

TAPHONOMY OF DIPTERA IN LACUSTRINE ENVIRONMENTS: A CASE STUDY FROM FLORISSANT FOSSIL BEDS, COLORADO

DENA M. SMITH¹* and AMY P. MOE-HOFFMAN²

¹CU Museum—Paleontology and Department of Geological Sciences, University of Colorado, Boulder, Colorado 80309-0265, USA;

²CU Museum—Paleontology, University of Colorado, Boulder, Colorado 80309-0265, USA

e-mail: dena@colorado.edu

ABSTRACT

The purpose of this paper is to study the taphonomy of fossil flies (Diptera) preserved in the lacustrine deposits of the Florissant Fossil Beds (late Eocene), Colorado, United States. Three hundred and twenty-six fossil Diptera were examined, collected from a nearshore ($n = 215$) and an offshore ($n = 111$) site. The degree to which a specimen's preservation quality correlated with the ability to identify the specimen to various taxonomic levels and whether specimen size, orientation, or disarticulation had an effect on a preservation quality were evaluated. Also examined was the influence of depositional environment on these variables. Preservation quality was found to be important for identification to species level, but specimens of low preservation quality were still identifiable to the family and genus levels. Specimen size, orientation, and disarticulation were not correlated with the identifiability of a specimen. There was no significant difference in the orientation, disarticulation, or preservation quality of specimens found in the nearshore and offshore sites. There was a significant difference in the size of specimens preserved at each site, with larger specimens being found offshore. More specimens were found in the offshore site, but species richness did not differ between the two sites. Composition of taxa did differ depending on the site. These results demonstrate the importance of collecting all specimens, as even poor quality and disarticulated specimens are identifiable and useful in studies of insect ecology and evolution. In addition, depositional environments should be documented, as size sorting can bias the taxonomic composition of assemblages.

INTRODUCTION

This study examines the taphonomy of fossilized Diptera preserved within the lacustrine deposits of the Florissant Fossil Beds. Specifically, the degree to which preservation quality of insect specimens correlated with the ability to identify the specimens to various taxonomic levels was tested. Also examined was whether specimen size, orientation, or disarticulation had an effect on a specimen's preservation quality. In addition, specimens from two sites, a nearshore site and an offshore site, were studied to determine the influence of depositional environment on size, orientation, disarticulation, and preservation quality of fossil flies (Diptera).

Some of the best-known lake deposits for insect preservation are the upper Eocene Florissant Fossil Beds. Over 1500 insects have been described from the Florissant Formation and represent at least 21 insect orders, all of which are extant (Drummond, 2004). Florissant has received a great amount of attention from paleontologists who have worked on insect taxonomy because of its diversity of fossil insects (Scudder, 1890, 1893; Cockerell, 1907a, 1907b, 1909, 1914, 1917), ecological interactions (Smith, 2000b), and presence of insects as climatic indicators (Moe and Smith, 2005).

Insects are both abundant and diverse in modern continental environments. Although often considered to be soft-bodied organisms by paleontologists, fossil insects can be preserved in high numbers and in excellent condition when given the right preservation conditions (Carpenter, 1992; Labandeira and Sepkoski, 1993; Rasnitsyn and Quicke, 2002; Grimaldi and Engle, 2005). Insect fossils are preserved in a number of environments, including shallow marine, fluvial, palustrine, and lacustrine deposits and as inclusions within fossilized resins (Rasnitsyn and Quicke, 2002; Grimaldi and Engle, 2005). While insects are preserved in a variety of environments, lakes are the most common environment in which to find insect fossils (Labandeira, 1999; Smith and Cook, 2001).

Taphonomic studies are important for evaluating what factors influence insect accumulation and preservation and for using fossil insects more effectively in paleobiological analyses. Various studies have elucidated biases in insect preservation and demonstrated how understanding these biases can improve our ability to use the fossil record to study insect evolution and ecology. For example, the chemical composition (Miller, 1991; Briggs et al., 1993, 1998; Baas et al., 1995; Briggs and Wilby, 1996; Bierstedt et al., 1997; Stankiewicz et al., 1997; Briggs, 1999) and morphology (Stankiewicz et al., 1997; Briggs, 1999; Smith, 2000a; Smith et al., 2006) of insects influence their preservation, as do the ecology of insects and the depositional environment (Wilson, 1980, 1988; Martínez-Délclòs et al., 1991, 2004; Henwood, 1993a, 1993b; Smith, 2000a).

