct long-term paleoecological changes and seasonal variation in sloth diet (Martin et al., 1961; Hansen, 1978; Mead, 1981). Schmidt et al. (1992) reported on parasites and their eggs found within sloth coprolites.

Rampart Cave also yielded coprolites of *Oreamnos harringtoni* dated to approximately 18,430 years B.P. (Fig. 2I; Mead et al., 1986c; Mead and Agenbroad, 1992). Deposits of material interpreted as chiropteraguanolite (bat guano) located near the rear of the cave are among the oldest deposits in the cave, having been dated to >35,500 years B.P. (Long and Martin, 1974). Packrat paleomiddens (neotomalites) are abundant at Rampart Cave, with 30 indurated (cemented) paleomiddens found both in and around the cave (Phillips and Van Devender, 1974). One 33-cm thick paleomidden layer was dated between 24,000 and 14,000 years B.P., and may have constituted the largest Pleistocene packrat deposit ever found (Phillips and Van Devender, 1974).

Vulture Cave contains 15 packrat paleomiddens and a large *Bassariscus astutus* refuse area encompassing more than one square meter (Mead and Van Devender, 1981). The Late Holocene remains in the refuse deposit were interpreted as being dietary remnants.

The Muav Caves are three small caves upstream from Rampart Cave that contain *Nothrotheriops shastensis* latrinites and coprolites that have been radiocarbon dated to between 11,810 and 10,650 years B.P. (Harrington, 1936; Long and Martin, 1974; Mead and Agenbroad, 1992). Stanton's Cave contains groups of large *Oreamnos harringtoni* coprolites that have been dated to between 17,300 and 10,870 years B.P., together with coprolites of a large artiodactyl, perhaps *Ovis canadensis*, and small coprolites (Mead and Agenbroad, 1992; Emslie et al., 1987).

Four groups of *O. harringtoni* coprolites from Tse'an Bida Cave have been used for pollen analysis and radioisotopically dated between 24,190 and 11,850 years B.P. (Mead et al., 1986c; Mead and Agenbroad, 1992). This cave also contains several packrat paleomiddens (Cole and Mead, 1981).

Sandblast Cave is a series of three caverns merging together to form a small cave complex. The complex probably represents a nest or roost for raptors, including the condor *Gymnogyps californianus*, as evidenced by the extensive remains (Emslie, 1986, 1987, 1988). Thousands of bones of fish, lizards, snakes, birds, and rodents are scattered on the floor of the cave (Emslie, 1988). An unconsolidated packrat paleomidden has yielded bones and bone fragments of large mammals (*Equus*, *Bison*, *Camelops*, *Oreamnos*, *Mammuthus*) (Emslie, 1988). These bones, together with the small bones littering the floor, probably represent condor food debris. Coprolite pellets of *O. harringtoni* were also recovered and radiocarbon-dated (Mead and Agenbroad, 1992).

Shrine Cave is an important archeological site that contains more than 33 rock cairns and two split-twig figurines (Emslie et al., 1987). In many cases fossil material, including coprolites, are associated with the archeological resources, which may indicate the use of paleontological resources as cultural artifacts (Santucci et al., 2001). For example, many of the cairns include packrat paleomiddens (neotomalites), and some of the split-twig figurines are associated with coprolites (probably of *Ovis canadensis*), which may have been wrapped inside of them (Emslie et al., 1987). Pre-occupation paleomiddens in the cave sometimes contain coprolites of either *Oreamnos harringtoni* or *Ovis canadensis* (Emslie et al., 1987).

The floor of Skull Cave is littered with the coprolites of *Neotoma* and *Peromyscus* (Santucci et al., 2001). Hummingbird Cave contains numerous rodent coprolites (probably *Peromyscus*) (Emslie, 1988). Crescendo Cave contains a latrinite probably representing *Oreamnos harringtoni* and a packrat paleomidden (Emslie et al., 1995). Rebound Cave contains a latrinite representing *Ovis canadensis* or *Oreamnos harringtoni* and packrat paleomiddens (Emslie et al., 1995). Left Eye Cave includes a latrinite of *Ovis canadensis* or *Oreamnos harringtoni* coprolites and a packrat paleomidden (Emslie et al., 1995). A packrat paleomidden has been reported from Right Eye Cave (Emslie et al., 1995). Five Windows Cave contains a single packrat paleomidden and a latrinite of *Oreamnos* or *Ovis* (Santucci et al., 2001). *Oreamnos* or *Ovis* coprolites have been reported from White Cave (Emslie et al., 1995). Mead and Agenbroad (1992) dated coprolites and a latrinite of *Oreamnos harringtoni* from Chuar Cave. Disappearing Cave is a small limestone shelter that contains some dated coprolites of *O. harringtoni* and many packrat paleomiddens (Mead and Agenbroad, 1992). Tse'an Kaetan Cave contains coprolites of *O. harringtoni* that have yielded radiocarbon dates between 30,600 and 14, 220 years B.P. (Mead and Agenbroad, 1992). Stevens Cave has produced coprolites, as well as hair and bones, of *O. harringtoni* (Emslie, 1988). Midden Cave contains multiple paleomiddens, as its name suggests.

