PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2023, v. 38, 22–30
Research Article
DOI: http://dx.doi.org/10.2110/palo.2021.039

THE BISON AND THE BLOW FLY: USING PUPARIA OF THE BLACK BLOW FLY (*PHORMIA REGINA*: DIPTERA, CALLIPHORIDAE) TO CONSTRAIN THE SEASON OF DEATH AND TAPHONOMIC HISTORY OF AN EARLY HISTORIC-AGE BISON, CARSON CITY, NEVADA, USA

STEPHEN M. ROWLAND,[1,2,] TERRY L. WHITWORTH,[3] MICHELE JONES,[1] JOHN DOOLEY,[4,5] ERIC CHAMEROY,[1,2] AND THOMAS GORDON[6]

[1]*Las Vegas Natural History Museum, 900 Las Vegas Blvd., N., Las Vegas, Nevada 89101 USA*
[2]*Department of Geoscience, University of Nevada Las Vegas, 4505 S. Maryland Parkway, Las Vegas Nevada, 89154-4010 USA*
[3]*Department of Entomology, Washington State University, 100 Dairy Road, Pullman, Washington, 99164 USA*
[4]*Nevada State Museum, 309 S. Valley View Blvd., Las Vegas, Nevada, 89107 USA*
[5]*USDA, APHIS, PPQ South San Francisco, California, 94080 USA*
[6]*Gordon Bison Site, Carson City, Nevada, 89701 USA*
email: steve.rowland@unlv.edu

ABSTRACT: **We report the occurrence of abundant dipteran puparia of *Phormia regina*, the black blow fly, in association with an early historic-age bison skeleton excavated near Carson City, Nevada. Cut marks on some of the bones indicate that the bison was butchered and probably skinned by humans. Radiocarbon dating provides two possible age intervals for the death of the bison: (1) latest seventeenth to early eighteenth century or (2) early nineteenth to early twentieth century; we consider the more recent age to be more plausible. The purpose of this study is to explore how the presence of puparia of this well-studied, necrophagous fly species can be used to help constrain the season of death and inform the interpretation of the taphonomic history of the bison.**

The life cycle of *P. regina* requires a minimum of 8.8 days within a temperature range of 14°C to 35°C, so the bison carcass must have been exposed to the air for at least that long within that temperature range. However, of the thousands of recovered puparia, 35% remain closed and did not produce adult flies; of this cohort, only a tiny percentage exhibit small exit holes attributable to parasitoid wasps. Cold temperatures, and not parasitoid wasps, are the most probable cause of the high pupal mortality. Climate data for the region, along with *P. regina* temperature constraints and streamflow and flooding records for the Carson River watershed, indicate that the bison died and was colonized by black blow flies in the spring, when night-time temperatures were low. A short time later the skinned and butchered skeleton was buried by floodplain sediments. Blow fly puparia can contribute useful information for the taphonomic analysis of vertebrate fossil sites.

INTRODUCTION

Necrophagous insects play a significant ecological role in the decomposition of animal carcasses. The purpose of this study is to explore how the presence of sclerotized pupal casings (puparia) of a well-studied, necrophagous blow fly species can be used to help reconstruct the taphonomic history and season of death of an early historic-age bison.

On private land on the east side of Carson City, Nevada, we excavated skeletal remains representing at least four *Bison bison* individuals and skeletal elements of one pronghorn (*Antilocapra americana*) (Fig. 1). The site lies in Carson Valley, within the territory traditionally occupied by the Washoe people. Because of archaeological aspects of the site, traditional cultural practices of the Washoe are relevant to this study. We conferred with Washoe tribal historic preservation officer Darrel Cruz regarding our interpretation of the site.

One of the bison, from pit GOR-1, consisted of a nearly complete, articulated skeleton; the other bison and the pronghorn are known only from isolated skeletal elements. The GOR-1 bison skeleton was missing portions of its spinal column, including most of the thoracic, lumbar, and caudal vertebrae, and also the terminal phalanx (the hoof phalanx) on its left foreleg. The pelvic girdle was inadvertently damaged by the ditch-digging machine being used by the landowner to dig a trench for a waterline; this was how the bones were discovered. In general, the bones of the GOR-1 bison are very well preserved, exhibiting no sign of cracking or flaking due to weathering (Fig. 2). These are bone-weathering characteristics of Stage 0 of Behrensmeyer (1978), which indicates that the bones were buried less than a year after death. Conspicuous cut marks on some of the bones (Fig. 2) indicate that this was a butchering site; we have named it the Gordon Bison Butchering Site.

The animals were probably butchered by members of the Washoe Tribe, who have continuously inhabited the Carson Valley/Lake Tahoe region from pre-colonization time to the present day. Non-Washoe people are not known to have made regular use of Carson Valley in aboriginal times (D'Azevedo 1986). However, due to uncertainties about the age of the site (see below), we cannot rule out the possibility that Euro-Americans were involved.

While excavating the GOR-1 bison skeleton, we encountered thousands of dipteran puparia in the sediment adjacent to the animal's rib cage. These are non-mineralized, desiccated organic remains. A more complete description and interpretation of the vertebrate paleontology and archaeology of the site will be presented in a separate paper. Here we document the presence of the puparia, and we explore their taphonomic significance with respect to the bison skeleton.

Published Online: January 2023

FIG. 1.—Site location. **A**) Index map. **B**) Photo of Excavation Pit GOR-1 at the Gordon Bison Butchering Site, beneath the blue canopy. The puparia were recovered from the bottom of this pit.

Fly puparia have been occasionally reported from mummified human corpses (Giordani et al. 2018) and burial sites (Gilbert and Bass 1967; Teskey and Turnbull 1979; Panagiotakopulu 2004), as well as from Holocene (Johnson et al. 2005) and Pleistocene (Stock 1956; Gautier and Schumann 1973; Erzinçlioğlu 2009; Lister 2009; Mähler et al. 2016) non-human vertebrate fossils. As in forensic science, the presence of necrophagous insect remains in association with the body of a vertebrate animal may contribute valuable information regarding the postmortem history of the animal. In this particular case we are able to identify the species of fly involved, which is a well-studied extant species, thus providing unusually detailed environmental data that are useful for constraining the season of death, as well as the taphonomic history of the carcass.