METHODS AND MATERIALS

The Florissant lakebeds formed 34.07 ± 0.10 Ma by the damming of the original drainage basin by lahars from the Thirty-Nine Mile Volcanic Field (Evanoff et al., 2001; Meyer, 2003). Fly specimens examined in this study were collected from Florissant by T.D.A. Cockerell from 1906 to 1908 and are housed at the University of Colorado Museum (UCM). Cockerell and his team collected all the fossil insect and plant specimens they encountered, regardless of preservation quality. This study uses material from two localities: UCM 83013 and UCM 83014 (Cockerell's sites 13 and 14, respectively). These sites are among the most insect-rich fossil sites in the Florissant lakebeds, and nearly 1200 insect specimens from these sites are housed at the University of Colorado Museum.

Sites 13 and 14 are located approximately 1.5 km southwest of the town of Florissant (Teller County, Colorado) in a small inlet that branches from the main Florissant lake basin (Cockerell, 1907b; CU Museum—Paleontology's archive of locality information, Boulder, Colorado). Site 13 is located nearshore; site 14 is located ~ 160 m south of site 13 and is considered to be offshore based on the current topography, which is thought to reflect ancient lake boundaries (Meyer, 2003; Fig. 1). Plants, mollusks, and arachnids have been collected from both sites, with greater plant abundance and diversity being found in the offshore site. Fish have also been found at both sites, but in very low numbers. Fossil specimens are found preserved typically among large amounts of organic debris, and multiple insect specimens are often found on the same piece of shale. Laminated sediments are found at both sites, with site 13 having slightly coarser, fine-grained sediments than what is found at site 14. Sites 13 and

* Corresponding author.

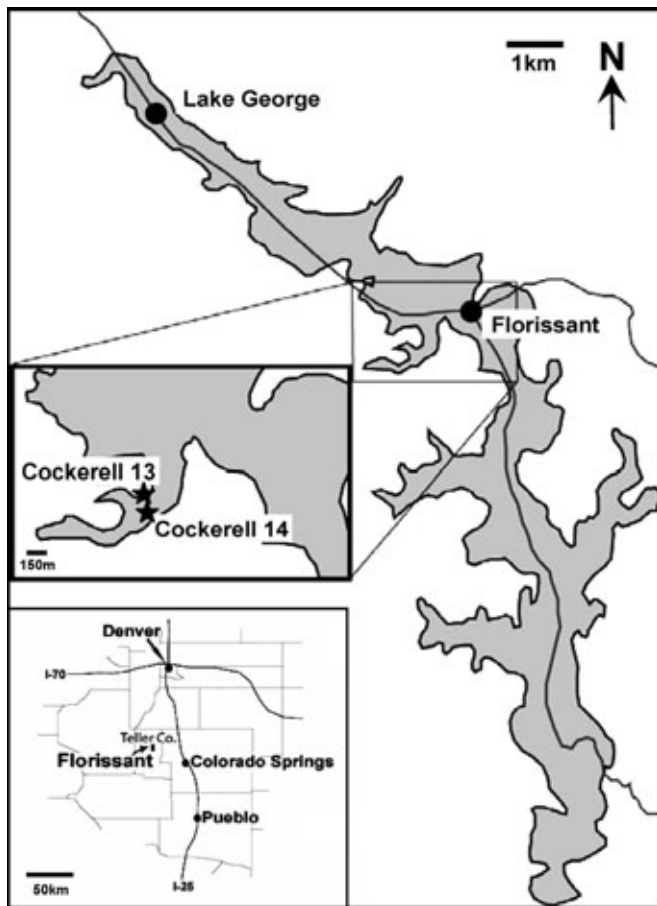
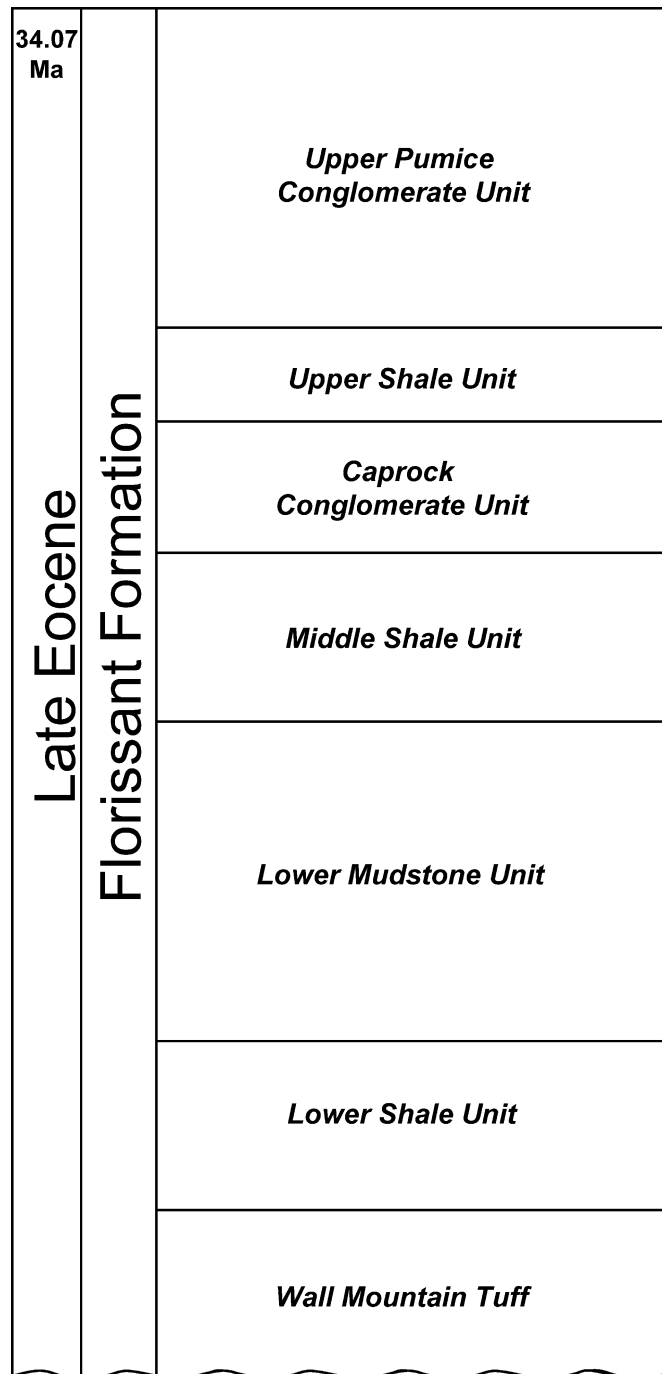


