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LATE PLEISTOCENE MOLLUSKS FROM THE SOUTHERN BLACK HILLS, SOUTH DAKOTA

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ABSTRACT.—Pleistocene-age mollusks recovered from the Nelson-Wittenberg Site and Mammoth Site provide information on paleoenvironments of the southern Black Hills, South Dakota. New mollusk records for the Mammoth Site include *Vertigo modesta, Catinella* sp., and *Gyraulus parvus.* The presence of *V. modesta, Columella columella alticola,* and *Pupilla muscorum* at the Nelson-Wittenberg Site suggests cooler than modern conditions in the Black Hills during the Pleistocene. Although the majority of identified taxa are consistent with previous interpretations of an arid, shrub-steppe environment for the Black Hills during the Wisconsin Glaciation, *V. modesta* and *C. c. alticola* suggest the presence of at least some isolated, local mesic areas.

Key words: Black Hills, mollusks, Late Pleistocene, paleoenvironments, Mammoth Site, Nelson-Wittenberg Site.

The Black Hills of South Dakota, aptly described as "a forested island in a grassland sea" (Froiland 1990:1), occupy a unique physiographic position within the northern Great Plains (Fig. 1). The Black Hills are situated approximately 610–2100 m higher than the surrounding northern Great Plains, with the local vegetation containing representatives from all adjoining plant communities (Weedon and Wolken 1990). Reconstructions of paleoenvironments for the northern Great Plains rarely address the Black Hills. Due to the varied topographic and biotic nature of the Black Hills, paleoenvironmental reconstructions based on data recovered from the surrounding northern Great Plains may not provide an accurate picture of conditions within the Black Hills during the Pleistocene (1.77 Ma [*meg annum*; million years ago] to approximately 10,000 yr B.P.; years before present). Although the Black Hills have no direct evidence of glaciation (Lemke et al. 1965), the close proximity of the Black Hills to the Laurentide ice cap (~240 km to the east) during the Late Pleistocene surely influenced the composition of local biotic communities.

Data on Pleistocene environments in the Black Hills are not abundant. Due to a lack of natural lakes and ponds, the potential for palynological study for the reconstruction of past environments is limited. Fredlund (1996) provides geomorphic evidence of latest Pleistocene and Holocene deposits. At present, only 2 Pleistocene paleontological localities, Salamander Cave (Mead et al. 1996) and the Mammoth Site (Agenbroad et al. 1990), are published from the Black Hills proper. Most paleoenvironmental data for the northern Great Plains during the Late Pleistocene were derived from research at localities in adjacent geographic areas outside the Black Hills. Using data from areas peripheral to the Black Hills, some researchers have inferred that portions of the Great Plains, including the Black Hills, were covered with spruce (*Picea*) forest during the Late Pleistocene (see Mead et al. 1994 for discussion). Other interpretations, based on faunal evidence, suggest steppe environments for portions of the northern Great Plains during the Pleistocene (Taylor 1960, 1965, Voorhies and Corner 1985).

Molluscan and vertebrate data from the Late Pleistocene Lange-Ferguson Site (10,670 yr B.P.), east of the Black Hills (Fig. 1), suggest more mesic conditions than modern, with brush and/or woodlands occurring at the site (Leonard 1982, Martin 1987). Whether Lange-Ferguson fossils represent an overall "mesic" regional trend is unknown; drier, grassland environments may have occurred in areas away from Lange-Ferguson (Martin 1987).

To the west of the Black Hills, mammalian faunas are the primary source of paleoenvironmental reconstructions (Mead et al. 1994).

