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Senior Thesis

Paleoecologic and Paleogeographic Implications of a Hemphillian (7-4.5 MA) Snake
Assemblage in Washington County, Tennessee

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April 5, 2005

Abstract

The Gray Fossil Site, a Miocene deposit in Washington County, Tennessee, has yielded a wide variety of fossilized vertebrate remains since its discovery in the summer of 2000. Preliminary geologic and paleoecologic studies indicate that the Gray Site was once a sinkhole lake, which was subsequently filled with sediment and remains of various vertebrates, invertebrates, and plants. Snake fossils previously identified from this locality include *cf. Regina* and *cf. Sistrurus*. While some of the fossilized snake remains are too poorly preserved to be identified beyond colubrid or erycine boid, others are much more enlightening. Additional remains belong to the genus *Vipera*, the first members of this genus discovered in North America and potentially a previously unknown species. The presence of *cf. Vipera*, as well as other Eurasian species, in eastern Tennessee calls the current understanding of Miocene migrations and dispersal corridors into question. The specific species represented at the Gray Site is consistent with the current paleoecologic interpretation of the deposit. However, further research on the snake remains of the Gray Site needs to be performed in order to clarify the large-scale patterns of snake species found there and to help further our understanding of the paleoenvironment.

Introduction

In May of 2000, Tennessee Department of Transportation (TDOT) workmen uncovered a vertebrate fossil-rich deposit in Washington County, Tennessee. Named the Gray Fossil Site, in honor of the nearest town, this assemblage has proven to be one of the largest, best preserved Miocene vertebrate deposits found in North America. The locality bed has been granted state protection and funding placing it under the care of East Tennessee State University (ETSU) and the soon-to-be constructed East Tennessee Museum of Natural History (ETMNH). The site is approximately 220 m by 100 m in surface area and 36 m in depth, making the total volume roughly 792,000 m² (Smith, 2003). The state of Tennessee and ETSU are currently in negotiations to buy surrounding property, so it is very likely that the site itself is actually much larger (Bristol, 2004).

Five years into excavations, the Gray Site is still producing large quantities of fossils. The most common remains recovered belong to the tapir *Tapirus polkensis*. The discovery of *Plionarctos*, a short-faced bear (Smith, 2003), and *Teleoceras*, a pot-bellied rhinoceros (Parmalee et. al, 2002), place this site between 4.5 and 7 MA, in the Hemphillian Land Mammal Age. Other notable vertebrate finds include gomphotheres, saber-toothed cats, camels, alligators, fish, frogs, and snakes (Wallace, 2004). Remains of invertebrates include gastropods and clams (Parmalee et. al., 2002). Plant micro- and macrofossils are dominated by oak, hickory, and pine (Wallace, 2004).

Until recently, most fossils collection occurred on the surface and in the hills of debris moved by TDOT crews before the nature of the Site was noted. Consequently few small remains, such as snakes, were collected. However, water-screening of excavated material began in spring of 2004 and literally hundred of snake fossils have since been recovered. This paper will attempt to cover the paleoecologic and paleogeographic implications of some of the early finds of snake remains at the locality.

Geology

During the late Miocene, the Gray Fossil Site was forming in what would become eastern Tennessee. Originally a sinkhole lake, the steep-sided depression slowly filled with sediments over time. Sinkholes of this type form when karst caves collapse, exposing the caverns on the surface. The lake could have formed when its drainage system was plugged by sediment, when the sinkhole collapsed further, or by a dramatic rise in the water level (Shunk, 2003). Others have noted that the Gray Site occurs over a fault, and that earthquakes might have triggered the blocking of the drainage system (Whisner & Hatcher, 2003). Also, since this is an east-west trending fault, which is rare in the Valley and Ridge Province, it has been theorized that other localities, similar to the Gray Site in age and quality, may be found along other east-west faults in the same geologic and geographic area (Whisner et. al, 2001).

At the Gray Site itself, the surrounding rock is Middle Ordovician Knox Group dolomite, and debris from this unit can be found within the lake sediments (Shunk, 2003). Previous studies have separated the sediments of the Gray Site into four sections. The oldest section is made up of graded beds with little organic carbon. Each layer grades upwards from fine sands into silts and clays and have been interpreted as storm events (Shunk, 2003).