Mead et al. (2003) reported on coprolites from caves in eastern GRCA. Cave CC:5:1 contains some packrat paleomiddens (neotomalites) and small deposits of *O. harringtoni* coprolites. Packrat paleomiddens occur in Cave CC:5:2. Cave CC:5:3 has unindurated packrat paleo middens and modern raptor pellets in its entrance room, and coprolites of *O. harringtoni* are common on the cave floor. Cave CC:5:4 includes several latrinites (*sensu* Hunt and Lucas, 2012) of *O. harringtoni* as well as numerous paleomiddens. Indurated (urine-cemented) packrat paleomiddens are common in Cave CC:5:5. Cave CC:5:6 contains coprolites, including some identified as pertaining to *O. harringtoni*. NAUQSP Locality 991 is a single packrat paleomidden from an isolated crevice.

GRAND CANYON-PARASHANT NATIONAL MONUMENT (PARA)

Undescribed packrat paleomiddens have been found in this Arizona monument (Tweet et al., 2012).

GREAT BASIN NATIONAL PARK (GRBA)

At least four packrat paleomiddens have been studied from Great Basin National Park, Nevada (Tweet et al., 2012).

GUADALUPE MOUNTAINS NATIONAL PARK (GUMO)

Twenty-seven caves have been documented within Guadalupe Mountains National Park, Texas. The caves contain significant Pleistocene and Holocene fossils, including coprolites, paleomiddens and strigilites (Santucci et al., 2001).

Pratt Cave yields bones of an extinct roadrunner and a turkey that McKusick (1978) concluded were deposited as owl pellets. Dust Cave has yielded packrat paleomiddens and ground sloth coprolites (Spaulding and Martin, 1979; Santucci et al., 2001). Lower Sloth Cave contains several types of bromalites, including sloth coprolites, carnivoran coprolites, strigilites (owl pellets), and packrat paleomiddens (Logan, 1977). Sloth coprolites from this cave have yielded a radiocarbon date of 10,750-11,060 years B.P. (Logan, 1977; Logan and Black, 1979; Spaulding and Martin, 1979). Small bone accumulations are associated with owl pellets and coprolites of the small carnivores *Bassariscus*, *Spilogale* and *Canis* (Logan, 1977).

Upper Sloth Cave preserves packrat paleomiddens (neotomalites) that yield radiocarbon dates to about 13,000 years B.P., and sloth coprolites from the cave yielded a radiocarbon date of approximately 11,760 years B.P. (Logan, 1975; Spaulding and Martin, 1979). Williams Cave (Indian Cave) has produced well-preserved sloth coprolites, and remnants of packrat paleomiddens are plastered to the walls (Ayer, 1936; Spaulding and Martin, 1979). Packrat paleomiddens are also known from other localities at GUMO (Tweet et al., 2012).

HAGERMAN FOSSIL BEDS NATIONAL MONUMENT (HAFO)

The first discovery of a coprolite from Hagerman Fossil Beds National Monument, Idaho, was made by Greg McDonald during the early 1990s. The coprolite specimen contains small vertebrate bones and is believed to be from a carnivore (Greg McDonald, pers. commun., 2012).

HUBBELL TRADING POST NATIONAL HISTORIC SITE (HUTR)

Hubbell Trading Post National Historic Site, Arizona, reportedly has a coprolite in the park museum collection (Tweet et al. 2012).

JEWEL CAVE NATIONAL MONUMENT (JECA)

Jewel Cave National Monument, South Dakota, has yielded the northeasternmost packrat paleomiddens (neotomalites) in the NPS (Tweet et al., 2012).

JOHN DAY FOSSIL BEDS NATIONAL MONUMENT (JODA)

There are 58 coprolites in the John Day Fossil Beds National Monument, Oregon, museum collection from the Turtle Cove Member of the John Day Formation (Fig. 2C; Chris Schierup, pers., commun., 2009).

