

## FIRST REPORT OF FOSSIL *AMPHIUMA* (AMPHIBIA: CAUDATA: AMPHIUMIDAE) FROM SOUTH CAROLINA, USA

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### ABSTRACT

Twenty-five fossil *Amphiuma* vertebrae have been collected from five sites in eastern South Carolina. These specimens constitute the first fossil records of this amphibian from the state and the northernmost record of the genus within the Atlantic Coastal Plain. Eleven specimens from one site in Dorchester County are assigned to the late Blancan North American Land Mammal Age (NALMA) and represent the oldest Pleistocene record (Gelasian Stage) of the genus. A vertebra from a second Dorchester County site was collected from strata thought to have been deposited during the middle Pleistocene (Ionian Stage), within the late Irvingtonian NALMA. Twelve specimens from two exposures of the Wando Formation represent middle Rancholabrean NALMA occurrences within the late Pleistocene (70,000 to 130,000 Ka; Tarantian Stage). A single specimen from Colleton County represents a new addition to the Edisto Beach faunal assemblage, which contains an assortment of fossil taxa ranging in age from late Miocene to late Pleistocene. All of the specimens reported herein are tentatively referred to *Amphiuma means* based on trunk vertebra morphology and Recent distributions of the three extant species.

### INTRODUCTION

The southern portion of the Atlantic Coastal Plain, here defined as the region from the North Carolina-South Carolina state line south to the Georgia-Florida state line, contains a rich trove of Cenozoic vertebrate fossils, especially from the Pliocene and Pleistocene epochs. However, the fossils from this area have received comparatively little attention except from the hobby collecting community. Hulbert (2002) presented an overview of the vertebrate paleofaunas of Florida (listing over 1,100 taxa of fossil vertebrates) that provides some idea of the species that may also have inhabited Georgia and South Carolina. A review of the published records for South Carolina and Georgia revealed that only in the past three decades concerted efforts have been made to study the Plio-Pleistocene paleofaunas from this geographic region.

Recent studies by Hulbert and Pratt (1998) and researchers from Georgia College and State University, Milledgeville, have begun to elucidate the structure of Pleistocene paleofaunas of Georgia (i.e., Mead et al., 2006; Parmely et al., 2007). In South Carolina the most popular hobby-collecting site is on Edisto Beach, and the Edisto Beach faunal assemblage (fa) was discussed by Roth and Laerm (1980), Holman (1995), and Sanders (2002). The best-known Pleistocene

fauna, the Ardis Local Fauna (LF), was collected at the Giant Cement quarry, just north of Harleyville, Dorchester County, from solution cavities in the upper Eocene Tupelo Bay Formation that were infilled with overlying fluvial sands and clays. The Ardis LF contains a wide variety of mammalian taxa (Bentley et al., 1994), turtles (Bentley and Knight, 1993, 1998), and birds (Chandler and Bentley, 2007). Plio-Pleistocene elasmobranch taxa are also receiving close analysis (i.e., Cicimurri and Knight 2009; Cicimurri and Knight unpublished data). Local faunas representing the late Blancan (lowermost Pleistocene), late Irvingtonian (middle Pleistocene), and Rancholabrean (middle to late Pleistocene) North American Land Mammal Ages (NALMA), in the collections of the South Carolina State Museum, are in various stages of study and will be reported on in the future. Although a considerable number of fossil collections have been made, a great deal of research remains to be conducted in order to claim even a partial understanding of Plio-Pleistocene ecologies and faunas in South Carolina.

The purpose of this report is to discuss the significance of fossil amphibian remains, all referred to the genus *Amphiuma*, collected in South Carolina (Figure 1). These remains represent: 1) the oldest Pleistocene record of the Family Amphiumidae; 2) the northernmost Pleistocene record of *Amphiuma* from the

Atlantic Coastal Plain of the United States; 3) the first amphibian fossils reported from South Carolina; and 4) the first fossil amphibian records for both the Edisto Beach faunal assemblage and the Wando Formation.