The next section is composed of paired dark brown or black sediments and gray silt and clay sediments. These couplets seem to be varved layers with the darker, organic-rich layers representing wetter periods of the year and the gray, silty layers being deposited during the drier seasons. The rate of sedimentation remained relatively constant throughout this section (Shunk, 2003). It is in this dark section that the vast majority of fossils have been found. The lake bottom seems to have been extremely low in oxygen, preventing biotic interruptions and accounting for the unusually good preservation and articulation in the fossil remains (Smith, 2003).

A shift towards a drier climate seems to have exposed the uppermost varved sediments to the air, which formed paleosols. The area was subsequently covered by alluvium and a cherty gravel cap formed over the entire filled sinkhole. Differential weathering wore the surrounding area away, making the once-depression into a small hill

(Shunk, 2003). The regolith cap protected the fossils within the Gray Site by trapping water under pressure within the beds. It was only in 2000 when road crews broke through the cap that drying started, compromising the quality of preservation of the fossils contained there (Bristol, 2004).

General Paleocology

The structure of the Gray Site indicates it was originally a steep-sided sinkhole consistent with those found in present day Central America, which form under wet, warm conditions. Since the oldest layers represent storm events, the shift towards undisturbed, annual varves either indicates a shift in environment to a calmer climate, or a change in basin shape or depth, placing the lake bottom out of the reach of the storms. Either of these situations, and the type of sedimentation, indicate that the climate was getting progressively wetter when the second section was deposited (Smith, 2003).

Analysis of the plant macro- and microfossils indicates that the lake was surrounded by an oak-hickory forest at the time, not unlike the modern forests of eastern Tennessee. This makes the Gray Site unusual among other Miocene finds in North America that generally represent C4 grasslands that were evidently common at the time (Bristol, 2004).

The Gray Site has produced fossils of aquatic and semi-aquatic animals that would have lived within and around the lake itself, as well as terrestrial animals that would have used the lake as a watering hole. It has been suggested that the steep sides of the sink-hole lake would have made it function as a trap if drinking animals fell into the water (Wallace, 2002). However, others contend that modern watering holes attract predators, which pick off the unwary, and sick or dying animals making such areas perfect places to find a wide variety of remains (Bristol, 2004).

Problems With Snake Identification

Before addressing the identifications of the remaining fossils, it is important to cover the problems inherent in fossil snake identification. Identifying individual snake

species can be problematic at best. Most snake species are differentiated by the size, shape, and positioning of their vertebral processes. However, these features are often very similar between species. Many modern species are completely indistinguishable osteologically (Holman, 2000). Therefore, the study of snake paleoecology is hindered somewhat by the morphology of the snakes themselves.

To compound matters, most snake remains are extremely small and fragile. Snake vertebrae are rarely preserved whole, which obscures characteristics of the bone necessary for correct identification. Especially at the species level, errors can be made by even the most trained of eyes. Unfortunately, many snakes also have extremely similar skeletal structures. Many modern species are differentiated by coloration and geographic location (Holman, 2000). Since neither of these traits are represented in the fossil record, species-level identifications can become impossible.

Habits within the paleoherpetological field also make for problems when dealing with snakes' identifications and ranges. In the 1950s, there was a trend to name as many different species as possible. This led to single species having multiple names and expanded assumptions about diversity. In the backlash, modern herpetologists tend not to identify a fossil as a new species at all since such findings are often poorly received by their peers (Holman, 2000).

The end result of this mindset is that many modern paleoherpetologists work under the assumption that snake fossils, even very ancient ones, correlate perfectly with modern species. Many modern snake species that are currently identified by their geographic range are also identified this way for ancient remains regardless of the fact that their ranges could have shifted during the intervening years. Many do not attempt to see if a fossil could be from a new species of extinct snake and simply categorize their finds with modern names. This hinders the understanding of snake evolution and potentially decreases the amount of diversity predicted in past ecosystems (Holman, 2000). These issues are perpetuated throughout the literature. Additionally, snake taxonomy and evolution is still being hotly debated. Keeping these limitations in mind, snakes can be useful tools in understanding the paleoecology of past environments, such as that represented by the Gray Fossil Site.