JOSHUA TREE NATIONAL PARK (JOTR)

More than 100 packrat paleomiddens (neotomalites) have been studied from Joshua Tree National Park, California (Tweet et al., 2012).

LAKE MEAD NATIONAL RECREATION AREA (LAME)

Lake Mead National Recreation Area, Nevada, has a number of rock shelters with Neotoma paleomiddens. Paleomiddens have been described from three general areas: Black Mountains, Iceberg Canyon and Newberry Mountains (Tweet et al., 2012).

LAVA BEDS NATIONAL MONUMENT (LABE)

Packrat paleomiddens have been described from lava tubes and rock shelters at Lava Beds National Monument in northern California (Tweet et al., 2012).

MAMMOTH CAVE NATIONAL MONUMENT (MACA)

Jegla and Hall (1962) and Toomey et al. (1998, 2000) described a large *Tadarida* (bat) latrinite of chiropteraguanolite dated to more than 38,000 years B.P. from Mammoth Cave National Park, Kentucky. Toomey et al. (1998) documented large quantities of *Procyon lotor* (raccoon) coprolites containing a high percentage of bat bones. They dated bat bones, chiropteraguanolite (bat guano), and raccoon coprolites with radiocarbon dating and obtained a range of dates, from 8,700 years B.P. to 100 years B.P. Most of the material yielded dates less than 1,000 years B.P. (Toomey et al., 1998).

MESA VERDE NATIONAL MONUMENT (MEVE)

Cretaceous marine coprolites occur in the Mancos Shale at Mesa Verde National Park, Colorado, with one specimen in the park museum collection (JST personal observation). Stiger (1977) described 22 human coprolites from the Basketmaker II site of Step House. Pueblo III coprolites are also known from Step House and Hoy House (Stiger, 1977). Recent packrat paleomiddens also occur at MEVE (Tweet et al., 2012).

MOJAVE NATIONAL PRESERVE (MOJA)

Late Pleistocene and mid-Holocene packrat paleomiddens have been documented and studied at Mojave National Preserve, California (Tweet et al., 2012).

NATURAL BRIDGES NATIONAL MONUMENT (NABR)

Bare Ladder Shelter is a cave formed in the Permian Cedar Mesa Sandstone at Natural Bridges National Monument, Utah. A large number of indurated and unconsolidated Rancholabrean packrat paleomiddens are preserved in Bare Ladder Shelter (Mead et al., 1987; Santucci et al., 2001; Tweet et al., 2012). There are at least two coprolite-rich layers of specimens identified from *Oreamnus harringtoni* and three main layers of paleomiddens (Tweet et al., 2012). *O. harringtoni* coprolites have been dated to more than 39,800 years B.P., making this the oldest, directly-dated occurrence of this species (Mead et al., 1987; Mead and Agenbroad, 1992). Additional coprolites yield younger dates, ranging in age from 23,350 to 9,660 years B.P. (Mead et al., 1987).

NAVAJO NATIONAL MONUMENT (NAVA)

Stiger (1977) described human coprolites from the Pueblo II period within Inscription House at Navajo National Monument, Arizona. Additional coprolites have been found at Turkey Cave and Keet Seel Ruin at NAVA.

ORGAN PIPE CACTUS NATIONAL MONUMENT (ORPI)

Packrat paleomiddens (neotomalites) occur in both the Ajo Range and Puerto Blanco Mountains in the east-central portion of Organ Pipe Cactus National Monument, Arizona. The paleomiddens have yielded significant arthropod and vertebrate body fossils as well as paleobotanical remains (Tweet et al., 2012). A packrat paleomidden exhibit is on display at the Organ Pipe National Monument Visitor Center.

PETRIFIED FOREST NATIONAL PARK (PEFO)

Vertebrate coprolites are locally common in strata of the Upper Triassic Chinle Group at Petrified Forest National Park, Arizona (Hunt et al., 2007; Fig. 2A). The Chinle Group section at PEFO consists of, in ascending order, the Bluewater Creek Formation, the Blue Mesa, Sonsela and the Painted Desert members of the Petrified Forest Formation, and the Owl Rock Formation. The vast majority of fossils occur in the Blue Mesa and Painted Desert members.

Hunt et al. (1998) described *Heteropolacopros texaniensis* as occurring in the Blue Mesa Member of the Petrified Forest Formation of northeastern Arizona, including at PEFO (Hunt and Santucci, 1994). Murry (1989) and Heckert (2001, 2004) noted the occurrence of coprolites, some of which contain fish scales, teeth and plant debris, from the Blue Mesa Member at the "Dying Grounds" locality in PEFO. Wahl et al. (1998) described coprophagy in coprolites from the Blue Mesa Member at Petrified Forest National Park. Other localities in the Blue Mesa Member have also yielded significant coprolites, such as at Dinosaur Ridge.