AGE OF THE FOSSILS

The bison and antilocaprid fossils at the Gordon Bison Butchering Site are early historic in age in a regional sense, although they may predate historical records in Carson Valley. Due to fluctuating levels of atmospheric ^{14}C in the eighteenth and nineteenth centuries, radiocarbon dating of a fragment of bison rib yielded two possible age windows: 1694–1728 cal AD and 1812–1919 cal AD (Beta Analytic No. 574529). Some of the cut marks on the bison bones are too narrow and deep to have been made with stone tools (Fig. 2A); steel tools were apparently used, which bears on the question of the age of the fossils. The earliest documented contact between Washoes and people of European ancestry was in May 1827 when the American fur trapper Jedediah Smith and two companions wandered into Washoe territory as they crossed the Sierra Nevada (Makley 2018). Seventeen years later, in 1844, a party led by John C. Frémont interacted with a group of Washoes in Carson Valley. Five years after Frémont's visit, in 1849, the first wave of California-bound Euro-American travelers passed through Washoe territory on the "Carson Route" across the Sierra Nevada, on their way to the gold fields (Makley 2018). And in 1859 the Comstock silver rush attracted many more immigrants to the region.

By mid-nineteenth century, therefore, steel tools doubtless were present in Carson Valley. Well before direct contact occurred between Washoes and Euro-Americans, however, a wide variety of trade goods, including steel knives and axes, found their way into the Great Basin (Hughes and Bennyhoff 1986). It is very likely that Washoes acquired trade goods of Spaniard origin in the early nineteenth century (M.S. Makley personal communication 2022), and perhaps earlier, as the California mission network expanded northward in the eighteenth century. However, the early radiocarbon window for fossils in this study, 1694–1728, predates the California missions.

We conclude, therefore, that the later of the two radiocarbon intervals, 1812–1919, is the more likely of the two possible ^{14}C age intervals. We can further constrain the probable age due to the fact that, by the early 1880s, North American bison had been severely overhunted, to the brink of extinction (Lott 2002). So the bison and antilocaprid fossils at this site probably date to sometime between 1812 and the 1870s.

SITE DESCRIPTION AND SURFACE HYDROLOGY OF THE CARSON RIVER WATERSHED

The site lies on flat terrain, at an elevation of 1,400 m (~ 4,600 feet). The latitude is approximately 39°N. The site was mapped by Stewart (1999) as "Quaternary alluvium," adjacent to "Quaternary younger fluvial deposits", however the latter description is more appropriate. The sediments at the fossil site consist of poorly sorted, organic-rich sand, with angular pebbles of granite up to 0.5 cm in diameter. We infer these sediments to be floodplain overbank deposits that buried the fossils at this site, followed by the development of a sagebrush-dominated plant community. Prior to the development of home sites, the vegetation at the site consisted of a mature sagebrush (*Artemisia tridentata*) community within the Great Basin Desert. The modern, artificially channelized course of Clear Creek, a tributary to the Carson River, is approximately 600 m

