Taphonomy of Insects from the Florissant Formation, Colorado

by

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This thesis entitled:
Taphonomy of Insects from the Florissant Formation, Colorado
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The final copy of this thesis has been examined by the signatories, and we
Find that both the content and the form meet acceptable presentation standards
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Thoene, Jenell Jo (M.S., Museum and Field Studies)

Taphonomy of Insects from the Florissant Formation, Colorado

Thesis directed by Associate Professor Dena M. Smith

The purpose of this study is to understand how sedimentary environments influence fossil insect preservation. Eight hundred and twenty-four fossil insects were collected from the lacustrine deposits of the Florissant Formation (Late Eocene) to study how sedimentary environments affect the completeness, quality, and orientation of fossil insects. Also examined was the level of decay and disarticulation different insect orders exhibited amongst different sedimentary environments, as well as the representation of insect diversity throughout an extensively sampled section of the Florissant Formation. Two years of intensive field collecting resulted in a collection that was under-sampled and therefore did not capture the diversity of fossil insects in the Florissant Formation. Thus, to study insect diversity within the Florissant Formation, sampling efforts must increase greatly. No significant differences were found in insect completeness, preservation quality, or orientation between the different sedimentary environments; however, there were significantly smaller specimens found in the siltstone layer. The diatom and bacterially-generated biofilm model as a mechanism for exceptional preservation is no longer supported. Finally, levels of disarticulation, decay, and the orientation varied depending on the insect order. It is recommended that actualistic taphonomic studies be conducted to further understand how insects settle through the water column.

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INTRODUCTION

Insects have a rich fossil record. However, depositional environments and large scale taphonomic factors that influence the fossilization of insect assemblages are poorly understood and rarely described in the paleoentomologic literature (Smith and Moe-Hoffman, 2007). The bulk of the research and literature currently centers on the molecular taphonomy of insect cuticles and the taxonomic descriptions of fossil insects. Understanding the depositional environments that influence taphonomic processes is important in order to be able to use these fossil insects for phylogenetic and paleobiological studies (Martínez-Délclòs et al., 2004), and to help reconstruct paleoenvironments.

Exceptionally preserved insect fossils occur in a variety of environmental settings, including lake deposits, amber, peat, tar deposits, and calcium carbonate precipitates (Martínez-Délclòs et al., 2004). Among the environments that best preserve insects are in amber and fine-grained laminated sediments in lacustrine and shallow marine settings (Martínez-Délclòs et al., 2004). These environments are excellent for preserving the labile soft-tissues and the cuticle of insects. The most remarkably preserved insects occur in *Konservat-Lagerstätten*, where non-biomineralized soft part tissues are preserved in the form of impressions or compressions. Lagerstätten deposits are often the result of anoxic conditions, such as oxygen-free lake mud, that can prevent bacterial decomposition for the delicate soft body parts to be preserved. Preserving non-biomineralized tissues of insects is a complex process, not only involving microbial activity, but geochemistry of the environment as well (Allison and Briggs, 1991a,b). Preservation of these non-biomineralized tissues is crucial in providing palaeobiological data that cannot be obtained from the "shelly" fossil record (Briggs, 1995). Microbial mats in lagerstätten are also thought to help aid in the taphonomic process of insects by secreting biofilms that encapsulate and protect the fossil material (O'Brien et al., 2008). Such biofilms have been documented around Florissant insect fossils (O'Brien et al., 2008).

This study will focus on three primary questions related to the preservation of fossil insects in lacustrine deposits: 1) how does sedimentary environment affect insect completeness, quality, and orientation, 2) are different taxonomic groups more susceptible to decay and disarticulation than others, and 3) how representative of insect diversity is on an extensively sampled section related to the overall insect diversity in the Florissant Formation?

Background

Insect taphonomy is a key component for interpreting sedimentary and ecological paleoenvironments where insects lived and died. Taphonomic processes influence phylogenetic and paleobiogeographic studies by assessing the factors that affect insect accumulation (Smith and Moe-Hoffman, 2007), and is a requirement for recreating fossil insect assemblages and establishing the origin and extinction of insect groups. Understanding the taphonomic conditions and the biases introduced by the processes of fossilization is important in order to interpret the role of insects in their ecosystem (Martínez-Délclòs et al., 2004).

Several studies have focused on what the insect cuticle can tell researchers about organic matter diagenesis and kerogen formation by the selective preservation of chemically resistant molecules in the insect cuticle (Stankiweicz et al., 1998). Other research has discovered that fossilized insect cuticle can help provide evidence of the factors controlling the growth of minerals in the sediments (Martínez-Délclòs et al., 2004). Insects are often preserved as organic remains of the cuticle in lacustrine deposits, or as a mold where the cuticle is lost during diagenesis or weathering (Martínez-Délclòs et al., 1995). The morphology of the insect exoskeleton can be replicated by early mineralization in calcium, pyrite, or calcium phosphate (McCobb et al 1998; Duncan et al 1998), indicating the type of geological setting in which the insects were deposited and the environmental factors that influenced mineralization, such as water temperature, current flow, density, and salinity.

It has been shown that the ecology and morphology of insects and depositional environments also influence preservation. Smith and Moe-Hoffman (2007) found that when studying the taphonomy of fossil flies from two different localities of the Florissant Formation, there was a significant difference in the size of specimens preserved at the localities. Larger specimens were found at the offshore locality of the lake, and although there was a greater abundance of specimens offshore, species richness did not differ between the two localities (Smith and Moe-Hoffman, 2007). Wilson (1988) also found differences between near shore and offshore environments when examining the preservation of insects in lacustrine deposits. Wilson found that more fossil insects were preserved in near shore lacustrine deposits of Tertiary lakes in North America. Yet, the preservation quality of the specimens was not as pristine as the offshore deposits, which were less disarticulated. Clearly, the environment in which insects are deposited plays an important role in the preservation of these organisms.

To date, there have been four general ideas of how the insects in the Florissant Formation have been preserved (see Table 1). The first idea is the Insect Pompeii model proposed by Cockerell. Cockerell (1908) suggested that during large volcanic eruptions, violent gusts of wind and blowing cinders would form a large cloud of fine ash that carry down flying insects into the bottom of the lake, preserving them in fine grained siltstone layers. This scenario is not supported by the geologic evidence.

Table 1 – Summary of preservation models and the type of fossilization found in each model.

Preservation Model	Expected Type of Fossilization
Insect Pompeii	Dismissed – No geologic evidence in support.
Boiling Lake	Dismissed – No geologic evidence in support.
Anoxic environment	Possible mechanism for exceptional preservation Sediment: sapropel and siltstone Insects: all insects will be found in these layers since the presence of these layers indicates an environment of accumulation that is unoxygenated with minimal circulation (McLeroy and Anderson, 1966). Completeness: Complete Quality: Good Orientation: No specific orientation Size sorting: None
Diatom and Bacterially-Generated Biofilm	Possible mechanism for exceptional preservation. Sediment: diatomaceous shale Insects: all insects will be preserved in shale layers due to the algal and bacterial biofilm mats that formed and protected the microfossils from deterioration (Harding and Chant, 2000; O'Brien et al., 2002). Completeness: Very Complete Quality: Excellent Orientation: No specific orientation Size sorting: None

The second proposed model of preservation at Florissant was proposed by Melander in 1949 in which he claimed that outbursts of molten lava from the nearby volcanic field boiled the water of the ancient lake and "sterilized" the insect bodies. The result of the boiling water was thought to have left the abdomens of the insects bloated and expanded, evidenced by the wide interstices between the sclerites of the fossil insects (Melander, 1949). Melander (1949) claims that such processes can be seen in Yellowstone National Park when an insect drops into the hot pools. The bloated insects would then be covered with ash, preserving their extended abdomens as fossils. Licht (1986) also proposed that as ash from a volcano entered the lake, it raised the temperature of the water, killing spiders that had fallen within and causing them to extend their legs in a relaxed position. Microfossils are not associated with airborne ashbeds and there are no lava flows in the Florissant Formation, therefore neither of these scenarios is supported by the geologic record.

The third model proposed by McLeroy and Anderson (1966), focused on sedimentological and stratigraphic evidence and emphasized that preservation relies on a chemically stratified lake with minimal circulation and an anoxic lake bottom. The ancient lake would have been slightly alkaline in the upper lever, and oxygen depleted in the lower level (McLeroy and Anderson, 1966). Organic material that sank to the bottom of the lake would have only partially decomposed through reactions with anaerobic bacteria, and this partially decomposed material would have accumulated as sapropel (McLeroy and Anderson, 1966).

The fourth model of preservation that has been proposed is that of diatoms and bacterially generated biofilms acting as agents of preservation. In this model diatoms or bacteria are thought to produce a biofilm that encapsulates the remains of insects, protecting them from further deterioration (Harding and Chant, 2000; O’Brien et al., 2002). The shale layers of the Florissant Formation are the only sedimentary layers that contain abundant diatomaceous material and these appear to be the most fossil rich layers as well. Although this study does not directly test these models, the results will have a bearing on the likelihood of the models.