Undescribed coprolites occur in the Painted Desert Member of the Petrified Forest Formation. The most significant accumulations are in the lower part of the Painted Desert Member, at localities that include Dinosaur Hill (Hunt and Lucas, 1993).

PIPE SPRING NATIONAL MONUMENT (PISP)

Recent packrat middens are present at Pipe Spring National Monument, Arizona (Tweet et al., 2012).

SAGUARO NATIONAL PARK (SAGU)

Packrat paleomiddens (neotomalites) are present at Saguaro National Park, Arizona, but only one paleomidden has been studied in detail (Tweet et al., 2012).

SEQUOIA/KINGS CANYON NATIONAL PARKS (SEKI)

Sequoia and Kings Canyon National Parks are two units of the National Park Service that are administered together. Packrat paleomiddens (neotomalites) were discovered in Bear Den Cave and at least seven other localities (Cole, 1983). One paleomidden, King's Canyon No. 8, produced identifiable vertebrate skeletal remains indicating an early to middle Wisconsin record (Mead et al., 1985).

TIMPANOGOS CAVE NATIONAL MONUMENT (TICA)

Packrat paleomiddens (neotomalites) are common in the caves of the Timpanogos Cave National Monument, Utah. Paleomiddens have been documented from the entrance room to Hansen Cave, the Boneyard near the natural entrance of Timpanogos Cave, the entrance to Middle Cave, and Hidden Mine Cave (George, 1999; Santucci et al., 2001; Tweet et al., 2012). The similarity between the paleomidden assemblage and the present-day mammal fauna supports a Holocene age (George, 1999).

WUPATKI NATIONAL MONUMENT (WUPA)

Twenty-two packrat paleomiddens (neotomalites) representing a variety of ages (Pleistocene and Holocene) have been described from Wupatki National Monument, Arizona (Tweet et al., 2012).

YELLOWSTONE NATIONAL PARK (YELL)

Lamar Cave at Yellowstone National Park, Montana and Wyoming, preserves Holocene packrat paleomiddens and carnivore den materials (Tweet et al., 2012).

SIGNIFICANCE OF NPS COPROLITE RECORD

Vertebrate coprolites are an understudied resource in many National Park Service (NPS) areas. The three most important coprolite assemblages are at Badlands National Park (BADL), Grand Canyon National Park (GRCA) and Petrified Forest National Park (PEFO) (Hunt et al., 2009). These vertebrate coprolite assemblages represent three of the acme zones for vertebrate coprolites in North America: Late Triassic at PEFO (Chinle Group), Eocene-Oligocene at BADL (White River Group) and Pleistocene at GRCA (cave deposits) (Hunt and Lucas, 2005, 2007) and have been central to recent work on paleoecology and biochronology.

The Blue Mesa and Painted Desert members of the Petrified Forest Formation (Chinle Group) at PEFO yield abundant vertebrate coprolites. The superposition of vertebrate coprolite assemblages at PEFO demonstrates the biostratigraphic and biochronologic significance of Late Triassic coprolites, such as *Dicynodontocopros* and *Heteropolacopros*, which are restricted to the upper Carnian (Adamanian) portion of the section (Hunt et al., 1998).

The White River coprolites of BADL and surrounding areas are the most studied Cenozoic vertebrate coprolites. Some contain casts and molds of hair and occasionally microvertebrate bones. These coprolites have been the focus of significant studies of Oligocene bone processing by predators/scavengers.

The numerous caves developed in Paleozoic limestones at GRCA yield an abundance of Pleistocene vertebrate coprolites representing several mammals and raptors (e.g., Santucci et al., 2001; Mead and Swift, 2012). The largest coprolite deposits represent the Shasta Ground Sloth and have been at the core of several paleoecological studies (diet, DNA, parasitology, trace elements). In summary, vertebrate coprolite assemblages from NPS units represent a significant paleontological resource that has been pivotal to recent advances in the study of coprolites.