#### METHODS

*Amphiuma* vertebrae have been collected from five sites in the South Carolina Coastal Plain (Fig. 1), and all of the specimens reported herein are housed in the collections of the South Carolina State Museum (SC) in Columbia. Vertebrae in the Walrus Ditch, Crowfield, and Rodent Ditch local faunas were obtained both by surface collecting of weather-exposed fossils and screen-washing *in situ* matrix (down to 0.25 mm mesh size). The specimen from the Camelot LF was recovered through screen-washing of matrix associated with a large sloth pelvis that was excavated at the site. Precise geographic information for these four sites is not listed here because they are currently on private property, but the information is on file at SC. The single specimen recovered from Edisto Beach had washed ashore and was found by a hobby collector while beachcombing. Fossil collecting is currently allowed in Edisto Beach State Park.

#### SYSTEMATIC PALEONTOLOGY

##### Order Caudata

##### Family Amphiumidae

*Amphiuma* sp. cf. *A. means* Garden, 1821

##### Figure 2

According to Gardner (2003), amphiumid trunk vertebrae are diagnostic and can be differentiated from those of other salamanders by a suite of features. Centra are amphicoelous with deeply concave cotyles (and we have observed that these are usually vertically oriented and oval; see Figure 2A, E, T) and the notochordal pit is retained (Figure 2E, F, J, K, O, P). Spinal foramina are absent. The neural crest is elongate (Figure 2H, M), moderately high, and often bears paired, posteriorly divergent neural spines (Figure 2B, Q). Transverse processes are weakly bicipitate on anterior-most trunk vertebrae but unicipitate on other trunk vertebrae. The ventral surface bears a longitudinal keel (Figure 2D, I, N, S) and a pair of well-developed anterior basapophyses (Fig. 2A, F, K, P). The trunk vertebrae and all but the posterior-most caudals of fossil and extant amphiumid salamanders bear a pair of dorsal postzygapophyseal crests adjacent to the neural crest (Figure 2C, G, H, L, M, Q, R), an apomorphy that is unique among salamanders (Gardner, 2003).

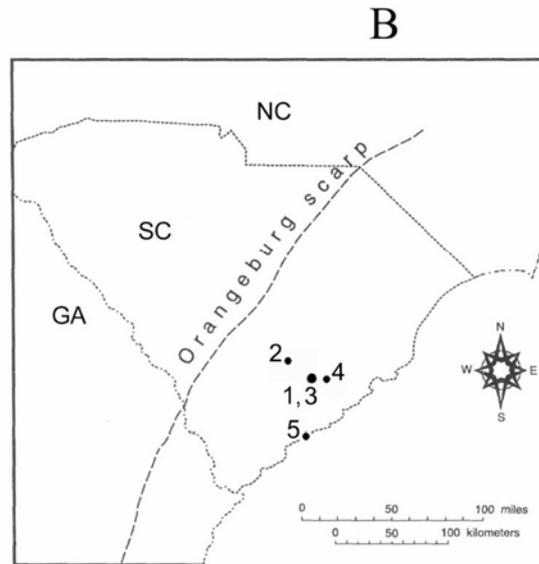


FIGURE 1. A, Geographic map of the eastern United States showing locations of some southeastern coastal states. B, Geographic map of South Carolina showing locations of the five fossil localities discussed in the text: 1 = Walrus Ditch site; 2 = Camelot site; 3 = Crowfield site; 4 = Rodent Ditch site; 5 = Edisto Beach site. Abbreviations: GA = Georgia; NC = North Carolina; SC = South Carolina. Base map in A adapted from Case (1994:text-fig. 1).

