

Trends in plant-insect interactions in the Cenozoic

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ABSTRACT

The Cenozoic era was a time of global-scale changes not only in climate, but also in the levels of angiosperm and insect diversity. Previous work on plant-insect relationships suggests that these temporal and climatic factors may have played a role in the evolution of such interactions. To test these hypotheses, a study of the patterns of insect mediated leaf damage was conducted by comparing six, well-preserved lacustrine deposits in western North America. The Cenozoic formations examined span a 30 million year time interval and have varying climate that allowed us to determine which variables might be better predictors of the amount and types of insect damage present in these fossil assemblages.

Two-thousand three hundred and ninety leaves were examined in total to measure overall damage levels for each assemblage, as well as damage levels for specific plant families. Plant families were chosen because they appeared in more than one assemblage, and this would provide a control for overall taxonomic differences that might exist between assemblages. For sites where greater information about the depositional environment was known, a chi-square analysis was used to further determine whether the position of a deposit relative to the lake margin had an effect on insect damage levels.

Neither overall assemblage damage levels nor damage levels within specific families were shown to correlate with climatic factors (temperature and precipitation) or age. Furthermore, significant differences in damage levels were recorded in a single lacustrine deposit depending on whether an assemblage was preserved near- or offshore, and whether it was on the east or west side of the lake. These findings suggest that there are many micro-scale climatic and environmental factors that must be taken into account and controlled for when making macro-scale time and space comparisons of insect feeding damage.

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1. Introduction

Plants and insects are the two most species-rich groups, and together they make up most of the Earth's biodiversity (Wilf and Labandeira 1999). Given the strong positive correlation between the regional richness of plant and insect species (Gaston 1992), and the fact that phytophagous insects constitute over a quarter of all macroscopic organisms (Bernays and Chapman 1994) it becomes apparent that interactions between these two groups are very important. In fact, researchers have suggested that the biodiversity of both groups are a result of these numerous interactions and subsequent coevolution (Ehrlich and Raven 1964).

Coevolution, as defined by Janzen (1980), is “an evolutionary change in a trait of the individuals of one population in response to a trait of the individuals of a second population, followed by an evolutionary response of the second population to the change in the first.” This model is particularly attractive for describing the evolution of insect-plant interactions because over 75% of all plant-feeding insects are monophagous or oligophagous, suggesting that insect herbivores have very specialized relationships with their host-plants (Bernays and Chapman 1994). These highly specialized relationships allow the insect to develop many adaptations for obtaining nutrients and resources from the host plant, and in turn also allow the host plant to develop defenses against the insect herbivore. It is believed that this pattern of plant defense and insect counter-defense has, over time, given rise to the current number of insect and plant species (Ehrlich and Raven 1964).

While many studies have focused on the coevolutionary aspects of insect-plant interactions, recent research suggests that climatic factors may also affect the evolution of insect-plant interactions. The latitudinal hypothesis predicts that as latitude decreases insect and plant species diversity should increase such that greater herbivore pressure is exerted on each host plant as temperature increases, resulting in greater leaf damage (Wilf and Labandeira 1999). Wilf and Labandeira (1999) tested this hypothesis by documenting and characterizing leaf damage on fossil leaves from the Paleocene and Eocene, a period of time where temperatures increased. As they expected, insect damage increased with the increase in global temperature. Other studies (Smith 2000; Wilf et al. 2001) confirmed this general trend by documenting decreasing levels of herbivory during the middle to late Eocene, a time of global cooling.

Although these models provide a useful framework for thinking about the possible factors affecting plant-insect interactions, neither one has been used to look at insect-plant interactions at time scales greater than 12 my. This study proposes to study interactions over a 30 my time period by comparing data from previous studies with data collected from the Green River, Florissant, Crede, Latah, Stewart Valley and Buffalo Canyon formations. In addition to the broader time interval, these formations have varying climate parameters that will allow us to determine whether insect damage patterns in the fossil record more closely follow the predictions of the coevolutionary model or the climate-driven model for insect-plant interactions.