Florissant Geology

The Florissant Formation of the Late Eocene is an ideal location for studying the preservation of fossil insects, as it is a lacustrine Lagerstätten deposit known for its exceptional preservation of fossil insects (Evanoff et al., 2001) and nearly 1,580 insect species and Arachnids have been studied and described (Meyer 2003, Meyer et al. 2004). The lake was formed by a large lahar (volcanic debris flow) from the Thirty-Nine Mile Volcanic Field, damming the original drainage basin and forming two lake episodes by impoundment of the Florissant paleodrainage from lahars (Evanoff et al., 2001; Meyer, 2003). The Florissant Formation is comprised of shale, tuffaceous mudstone and siltstone, tuff, and volcaniclastic sandstone and conglomerate, and consists of six informal units: the lower shale unit, lower mudstone unit, middle shale unit, caprock conglomerate unit, upper shale unit, and upper pumice conglomerate (Evanoff et al., 2001, Figure 1). The three fossiliferous “paper shale” units are thinly laminated shales composed of the alternation of couplets of diatoms and weathered volcanic ash. These couplets average less than or equal to 1 mm in thickness (O’Brien et al., 2002), and are thought to represent annual layers (varves) produced by spring diatom blooms (McLeroy and Anderson 1966). However, O’Brien et al. (2002) and others believe that the spring diatom blooms creating the shale layers not only resulted from seasonal variations, but from influx of ash and clay into the lake from runoff, altering the chemistry of the lake and promoting the growth of diatoms (O’Brien et al., 2002). Depositional duration of these diatom couplets is thought to represent 2,500-5,000 years (McLeroy and Anderson, 1966). ^{40}Ar/^{39}Ar dating indicates that the upper part of the Florissant Formation was deposited 34.07 ± 0.10 Ma (Evanoff et al., 2001). The middle shale unit is where insect fossils for this study were collected.

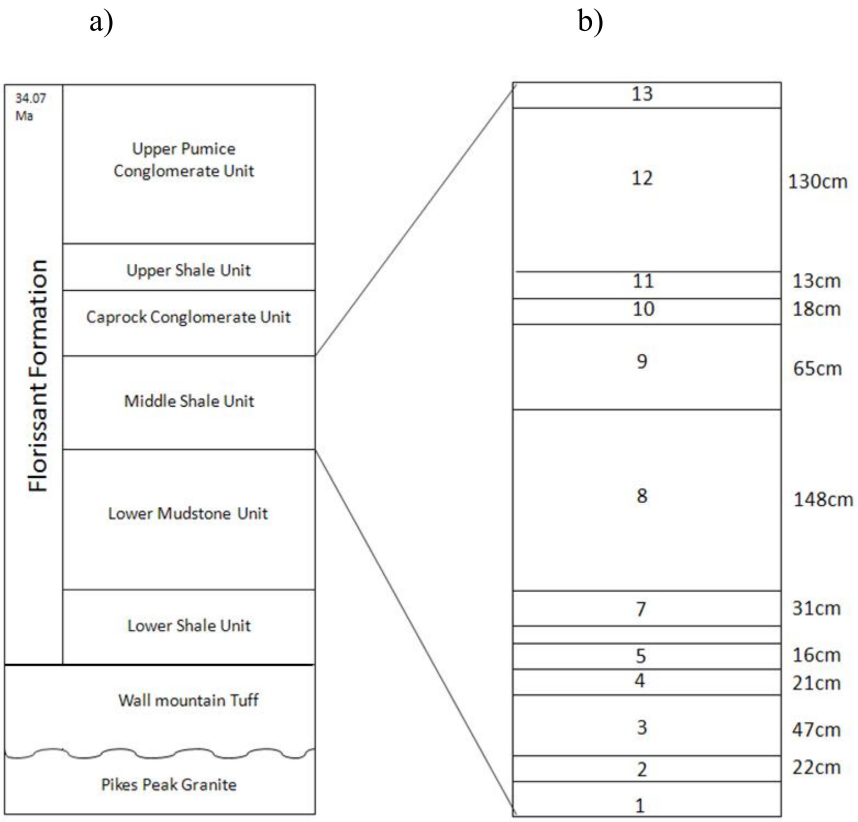

Figure 1 – Basic stratigraphy of the Florissant Formation redrawn from Evanoff et al., 2001 (a), and a specific section of the excavation site, Card 2010 (b).

CHAPTER 2:

METHODS

Fossil insects were collected from Florissant Fossil Beds National Monument in Teller County, Colorado during the summers of 2009 and 2010. The specimens were collected from FLFO Site 9 (equivalent to Inventory and Monitoring site 15) in the northwest area of the park. Based on current topography representing the ancient lake, it has been determined that the collection site is located near the center of ancient Lake Florissant, probably near the opening of a tributary inlet (Figure 2). The fossil insects were collected from the Middle Shale Unit of the Florissant Formation (Evanoff et al., 2001) by National Park staff and interns of Florissant Fossil Beds. The middle shale unit measured at this site consists of 13 informal units described by Katherine Card (Figure 3). Units 2, 4, and 8 are composed of alternating laminae of shale, siltstone, and tuff (Card, 2010; Figure 4). In contrast, Units 3, 5, 7, 9, and 12 consist of alternating layers of siltstone, mudstone, claystone, tuff, and very little shale (Card, 2010; Figure 4). Based on Card's (2010) stratigraphic column, it has been determined that the three most common sediment types in which insect fossils could be found is shale, siltstone, and mudstone. I will be using these three rock types to conduct the various taphonomic studies. The reason these three rock types were chosen for this study is because although they are very similar in grain size, siltstone has a slightly larger grain size (Table 2). In addition, siltstone was most likely deposited in a relatively higher energy event, whereas shale and mudstone were deposited in a low-energy suspension-settling event with the shale having a large diatom component as well. This will allow for a comparison of insect taphonomy in three different depositional settings.

Table 2 – Shale, mudstone, and siltstone geologic and environmental differences.

	Grain Size	**Environmental Energy**	**Seasonal/ Depositional Environment**
Shale	Clay < 4 µm and Siltstone Particles	low-energy	suspension-settling and abundant diatomaceous laminae
Mudstone	Clay < 4 µm and Siltstone Particles	low-energy	suspension-settling, rare diatoms
Siltstone	Coarsest; 4 to 62 µm	episodic high energy events	suspension-settling/ intense stream run-off, rare-absent diatoms

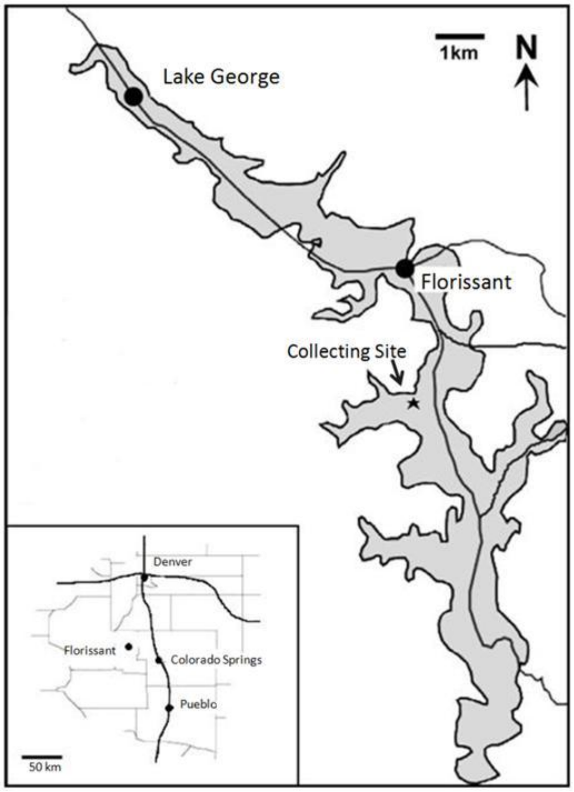

Figure 2 – Map of the ancient Florissant Lake with the current collecting site starred. Modified from Smith and Moe-Hoffman (2007).