Snake Identification

The end of the Miocene was marked by a rapid change in snake diversity across North America. Boid species were being forced south by the changing climate and colubrids experienced a rapid evolutionary radiation to fill the ecologic voids. Many modern species of colubrid and crotaline snakes were present by the end of the Miocene (Holman, 2000). Some of the snakes found at the Gray Site fit nicely into this general characterization of the late Miocene, but others pose interesting problems.

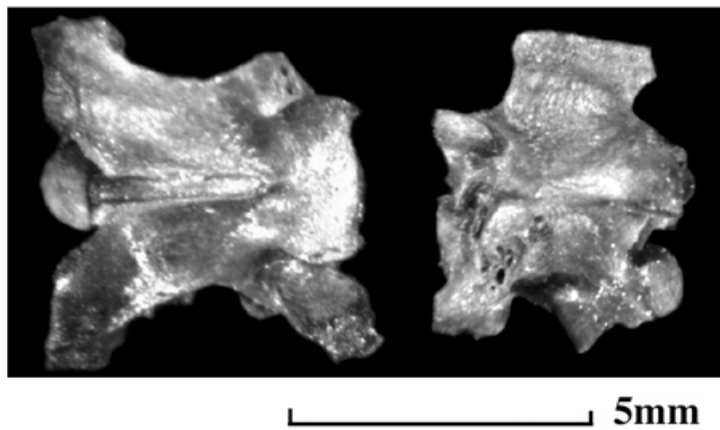


Figure 1: Dorsal (left) and lateral (right) views of the *cf. Sistrurus* specimen recovered in June of 2000

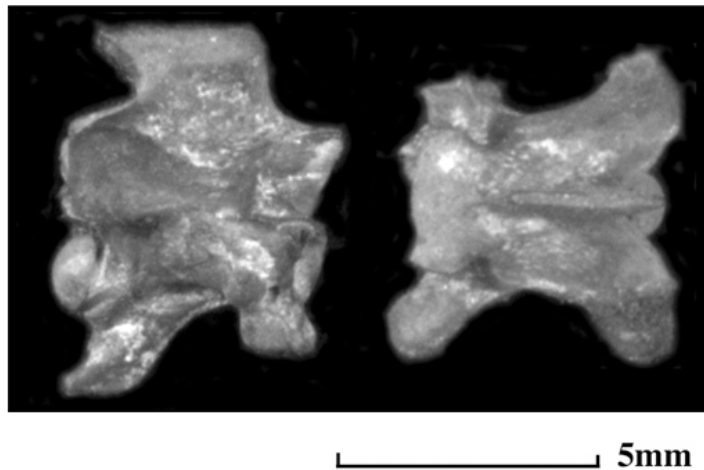


Figure 2: Lateral (left) and dorsal (right) views of the *cf. Regina* specimen recovered in June of 2000

Two snake fossils had been identified prior to this study as *cf. Sistrurus* (Figure 1), making it a relative of modern massasaugas and pygmy rattlesnakes, and *cf. Regina* (Figure 2), a crayfish snake (Holman, 2001). These fossils were found during the excavation of the first tapir skeleton in June of 2000 (Parmalee, 2001). The remainder of the fossils was collected on the surface between 2000 and 2004, and no additional location data, either within the site or between the fossils themselves was provided. Until water-screened fossils become available for study, the snake fossil record will be skewed towards larger, more complete remains.