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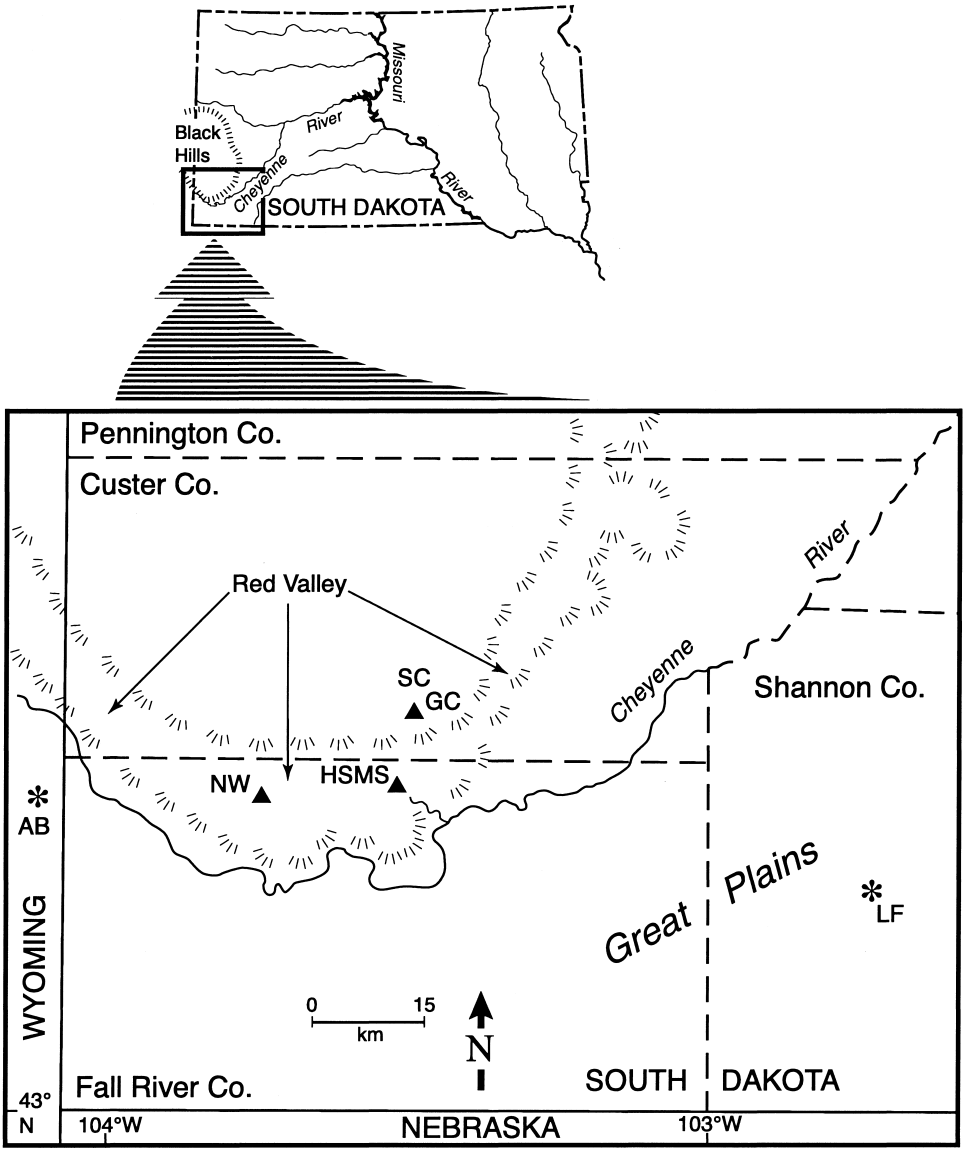

Fig. 1. Map depicting locations (triangles) of Graveyard Cave (GC), Mammoth Site of Hot Springs (HSMS), Nelson-Wittenberg Locality (NW), Salamander Cave (SC), and PaleoIndian sites (asterisks) containing mollusks, including Agate-Basin (AB) and Lange-Ferguson (LF).

Alpine tundralike conditions and more equable climates may have dominated much of Wyoming at approximately 22,000–18,000 yr B.P. (Walker 1987). At that time boreal forest environments were more widespread than today (Walker 1987). Immediately west of the Black Hills, faunal remains from the Late Pleistocene–Early Holocene Agate Basin Site (Fig. 1) indicate a steppe savanna for the terminal Pleistocene (Walker 1982). Mollusks from Agate Basin are indicative of more mesic conditions than today, at least in the immediate area of the locality (Evanoff 1982).

Reported Pleistocene localities from the Black Hills include Salamander Cave (Fig. 1), which has a minimum age of 252,000 yr B.P. (Mead et al. 1996), and the Mammoth Site of Hot Springs (Agenbroad et al. 1990, Agenbroad and Mead 1994). Using faunal and limited pollen data from the Mammoth Site, several authors (Czaplewski and Mead 1994, Mead et al. 1994, and others) suggested the presence of a cold steppe-grassland in the Black Hills at 26,000 yr B.P. More mesic conditions and geomorphic stability, relative to modern, existed in parts of the southern Black Hills during the transition from Late Pleistocene to Early Holocene (14,000 yr B.P. to 9000 yr B.P.; Fredlund 1996). An interpretation of more mesic than modern conditions from the Late Pleistocene through the Early Holocene is consistent with paleoenvironmental data from a variety of localities peripheral to the Black Hills (see summary in Fredlund 1996). Fossil mollusks from a third Pleistocene locality within the Black Hills, the Nelson-Wittenberg Site, provide evidence for the reconstruction of past environments in the southern Black Hills. Here we present identifications of mollusks from the Nelson-Wittenberg Site as well as additional specimens from the Mammoth Site. We use these mollusks to further assess environmental conditions in the southern Black Hills during the Late Pleistocene.

STUDY AREA

Locality Descriptions

Currently, Pleistocene-age fossil sites in the Black Hills are known only from the southern Black Hills.