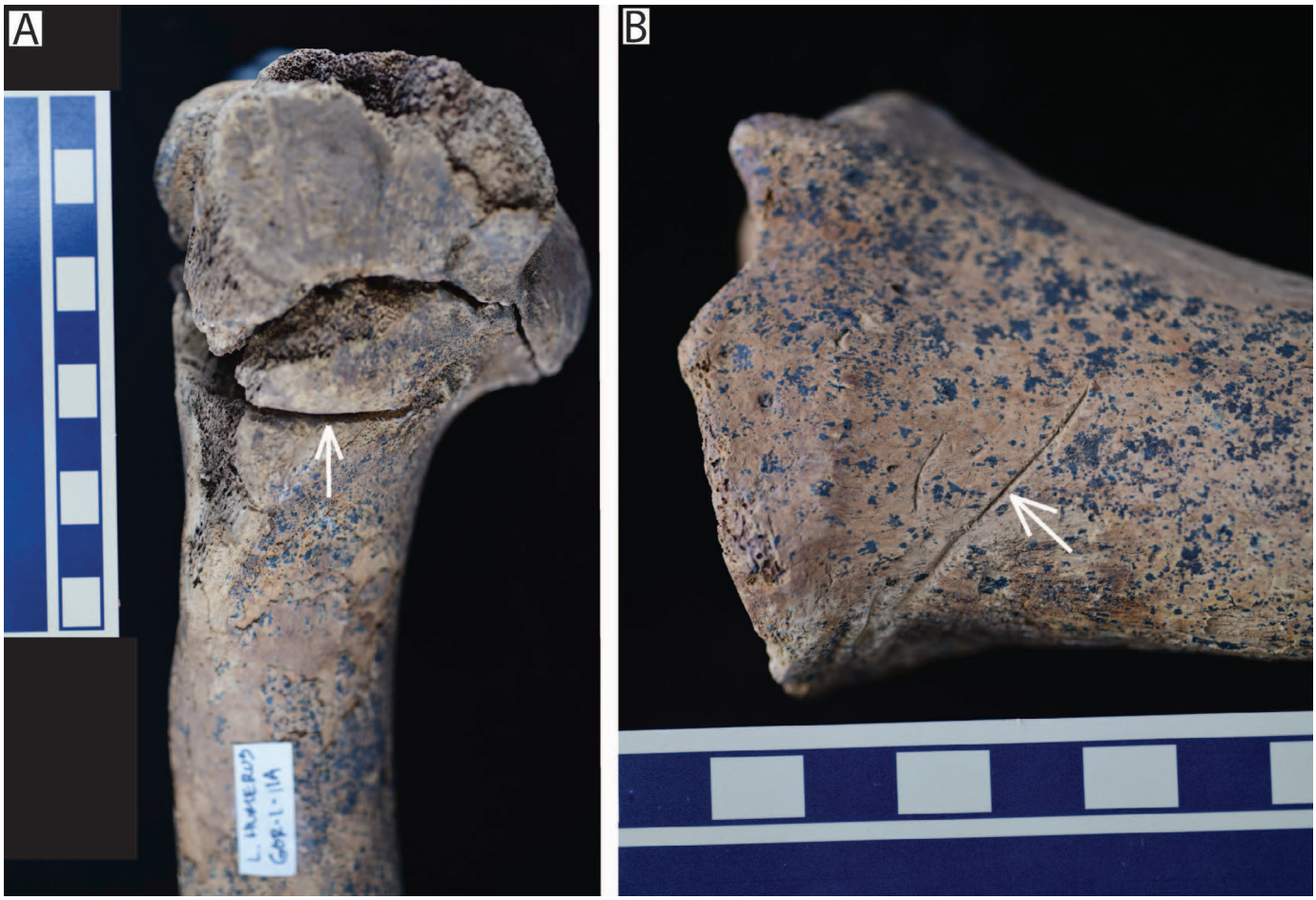

FIG. 2.—Specimens recovered. **A**) Proximal end of humerus GOR-1-11. Arrow points to a deep and narrow cut mark that we interpret to have been made with a steel tool. The epiphysis of this humerus is not fused to the shaft. **B**) Proximal end of fused radius/ulna GOR-1-13. Arrow points to a cut mark.

from the fossil site; it may have been much closer in the nineteenth century. Clear Creek joins the Carson River 1,500 m to the southeast. The confluence of the east and west forks of the Carson River is a few km upstream from the mouth of Clear Creek.

We interpret the bones and puparia at this site to be buried in floodplain sediments, probably deposited in a single major flood event. The headwaters of the Carson River are in the Sierra Nevada, south of the Lake Tahoe Basin. High-magnitude floods are well known in this drainage basin, typically caused by a heavy snowfall followed by warm rains. The earliest such flood in recorded history occurred in December–January, 1861–1862, with several others occurring in subsequent decades (Dangberg 1972). The flood of January 1997 is described below.

The Carson River drainage is one of the most intensively studied river basins in the U.S. due to contamination by mercury. The Comstock Lode, a rich source of gold and silver ore, occurs within the Carson River watershed. During the late nineteenth century this ore body was intensively mined, and Hg-amalgamation was used to extract the precious metals from the ore. Streamflow on the river has been monitored since 1890 (Fig. 3). In 1991 the Carson River was designated a Superfund site due to the presence of mercury-contaminated mine tailings (Carroll et al. 2004; Morway et al. 2017). Runoff volume typically rises sharply in April, as the snow melts in the Sierra Nevada. It peaks in May and June, and abruptly drops in the summer and fall. Sixty-one percent of the streamflow occurs in April, May, and June (Fig. 3).

A high-magnitude flood in January 1997 produced widespread overbank deposits that in some places exceeded two meters in depth (Miller et al. 1999; Carroll et al. 2004). Such a flood event is a plausible mechanism by which the GOR-1 bison was buried. The abundant blow fly puparia

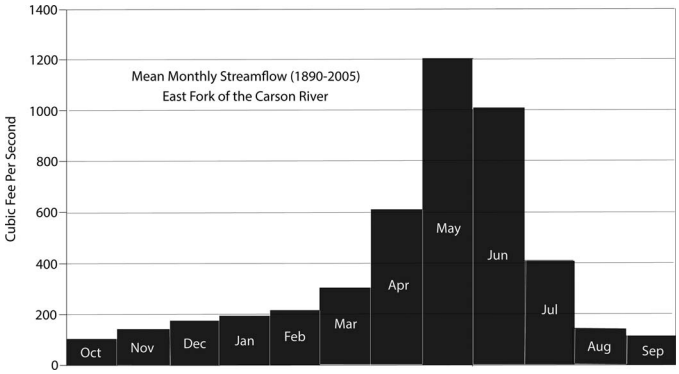

FIG. 3.—Mean monthly streamflow (1890–2005) on the East Fork of the Carson River near Gardnerville, NV, approximately 10 km upstream from the study area. The confluence of the West and East forks is between Gardnerville and the study area, so the streamflow in the region of the study area was substantially greater than shown. USGS data from Nevada Division of Environmental Protection report, Carson River: Total maximum daily loads for total suspended solids and turbidity, 2007.

FIG. 4.—Photographs of two puparia. The anterior end of the upper puparium has broken off due to the emergence of the adult fly.

associated with this bison skeleton provide a seasonally sensitive environmental signal that helps to constrain the season of this hypothesized bison-burying flood.

SPECIES IDENTIFICATION OF THE PUPARIA

The puparia are mottled dark brown and black. They are 7–8 mm long and about 3 mm wide. They are fusiform in shape, with the anterior end more tapered than the posterior end (Fig. 4). The characteristics of these puparia are diagnostic of blow flies. There is a key to adult blow flies of North America (Jones et al. 2019), but there are no comprehensive keys to North American blow fly puparia. To identify the species of these puparia we studied specimens of known species reared from puparia and compared morphological features between these specimens. The puparia from this site have a distinctive stigmatal region at their posterior end (Fig. 5). The spiracles are in a distinctive, deep depression, and there is a pair of prominent, horn-like tubercles dorsally above the stigmatal area. The dorsum and venter of the puparium have rows of spinules (short spines) which closely match those of modern *Phormia regina*. Based on these features, together with the arrangement, position, and shapes of the spinules, bands, and spiracle, we are able to identify the puparia as those of the black blow fly, *Phormia regina* (Meigen 1826) within family Calliphoridae—the blow fly family. Voucher specimens of the puparia are curated at the Las Vegas Natural History Museum, with the following accession number: GOR2021.001.1.

Phormia regina is locally abundant in northern states of the U.S. during the summer months and in southern states in the winter months, especially around human habitation (Haskell 1993; Byrd and Allen 2001). This species often comprises more than 50% of the blow fly fauna (Bird and Allen 2001). In central California, *P. regina* is the dominant species of calliphorids during the warmer months (Denno and Cothran 1975).