2. Methods and Materials

A study of two competing models of the evolution of plant-insect interactions was conducted by comparing the fossil flora from six well-preserved lacustrine deposits in western North America. See Figure 1. The two models examined were the climate-driven model (Wilf and Labandeira 1999) and the coevolutionary model (Smith, In Press). The predictions of the

climate driven model suggest that localities with higher mean annual temperatures (MAT) and/or mean annual precipitation (MAP) should have higher damage levels, while the predictions of the coevolutionary model suggest that older deposits should have lower levels of insect damage than geologically younger deposits.

To test these hypotheses damage levels were calculated for the entire floral assemblage at each formation. Damage levels were also calculated separately for families occurring in multiple formations to control for possible taxonomic differences. Additionally, for the Florissant and Stewart Valley formation, where more information was known about the depositional environment, we examined whether the position of the deposit relative to the lake margins affected insect damage levels.

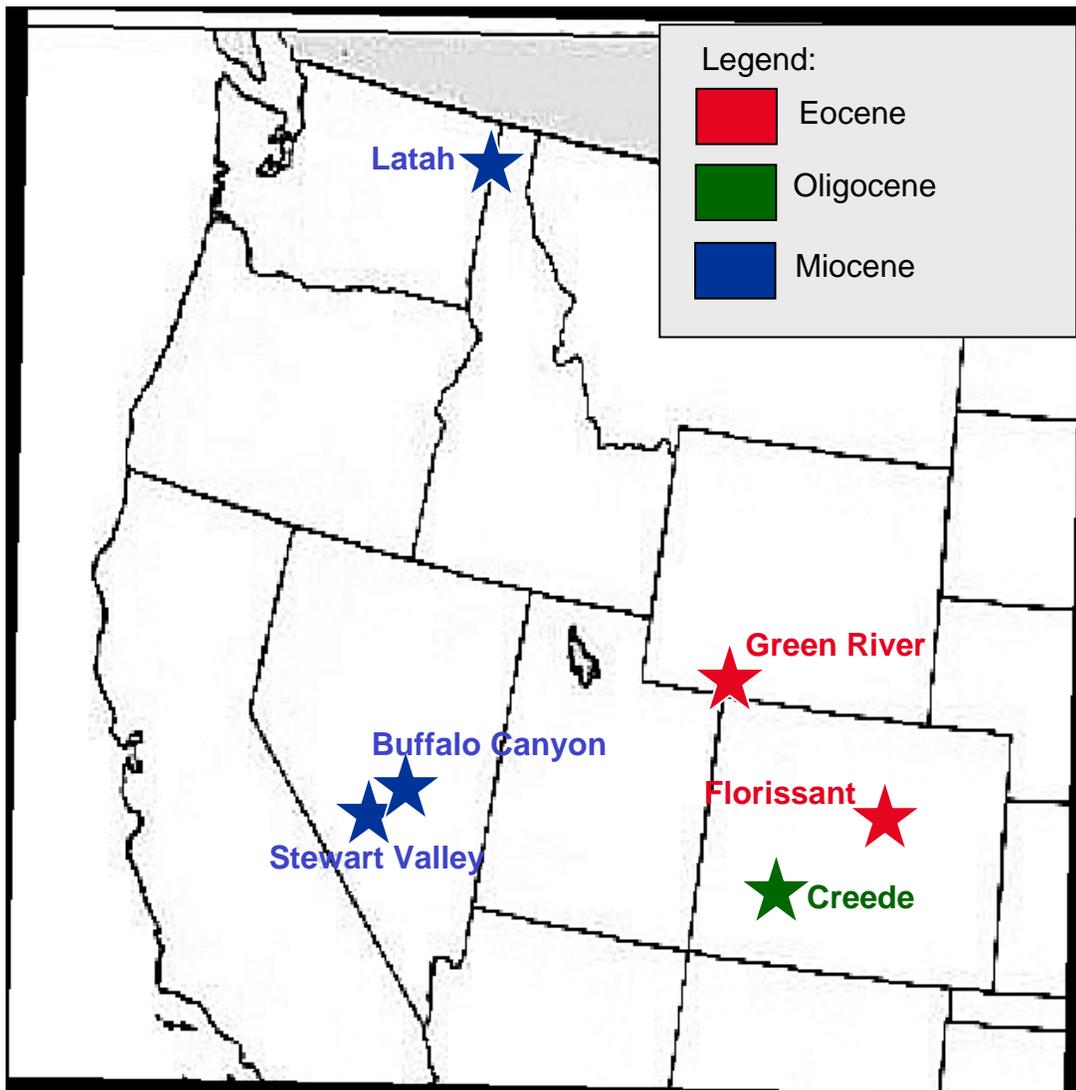


Figure 1. Map of western North America with fossil formation locations.