MAMMOTH SITE.—The Mammoth Site of Hot Springs is a 26,000-year-old deposit located in the southern Black Hills (Fig. 1). Detailed descriptions of the geology, chronology, and vertebrate paleontology of the Mammoth Site are presented in Agenbroad et al. (1990) and Agenbroad and Mead (1994). The Mammoth Site represents an artesian spring-fed pond environment contained within a sinkhole (Agenbroad 1994). The sinkhole was likely in-filled with sediment over a time period of 175 to 700 years (Laury 1994). Timing of cessation of spring discharge into the sinkhole is not known (Laury 1994).

Various aspects of the molluscan and vertebrate fauna from the Mammoth Site are discussed in Agenbroad and Mead (1994). Mead et al. (1994) describe mollusks recovered from the first 20 years of excavation at the Mammoth Site. From 1990 to 1999, sediments were washed through 1-mm-mesh screens and were stored at the site for future analyses. Sorting of these sediments began in July 1998 and produced additional fossil mollusk taxa which are reported here (see Table 1). Recovered mollusks come from bulk samples and cannot be strongly correlated to a particular time or stratigraphic unit within the depositional framework established by Laury (1994).

NELSON-WITTENBERG SITE.—The Nelson-Wittenberg Site is a small alluvial deposit in the southern Black Hills, located west of the Mammoth Site (Fig. 1). The structure of this small deposit shows uniform, yet limited, stratigraphy (Mead personal observation). The locality appears to be a remnant drainage channel that might have originated from a spring deposit, but apparently not one containing any pooled water. No spring occurs in the area of the locality today. A sample of fine-grained sediments from around a *Mammuthus* tusk and *Bison* tooth produced a thermoluminescence date of 37,900 ± 2900 yr B.P. (W2611). We feel this is an approximate age but verifies assignment of the deposit to the Late Pleistocene. If the thermoluminescence date is correct, the locality lies well within the most recent glacial phase (Wisconsinan Glaciation) and dates older than the Mammoth Site. Microfaunal elements discussed herein come from salvaged bulk sediment samples (washed through 1-mm sieve). Small mammals from the locality include *Lemmiscus curtatus* (sagebrush vole; see Bell and Mead 1998 for identification of characters) and *Microtus* sp. (vole).

Modern Environments

As a result of an updoming event that began during the Laramide Orogeny, the geologic structure of the Black Hills region is characterized by a "layer cake" or anticlinal pattern in which the oldest rock formations are encircled by younger rock formations as one progresses outward from the core (Froiland 1990). The 4 major physiographic regions of the Black Hills include the Crystalline Core, Limestone Plateau, Red Valley, and Hogback Ridge. The Mammoth and Nelson-Wittenberg sites are situated on erosional remnants of the Permo-Triassic sediments that make up the Red Valley. In the southern Black Hills this region is currently dominated by grassland, interspersed with an open ponderosa pine (*Pinus ponderosa*) forest. Fredlund (1996) considered the Red Valley an extension of the grasslands that surround the Black Hills. Local artesian springs (some thermal) provide

TABLE 1. Fossil molluscan faunas from the southern Black Hills. For fossil and subfossil taxa, X = present in this study (see text), 1 = Mead et al. (1994). Extant refers to the presence of fossil species as part of the modern snail fauna of the Black Hills. For extant, TR = this report, 2 = Frest and Johannes (1993). For a complete list of extant Black Hills mollusk taxa, see Frest and Johannes (1993). NW = Nelson-Wittenberg, MS = Mammoth Site, GC = Graveyard Cave. Provincial information for terrestrial gastropods is as follows: C = common, widespread, RM = Rocky Mountain, I = Interior, N = Northern, based on discussions in Bequaert and Miller (1973), Frest and Dickson (1986), Frest and Johannes (1993), and Woodman et al. (1996).