Puparia belonging to *P. regina* have previously been reported in association with human mummies in the crypt of a cathedral in Sardinia (Giordani et al. 2018), but they have not previously been definitively identified in association with vertebrate fossils. A closely related species, *Protophormia terraenovae*—the subarctic blow fly—has been reported from Pleistocene sites in Europe. Gautier and Schumann (1973) reported the presence of puparia of *P. terraenovae* in the skull and horn core cavities of a Pleistocene steppe bison, *Bison priscus*, in Belgium. Lister (2009) and Erzinçlioğlu (2009) reported puparia of *P. terraenovae* in the sinuses of one cranium and in two mandibles of juvenile woolly mammoths (*Mammuthus primigenius*) in the U.K. Stock (1956) reported the discovery of puparia of a blow fly within the marrow cavity of the broken forearm bone of a Pleistocene teratorn (a condor-like vulture) from the La Brea 'tar' pits. Without providing details, he mentioned that the fly responsible for the larval cases is related to the black blow fly. Johnson et al. (2005) reported the presence of dipteran puparia associated with late Holocene bison fossils in southeastern Nevada, but without any more specific taxonomy.

LIFE CYCLE CHARACTERISTICS OF *PHORMIA REGINA*

Phormia regina is an important species in the field of forensic entomology because the flies lay their eggs on dead bodies of vertebrates (Greenberg 1991; Byrd and Allen 2001; Lewis and Benbow 2011; Berg and Benbow 2013). If stages of this species' life cycle can be recognized on a human crime victim, for example, forensic investigators are able to estimate time since death. Primarily for this reason, the autecology and life cycle of *P. regina* have been well studied (Greenberg 1991; Haskell 1993; Byrd and Allen 2001; Nabity et al. 2006; Lewis and Benbow 2011; Berg and Benbow 2013; Strauss 2019).

Black blow flies typically mate on dung or carrion, after which the females seek a vertebrate carcass on which to lay their eggs. Under suitable environmental conditions, the flies locate a carcass within four to twelve hours after the animal's death (Mohr and Tomberlin 2015). At 40°C, hatching of the larvae peaks at 10 hours after the eggs are laid and is complete by 14 hours. At lower temperatures (14°C and above) all the larvae hatch within 24 hours (Byrd and Allen 2001). After hatching, the larvae (maggots) gain access to the flesh of the carcass through a wound or through one of the body's orifices. Larvae develop through three instars. The puparium, which is analogous to the chrysalis of a butterfly, forms by the sclerotization of the third larval instar, within which the pupa develops into an adult. The puparia may be preserved in the fossil record, as in this case. Adult flies eclose (emerge) from the puparia, and the life cycle repeats (Byrd and Allen 2001).

Controlled-temperature experiments with *P. regina* colonies have revealed that they can complete their life cycle within a temperature range of 14°C (57°F) to 35°C (95°F) (Byrd and Allen 2001; Nabity et al. 2006). At 35°C the interval from egg to adult may be as short as 8.8 days, with the mean being 11 days. With respect to low temperatures, no eggs hatch when the flies are raised at 10°C (Byrd and Allen 2001). At 12°C (54°F), eggs hatch and the larvae pupate, but adult flies do not emerge (Nabity et al. 2006). At 15°C the life cycle is completed, but it takes longer than at warmer temperatures (Byrd and Allen 2001).

Haskell (1993), who sampled wild populations of calliphorids in northwestern Indiana, reported that *P. regina* is common from May through late October, typically comprising greater than 50% of the calliphorids present. Haskell recorded total numbers of female calliphorids present at various temperatures, revealing a threshold low temperature of 24°C. At this temperature and above, calliphorids of various species were abundant, while below 24°C they were scarce.

DISCUSSION

Flooding was doubtless involved in the burial of the GOR-1 bison carcass, so a key question concerns the timing of the flooding, relative to the death of the animal. The fact that thousands of *P. regina* puparia were recovered from the rib cage area of the GOR-1 bison skeleton indicates that the carcass was exposed for a minimum of 8.8 days after death.