## 1. Walrus Ditch LF

**Material Examined**—SC 89.245.51, one vertebra (Figure 2A-E), SC 89.245.50, bulk lot of ten vertebrae.

**Comments**—The centrum length of the largest specimen in the sample measures 8.55 mm. It is likely that several individuals are represented in our sample because the vertebrae were found at different areas within the collection site. The Walrus Ditch LF was collected from the bank of a ditch flowing through a residential neighborhood adjacent to Summerville, Dorchester County. Remains of a considerable number of taxa have been recovered from the site, including terrestrial and marine mammals, birds, turtles, squamates, crocodylians, elasmobranchs, and teleost fish. Only the elasmobranchs have been studied in detail thus far (Cicimurri and Knight, unpublished data). The *Amphiura* vertebrae were associated with mammalian taxa recognized by Morgan and Hulbert (1995) as late Blancan NALMA indicator taxa, including *Nannippus peninsulatus*, *Holmesina floridana*, and *Canis lepophagus*. The late Blancan NALMA falls within the Gelasian Stage, and until recently this stage was part of the Pliocene Epoch. The Pliocene-Pleistocene boundary was placed at 1.8 Ma (see Haq et al., 1977), but on 30 June, 2009, the International Union of Geological Sciences ratified a request from the International Commission on Stratigraphy to move the Pliocene-Pleistocene boundary from 1.8 Ma to 2.6 Ma (see web page at [www.stratigraphy.org](http://www.stratigraphy.org)). The Gelasian Stage, an interval of time of roughly 800,000 years, is therefore now part of the Pleistocene Epoch. The occurrence of *Amphiura* in the Walrus Ditch LF should therefore be considered as the oldest Pleistocene record of the genus (Holman, 2006; Parmley et al., 2007).

## 2. Camelot LF

**Material Examined**—SC 2004.1.151, one vertebra (Figure 2F-J).

**Comments**—The preservation of this specimen is nearly perfect, with only minor damage to the anterior part of the left prezygopophys, the distal end of the left transverse process, and the right neural spine. The centrum measures 7.54 mm in length, and the width of the vertebra between the tips of the right and left transverse processes measures 12.41 mm. The Camelot local fauna was collected in an active limestone quarry (Giant Cement) located less than five km north of Harleyville, Dorchester County. The fossils are derived from fluvial sands and gravels of an undescribed formation that represent point bar, crevasse splay, and oxbow lakes that were part of a meandering river system. These fluvial deposits are

located under 3-4 m of unfossiliferous sediment and are exposed when overburden is removed in order to quarry the limestone.

Based on the mammalian component, which is very similar to the Coleman IIA LF of Florida (Morgan and Hulbert, 1995), the Camelot LF is assignable to the late Irvingtonian NALMA and is 450,000 - 400,000 years old. This interval of time is within the Ionian Stage (middle Pleistocene), and the fossiliferous deposit is temporally equivalent to the Ladson Formation found near the South Carolina coast.

## 3.4. Crowfield and Rodent Ditch local faunas

**Material Examined**—Crowfield local fauna: SC 2009.1.30, one vertebra (Fig. 2, K-O), SC 2009.1.31 bulk lot of ten vertebrae. Rodent Ditch local fauna: SC 99.43.1, one vertebra.

**Comments**—The Crowfield and Rodent Ditch local faunas were derived from the Wando Formation. The largest specimen in the Crowfield sample measures 9.40 mm in centrum length, whereas the single specimen in the Rodent Ditch LF measures 4.65 mm in centrum length. The Crowfield material was collected from the Crowfield Lake construction site located between Summerville and Goose Creek, Berkeley County. The lake, developed as an ornamental feature for the Crowfield neighborhood, was dug in such a fashion that a gentle slope was formed that cut through the Wando Formation and exposed the significant disconformity with the underlying upper Oligocene (Chattian) Chandler Bridge Formation. The Rodent Ditch collection site is less than 20 km from the Crowfield site, and the Wando Formation is exposed in creek and ditch banks in a number of places in the immediate region.

The Wando Formation consists of a series of sand, clay, and silt facies that are thought to be of fluvial to estuarine origin (Weems and Lemon, 1988). The formation has been dated to 130,000 to 70,000 Ka and is therefore predominantly within the Tarantian Stage (late Pleistocene). The mammalian component of the Crowfield and Rodent Ditch local faunas is assignable to the middle Rancholabrean NALMA. Fossil birds in the Crowfield LF include a grebe and at least four species of duck (Chandler and Knight, 2009), and these provide additional evidence for the presence of an aquatic environment nearby. Our specimens represent the first record of a salamander from the Wando Formation, as well as the first published amphibian records in the Crowfield and Rodent Ditch local faunas (other amphibian taxa are known from these faunas and will be reported on at a later date).