Taxa	NW	MS	GC	Extant	Province
SPHAERIIDAE					
Pisidium castertanum	—	X	—	—	—
Pisidium compressum	—	X, 1	—	—	—
Pisidium obtusale	—	1	—	—	—
Pisidium walkeri	—	X, 1	—	—	—
LYMNAEIDAE					
Fossaria parva	—	X	—	—	—
Fossaria cf. *dallia*	—	1	—	—	—
Fossaria sp.	—	1	—	—	—
PHYSIDAE					
Physella sp.	—	X, 1	—	TR	—
PLANORBIDAE					
Gyraulus parvus	—	1	—	TR	—
Gyraulus sp.	—	X	—	TR	—
PUPILLIDAE					
Columella simplex	—	1	—	2	I, N
Columella c. alticola	X	—	—	—	N, RM
Gastrocopta armifera	—	—	X	TR, 2	I
Gastrocopta procera	—	—	X	TR, 2	I
Pupilla muscorum	X	X, 1	—	—	N
Pupilla hebes-like	X	—	—	—	RM
Pupoides albilabris	X	—	X	2	C
Vertigo modesta	X	X	—	2	N
Vertigo gouldi hannai	X	—	—	—	I
VALLONIIDAE					
Vallonia gracilicosta	X	X, 1	X	2	RM
Vallonia cyclophorella	X	—	X	TR, 2	RM
SUCCINEIDAE					
Catinella sp.	X	X	X	TR	—
DISCIDAE					
Discus whitneyi	—	—	X	2	C
Discus sp.	X	—	X	—	—
ZONITIDAE					
Hawaiia minuscula	X	—	X	TR, 2	C
Zonitoides arboreus	—	—	X	2	C
LIMACIDAE					
Deroceras laeve	X	1	—	TR, 2	C

the potential for atypical microhabitats in the southern Black Hills. Riparian areas occur as a result of drainage from spring discharge and runoff, although perennial streams are not abundant.

The modern vegetative character throughout the Black Hills is complex. Elements of eastern deciduous forests, Rocky Mountain coniferous forest, northern coniferous forest, and northern Great Plains grassland all occur in the Black Hills (Froiland 1990, Weedon and Wolken 1990). Many plant species have only relictual populations in the Black Hills as a result of climatic changes through the Pleistocene/Holocene transition (Weedon and Wolken 1990).

Today, mean annual temperature for the Black Hills is 45.6°F (7.5°C); average precipitation is 73.6 cm (29 inches) at high elevations, with lower amounts occurring in the adjacent plains (Froiland 1990). Climates in the Black Hills are highly variable and differ from north to south. The southern Black Hills are characterized by less annual precipitation, warmer summer temperatures, and warmer winter temperatures than the northern hills (Froiland 1990, Weedon and Wolken 1990).

Until recently the modern molluscan fauna of the Black Hills region was not well known. Prior to 1993, four published surveys, primarily reporting specimens from the northern Black Hills, provided the only information on extant molluscan species of the Black Hills area (Over 1915, Henderson 1927, Roscoe 1954, Hubricht 1985). The most comprehensive report on extant Black Hills land snails is an unpublished United States Forest Service and United States Department of the Interior report (Frest and Johannes 1993). To our knowledge, no information concerning locally extant aquatic taxa is published.

When considering Black Hills molluscan fauna as a whole for comparisons of fossil faunas with locally extant taxa, we refer to the complete list of known Black Hills taxa presented in Frest and Johannes (1993). To supplement the data of Frest and Johannes (1993), in Table 1 we include records of taxa collected by us from disturbed and undisturbed habitats of the southern Black Hills. Mollusks from Graveyard Cave, a Late Holocene locality in the southern Black Hills (Fig. 1), are also presented in Table 1. Graveyard Cave mollusks represent a modern portion of the Black Hills malacofauna from outside the Red Valley, in open ponderosa pine forests of the adjacent Limestone Plateau (see Fig. 1).

Extant Black Hills mollusks have mixed affinities, with the majority of species associated with molluscan provinces to the north (Northern Province) and west (Rocky Mountain Province; Frest and Johannes 1993). The Red Valley malacofauna is less diverse than in other portions of the Black Hills, possibly due to the composition of the substrate (Frest and Johannes 1993). This model of a depauperate Red Valley may change with further sampling of microhabitats in the southern Black Hills.

METHODS

Methods of fossil snail recovery are discussed, in part, under site descriptions. The use of 1-mm sieves for mollusk retrieval at the Mammoth Site and Nelson-Wittenberg Site is possibly unfortunate, as some smaller taxa (i.e., *Vertigo* spp.) might not be recovered at that mesh size. A 0.7-mm (700-μm) sieve is typically more desirable for mollusk recovery and is now employed in all of our studies.

Unless otherwise indicated, species names follow Turgeon et al. (1998). Mollusk identifications (in part), descriptions, and anatomical terminology are based on Pilsbry (1946, 1948), Herrington (1962), Clarke (1981), and Burch (1962, 1989). Comparisons of modern and fossil specimens from Northern Arizona University, Quaternary Sciences Program, were also used for identifications. Institutional abbreviations are as follows: Northern Arizona University, Quaternary Sciences Program (NAUQSP); Mammoth Site of Hot Springs Laboratory (MSL); and Wind Cave National Park (WICA). Nelson-Wittenberg mollusks and extant mollusks reported here are curated at NAUQSP. Mammoth Site mollusks are curated at MSL. Graveyard Cave mollusks are under the auspices of WICA but are curated at the National Park Service Repository, Northern Arizona University, QSP.