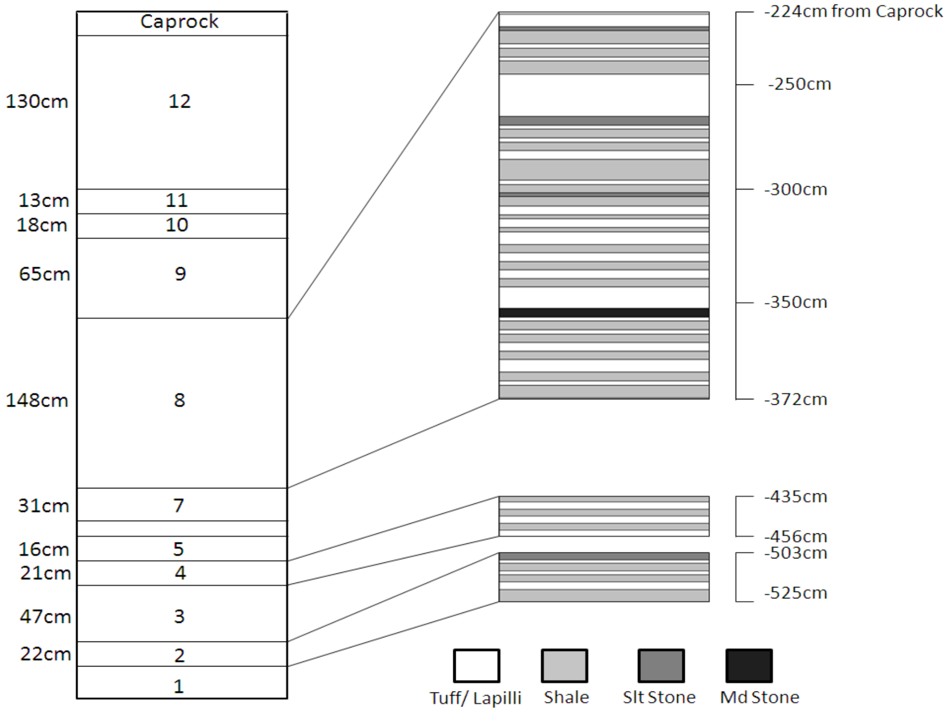

Figure 3 – Simplified version of shale layers from Katherine Card's stratigraphic column of the excavation site with units 2, 4, and 8 extensively sampled (2010).

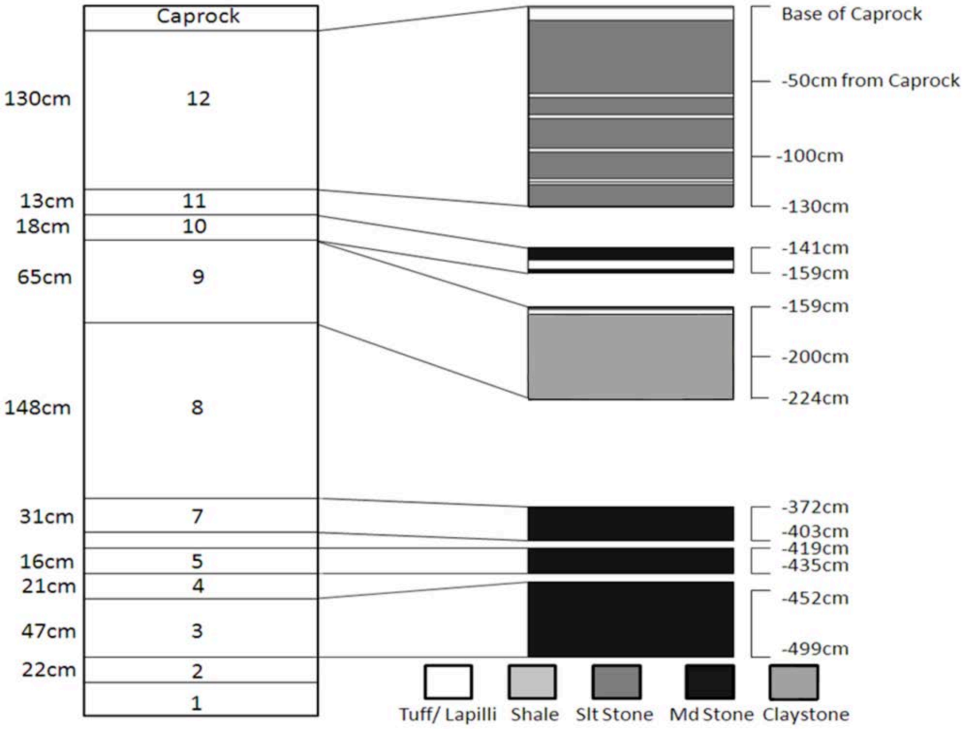

Figure 4 – Simplified version of siltstone, mudstone, and claystone layers from Card's stratigraphic column of the excavation site with units 3, 5, 7, and 12 extensively sampled (2010).

Stratigraphic levels were demarcated every 10cm along the trench of the collecting site to facilitate documentation of sedimentary environments. This startigraphic column was detailed by Card (2010). The base of the caprock at its contact with the middle shale was used as the datum for 0. All fossil insects encountered were collected, regardless of the quality of the preservation. When a specimen was collected, the date it was collected was recorded as well as the centimeter level from which it came, and who collected it. 824 fossil insects were collected during both years combined. The fossils were then sorted, grouped, and identified to the level of order and family when possible; these identifications used CSIRO (1991) and Borror, Tripplehorn and Johnson (1989). Specimens only from the shale layers were then categorized into morphotypes, which were distinguished by examining morphological characteristics and sorting into groups that were thought to represent distinct species groups. Morphological features used to distinguish different groups were wings and venation, antennae, presence of mouth parts, eyes, and head sutures (Smith and Moe-Hoffman, 2007).

Each individual fossil specimen was assessed based on completeness, quality, and orientation. For completeness, insects were categorized as complete (100%), incomplete (50-100%) or fragment (<50%). The quality of each specimen was then determined using the number of morphological characters present that could be used for identification of a specimen as well as criteria pre-programmed and defined in the National Park database software, Re:discovery (Re:discovery Software Inc, 2010; see Table 3). Each specimen was assigned a quality of excellent (no damage), good (minor damage), fair (some damage), or poor (significant damage) (Figure 5).

The orientation of each insect within the rock was then recorded as either dorsal or ventral side visible, lateral view visible, or twisted. Twisted specimens would often have the head pointing in one direction while the lower abdomen is pointed in an opposite direction, with morphological features of the abdomen hard to distinguish. Finally, the size of each specimen was recorded using digital calipers to measure the length and the width of the insect (Figure 6).

The most abundant and commonly occurring insect orders (Hymenoptera, Coleoptera, Diptera, and Hemiptera) were analyzed using their taphonomic data in JMP IN for Windows (SAS Institute, 1989-2000). Chi-square contingency tests were used to determine whether each of the four insect variables (completeness, quality, orientation, and size) is dependent on the main sediment types: shale, siltstone, and mudstone. Insects with an "unclear" orientation were left out of the orientation analysis so as to not skew the results. Additional chi-square contingency tests were conducted to determine whether each if the three taphonomic variables altered within shale and siltstone. Shale and siltstone insects were combined to conduct these contingency tests because results between the two rock types were not significantly different on their own. A one-way analysis of variance using a Tukey-Kramer test was used to determine if there is any bias in insect size depending on which sediment types these insects were deposited in.

To determine if the shale environment was effective at capturing insect diversity at the morphospecies level, an individual-based rarefaction analysis was performed using EcoSim 7.72 for Windows. Rarefaction allowed me to control for sampling and calculate species richness for each sample (stratigraphic interval). Chi-square contingency tests were then used to analyze whether there were differences within the shale sediment between each of the three taphonomic variables.

Table 3 – Detailed description of the quality assigned to each specimen.

Quality
Ex: Excellent [no damage or deterioration, at least three morphologic characters present]
GD: Good [minor damage, at least two morphologic characters present]
FR: Fair [some damage, at least one morphologic character present]
PR: Poor [significant damage, morphological characters not present]