a. Geologic Setting of Study Sites

1.) GREEN RIVER FORMATION

The Green River Formation is a 45 my old (H. Schorn, pers.Comm. 2007) lacustrine deposit that consisted of three, relatively large, shallow lakes whose margins fluctuated with the seasons. The ancient lakes spanned three states (Colorado, Wyoming, and Utah), and had a long geologic duration, existing from the late Paleocene to the middle Eocene. The Eocene climate was subtropical to warm temperate, with a mean annual temperature (MAT) of 16.6°C and a mean annual precipitation (MAP) of 22.5 cm (H. Schorn, pers.Comm. 2007).

2.) FLORISSANT FORMATION

The Florissant formation has been dated at 34 my (H. Schorn, pers.Comm. 2007), and the fossil beds were deposited when volcanic mudflows blocked a stream flowing through the valley producing a long, narrow lake. The paleoenvironmental conditions, as indicated by the flora and sediments, were likely temperate with relatively warm winters and hot summers (MacGinnitie, 1953). The MAT and MAP (as determined by CLAMP) were approximately 12.2° C and 18.5 cm, respectively (H. Schorn, pers.Comm. 2007).

3.) CREEDE FORMATION

The Creede Formation, located in southwestern Colorado, was once a site of active volcanism. A large eruption 27.4 mya created a caldera that later became a shallow mountain lake. The MAT was 11.4° C and the MAP was 13.5 cm, with dry summers and most precipitation occurring as snow (Wolfe and Schorn 1989).

4.) LATAH FORMATION

The Latah Formation was formed from the damming of ancestral streams by the Columbia River Basalts. The Lower to Middle Miocene flora has been dated at 16 Ma, with a MAT of 10.2° C and a MAP of 32.5 cm (H. Schorn, pers.Comm. 2007).

5.) BUFFALO CANYON

The Buffalo Canyon Formation was formed from drainage into basins created as a result of Basin and Range extension in western North America 15.6 mya (H.Schorn, pers.Comm. 2007). The MAT was 9.4° C and the MAP was 14.5 cm (H.Schorn, pers. Comm. 2007).

6.) STEWART VALLEY

The Stewart Valley Formation was formed from drainage into basins created as a result of Basin and Range extension in western North America 14.5 mya. The MAT was 10.9° C and the MAP was 12 cm.

b. Assessment of Herbivory

Each fossil leaf was examined for the presence or absence of leaf damage. Those leaves bearing damage were categorized as belonging to one of five functional feeding groups: 1) hole-feeding: external foliage feeding in which an insect feeds through the leaf leaving behind a hole; 2) margin feeding: external foliage feeding in which an insect feeds on the margin of the leaf; 3) skeletonizing: external foliage feeding in which an insect feeds on the soft tissues of the leaf, but does not feed on the veins; 4) leaf mining: internal feeding in which an immature insect lives and feeds within the leaf layers without eliciting a major histological response; 5) galling: internal

feeding in which an insect feeds and lives between the leaf tissue layers and the plant responds by developing histologically anomalous leaf tissue around the site (Labandeira 1998; Smith, In press). See Figure 3.