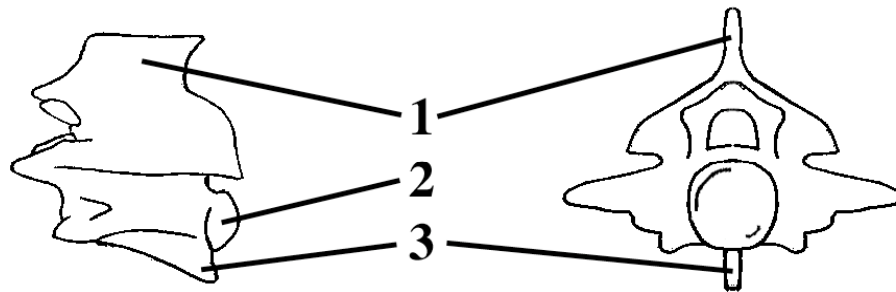


Figure 3: General snake vertebral markers - 1. neural spine, 2. condyle, 3. hypapophysis

Three of the specimens, ETMNH 523 (Figure 6), 539 (Figure 7), and 541 (Figure 5), shared a common trait that seemed unusual, their hypapophyses roughly formed a 45°, 45°, 90° triangle beneath the body of the vertebrae. This characteristic did not seem to match any North American snake species, either living or extinct. The only vertebra that seemed similar was MSUVP (Michigan State University of Vertebrate Paleontology) 1087, a specimen referred to the species *Neonatrix magna* (Holman, 2000).

However, the identification of the vertebra seemed questionable because the unusually shaped hypapophysis was not shared by the species' type specimen, MSUVP 943. It was suggested that looking among Eurasian species might be more helpful (Head, 2005). Expanding the search into Eurasian species seemed perfectly reasonable since it has long been thought that many North American colubrid, natricine, and viperid snakes

migrated from Asia in the early Miocene (Holman, 2000) and because other unusual Eurasian species, including a red panda and Old World badger, have recently been identified from the Gray Site (Wallace, 2004).

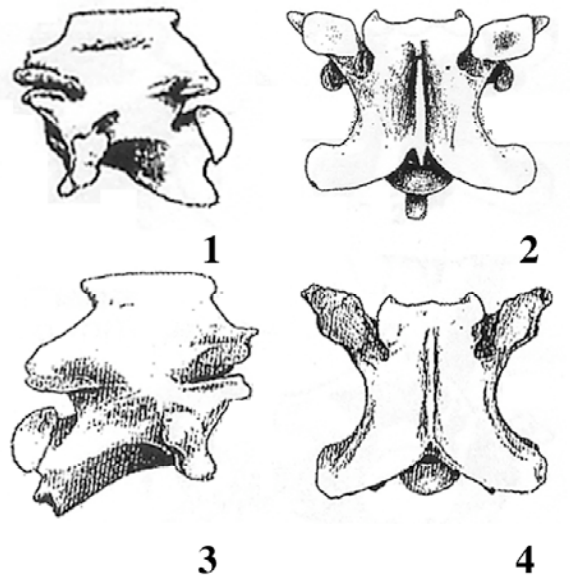
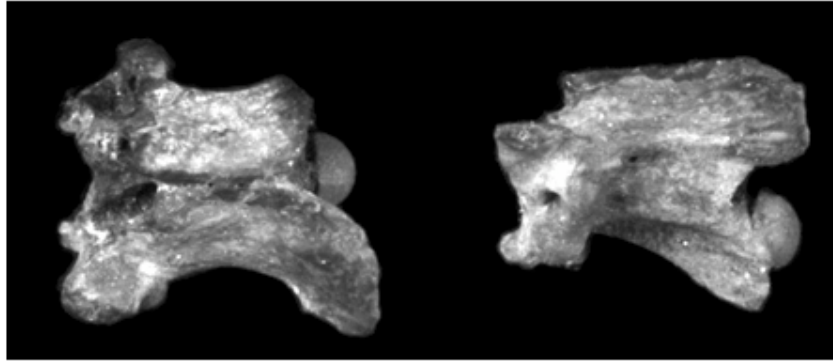


Figure 4: 1 (lateral) and 2 (dorsal) - *Vipera lebetina*, 3 (lateral) and 4 (dorsal) - *Vipera aspis* complex (Szyndlar & Rage, 1999)