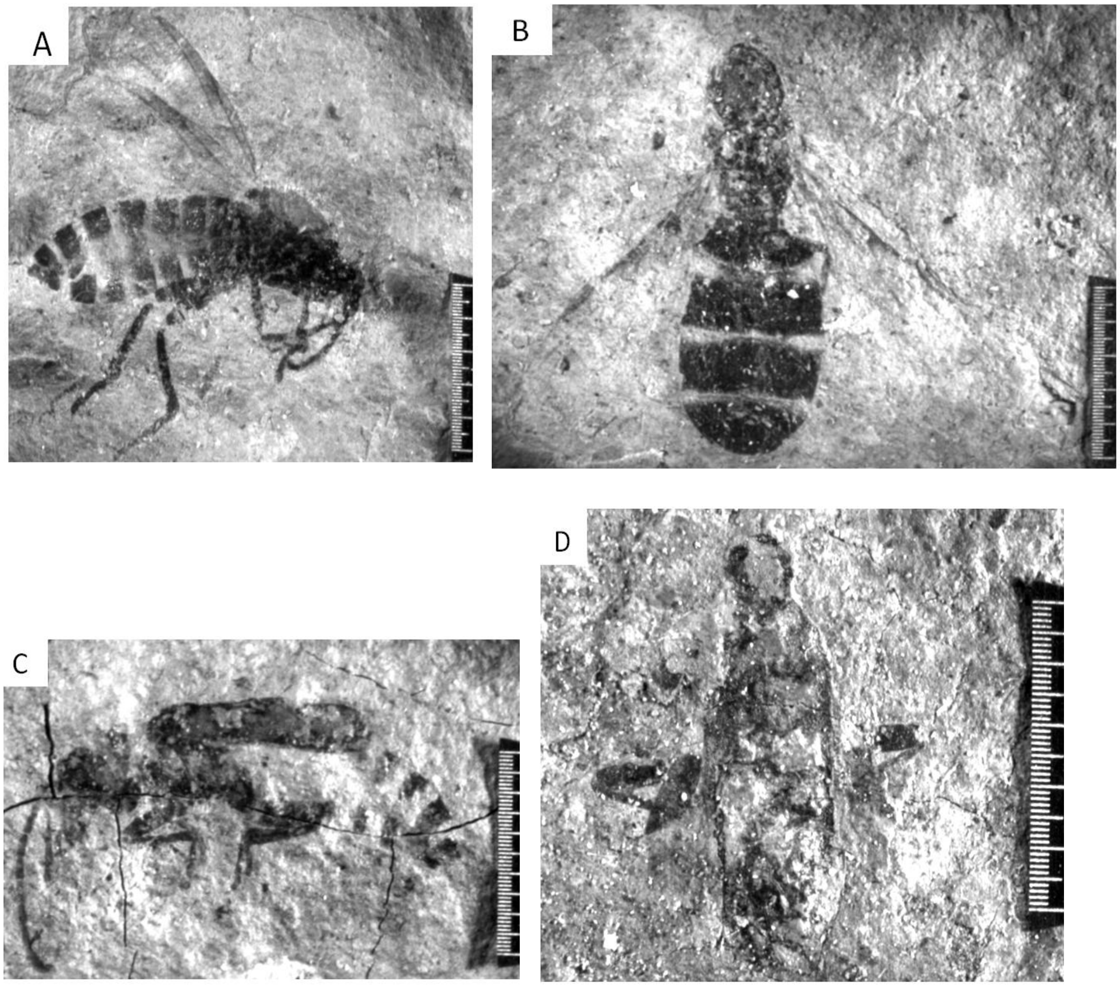

Figure 5 – Examples of insect specimen of different preservation qualities. Scale bar = 1 mm. A) Diptera, excellent (no damage, FLFO 7092). B) Hymenoptera, good (minor damage, FLFO 7320). C) Coleoptera, fair (some damage, FLFO 7743). D) Indeterminant, poor (significant damage, FLFO 7165).

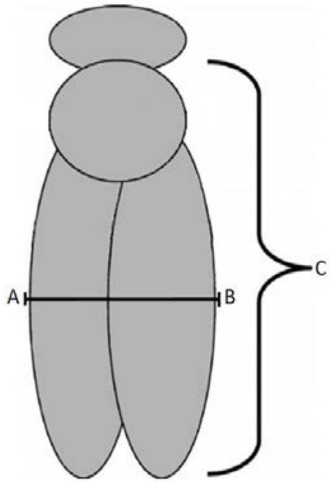

Figure 6 – Insect representation where width of the widest part of the insect was taken from A to B. Total length of the insect (thorax and abdomen) is characterized by C. Modified from Smith et al. 2006.

CHAPTER 3:

RESULTS

In total, 824 insects were collected from the section for this study. Insect fossils were preserved in all three rock types. There were 9 insect orders found overall, with the most abundant specimens being Hymenoptera (33%), Coleoptera (26%), Diptera (19%), and Hemiptera (9%). Fifteen percent of the specimens were not determinable to order (Figure 7). Of all of the insects identified to order, fifty-six percent were complete and forty-four percent were incomplete (Figure 8). Only ten percent of specimens were in excellent condition, and the majority (66%) had low (were either poor or fair) preservation quality (Figure 9). Of the insects collected, forty-six percent were dorsal-ventral oriented, forty-four percent were laterally oriented, two percent were twisted, and only eight percent had an orientation that could not be determined (Figure 10).

Completeness of a specimen was not dependent on the sediment type it was preserved in ($x^2 = 2.27$, df = 2, p = 0.32). There also was no difference in the preservation quality of specimens depending on the sediment type they were preserved in ($x^2 = 8.49$, df = 6, p = 0.20). Sediment type did not influence the orientation of insect specimens ($x^2 = 5.78$, df = 4, p = 0.259). Specimens preserved in the siltstone were significantly smaller in size (mean size 10.05 mm^2) than specimens preserved in shale and mudstone (F = 20.01, p <0.0001; Figure 11). Specimens preserved in mudstone and shale were not significantly different from one another (mean size 17.95 mm^2 and 16.77 mm^2, respectively).

When examining the combined shale and siltstone samples, Coleoptera and Hymenoptera were found to be much less disarticulated (77% and 64% complete) than Diptera and Hemiptera (52% and 46% complete; x^2 = 31.20, df = 3, p <0.0001; Figure 12). Although the majority of specimens were of fair preservation quality (41%), the majority of Dipteran and Hemipteran specimens were of low quality (69% fair to poor and 73% fair to poor), while coleopteran and hymenopteran specimens exhibited higher quality preservation (35% good to excellent, 42% good to excellent; x^2 = 23.95, df = 9, p = 0.0044; Figure 13). Nearly all Hemiptera (91%) were preserved in a dorso-vental position, whereas the other orders had the majority of specimens preserved in a lateral orientation and very few were twisted (x^2 = 57.73, df = 6, p<0.0001; Figure 14). Coleopteran specimens were significantly smaller than dipteran Specimens (mean size 11.05 and 17.88, respectively) but Diptera are not significantly larger than Hemiptera (15.86 mm^2) (F=5.85, p = 0.0006; Figure 15). Coleoptera have a mean size that is most similar to Hymenoptera (13.72 mm^2), but Coleoptera are not significantly smaller than Hemiptera (F=5.85, p = 0.0006; Figure 15). There is no statistical difference between Hemiptera and Hymenoptera. When focused on specimens preserved in the shale, Diptera (22.53 mm^2) are significantly larger than Coleoptera (13.45 mm^2), but are not significantly larger than Hemiptera (17.75 mm^2) (F=3.95, p = 0.0086; Figure 16). Hymenoptera (17.20 mm^2) and Hemiptera have a mean size larger than Coleoptera but they are not significantly larger (F=3.95, p = 0.0086; Figure 16). In contrast, when focused on the specimens preserved in siltstone, Hemiptera (13.94 mm^2) are significantly larger than Coleoptera (8.28 mm^2), but are not significantly larger than Diptera (11.53 mm^2) or Hymenoptera (9.39 mm^2). Hymenoptera and Diptera have a mean size that is larger than Coleoptera, but they are not significantly larger (F = 3.1663, p = 0.0249; Figure 17). There is no statistical difference between Diptera and Hymenoptera (F = 3.1663, p = 0.0249; Figure 17).

The individual-based rarefaction curve for all morphospecies preserved in shale does not come near asymptote (Figure 18). When sorted by order, it becomes clear that the Coleoptera are the most species rich, followed by Hymenoptera, then the Diptera and Hemiptera (Figure 19). All orders are undersampled, with Coleoptera being the most undersampled.

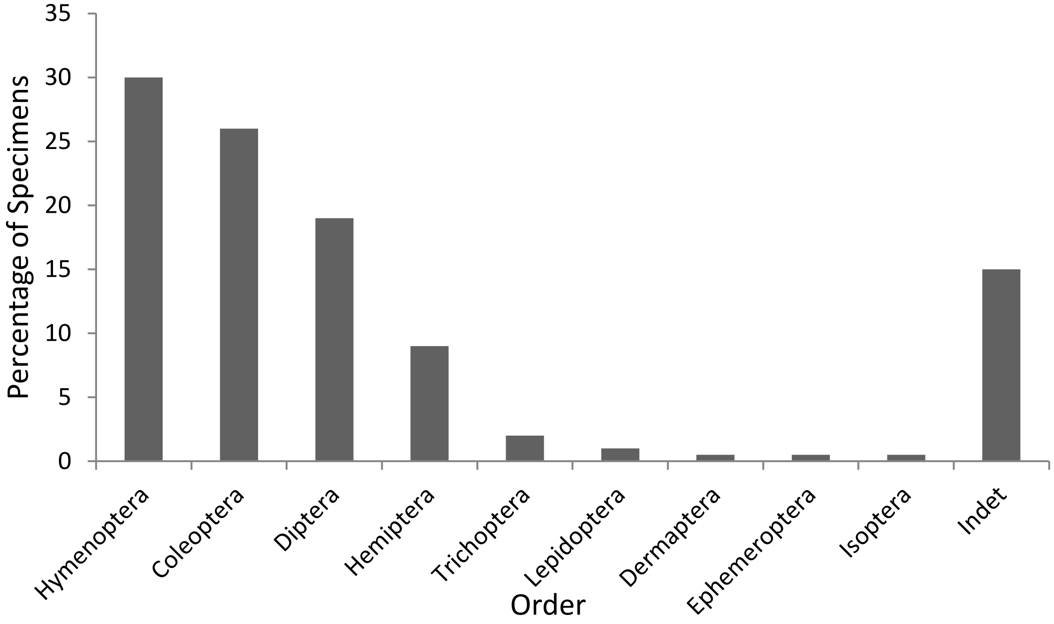

Figure 7 – Percentage of specimens from each order found during the excavation.