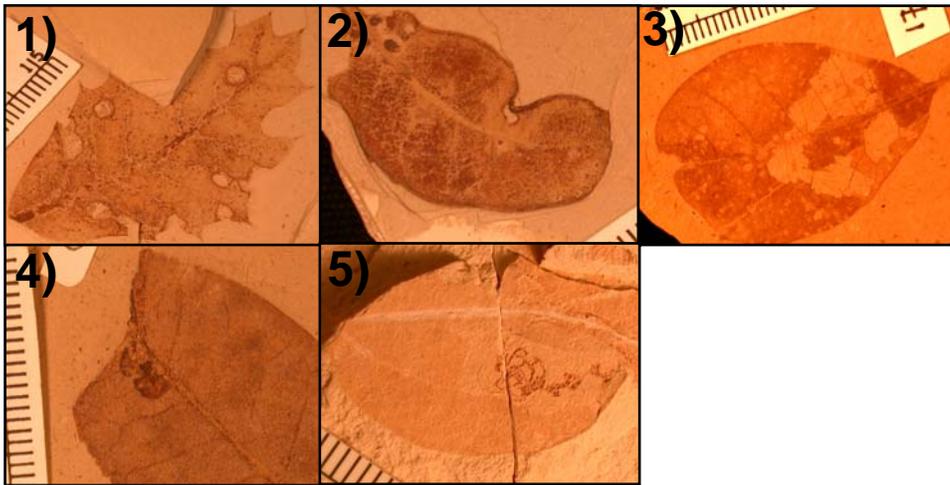


Figure 3. Insect Damage Types: 1)Hole-feed, 2)Margin-feed, 3)Skeletonizing, 4)Galling, 5)Leaf-mining.

The length and width of each leaf was also measured using digital calipers. Leaves with an area of less than 1 cm² were omitted from the study, as were leaves where the preservation quality hindered our ability to observe leaf damage.

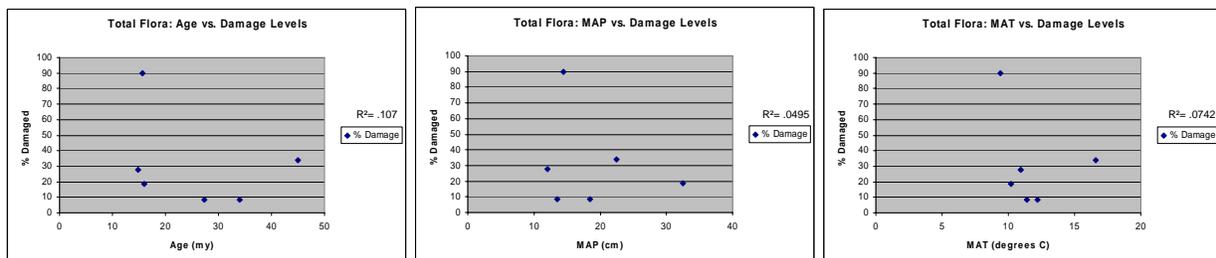
c. Statistical Methods

A linear regression was used to determine if there was a correlation between both the climatic and temporal variables and observed levels of insect damage. Chi-square analyses were also performed to determine whether the position of a deposit relative to the lake margin affected insect damage levels.

3. Results

a. Total Flora

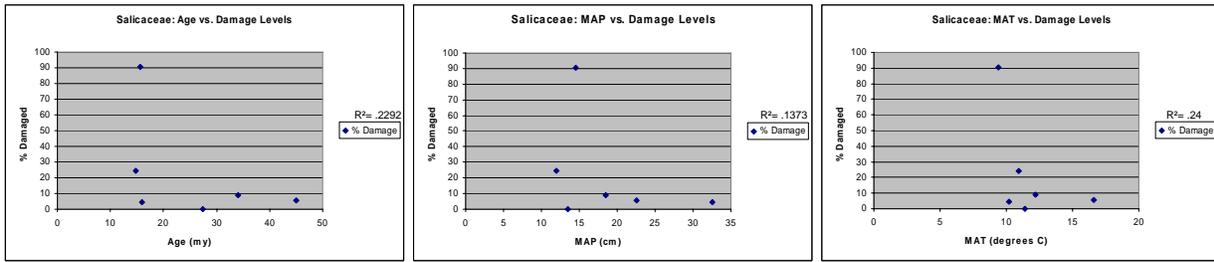
Overall insect damage levels did not show any correlation with mean annual temperature, mean annual precipitation, or age of formation.



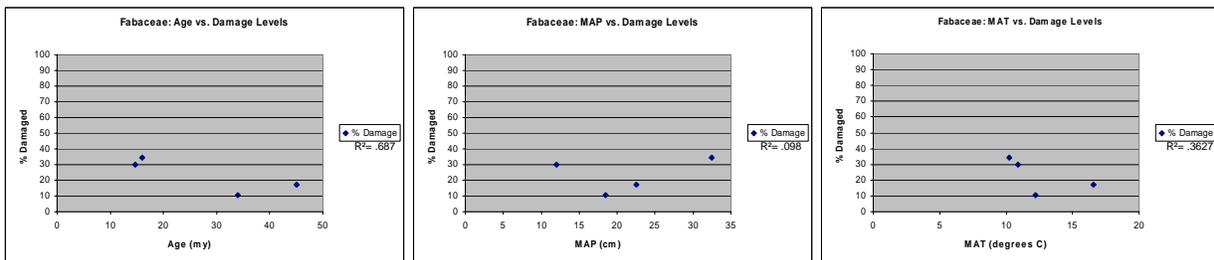
b. Salicaceae and Fabaceae

Only one family, Salicaceae, was abundant across all six formations. However the Salicaceae from the Creede formation were excluded from the study because they were all less