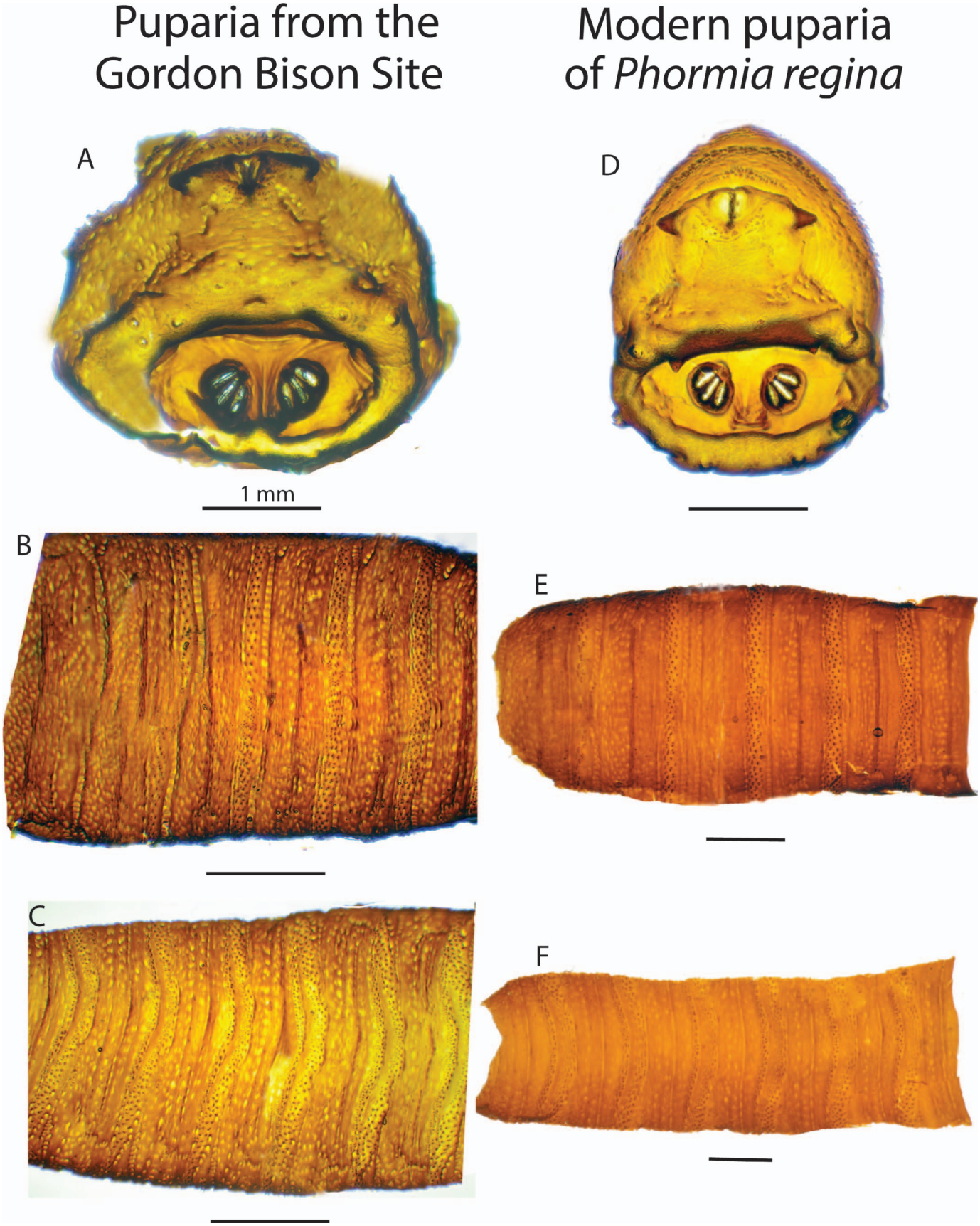

FIG. 5.—Comparison of slide-mounted fossil puparia (left) with modern *Phormia regina* puparia (right). **A**, **D**) Stigmatal region showing spiracles in a depression, with hornlike tubercles dorsally above. **B**, **E**) Dorsal views of puparia. **C**, **F**) Ventral views of puparia. Scale bars = 1 mm.

FIG. 6.—Artist's reconstruction of the skinning and butchering of the GOR-1 bison. Note position of left foreleg.

Considering the abundance of the puparia, it is likely that the carcass was exposed considerably longer. The closely related species *Protophormia terraenovae* does not lay its eggs on a wet carcass (Lister 2009), and we assume that this applies to *P. regina* as well. The puparia were found at the bottom of the excavation pit, 75 cm below ground level. Thus they predate the burial of the bison. We conclude, therefore, that this animal died and was colonized by black blow flies at least 8.8 days prior to being buried by floodplain sediments. The shallowest portion of the skeleton, the top of the skull, lay about 30 cm below ground level, and the deepest portion, the distal end of the right foreleg, extended vertically downward to about 65 cm below the top of the skull. Thus the skeleton was dorsoventrally compressed into a vertical interval of about 65 cm.

Articulated skeletons of vertebrate animals, such as the GOR-1 bison, are a rarity in the fossil record, due primarily to dismemberment by carnivores. The GOR-1 skeleton presumably avoided dismemberment by being buried by floodplain sediments soon after death. We entertained an early hypothesis that this animal drowned in a flood and was quickly buried. We ultimately rejected that hypothesis, however, in favor of a scenario in which the animal was killed by humans, placed on its stomach, skinned, and butchered prior to its burial. Several lines of evidence support this scenario: (1) the puparia at the bottom of the excavation pit indicate that the bison died and was exposed at this site for at least 8.8 days prior to being buried; (2) the posture of the bison—on its ventral side with its left foreleg projecting horizontally, parallel to the axis of the body (Fig. 6)—is an unlikely posture for a drowned animal; due to *rigor mortis*, a drowned bison would be more likely to have all of its legs projecting perpendicular to the axis of the body, and the animal would most likely be lying on its side; (3) some bison-hunting Native Americans are known to typically place a bison on its stomach prior to skinning and butchering, for the purpose of harvesting the highly desirable hump meat and to facilitate removal of the hide by cutting down the mid-dorsal line and peeling it back, also providing a clean surface on which to place the meat (Fig. 6) (Dibble and Lorrain 1968); (4) the absence of the terminal phalanx (the hoof phalanx) on the left foreleg strongly suggests it was removed by a human at the time the animal was being skinned; various groups of Native Americans are known to have used hooves in a wide range of ways, including for glue, rattles, spoons, cups, ladles, fire carriers, toys, and rituals (Barsness 1985; Maloney 2011); (5) a small number of thoracic and lumbar vertebrae suggests that the animal's dorsal region was not completely buried, leaving those bones exposed; (6) the absence of caudal (tail) vertebrae supports the interpretation that the animal was skinned prior to its burial by floodplain sediments; when skinning a bison, at least some Native American groups typically removed the tail with the skin (Barsness 1985). By the time the flood waters and overbank sediments arrived, the carcass was probably a skinless, butchered skeleton, which would explain why it did not float away.

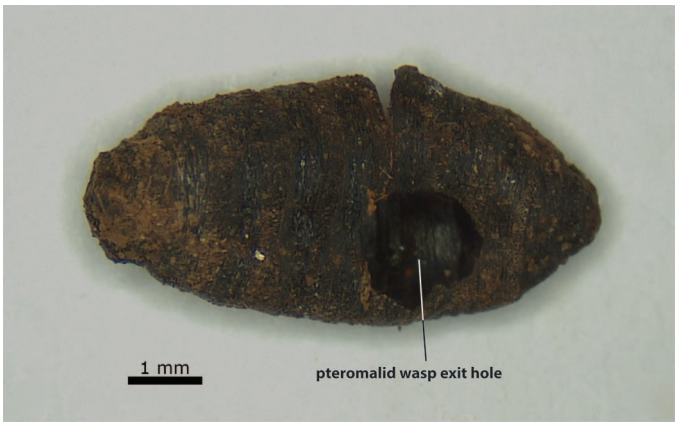

FIG. 7.—*Phormia regina* puparium with a small hole, presumed to be the exit hole of a parasitoid pteromalid wasp.

Phormia regina has been shown to be an especially generalist species of blow fly that is attracted to older carrion than are other species (Mohr and Tomberlin 2015). This may explain why this appears to be the only species represented among the puparia in this study. Perhaps other animals were processed prior to the skinning of the GOR-1 bison. By the time its flesh was exposed it may have been less attractive to calliphorid and sarcophagid species other than *P. regina*.

The seasonal streamflow pattern within the Carson River watershed (Fig. 3) indicates that the production of overbank deposits by flooding is most likely to occur in the spring. However, major floods are also known to occur in the winter (Dangberg 1972; Miller et al. 1999; Carroll et al. 2004). To better constrain the season in which the GOR-1 bison was buried by overbank deposits, we turn to the blow fly puparia.