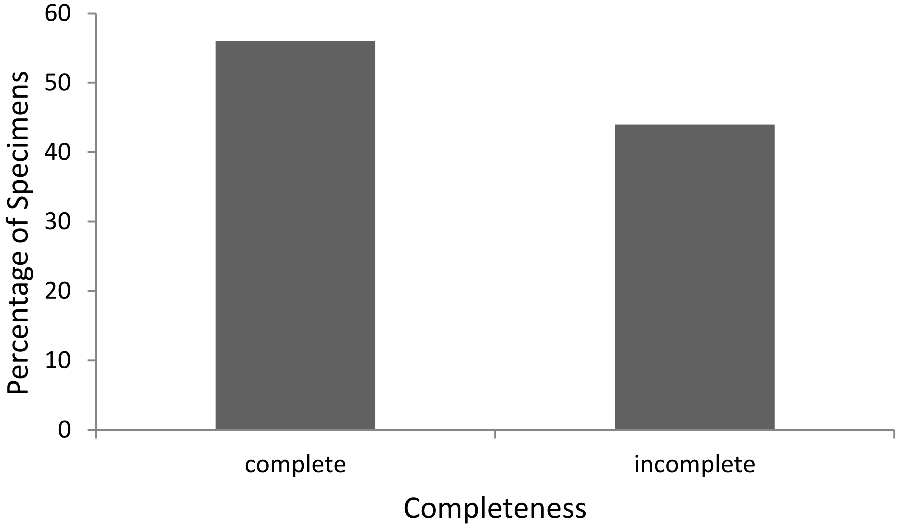

Figure 8 – Percentage of total specimens that were either complete or incomplete.

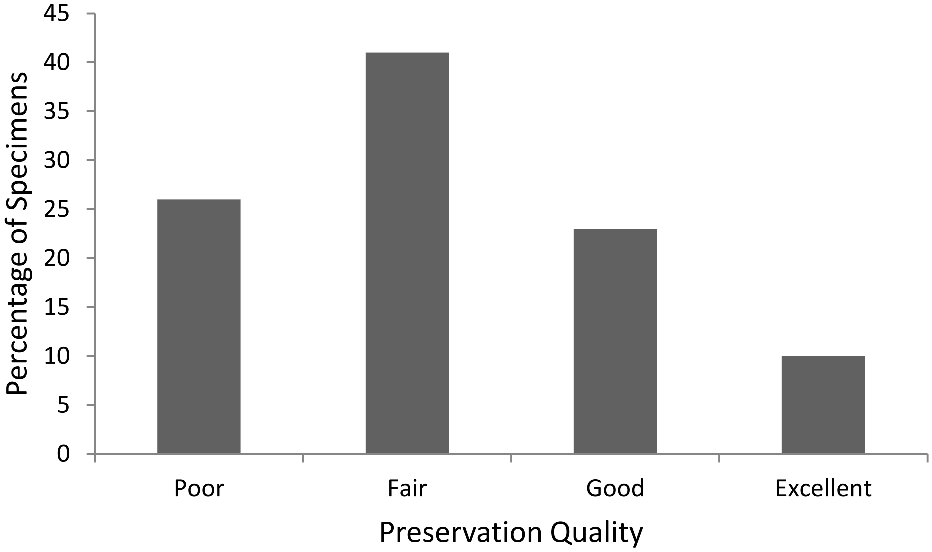

Figure 9 – Percentage of specimens with a preservation quality of either fair, poor, good, or excellent.

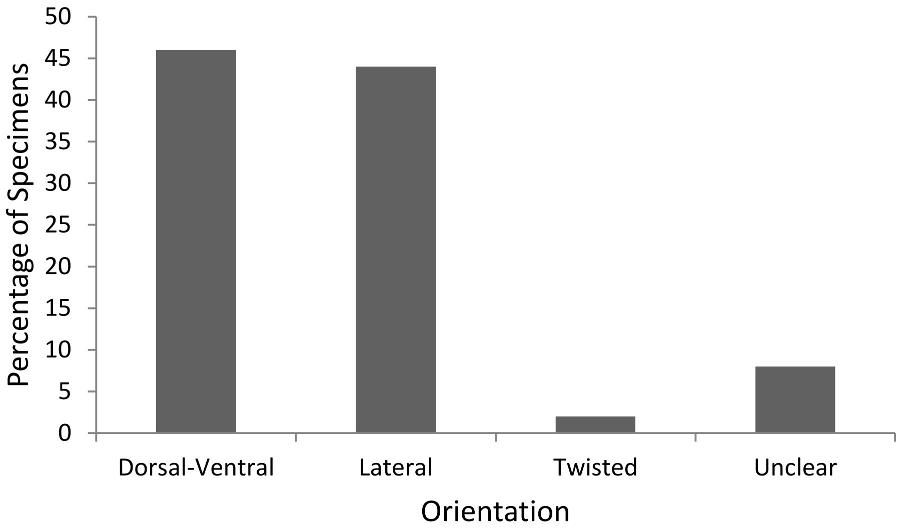

Figure 10 – Percentage of specimens with an orientation of dorsal-ventral, lateral, twisted, or an unclear orientation.

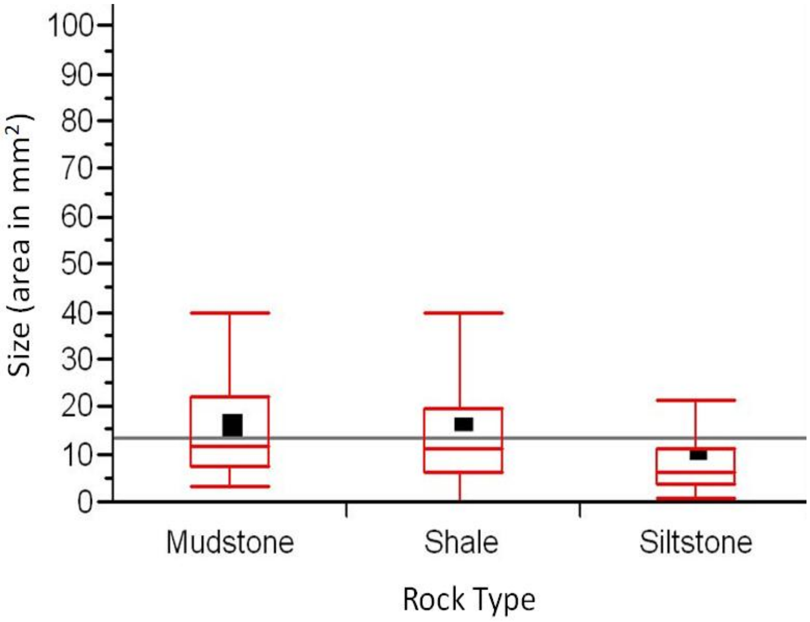

Figure 11 – Size of specimens found in each sediment type. ■ = mean size of specimens for each rock type (mudstone = 17.95 mm^2, shale = 16.77 mm^2, siltstone = 10.05 mm^2). Specimens found in siltstone were significantly smaller than those found in mudstone or shale ($F = 20.01$, $p < 0.0001$).

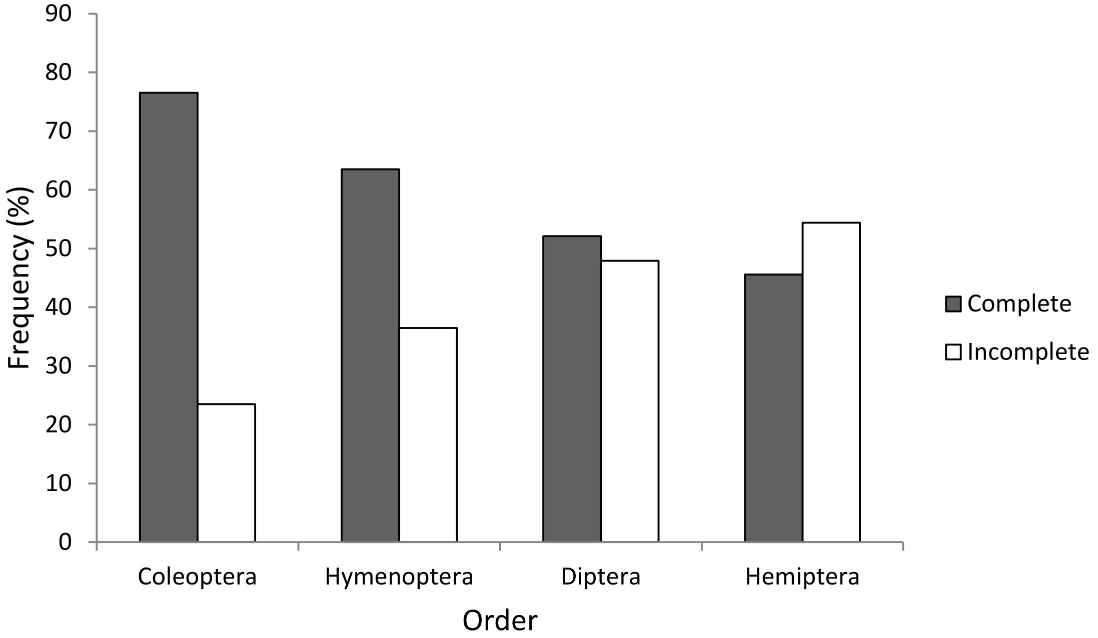

Figure 12 – Frequency in percent of the completeness of a specimen by order in shale and siltstone ($x^2 = 31.20$, df = 3, $p < 0.0001$).