than 1 cm². For the remaining five assemblages, there was found to be no correlation between MAT, MAP, or age of formation and insect damage levels within the Salicaceae family.



The next most abundant family, the Fabaceae, was found in four of the six formations: Green River, Florissant, Latah, and Stewart Valley. Again, no correlation was shown between MAT, MAP, or age of formation and insect damage levels within the Fabaceae family.



c. Depositional Environment

An examination of Florissant deposits revealed significant differences in damage levels between different depositional environments. For example, there was a significant difference ($\chi^2 = 17.549$, $P < .0001$) between damage levels observed from the nearshore locality (Locality #83013) and the offshore locality (Locality #83014). Insect damage levels were also found to be significantly different ($\chi^2 = 64.788$, $P < .0001$) when localities were located on different sides of the same lake deposit. See Figure 2.

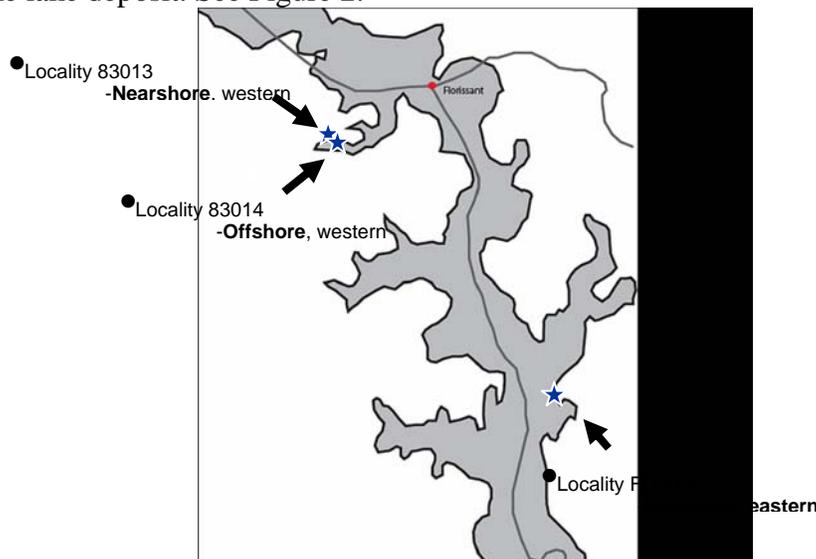
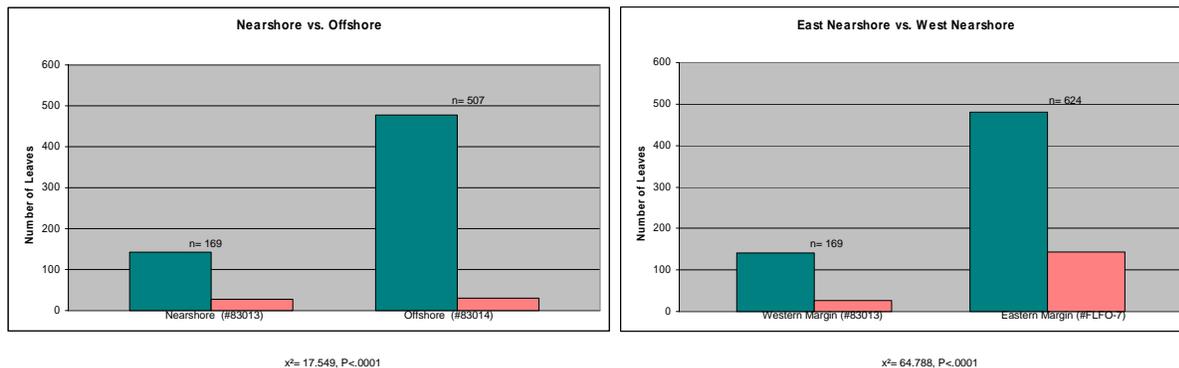