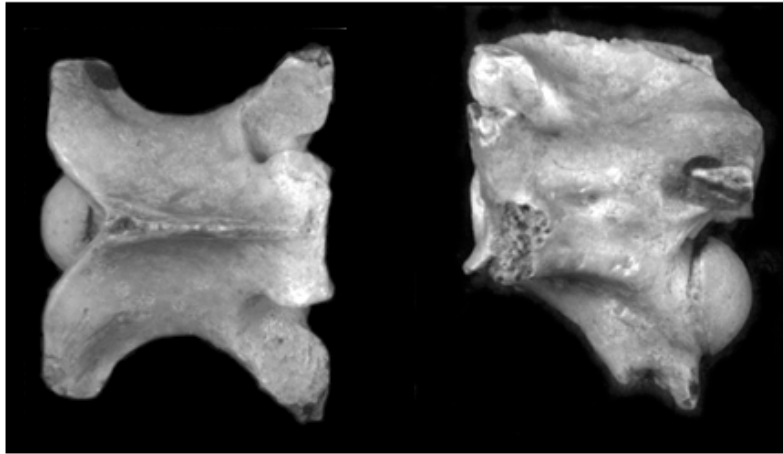
When compared to Old World members of the genus *Vipera* from the early and middle Miocene, the similarities are undeniable (Figure 4). Similar hypapophyses can be found in the middle trunk vertebrae of both *Vipera lebetina* and members of the *Vipera aspis* complex, a group of “Oriental vipers” that are virtually impossible to differentiate from one another or their modern analogs (*V. ammodytes*, *V. aspis*, and *V. latastei*). The vertebrae are very robust and the size, shape, and orientation of their processes all indicate that these fossils do in fact belong to the genus *Vipera* (Szyndlar & Rage, 1999). Of these three fossils, ETMNH 523 and 539 are extremely similar in size and form, lending to the idea that both belong to the same species. ETMNH 541 is much lower and longer than the other two when viewed laterally. These differences can either be interpreted as indicating that 541 belongs to another species, or that this vertebra simply

came from another part of the snake's anatomy. Considering the differences in age, geography, and process morphology, it seems very likely that these fossils represent one or more new species, the first members of this genus identified in North America.



_____ 5mm

Figure 5: Specimen ETMNH 541, identified as *cf. Vipera*



_____ 5mm

Figure 6: Specimen ETMNH 523, identified as *cf. Vipera*

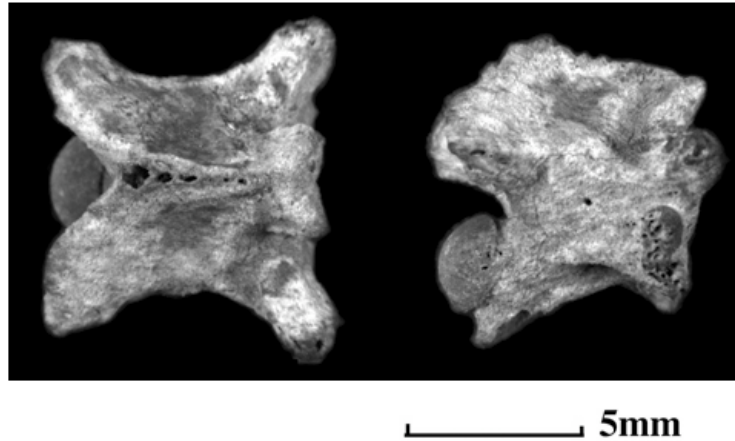


Figure 7: Specimen ETMNH 539, identified as *cf. Vipera*

ETMNH 540 is an even more problematic vertebra to identify (Figure 8). It is in fairly poor condition and the condyle is completely missing. It somewhat resembles erycine boids, but could also be some variety of colubrid (Head, 2005), one of the largest families of snakes and also one of the most debated and rearranged (Holman, 2000). Either identification seems reasonable since the late Miocene saw an explosion in colubrid species, and since erycine snakes were the last boid species to leave North America during the shift to colder climates.