Many of the puparia from this site had not produced an adult fly; they are without an opening on the anterior end (Fig. 4). We randomly selected 100 puparia and counted the number that are open and those from which adult flies had not emerged. Adults had emerged from 65 of the 100 puparia; 35 of the pupae had died within their puparia, which is a high mortality rate. A common cause of mortality of blow fly pupae, especially during the warm season, is parasitoid chalcidoid wasps belonging to the family Pteromalidae. These wasps puncture the shell of the puparia and lay one or more eggs inside (University of Florida web page, see references). After the eggs hatch, the wasp larvae consume the fly pupa and they continue to live within the fly puparium, where they pupate. One or more adult wasps ultimately emerge from the puparium, leaving a telltale emergence hole, approximately 1 mm in diameter. Of the 100 puparia examined microscopically in this study, only four were found to have such holes (Fig. 7). We conclude that pteromalid wasps were not the primary cause of high pupal mortality.

We suggest that temperature constraints, specifically low temperatures, were most probably the major cause of high pupal mortality. After death, in a process termed *algor mortis*, the body of a homeothermic, vertebrate animal undergoes progressive cooling toward the ambient temperature, following an initial stable temperature plateau. In the case of humans, a 'rule of thumb' is that the body cools at rate of about 1°C per hour, but the actual rate is quite variable depending on a wide range of factors (Rattenbury 2018). For an animal the size of a bison, there are no data regarding the postmortem body cooling rate (Brooks and Sutton 2018). We presume that the body of the GOR-1 bison would have cooled to ambient temperature within two to three days, by which time maggots would have been present. In a process called "maggot massing," an aggregation of maggots can cause a rise in temperature of the portion of a carcass where they are active. Such a temperature rise typically occurs four to six days after death (Johnson and Wallman 2014). In some cases, the temperatures of calliphorid maggot masses have been shown to be as high as 20°C above the ambient temperature (Charabidze et al. 2011). However, such maggot-generated heat does not protect the puparia from cold ambient temperatures, because the third larval instar typically moves away from the carcass into the adjacent soil to pupate (Australian Museum web page, see references). Moreover, *P. regina* maggots apparently do not form effective heat-generating masses, as do those of some other calliphorid species. The larvae of this species exhibit a wandering/meandering behavior that does not produce large, heat-generating concentrations (Strauss 2019). For these reasons, the *P. regina* puparia adjacent to the GOR-1 bison carcass would have been exposed to near-ambient temperatures.

The inference that low ambient temperatures were the cause of high pupal mortality at the Gordon site provides an opportunity to use the puparia as a constraint on the season of death of the bison. In Figure 8, the range of mean air temperatures throughout the year in the Reno/Carson City area is shown in blue, as recorded in the 1950s, prior to the warming trend of recent decades (Jaeger 1957). These air temperature data are superimposed on temperature intervals relevant to the life cycle of *P. regina*. The green and yellow bands together show the temperature range in which *P. regina* colonies are known to be viable, based on constant-temperature experiments (Byrd and Allen 2001; Nabity et al. 2006). The green band is the temperature interval in which *P. regina* is known to thrive. Haskell (1993) found calliphorids of various species, including *P. regina*, to be abundant in this temperature range. The yellow band is the temperature interval in which Haskell (1993) found calliphorids to be present but scarce. The red band is a temperature interval that is known to be too cold for *P. regina* to complete its life cycle.

The high pupal mortality in our study suggests that temperature conditions were not optimal for *P. regina* when the GOR-1 bison died and was colonized by *P. regina.* This eliminates summer as the likely season of death. The GOR-1 bison most likely died when temperatures were marginal, either in the spring, from late March through May, or in the fall, from late September through the beginning of November (Fig. 8). Streamflow patterns within the watershed (Fig. 3) eliminate the late fall as a plausible season for significant overbank flooding. Thus the spring is the only season in which the streamflow pattern and black blow fly temperature constraints are mutually compatible.

CONCLUSIONS: A TAPHONOMIC SCENARIO FOR THE GOR-1 BISON

Puparia of the black blow fly, *Phormia regina*, found in association with an articulated bison skeleton, provide valuable data that help to constrain the taphonomic history and season of death of the bison. It died in the spring, probably having been killed by humans. It was then placed on its stomach, butchered and skinned, and the carcass was colonized by *P. regina*. The carcass was exposed to the air for a minimum of 8.8 days, and probably considerably longer, allowing the flies to complete their life cycle. The near-completeness of the skeleton indicates that non-human mammalian carnivores did not scavenge the carcass, possibly due to the presence of humans. Cold night-time temperatures killed many of the fly pupae, causing a third of them to die in their puparia.

A major flood then occurred within the Carson River watershed, producing overbank deposits that that were approximately 65 cm deep at this site, partially burying the bison carcass. The dorsal portion of the skeleton remained exposed, allowing most of the thoracic and lumbar vertebrae to weather away. Subsequent flooding or other aggradational processes buried the skeleton to the depth at which it was discovered, with its shallowest portions being approximately 30 cm below ground level.

Blow fly puparia may occur unnoticed at other Pleistocene and Holocene terrestrial vertebrate sites. Where present, they can provide insightful taphonomic data.