Figure 2. Map of Florissant Localities



4. Discussion

Evidence of plant-insect interactions in the North America Cenozoic fossil record has given researchers the opportunity to study the evolution of this important relationship. Although previous research suggests that temporal and climatic variables have affected the evolution of these interactions, our data show that there is no readily discernible pattern to support either of these hypotheses. Rather, our data highlight the importance of controlling for micro-scale environmental and climatic factors that could possibly obscure the larger trends in plant-insect interactions.

Despite the fact that all fossils were collected from lacustrine depositional environments, there were still visible differences in preservation quality. Fossil plants from the Creede formation seemed to have the poorest preservational quality of all of the assemblages, with low levels of contrast between the fossil and the surrounding matrix, as well as poorly defined leaf margins. Leaves from the Latah formation also seemed to have relatively poor preservational quality, with many of the fossils appearing to be blotchy and faded in places. However, because the contrast between the surrounding matrix and the fossil were quite prominent, the observed fading may not be due to preservational issues, but rather due to the fact that the fossils had been lacquered. In contrast, leaves from the Green River and Florissant formation had excellent preservation, with high levels of contrast between the fossil and the surrounding matrix, and well-defined margins with visible venation.

The data indicate that size biases may have also been present in our sample. While the Latah formation had no leaves excluded from the study for size, over a quarter of all leaves examined from the Creede formation were excluded for size considerations. Within each formation there seemed to be only certain families that needed to be excluded due to size, and these families varied between the sites. For the Creede formation, the Rosaceae and Salicaceae families accounted for 25% of all leaves smaller than 1 cm², while in the Florissant formation the Anacardiaceae, Proteaceae, Roseceae, and Sapindaceae accounted for the 17% of all excluded specimens. The fact that the same families did not consistently have the smallest leaves in each of the formations suggests that there was a preservation bias related to size at each of the sites, as opposed to some formations simply having a taxonomic composition of larger leaves than others.

Furthermore, there were only two instances of leaf-mining recorded in a study sample of over two thousand leaves. Given that the insects responsible for leaf-mining have been found and documented throughout these formations; and the fact that leaf-mining, as a functional feeding group, has existed since the Mesozoic (Herrera and Pellmyr, 2002), it is curious that so few examples occurred when leaf-mining clearly existed at the time. This provides evidence that the overall lack of internal damage is not a function of a biological pattern, but rather a preservational problem that needs to be accounted for in future studies.

These preservational biases may be attributed to the fact that not all of the lakes sampled were created in the same manner. Within just the Rocky Mountain deposits alone there were significant differences in the history of formation of each lake. The Green River formation consisted of a series of three, freshwater lakes that formed from drainage into basins created by the uplift of the Rocky Mountains. The Florissant formation, on the other hand, was created when volcanic mudflows blocked an ancient river, producing a dendritic-like lake that was 12-miles long. Finally, the Creede formation was a caldera lake. The deposition of sediments in each of these different lake types will also vary, and this variance will lead to differences not only in what gets preserved, but also in quality.

Differences in lake types may also be responsible for the taxonomic differences observed between the formations. Each of the ancient lakes most likely fostered different environments and niches that helped dictate which plant species would colonize the margins. Controlling for taxonomic differences is especially important given the highly specialized interactions of plant and insects, and the possibility that this selective feeding on some plant families and not others, may be responsible for the differences in damage levels between sites. Evidence of this selective feeding was observed within the Creede formation, where only one out of nine families, the Rosaceae, accounted for all damage observed at the formation. Within the other formations there also seemed to be families that were preferred more over others, and these families were not always the most abundant in the formations (Smith, In press).

Even within a deposit, there can be environmental and preservational variability that can cause herbivory levels measured in the same deposit, but at different localities, to differ. Previous literature has shown that the position of a deposit relative to the lake margin has led to taphonomic differences in the preservation of fossil plants and insects in Eocene lakes (Wilson 1980, Smith, In press). Our study shows that some of these same biases may apply to leaves bearing insect damage, as significant differences were found between both nearshore and offshore sites, and sites located on the eastern and western margins of the Florissant lake.

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