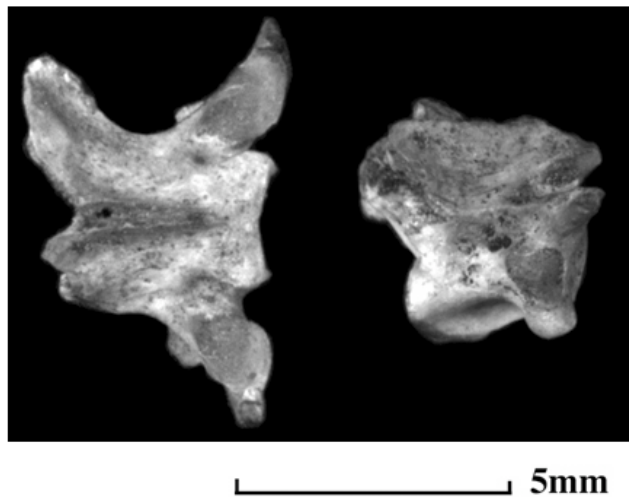


Figure 8: Specimen ETMNH 540, tentatively identified as either an erycine boid or a colubrid

Gray Snake Paleoecology and Paleogeography

The snakes identified above pose interesting problems from a paleoecological standpoint. Four of the six identified specimens are poisonous species, an oddity since nonpoisonous species outnumber poisonous ones by a large percentage throughout the fossil record in North America. It remains unknown why the environment that formed the Gray Fossil Site would support such a high number of poisonous snakes, or if this seemingly large percentage is simply a result of surface collection bias and the extremely small study group. Only further research of the Gray Site's snakes will stand to answer this question.

The presence of snakes of the genus *Vipera* simply add to the body of evidence that the Gray Site contains Eurasian species. These include *Pristinailurus bristoli*, a new species of red (lesser) panda and *Arctomeles dimolodontus*, an Old World badger. These species have led experts on the site to theorize that either migrations between Asia and North America extended further into the Miocene than previously estimated, implying unknown dispersal corridors, or that the wooded Gray Site functioned as a refugium for archaic species less able to adapt to the open grasslands so characteristic of the Miocene (Wallace, 2004).

If ETMNH 540 is in fact an erycine boid, it supports the theory that the Gray Site was a refugium since this subfamily, as well as all other kinds of boids, were rapidly disappearing from North America. If, however, this specimen is some variety of colubrid, very little can be gleaned from such a general identification.

The poisonous species, *cf. Vipera* and *cf. Sistrurus*, were more than likely generalists, so they can add little to the understanding of the Gray Site's ecology beyond their addition into diversity counts. The specimen of *cf. Regina*, is a little more enlightening. They are aquatic to semi-aquatic and can survive in subtropical to colder temperate climates. However, as their name suggests, crayfish snakes are only found in areas where crayfish, their primary food source, can be found (Holman, 2000). The highly specialized diet of members of this genus indicates that even though crayfish remains have not been recovered from the Gray Site, and due to the fragile nature of their

exoskeletons they may never be, it is reasonable to assume that they, or a closely related arthropod, were present.

Conclusions

The Gray Fossil Site provides a window into a part of geologic history that has been underrepresented in the eastern United States. Especially since this locality does not represent the grasslands that dominate other Miocene sites, it is an important tool for interpreting the larger picture of Hemphillian ecosystems. The Gray Site has already produced many unusual and scientifically important discoveries, but paleontologists there have barely scratched the surface of what the Site contains.

Even the most preliminary studies are helping build a picture of the environment represented by this site. The fossil beds are yielding extremely diverse fossils of plants, vertebrates, and invertebrates, giving scientists a better understanding of the entire ecosystem. Already, hundreds of snake remains have been discovered, but only a few have yet to be studied in detail. Only further studies will offer a more complete explanation of snake diversity in East Tennessee during the Miocene.

Currently, the Site has produced specimens of *cf. Sistrurus*, *cf. Regina*, and *cf. Vipera*. The specimen of *Regina* helps widen the understanding of the ecosystem as a whole with its specialized dietary needs. The presence of *Vipera* adds to the mystery regarding the presence of so many unexpected Eurasian organisms in the eastern United States. If trends in this study reflect large scale patterns in the Gray Site, the seemingly high ratio of poisonous to nonpoisonous snakes present there must also be addressed. As is often the case in preliminary paleoecology studies, only further excavation and research will be able to give answers to these questions.

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