### 5. Edisto Beach faunal assemblage

**Material Examined**—SC 2005.57.1, one vertebra (Figure 2P-T)

**Comments**—The specimen measures 8.05 mm in centrum length. The Edisto Beach faunal assemblage has long been considered to represent the Rancholabrean NALMA based on the mammals and turtles identified from the locality (Roth and Laerm, 1980; Holman, 1995; Sanders, 2002). However, we believe that there is some difficulty in assigning the various components of the assemblage to only a single NALMA. Edisto Beach specimens from other vertebrate groups, particularly the elasmobranchs and teleosts (currently under study), indicate a considerably broader temporal distribution spanning a time from some point in the Blancan NALMA (or even Hemphillian) well into or through the Rancholabrean (JLK and DJC unpublished data). Thus, the Edisto Beach faunal assemblage is heterochronic, and the *Amphiuma* vertebra could be as old as Pliocene or even late Miocene in age. This specimen represents the first fossil amphibian record for the assemblage.

### DISCUSSION

The Amphiumidae are a small family of aquatic salamanders endemic to North America (Gardner, 2003). The fossil record of the group is primarily known from the Pleistocene to Recent of the southeastern United States (i.e., Meylan, 1995; Parmley et al., 2007), but there are records from the late Maastrichtian or early Paleocene (Lancian or Puercan NALMA) of Montana, the late Paleocene of Wyoming, and the middle Miocene of Texas (Salthe, 1973; Holman, 1977; Estes 1981; Gardner 2003). The identification of a partial skeleton from the lower Eocene (Wasatchian NALMA) of western Wyoming (Rieppel and Grande, 1998) as an amphiumid was refuted by Gardner (2003) and Holman (2006).

In North America, five species have been assigned to the genus *Amphiuma*, including two fossil and three extant species. Of the fossil species, *A. jepsoni* was reported from the Polecat Bench Formation (late Paleocene, Tiffanian NALMA) of Park County, Wyoming (Estes, 1969). This taxon is known from incomplete skeletons and, contrary to the view of Rieppel and Grande (1998), Gardner (2003) considered *A. jepsoni* valid. *Amphiuma antica* was described by Holman (1977) from the Fleming Formation (middle Miocene, Barstovian NALMA) of Polk County, Texas. However, this taxon is based on a badly preserved trunk vertebra (Holman, 1977: fig. 2) and is considered a *nomen dubium* (Gardner, 2003; Parmley et al., 2007). A sixth *Amphiuma* species, *A. nordica*, was reported from the German Pleistocene, but the taxon is also a

*nomen dubium* because the holotype specimen is thought to belong to a teleost fish (Estes, 1981; Gardner, 2003). Genetic analyses by Bonett et al. (2009) indicate that the three extant species of *Amphiuma* diverged from a common ancestor four to ten million years ago, and *A. means* diverged from *A. pholeter* one to four million years ago. It seems reasonable to assume, therefore, that fossil *Amphiuma* remains occurring in Pleistocene through late Miocene strata can be assigned to one of the three extant species. We tentatively identify the South Carolina *Amphiuma* fossils as *A. means* based largely on the Recent distribution of the three extant species and because our material closely compares to a trunk vertebra of *A. means* illustrated by Gardner (2003, fig. 3F-H). Additionally, the large vertebrae in our sample are comparable in size and morphology to those of several Recent specimens of *A. means* we examined in the collection of the Georgia College and State University.

Modern *Amphiuma* salamanders occur along the Gulf Coast and southeastern Atlantic Coast of the United States (Conant and Collins, 1998; Petranka, 1998; Bonett et al., 2009). These salamanders have an elongate and superficially eel-like body, and a single gill slit but no external gills (Salthe, 1973; Duellman and Trueb, 1986; Conant and Collins, 1998). The one-toed *Amphiuma*, *A. pholeter*, is a small species (up to 33 cm in length) that occurs in disjunct populations from the Mobile Bay region of Alabama eastward through the central western coast of Florida (Petranka, 1998; Conant and Collins, 1998; Bonett et al., 2009). The three-toed *Amphiuma*, *A. tridactylum*, is a large species (up to 106 cm in length) that ranges from the lower Mississippi River valley of southeastern Missouri southwest to Houston Bay, and southeast to western Mississippi (Petranka, 1998; Conant and Collins, 1998; Bonett et al., 2009). The two-toed *Amphiuma*, *A. means*, is the largest of the three extant species (up to 116.2 cm in length) and occurs in the Gulf Coastal Plain from eastern Louisiana into Florida, and into the Atlantic Coastal Plain from Florida to southeastern Virginia (Conant and Collins, 1998; Bonett et al., 2009).