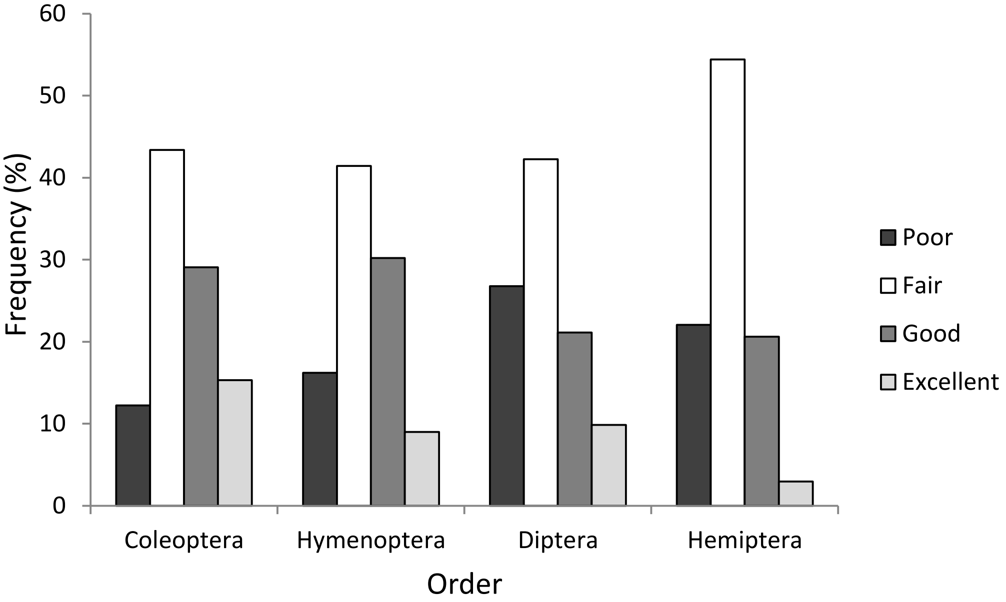

Figure 13 – Frequency in percent of the preservation quality of the common insect orders in shale and siltstone ($x^2 = 23.95$, df = 9, $p = 0.0044$).

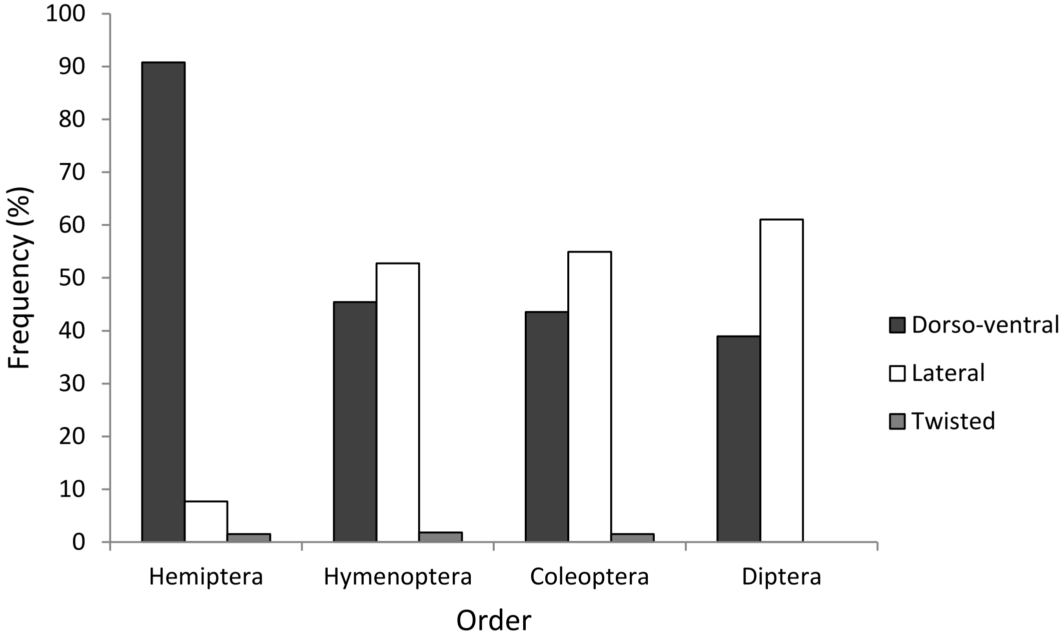

Figure 14 – Frequency in percent of insect orientation by order within shale and siltstone (x^2 = 57.73, df = 6, p<0.0001).

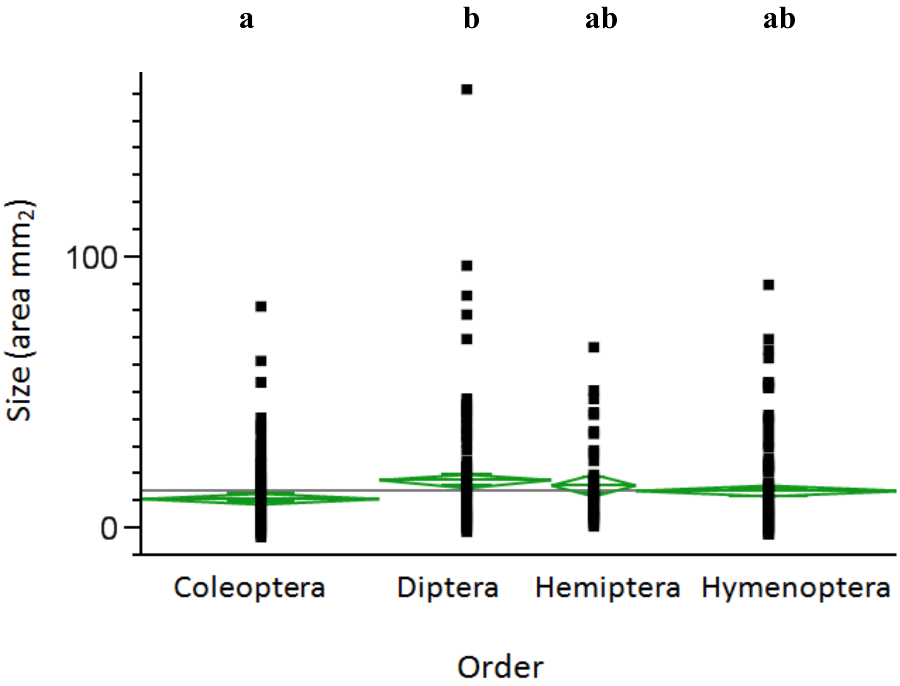

Figure 15 – Size class of the four main insect order types found within siltstone and shale combined. Diptera were significantly larger (17.88 mm^2) than Coleoptera (11.05 mm^2), but not Hemiptera (18.96 mm^2). There is no statistical difference between Hemiptera and Hymenoptera (13.72 mm^2) (F=5.85, p = 0.0006). Letters indicate significance levels at the $\alpha = 0.05$ level. Those with the same letters are not significantly different from each other, whereas those with different letters are significantly different from each other.

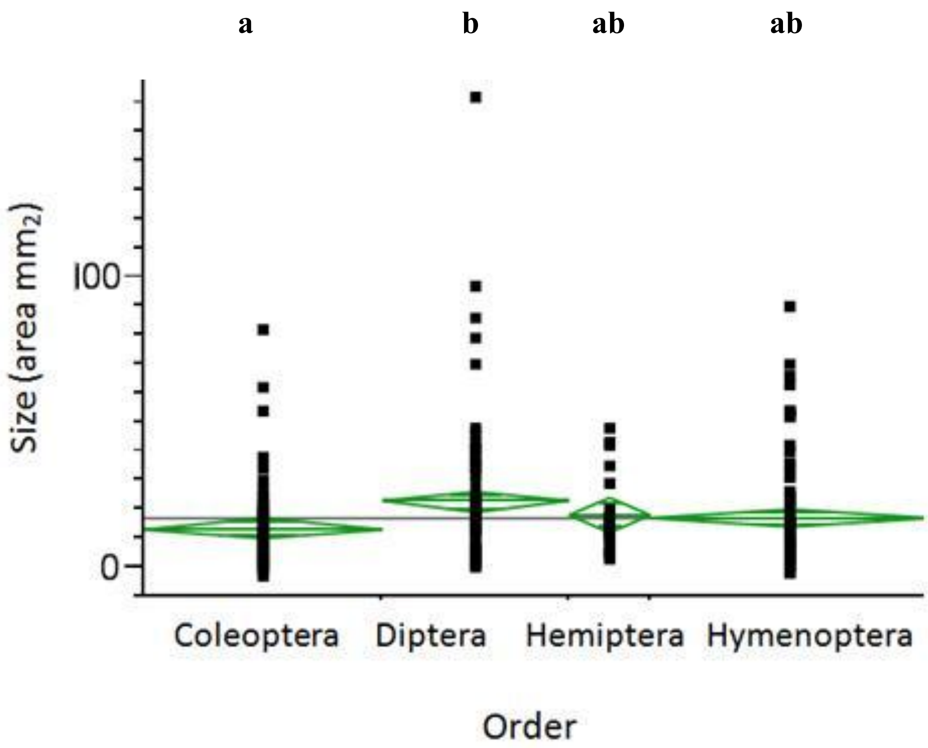

Figure 16 – Size of specimens in the four main insect orders found in shale (F=3.95, p = 0.0086). Diptera are significantly larger (mean size 22.53 mm^2) than Coleoptera (13.45 mm^2), but not Hemiptera (17.75 mm^2). There is no statistical difference between Hemiptera and Hymenoptera (17.20 mm^2). Hymenoptera (17.20 mm^2) and Hemiptera have a mean size larger than Coleoptera but they are not significantly larger. Letters indicate significance levels at the $\alpha = 0.05$ level. Those with the same letters are not significantly different from each other, whereas those with different letters are significantly different from each other