RESULTS

Table 1 provides a list of molluscan remains recovered from the Mammoth Site and the Nelson-Wittenberg Site. At least 13 fossil molluscan species are now known from the Mammoth Site (Table 1). *Vertigo modesta, Catinella* sp., and *Fossaria parva* are newly reported taxa from this locality. Twelve species of mollusks were recovered from the Nelson-Wittenberg Site (Table 1). For the most part, fossil mollusks from the Mammoth Site and Nelson-Wittenberg Site are extant in the southern Black Hills today. Identification of fossil taxa not found in the region today requires discussion of identification methods; these are presented below.

Pisidium walkeri
Sterki, 1895

Specimens of this small clam (MSL 1469, 1471–1473) include both left valves (with well-preserved C2 and C4) and right valves (with C3). The C2 is short, highly curved, and characteristically bent in the middle, with a rounded tip at the posterior end and tapering to a point at the anterior end.

Columella columella alticola
(Ingersol, 1875)

Columella columella alticola is the only North American form of the Holarctic species *C. columella.* Specimens (NAUQSP 11585) that can be confidently referred to this species conform to the characters outlined in Pilsbry (1948). In particular, the spire is rounded, weak striae are present, and the last whorl is more expanded than the preceding whorl (see Pilsbry 1948: figs 535–536). The cylindrical form of identified specimens (Fig. 2) is consistent with Pilsbry's (1948) description of *C. c. alticola* rather than the more tapering form of *Columella edentula* (Pilsbry 1948). *Columella columella alticola* is not reported in the aforementioned surveys of the modern Black Hills malacofauna. Several other specimens are probably *C. c. alticola*, but the state of preservation prevents an unequivocal identification.

Vertigo modesta
(Say, 1824)

The majority of specimens (MSL 1370; NAUQSP 11568–11574) conform to characters of the species outlined in Pilsbry (1948). The shell is irregularly striate or smooth. A parietal fold is present but minute. The columellar fold is barely present. A lower palatal fold is present and small, with a smaller labrum fold as either an upper palatal or interpalatal fold. Two specimens from the Nelson-Wittenberg Site have a small, angular lamella present in the aperture. These specimens (NAUQSP 11575–11576) conform to Pilsbry's (1948) description of *V. modesta parietalis* and so are referred to that taxon.

Vertigo gouldi hannai
Pilsbry, 1919, Pilsbry, 1948

Four shells (NAUQSP 11565–11567) contain an upper sinulus on the aperture. Striations are distinct but finely present. The angular fold is distinct and small. The parietal fold is strong and distinct from the angular. The columellar fold is large and distinct and separated from the smaller, subcolumellar fold. The upper and lower palatal folds are strong with a callus barely present to wanting. The longer, lower palatal fold is slightly inset deeper than the position of the upper. Shells are 1.8–1.9 mm in length and 1.1 mm in diameter within 4.25–4.50 whorls.

Our specimens fit into the *V. gouldi*-group as defined by Pilsbry (1948:971), who clearly states that select members may or may not contain an angular fold. Our specimens contain a subcolumellar fold (= basal fold of Pilsbry [1948:971]) that, along with the other characters listed above, would identify these specimens as belonging to *Vertigo gouldi hannai*. Some authors vary as to whether this taxon is a form of *V. gouldi* or a distinct species. Even Pilsbry varies as to its taxonomic placement (1948:971 vs. 976). Both Pilsbry and Hubricht (1985:11) placed this morph as a taxon restricted to Pleistocene-age deposits, with which we concur. We also agree with Pilsbry (1948:976) that "*V. g. hannai* is very closely related to *V. gouldi*, but differs by having slighter striations [and] a well-developed angular lamella. . . ." We see little reason based

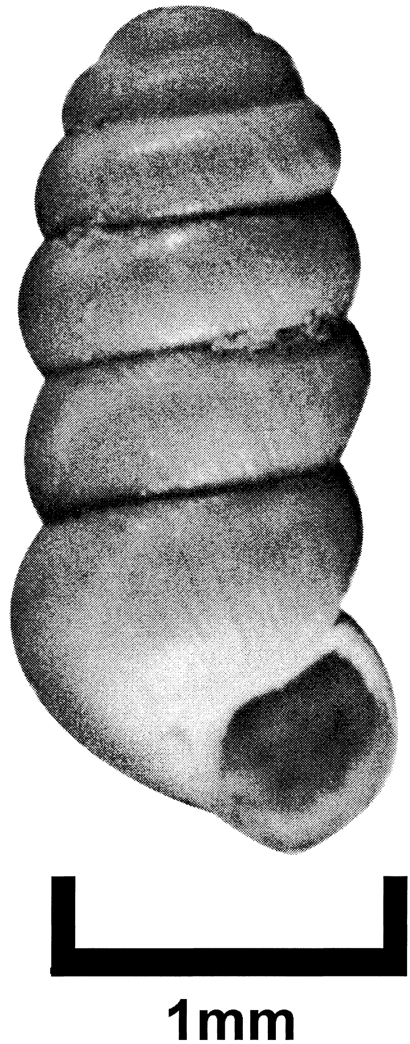

Fig. 2. *Columella columella alticola* (NAUQSP 11585) from the Nelson-Wittenberg Site.

on published accounts to relegate a slightly distinct and incompletely understood morph to species level due solely to chronological assignment. For this reason we have cautiously identified our specimens as *V. gouldi hannai* morph, with the hope that more specimens can be found in the future to better understand this apparently extirpated form.