The presence of *Amphiuma* in a paleofauna can serve as a paleoecological indicator. This large salamander is paedomorphic, obligate aquatic, gill-breathing, and occupies a wide variety of aquatic habitats, including bottomland swamps, bayous, cypress swamps, drainage ditches in suburban and agricultural areas, permanent ponds and lakes, isolated ephemeral wetlands, wet prairies and marshes, small streams, and individuals often inhabit crayfish burrows (Lannoo, 2005). *Amphiuma* only very rarely leaves the water, but individuals may move overland during and following heavy rains (Lannoo, 2005). Gibbons

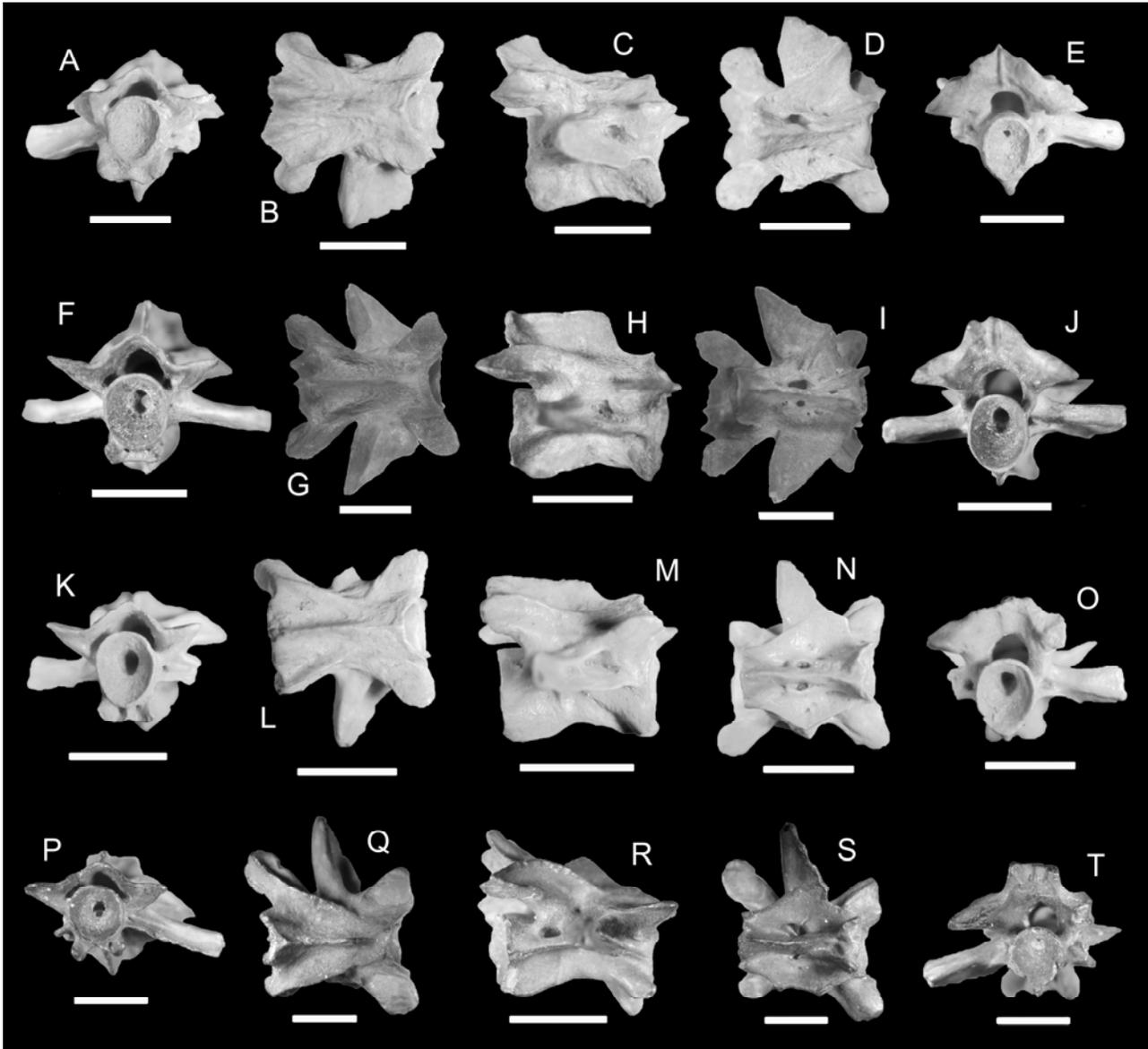


FIGURE 2. Trunk vertebrae referred to *Amphiura* sp. cf. *A. means*. Numbers in parentheses occurring after site names refer to locations on Figure 1B. A-E, SC 89.245.51, Walrus Ditch site (1). F-J, SC 2004.1.151, Camelot site (2). K-O, SC 2009.1.30, Crowfield site (3). P-T, SC 2005.57.1, Edisto Beach site (5). Anterior views in A, F, K, and P; dorsal views in B, G, L, and Q; right lateral views in C, H, and M, left lateral view in R (flipped horizontally); ventral views in D, I, N, and S (flipped horizontally); posterior views in E, J, O, and T. Anterior is at right in dorsal, lateral, and ventral views. Scale bars = 5 mm.

and Semlitsch (1991), working in the Savannah River Site (SRS) in south-central South Carolina, collected specimens in pitfall traps that were located away from aquatic situations. Snodgrass et al. (1999), also working at the SRS, found that the occurrence of *A. means* in depression wetlands decreased as the distance from the nearest intermittent habitat increased. Petranka (1998) observed *A. tridactylum* as much as 12 m away from water. The habitat preferences of extant

*Amphiura* strongly suggest that the discovery of *Amphiura* in a paleofauna will serve as a good indicator of standing or slowly flowing bodies of water in a coastal or more inland setting.