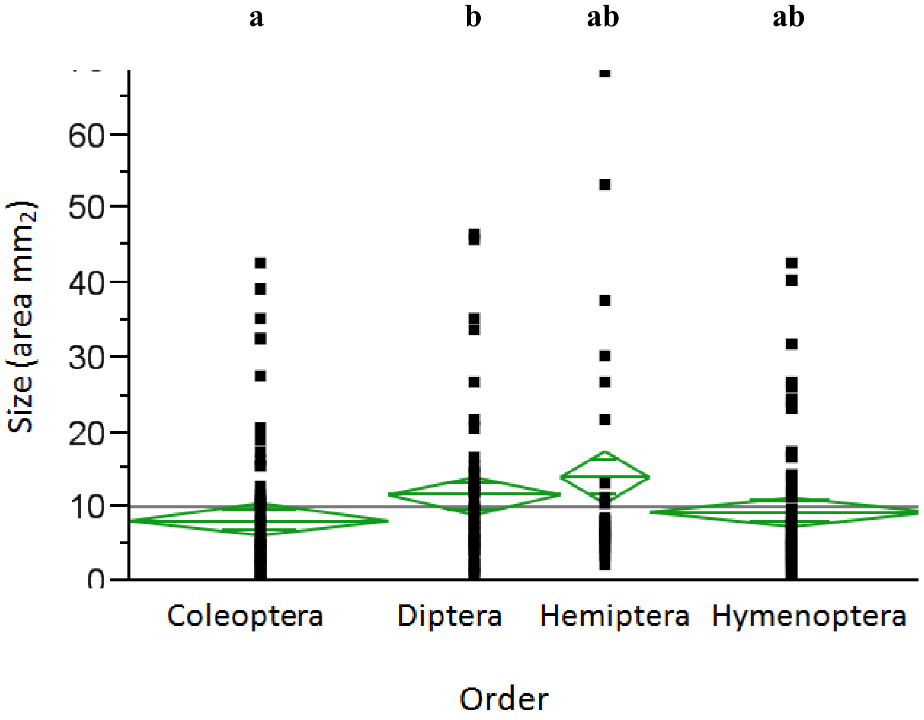

Figure 17 –Size of specimens in the four main insect order found in siltstone (F = 3.1663, p = 0.0249). Hemiptera are significantly larger (13.94 mm^2) than Coleoptera (8.29 mm^2), but not Diptera (11.53 mm^2) and Hymenoptera (9.39 mm^2). There is no statistical difference between Diptera and Hymenoptera. Letters indicate significance levels at the $\alpha = 0.05$ level. Those with the same letters are not significantly different from each other, whereas those with different letters are significantly different from each other

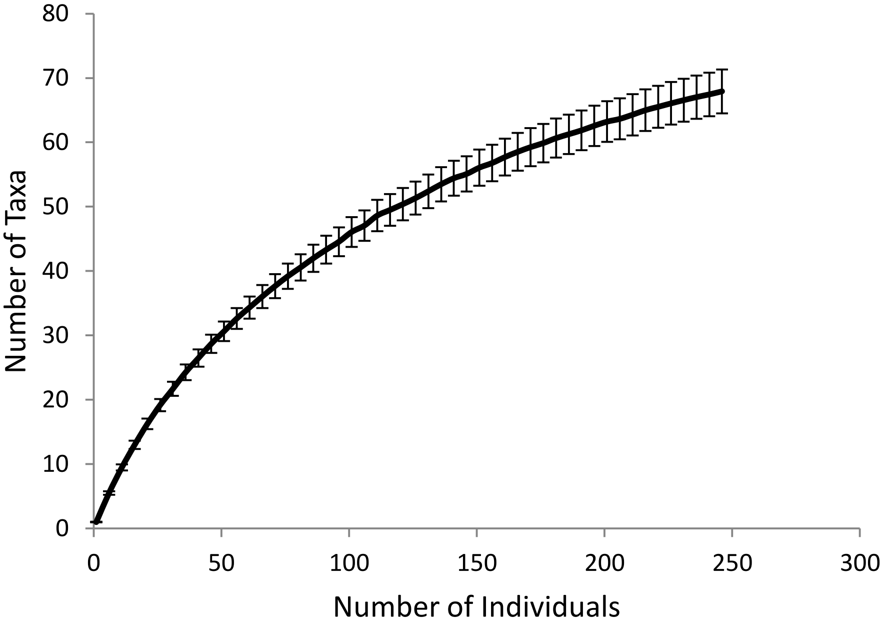

Figure 18 – Individual-based rarefaction curve that shows the accumulation of morphospecies diversity as the number of individual insects sampled increased.

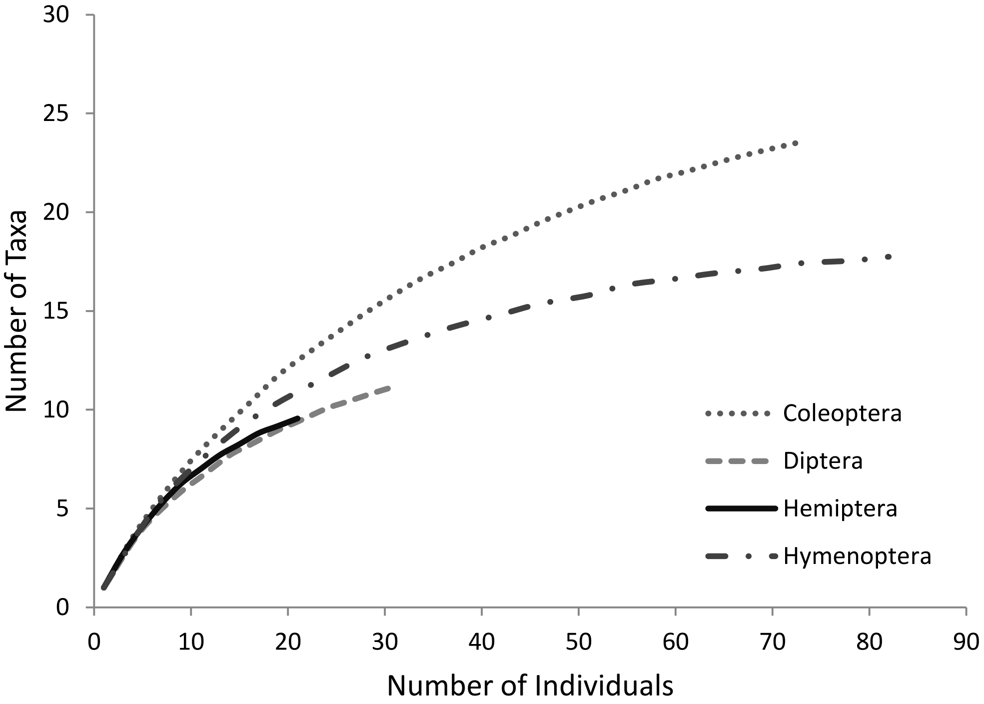

Figure 19 – Individual-based rarefaction curve showing the accumulation of morphospecies in each order as more individual insects are sampled.

CHAPTER 4:
DISCUSSION

Overall Diversity and Sampling

Two summers were spent collecting approximately 824 insects used for this study. Of the 824 insects, 121 insects were not identifiable. Coleoptera, Hymenoptera, Diptera, and Hemiptera represented the highest percentage of insects collected during both summers combined and the results are consistent with the findings of other researchers who have found that the four most species-rich groups described from the Florissant Formation are Coleoptera, Hymenoptera, Diptera, and Hemiptera (Drummond, 2004).