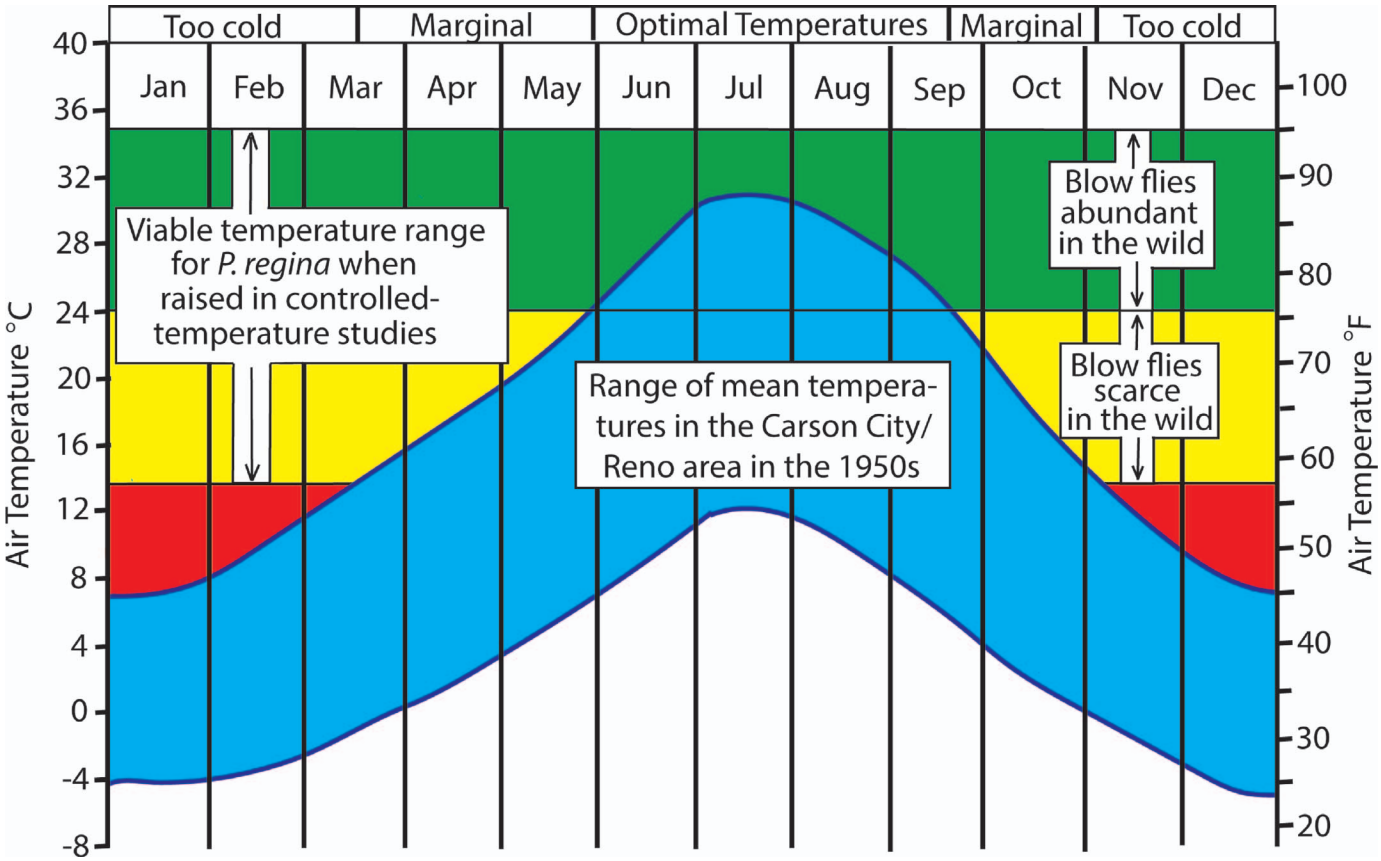

FIG. 8.—Mean temperature range for the Carson City region (blue) superimposed on known temperature constraints of *Phormia regina*. Red band is temperature range that is too cold. Yellow band is temperature range that is marginal. Green band is temperature range that is optimal.

ACKNOWLEDGMENTS

We thank patrons of the Las Vegas Natural History Museum and donors to the Paleontological Research Fund at UNLV for support of this research. Washoe Tribal Historic Preservation Officer Darrel Cruz provided very helpful guidance regarding Washoe cultural practices and some of the details illustrated in Figure 6. Historian Matthew S. Makley kindly shared his knowledge of Washoe history and the possible timing of the introduction of steel tools into Carson Valley. Thanks also to Aliera Gardner for photographing the puparia, and to Emily and Evan Jones for helping to pick puparia from the sediment. Two anonymous reviewers, an anonymous associate editor, and Editor Patrick John Orr provided very helpful comments that significantly improved the paper.

REFERENCES

AUSTRALIAN MUSEUM, 2022, New South Wales web page: https://australian.museum/learn/science/decomposition-fly-life-cycles/. Checked July 2022

BARSNESS, L., 1985, Heads, Hikes, Horns: the Compleat Buffalo Book: Texas Christian University, Fort Worth, 226 p.

BEHRENSMEYER, A.K, 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 4, p. 150–162.

BERG, M.C. AND BENBOW, M.E., 2013, Environmental factors associated with *Phormia regina* (Diptera: Calliphoridae) oviposition: Journal of Medical Entomology, v. 50, p. 451–457.

BROOKS, J.W. AND SUTTON, L., 2018, Postmortem changes and estimating the postmortem interval, *in* J.W. Brooks (ed.), Veterinary Forensic Pathology: Springer, Cham, Switzerland, p. 43–63.

BYRD, J.H. AND ALLEN, J.C., 2001, The development of the black blow fly, *Phormia regina* (Meigen): Forensic Science International, v. 120, p. 79–88.

CARROLL, R.W.H., WARWICK, J.J., JAMES, A.I., AND MILLER, J.R., 2004, Modeling erosion and overbank deposition during extreme flood conditions on the Carson River, Nevada: Journal of Hydrology, v. 297, p. 1–21, doi: 10.1016.jhydrol.2004.04.012.

CHARABIDZE, D., BOUREL, B., AND GOSSET, D., 2011, Larval-mass effect: characterization of heat emission by necrophagous blowflies (Diptera: Calliphoridae) larval aggregates: Forensic Science International, v. 211, p. 61–66.

DANGBERG, G., 1972, Carson Valley: Historical Sketches of Nevada's First Settlement: The Carson Valley Historical Society, Carson City, NV,147 p.

D'AZEVEDO, W.L., 1986, Washoe, *in* W.L. D'Azevedo (ed.), Handbook of North American Indians, vol. 11, Great Basin: Smithsonian Institution, Washington, DC, p. 466–498.

DENNO, R.F. AND COTHRAN, W.R., 1975, Competitive interactions and ecological strategies of sarcophagid and calliphorid flies inhabiting rabbit carrion: Annals of the Entomological Society of America, v. 69, p. 109–113.