The above hypothesis is supported by the *Amphiura* fossils within the Walrus Ditch, Crowfield, and Rodent Ditch local faunas. These local faunas contain a mixture of marine organisms (elasmobranchs, cetaceans, and sirenians) and terrestrial taxa like

artiodactyls, perissodactyls, canids, felids, and xenarthrans. These suggest very close proximity to a marine shoreline, where the remains of marine and terrestrial animals were mixed together. The compositions of the turtle communities within each LF, coupled with other associated fossils, further indicate the existence of standing or slowly moving bodies of fresh water in some portion of the habitat.

#### CONCLUSIONS

Twenty-five fossil *Amphiura* vertebrae tentatively identified as *A. means* were collected from coastal plain strata of South Carolina. Isolated *Amphiura* vertebrae collected from Pleistocene and Holocene sites elsewhere have been referred to *A. means* or simply *Amphiura* sp. (see summary in Gardner, 2003). Parmley et al. (2007) stated that specific identifications based on vertebral morphology could not be clearly supported because of similarities between vertebrae of the three extant species. Previously published reports of Pleistocene *Amphiura* sp. or *A. means* are from Florida (Brattstrom, 1953; Weigel, 1962; Hirschfield, 1969; Holman, 1995; Meylan, 1995), Georgia (Hulbert and Pratt, 1998; Parmley et al., 2007), and Texas (Holman, 1965; Slaughter and McClure, 1965). If the Texas material is correctly identified as *A. means* (Holman, 1965), then the western range of the species has been reduced by several hundred kilometers. The South Carolina fossils represent the northernmost Pleistocene record of *Amphiura* in the Atlantic Coastal Plain, and with the placement of the Plio-Pleistocene boundary shifted to 2.6 Ma (previously 1.8 Ma), the specimens from the Walrus Ditch LF are the oldest Quaternary record of the genus (early Pleistocene; Gelasian Stage; late Blancan NALMA).

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