Pupilla muscorum
(Linnaeus, 1758)

Identification of *Pupilla muscorum* follows Pilsbry (1948). The aperture of some referred specimens (MSL 1350–1360, NAUQSP 11597–11604) contains a thickened calcareous deposit, which separates them from *Pupilla hebes. Pupilla muscorum* is not known to be extant in the Black Hills.

A large number of specimens of *Pupilla* from Nelson-Wittenberg are "*Pupilla hebes*-like" (NAUQSP 11590–11596). The primary character used to separate *P. muscorum* and *P. hebes* is the lack of a thickened calcareous deposit in the aperture of the latter. Separation of *P. hebes* from *P. muscorum* in the fossil record is problematic, and we are not overly confident in our ability to distinguish fossil or modern shell specimens of these species. Although size variation, paralleling climate change, in fossil *Pupilla muscorum* is recognized (Rousseau 1989), there are currently no published diagnoses on natural variation in anatomical shell characters of fossil or modern *P. muscorum* and *P. hebes*. We identify a large number of *Pupilla* specimens as "*Pupilla hebes*-like" based on the lack of a thickened calcareous deposit in the aperture (Table 1).

DISCUSSION

Knowledge of the biology/ecology of extant animals allows us to address the meaning of their remains in Pleistocene fossil deposits. That is not to say that all fossil species have a modern analog or that extant animals could not have existed under slightly differing ecological conditions in the past. Rather, studies of the habitat preferences, biogeography, and ecology of extant mollusks, as well as vertebrates, provide us a starting point in addressing paleoenvironmental questions.

Most data on habitats associated with particular molluscan taxa come from regional and local surveys of modern malacofaunas. For habitat information concerning extant mollusks of the Black Hills, we refer to Frest and Johannes (1993). These data provide a baseline for comparison of habitat preferences associated with particular modern or fossil taxa in the Black Hills (i.e., found only in moist areas).

The geographic distributions of extant North American mollusks are fairly well known, although the factors that control such distributions are not completely understood. Specifically, the ecological factors that control modern land snail distributions (e.g., moisture, vegetation, temperature, etc.) are numerous and the relationships between those factors in limiting geographic distributions are not well known (Goodfriend 1992). Nonetheless, preliminary statements on the paleoenvironmental meaning of fossil mollusks can be extrapolated using available data on extant mollusk distributions and their associated habitat preferences.

The Mammoth Site, dating to 26,000 yr B.P., was previously sampled for mollusks, and a preliminary account of recovered species was presented in Mead et al. (1994). Sediments and mollusks from the site indicate the presence of abundant, open water. The aquatic genus *Physella* is by far the most abundant component of the Mammoth Site molluscan fauna (Table 2). Previous interpretations by Agenbroad and Mead (1994) state that the ponding water may have been warm and that the local environment was treeless. Having a molluscan fauna highly depauperate in diversity but dominated by physid snails was considered consistent with a warm-water regime. The additional taxa reported here do not clarify this interpretation.

The Nelson-Wittenberg Site, possibly dating to about 37,900 yr B.P., most likely represents drainage from a nearby spring. There is no indication of a warm-water spring at Nelson-Wittenberg. Unlike the Mammoth Site, there is no indication either in sediments or molluscan species that the spring supported a body of open, ponded water at, or adjacent to, this locality. All molluscan taxa are terrestrial forms. *Catinella* sp. is the most abundant snail from Nelson-Wittenberg (Table 2) but is not of great utility for paleoenvironmental interpretation. The affinities of snails from Nelson-Wittenberg are primarily with the Rocky Mountain or Northern molluscan provinces.

TABLE 2. Relative abundance of mollusks reported here from the Mammoth Site and Nelson-Wittenberg Site, to nearest 0.1%. MSL 1300–1478 are included here as representative of the Mammoth Site. Ongoing excavation at the Mammoth Site will likely produce additional specimens. The value of calculated relative abundance is limited due to sampling methods. NISP reflects the number of individual specimens of each species. For easily broken shells (*Catinella, Physa, Fossaria*), NISP was calculated by counting the apex in order to eliminate a bias toward less friable species. For others (Pupillidae), complete apertures were counted. Unless indicative of a distinct genus or species (*Discus* sp.), specimens referred to "sp." (e.g., *Pupilla* sp.) were not counted. Nelson-Wittenberg total NISP = 829; Mammoth Site total NISP = 203.