DIBBLE, D.S. AND LORRAIN, D., 1968, Bonfire Shelter: a stratified bison kill site, Val Verde County, Texas: Texas Memorial Museum, Austin, Miscellaneous Papers No. 1, 138 p.

ERZINÇLIOĞLU, Y.Z., 2009, Fly puparia associated with the Condover mammoths, Appendix, *in* A.M. Lister (2009): Geological Journal, v. 44, p. 474–479.

GAUTIER, A. AND SCHUMANN, H., 1973, Puparia of the subarctic or black blowfly *Protophormia terraenovae* (Robineau-Desvoidy, 1830) in a skull of a late Eemian (?) bison at Zemst, Brabant (Belgium): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 14, p. 119–125.

GILBERT, B.M. AND BASS, W.M., 1967, Seasonal dating of burials from the presence of fly pupae: American Antiquity, v. 32, p. 534–535.

GIORDANI, G., TUCCIA, F., FLORIS, I., AND VANIN, S., 2018, First record of *Phormia regina* (Meigen, 1826) (Diptera: Calliphoridae) from mummies at the Sant'Antonio Abate Cathedral of Castelsardo, Sardinia, Italy: PeerJ, v. 6, e4176, doi: 10.7717/peerj.4176.

GREENBERG, B., 1991, Flies as forensic indicators: Journal of Medical Entomology, v. 28, p. 565–577.

HASKELL, N.H., 1993, Factors affecting diurnal flight and oviposition periods of blow flies (Diptera: Calliphoridae) in Indiana: Unpublished Ph.D. dissertation, Purdue University, West Lafayette, 157 p.

HUGHES, R.E. AND BENNYHOFF, J.A., 1986, Early Trade, *in* W.L. D'Azevedo (ed.), Handbook of North American Indians, Volume 11, Great Basin: Smithsonian Institution, Washington, DC, p. 238–255.

JAEGER, E.C., 1957, The North American Deserts: Stanford University Press, Stanford, 308 p.

Johnson, A.P. and Wallman, J.F., 2014, Effect of massing on larval growth rate: Forensic Science International, v. 241, p. 141–149.

Johnson, W.G., Sharpe, S.E., Bullard, T.F., and Lupo, K., 2005, Characterizing a first occurrence of bison deposits in southeastern Nevada: Western North American Naturalist, v. 65, p. 24–35.

Jones, N., Whitworth, T.L., and Marshall, S.A., 2019, Blow flies of North America: keys to the subfamilies and genera of Calliphoridae and to the species of the subfamilies Calliphorinae, Luciliinae, and Chrysomyinae; Canadian Journal of Arthropod Identification, Issue 39, p. 1–191.

Lewis, A.J. and Benbow, M.E., 2011, When entomological evidence crawls away: *Phormia regina* en masse larval dispersal: Journal of Medical Entomology, v. 48, p. 1112–1119.

Lister, A.M., 2009, Late-glacial mammoth skeletons (*Mammuthus primigenius*) from Condover (Shropshire, UK): anatomy, pathology, taphonomy and chronological significance: Geological Journal, v. 44, p. 447–479.

Lott, D.F., 2002, American Bison: A Natural History: University of California Press, Berkeley, CA, 229 p.

Mähler, B., Wappler, T., Sanmugaraja, M., Menger, F., and Von Koenigswald, W., 2016, Upper Pleistocene blow flies (Diptera: Calliphoridae) trapped in fossilized crania of large mammals discovered from gravel pits in the Rhine rift valley from Hesse (Germany): Palaeontologia Electronica, 19.2.13A, p. 1–12.

Makley, M.S., 2018, The Small Shall Be Strong: A History of Lake Tahoe's Washoe Indians: University of Massachusetts Press, Amherst, 234 p.

Maloney, C.J., 2011, Death Wind for My People: The Societal Response to the Slaughter of the North American Bison: Unpublished M.A. thesis, The George Washington University, Washington, DC, 119 p.

Miller, J., Barr, R., Grow, D., Lechler, P., Richardson, D., Waltman, K., and Warwick, J., 1999, Effects of the 1997 flood on transport and storage of sediment and mercury within the Carson River Valley, west-central Nevada: The Journal of Geology, v. 107, p. 313–327.

Mohr, R.M. and Tomberlin, J.K., 2015, Development and validation of a new technique for estimating a minimum postmortem interval using adult blow fly (Diptera: Calliphoridae) carcass attendance: International Journal of Legal Medicine, v. 129, p. 851–859.

Morway, E.D., Thodal, C.E., and Marvin-Dipasquale, M., 2017, Long-term trends of surface-water mercury and methylmercury concentrations downstream of historic mining within the Carson River watershed: Environmental Pollution, v. 229, p. 1006–1018.

Nabity, P.D., Higley, L.G., and Heng-Moss, T.M., 2006, Effects of temperature on development of *Phormia regina* (Diptera: Calliphoridae) and use of developmental data in determining time intervals in forensic entomology: Journal of Medical Entomology, v. 43, p. 1276–1286.

Panagiotakopulo, E., 2004, Dipterous remains and archaeological interpretations: Journal of Archaeological Science, v. 31, p. 1675–1684.

Rattenbury, A.E., 2018, Forensic Ecogenomics, *in* T.K. Ralebitso-Senior (ed.), Forensic Taphonomy: Academic Press, London, p. 37–60.

Stewart, J.H., 1999, Geologic map of the Carson City 30 × 60 minute quadrangle, Nevada: Nevada Bureau of Mines and Geology, Reno, Map 118.

Stock, C., 1956, Rancho La Brea: A record of Pleistocene life in California (6/e): Los Angeles County Museum of Natural History, Science Series No. 20, Paleontology No. 11, 81 p.

Strauss, B.H., 2019, Density and mass effect on the development of *Phormia regina*: Unpublished M.S. thesis, University of Nebraska, Lincoln, 35 p.

Teskey, H.J. and Turnbull, C., 1979, Diptera puparia from pre-historic graves: Canadian Entomologist, v. 111, p. 527–528.

University Of Florida, 2021, Web page: https://entnemdept.ufl.edu/creatures/BENEFICIAL/ WASPS/Muscidifurax.raptor.htm. Checked August 2021.

Received 16 August 2021; accepted 7 November 2022.