MANAGING THE COPROLITE RESOURCE IN NPS UNITS

The National Park Service manages fossil coprolites similarly to any other paleontological resources, in consideration of their scientific and educational values. Coprolites typically do not require any specific management action, with the exception of some of the Pleistocene or Holocene coprolites, dung and middens that occur in National Park Service caves. The history associated with the partial destruction of sloth coprolite deposits by park visitors at Rampart Cave (GRCA) illustrates the need for park management action and implementation of preservation strategies to protect rare and sensitive paleontological resources. Park managers have the authority to close and limit access to caves in order to protect fragile and sensitive resources, as well as to insure public safety. The National Park Service uses a number of authorizations to close or restrict public access into caves, including the Archeological Resources Protection Act (1979), the Federal Cave Resources Protection Act (2004), the Paleontological Resources Preservation Act (2009), and the Code of Federal Regulations (36 CFR, 1.5).

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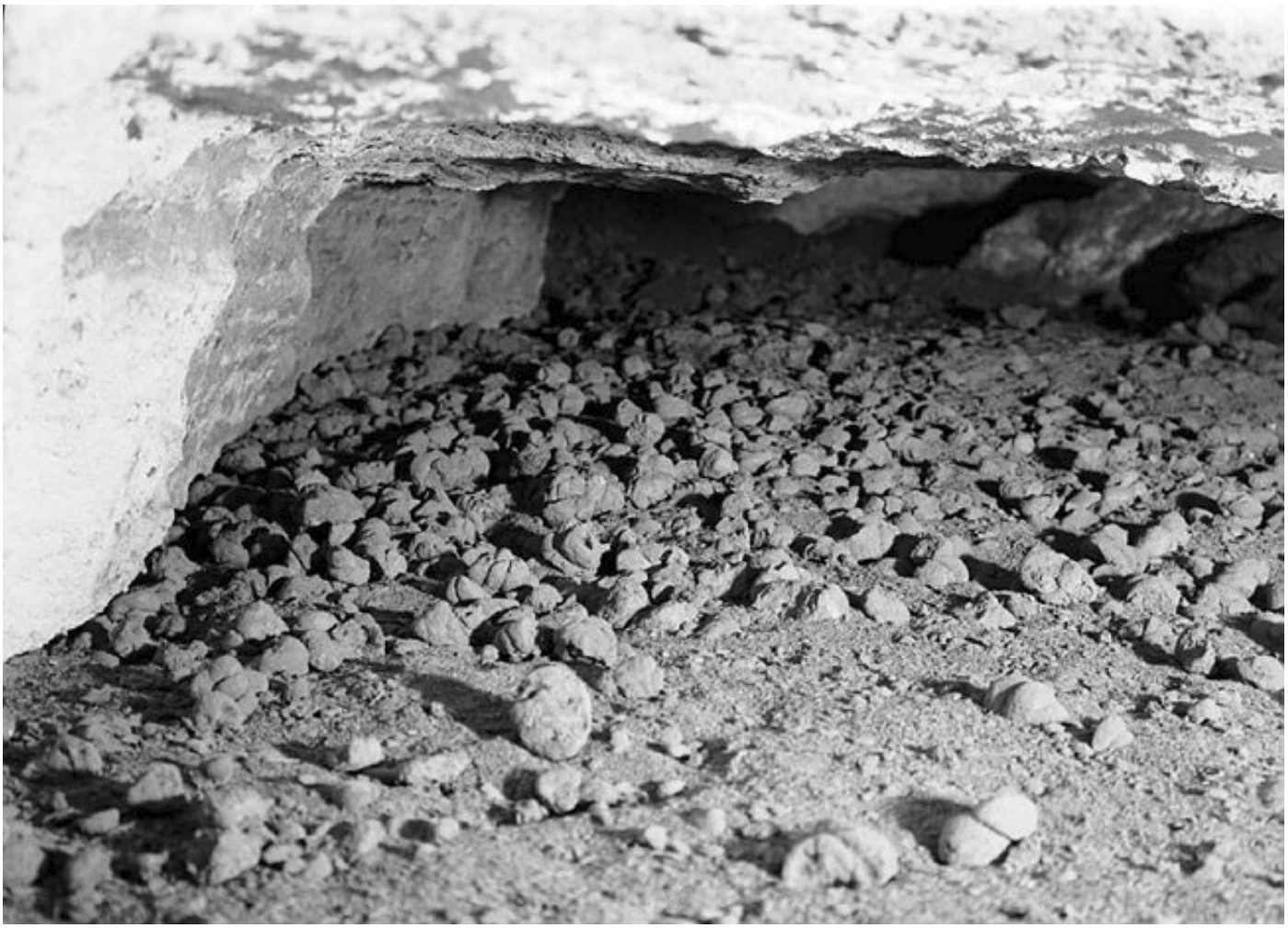

Rampart Cave latrinite.