	Nelson-Wittenberg		Mammoth Site	
	NISP	Rel. Abund.	NISP	Rel. Abund.
Pisidium casertanum	—	—	1	0.5
Pisidium compressum	—	—	2	1.0
Pisidium walkeri	—	—	4	2.0
Fossaria parva	—	—	1	0.5
Physella sp.	—	—	132	65.0
Gyraulus sp.	—	—	2	1.0
Columella columella alticola	4	0.5	—	—
Pupilla muscorum	90	10.8	14	6.9
Pupilla hebes-like	122	14.7	—	—
Pupoides albilabris[a]	1	0.1	—	—
Vertigo modesta	202	24.4	1	0.5
Vertigo modesta parietalis	2	0.2	—	—
Vertigo gouldi hannai	4	0.5	—	—
VALLONIIDAE				
Vallonia gracilicosta	145	17.6	31	15.3
Vallonia cyclophorella	4	0.5	—	—
SUCCINEIDAE				
Catinella sp.	216	26.1	15	7.4
DISCIDAE				
Discus sp.	3	0.4	—	—
ZONITIDAE				
Hawaiia minuscula	6	0.7	—	—
LIMACIDAE				
Deroceras laeve	29	3.5	—	—
TOTALS	828	100.0	203	100.0

[a]Appears to be a modern contaminant.

Widespread species, such as the slug (*Deroceras laeve*) and the snail (*Hawaiia miniscula*), are also present. The Nelson-Wittenberg molluscan fauna, as a whole, lacks some of the eastern and southern elements (e.g., *Gastrocopta procera, G. armifera*) found in the Late Holocene Graveyard Cave fauna and local modern surveys (Table 1).

The presence of *Vertigo modesta, Columella columella alticola,* and *Pupilla muscorum* at the Nelson-Wittenberg Site is noteworthy. *Vertigo modesta* is common at the Nelson-Wittenberg Site (Table 2). Frest and Johannes (1993) reported *V. modesta* (as *V. m. modesta*) from wet, lowland areas of the central Black Hills. Certainly, more mesic local conditions than today existed in order to support species such as *Vertigo modesta, Catinella* sp., and *Deroceras laeve* at the Nelson-Wittenberg Site. Indication of spring drainage further supports the idea of a moist, local setting. Such a scenario does not necessarily imply more mesic conditions for the southern Black Hills as a whole, but may merely record the existence of a greater number of areas of spring discharge.

The lack of modern *Columella columella alticola* specimens in the Black Hills is puzzling considering the affinity of Black Hills mollusks with Rocky Mountain forms. *Columella columella alticola* is typically a boreal form from the Rocky Mountain molluscan province (Bequaert and Miller 1973). At the more southern end of its range, *C. c. alticola* is usually found at high elevations where moister conditions occur (Bequaert and Miller 1973). La Roque's (1970) data on the ecology of the species indicate an affinity for moist areas. *Columella columella alticola* is a rare species from the deposit; only 4 specimens were confidently assigned.

Pupilla muscorum (considered a Northern Province species by Frest and Johannes 1993) is not reported in modern surveys of the Black Hills, and yet this taxon was relatively common at the Nelson-Wittenberg Site, more so if the *P. hebes*-like forms are actually *P. muscorum* (Table 2). As with *Columella columella alticola,* at the southernmost portion of its range (Arizona and New Mexico), *P. muscorum* is usually found at high elevations (2043–569 m [6700–12,000 feet]; Bequaert and Miller 1973).

Based on modern geographic and altitudinal distributions, we hypothesize that the presence of *Pupilla muscorum* and *Columella columella alticola* at Nelson-Wittenberg implies cooler or more equable temperatures (i.e., a lack of extremes, especially hot summer temperature) than those existing today. Although Black Hills climates are fairly mild today compared to the surrounding plains, temperature extremes are not uncommon (Froiland 1990).

By themselves, mollusks from Nelson-Wittenberg do not support (or refute) previous environmental interpretations for the southern Black Hills during the Pleistocene (see discussion above). The presence of *Columella columella alticola* and *Vertigo* spp. suggests that a fairly well-vegetated area (possibly a wet meadow or woodland) was nearby, whether at or adjacent to a spring. The mollusks do appear to indicate cooler, possibly more equable, regional climates and a greater number of local mesic microhabitats. Such an interpretation fits a pattern seen in the paleoenvironmental records from Agate Basin and Lange-Ferguson (Evanoff 1982, Martin 1987). Although these sites are not chronologically equivalent to our data sets, they indicate the presence of (at least) a higher number of localized mesic areas in or near the Black Hills during the Pleistocene. When the mollusks are compared with small mammal species from Nelson-Wittenberg for the purpose of paleoenvironmental interpretation, some unique differences are evident.