One of the main goals of this study was to assess how representative this sample was in terms of the overall insect diversity found in the Florissant Formation. Based on the individual-based rarefaction curve it is clear that many more specimens need to be collected in order to capture the actual diversity, even at this single locality. Perhaps this is not surprising, as the Florissant Formation has been studied and collected off and on for more than 130 years and has over 1,500 described species of insects (Drummond, 2004), whereas our current study was conducted over a two year period from one locality.

In addition to under-sampling insect species richness, those specimens that were collected were often disarticulated (44%) and the majority (66%) were classified as having fair to poor preservation quality. These results were surprising as the Florissant Formation is often lauded for both its high diversity and exceptional preservation quality. Despite its reputation, it is clear that numerous specimens need to be collected before finding a sufficient sample of well-preserved and complete specimens, as low quality specimens are the norm.

Influence of Sedimentary Environment

No differences between were observed the three sediment types in terms of insect quality, completeness, orientation, or taxonomic representation. A common conception is that the diatom mats covering the ancient lake helped preserve the insects within the lake sediments. If this were the case, it would be expected that the shale, which is diatom-rich, would have preserved greater diversity and higher quality insects than either the mudstone or siltstone. However, since there were no taphonomic differences found between the different sedimentary environments, perhaps the co-occurrence of diatom fossils with the insect fossil is just coincidental and not causal in terms of insect preservation. Therefore, the diatom and bacterially-generated biofilms model of preservation needs to be re-evaluated to determine the role, if any, diatoms play in insect preservation.

In contrast to the taphonomic variables examined, insect size was found to differ depending on sedimentary environment and insects preserved within siltstone were significantly smaller than those preserved in shale or mudstone. Siltstone is a coarser grained sediment than shale and mudstone and is most likely the result of episodic higher energy events like stream deposition into the lake. Sedimentation of silt is often precipitated by winter snow melt and from weathering of allochthonous rock sources (Dean et al., 1999).

In general, it is expected that during intense run-off events, a larger range of specimen sizes will be captured (Behrensmeyer et al., 2000). However, since sedimentation of siltstone was likely the result of episodic higher energy events compared to shale, the insects that were captured were from brief moments in time, thus the sampling interval was shorter and a smaller proportion of the assemblage was captured. In addition, insect sorting associated with deposition of the siltstone (smaller-sized clasts) could have occurred, influencing why smaller insects are found in siltstone. In contrast, the insects preserved in the shale and mudstone sediments were captured over a longer time frame where sediment input was slower and the sampled insect assemblage was therefore more time averaged. Slower sedimentation over a longer period of time would allow a more diverse fauna to be captured (Behrensmeyer et al., 2000) and thus a bigger size range is represented within these two sediments. In general, the sedimentary environments of the Florissant Formation have captured ranges that represent episodic or seasonal events which results in different levels of time averaging and greater differences in insect size ranges.

This study demonstrates how subtle depositional events can impact insect assemblages. Time averaged assemblages are often discussed on a scale in which hundreds or thousands of years of input can occur (Behrensmeyer et al., 2000). For example, Behrensmeyer et al. (2000) estimate that organisms in a lake setting represent a time averaged assemblage anywhere from 100 years to 10,000 years. However, even at a smaller time scale (seasons to decades), changes amongst assemblages can be captured. Unfortunately, little research has been done to compare time averaged assemblages to single event assemblages of fossil insects. From this study, it is evident that the Florissant Formation has captured insect assemblages representing both time averaged events (shale and mudstone) as well as brief moments captured in time (siltstone).

Taxonomy and Taphonomy

Based on previous studies, the taxonomy of an insect also influences its preservation potential (Smith et al., 2006 and Wilson, 1980). For example, Coleoptera are often very sturdy, compact, and robust; all features that have been found to be favorable to preservation (Gullan and Cranston, 2005, Smith et al., 2006). In this study, Coleoptera had the highest percentage of complete specimens and high quality (good-excellent) preservation. The surprising results from this study were the low levels of disarticulation and high quality of preservation amongst the Hymenoptera. High preservation quality of Hymenoptera is not often mentioned in insect taphonomy studies, especially compared to Diptera. In addition, Hymenoptera were found to be very diverse and abundant which was another unexpected result. However, newly sampled material from other exceptionally preserved lacustrine deposits has shown very high diversity, abundance, and preservation quality of Hymenoptera (Smith, unpublished data, 2011).

Our results indicate that nearly half of insects were preserved dorsal-ventrally and the other half were in a lateral orientation. Striking was the orientation of Hemiptera, with 90.77% preserved dorsal-ventrally, a result that was likely related to the morphology of this group of insects. Hemiptera are commonly dorsal-ventrally flattened with their weight distributed laterally, similar in shape to coin. As these insects entered the water column, it is likely that they dropped straight down and landed in the bottom lake sediment to be preserved dorsal-ventrally because it would have been difficult for the insect to land on its narrow side. It is also likely that more differences in orientation would be seen if the analyses were conducted at the family level.

For example, the Curculionidae (Coleoptera) are nearly always preserved in a lateral position. This is likely due to their stout bodies and positioning of the limbs, resulting in the tipping of Curculionidae onto their sides. Settling experiments would be the clear next step to see when and how morphology influences insect position on lake bottoms.

Very little research has been performed to directly compare different insect orders and study how their taphonomy may differ. It would be interesting to conduct further actualistic experiments comparing the four main orders used in this study (Coleoptera, Hymenoptera, Diptera, and Hemiptera) and determine how each order sinks to the sediment bottom and disarticulates in environments with different energy levels. Martínez-Délclòs and Martinell (1992) did do some work that found that different insect groups behaved differently during particular stages of preservation based upon morphological and physiological characteristics. For example, wingless insects were found to sink almost instantaneously in a calm environment, furthering their chances for little disarticulation, whereas those with wings covering a large surface area stayed on the water surface for a long period of time, which greatly enhanced the chance of becoming disarticulated (Martínez-Délclòs and Martinell, 1992).

Finally, Diptera were the largest insects found within all three sediment types. This was due to numerous Tipulidae that were found throughout the stratigraphic column, which are the largest members of the Diptera. Some Tipulidae even have a body length exceeding 35 mm (Borror et al., 1989). Hempitera and Hymenoptera were the next largest in size and Coleoptera were the smallest. Though Coleoptera can have vast ranges in body size, the small body size found within the Florissant Formation is most likely attributable to the large number of Curculionidae collected (41% of Coleoptera). In addition, taphonomic work on Coleoptera has shown a preservation bias favoring Coleoptera that are smaller (Smith et al., 2006 and Smith and

Moe-Hoffman, 2007). Curculionidae is a large family of beetles with more than 3,100 extant species found in North America ranging in all different sizes (Borror et al., 1989) and they are preserved in great abundances in fossil deposits (DM Smith, pers. comm.). This is also the case at Florissant, where the majority of fossil Curculionidae collected in this study had an average area size of 1.5 mm^2. Interestingly, siltstone had smaller insects overall, but the Hemiptera were larger than the other groups, perhaps due to seasonal, high energy deposition.

Conclusion

The Florissant Formation is known for its abundant, diverse and high quality fossil specimens. However, in a given sample, specimens are typically of low quality and are often disarticulated. In addition, two years collecting resulted in an under-sampled collection that did not capture the diversity of insects at the locality. Therefore, a greater number of specimens need to be collected in future studies to get an adequate sampling of the high quality and high diversity of insects that has made the Florissant Formation renowned.

Careful sampling, within the context of different sedimentary environments, can reveal subtle differences in assemblages related to differential time-averaging. This was demonstrated to be the case in terms of sampling duration and the resultant size range of insects in samples. In addition, we found no strong support for diatoms aiding in insect preservation, as there were no significant differences in the taphonomy of specimens preserved in diatom-rich vs. diatom-poor sediments. Instead, the diatoms found to co-occur with macrofossils in the Florissant Formation should be viewed as just another component of the past ecosystem and not as a driver of insect preservation.

As expected, Coleoptera had the highest preservation quality with the least amount of disarticulation. Unexpectedly, Hymenoptera were found to have high preservation quality and were very diverse and abundant. Often absent in previous studies of insect taphonomy, Hymenoptera should be incorporated in future work that examines preservation bias in lacustrine systems.

Interestingly, about half of all the insects collected had a dorsal-ventral orientation, while the other half were lateral and very few insects were in a twisted position, suggesting a relatively calm setting for preservation. We recommend future settling studies to further identify why the insects settle the way they do within a water column and how morphological variables will influence their final orientation.

The study found that there were size differences amongst the particular representatives of the different groups of insects at Florissant, with Coleoptera being smallest and Diptera being the largest overall. These size differences are likely due to which groups within each order were sampled most often. Many of the Coleoptera collected were small Curculionidae while Tipulidae were the largest of the Diptera.

Because of the results of this study, we now understand more clearly that different sedimentary environments, in and of themselves, did not have a large impact on insect preservation except in terms of time averaging and the size range of the insect preserved. In contrast, there were great differences in preservation based on which order an insect belonged to. This indicates a need to not only discern sedimentary environment, but also to examine the effects of taxonomy when studying the taphonomy of fossil insect assemblages.

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