The presence of *Lemmiscus curtatus* (NAUQSP 11629) at Nelson-Wittenberg is notable given our fossil mollusk-based hypothesis of a more vegetated, moist locality (relative to modern). The closest extant population of sagebrush vole is distributed north and west of the locality by approximately 200–240 km. Sagebrush voles inhabit temperate-arid, shrub-steppe habitat from northwestern South Dakota to northern Colorado, eastern California, and southern Canada (Jones et al. 1985). The presence of sagebrush voles in the southern Black Hills during the Pleistocene is consistent with the previous interpretations of a shrub-steppe environment discussed by Mead et al. (1994) and others mentioned above. Shrub-steppe environments may have surrounded the moister and possibly more vegetated spring area at Nelson-Wittenberg. There appears to be some disparity between molluscan and mammalian environmental indicators at Nelson-Wittenberg. These differences suggest the presence of a mosaic of communities or microhabitats for the Pleistocene in the southern Black Hills, much in the same way that the modern Red Valley is predominantly grassland with interspersed riparian and ponderosa pine microhabitats. The presence of extralimital, boreal-adapted molluscan species may reflect the presence of a localized woodland or wet meadow community (spring discharge-based) interspersed with a regional shrub-steppe community as indicated by *Lemmiscus* and other regional studies.

Paleoenvironmental indicators for the southern Black Hills during the Late Pleistocene hint at a more equable climate. The recovery of taxa typically associated with more boreal or northern habitats indicates some changes in local environments from the Pleistocene to recent. Certain species (e.g., *Columella columella alticola, Pupilla muscorum*) may not have been able to adapt to changes in the southern Black Hills environment through the Pleistocene/Holocene transition. The altithermal (8000 yr B.P. to 4500 yr B.P.) in the Red Valley of the southern Black Hills was shown to be characterized by much different climatic conditions than the Pleistocene (Fredlund 1996). Presently, however, subtle local-level changes in the southern Black Hills environment and malacofauna do not appear as drastic as seen in other areas of the Great Plains.

When compared with other Late Pleistocene malacofaunas, one unique aspect of Mammoth Site and Nelson-Wittenberg Site mollusk assemblages is their overall similarity to the modern molluscan fauna of the Black Hills (Table 1). Both localities indicate that a portion of the extant Black Hills molluscan fauna may have been established by at least the Late Pleistocene, during a glacial climatic phase. The majority of species recovered from fossil deposits in the southern Black Hills are still extant in the region today (Table 1). This is in stark contrast to other localities in the Great Plains where Pleistocene mollusk diversity was greater and representative of more biogeographic heterogeneity than modern (Baker et al. 1986, Frest and Dickson 1986). Whether this will be a consistent trend in the Black Hills or simply an artifact of sampling is presently unknown.

CONCLUSIONS

The assemblages under consideration are distinct from one another in time and character. Neither locality contains a long stratigraphic record, and both appear to have short depositional histories. The Mammoth Site molluscan fauna is indicative of a unique local microhabitat. Recovered mollusks are predominantly aquatic, indicating abundant water. The Nelson-Wittenberg mollusks, along with recovered mammalian species, provide a further glimpse into Pleistocene environments in the Black Hills. Recovered mollusk taxa suggest cooler or more equable temperatures than modern. Based on the recovery of extralimital (*Columella collumella alticola*) and extralocal (*Vertigo modesta*) taxa, a wet meadow or woodland is inferred for portions of the southern Black Hills at approximately 37,900 yr B.P. Remains of sagebrush vole indicate shrubsteppe in areas of the Red Valley. Together, Pleistocene mollusks and mammals suggest a slightly different mosaic of communities than occurs in the southern Black Hills today.

Future studies may provide greater accuracy in depicting long-term environmental and climatic changes or lack thereof. Additional molluscan records from the region will help further clarify small-scale environmental change (microhabitat-level) from large-scale patterns of paleoenvironmental change or stasis. Presently, the lack of reliable, stratigraphically continuous records prohibits any interpretation beyond a localized, site-by-site basis. As localities of different ages are identified, the faunal record of the Black Hills will become more useful in answering questions about long-term paleoenvironmental change.

The validity of our hypothesis of "cooler" or more equable temperatures depends entirely on the influence of specific ecological factors in controlling the distribution of *C. c. alticola* and *P. muscorum* in North America. More research on the physical and biotic factors that control mollusk distributions is sorely needed.

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