FIGURE 1—Map of the Florissant Formation exposures with UCM 80313 (Cockerell 13) and 80314 (Cockerell 14).

14 are within the Middle Shale Unit of the Florissant Formation (Evanoff et al., 2001; Fig. 2), which has produced the majority of described insect and plant macrofossils.

All fly specimens collected by Cockerell at sites 13 ($n = 215$) and 14 ($n = 111$) are included in this study. A list of these specimens and their associated data can be found in the Supplementary Data¹. These specimens have received thorough examination, with the majority of work on the taxonomy completed by T.D.A. Cockerell in the 1900s, F.M. Brown in the 1980s, and by V. Scott in 2002 (see the CU Museum Invertebrate Paleontology Database, Boulder, Colorado). Several authors also reexamined specimens to check for consistency in the identifications and any updates to the nomenclature (Bequaert, 1930; James 1937, 1939; Evenhuis, 1994). Unidentified specimens are thus far not identifiable, rather than being unidentified because they had not yet been examined by an expert.

Taphonomic grade (preservation quality) was determined by the presence of morphological characters and number of characters that could be used for identification of a specimen. A Bausch & Lomb Stereozoom 5 microscope with $0.8\times$ – $4.0\times$ magnification was used to group fly specimens into one of five potential taphonomic grades and to examine whether preservation quality determined the taxonomic level to which specimens were identified. Important characters for identification included wings with apparent venation, head sutures, and the presence of mouthparts, antennae, setae, eyes, and reproductive parts. The characteristic of having wings with visible venation was viewed as more important in the assignment of taphonomic grade than the other characters because it is a



Pikes Peak Granite

FIGURE 2—Generalized stratigraphy of the Florissant Formation (based on Evanoff et al., 2001). Most fossil insects have come from the Middle Shale Unit.

key character emphasized heavily in the identification of both modern and fossil Diptera (McAlpine et al., 1981). Taphonomic grades (Table 1) ranged from 1 through 5, with level 1 the poorest quality of preservation and level 5 the highest quality of preservation (Fig. 3).

To prevent researcher bias whereby a fossil might be determined to be of higher quality because it was previously identified, the identification tags were not made accessible during the assignment of taphonomic grade for specimens. While the measurement of taphonomic grade relied on the presence of key characters used by taxonomist to identify fly specimens, it was separately noted whether a specimen was articulated or disarticu-

¹ www.paleo.ku.edu/palaios

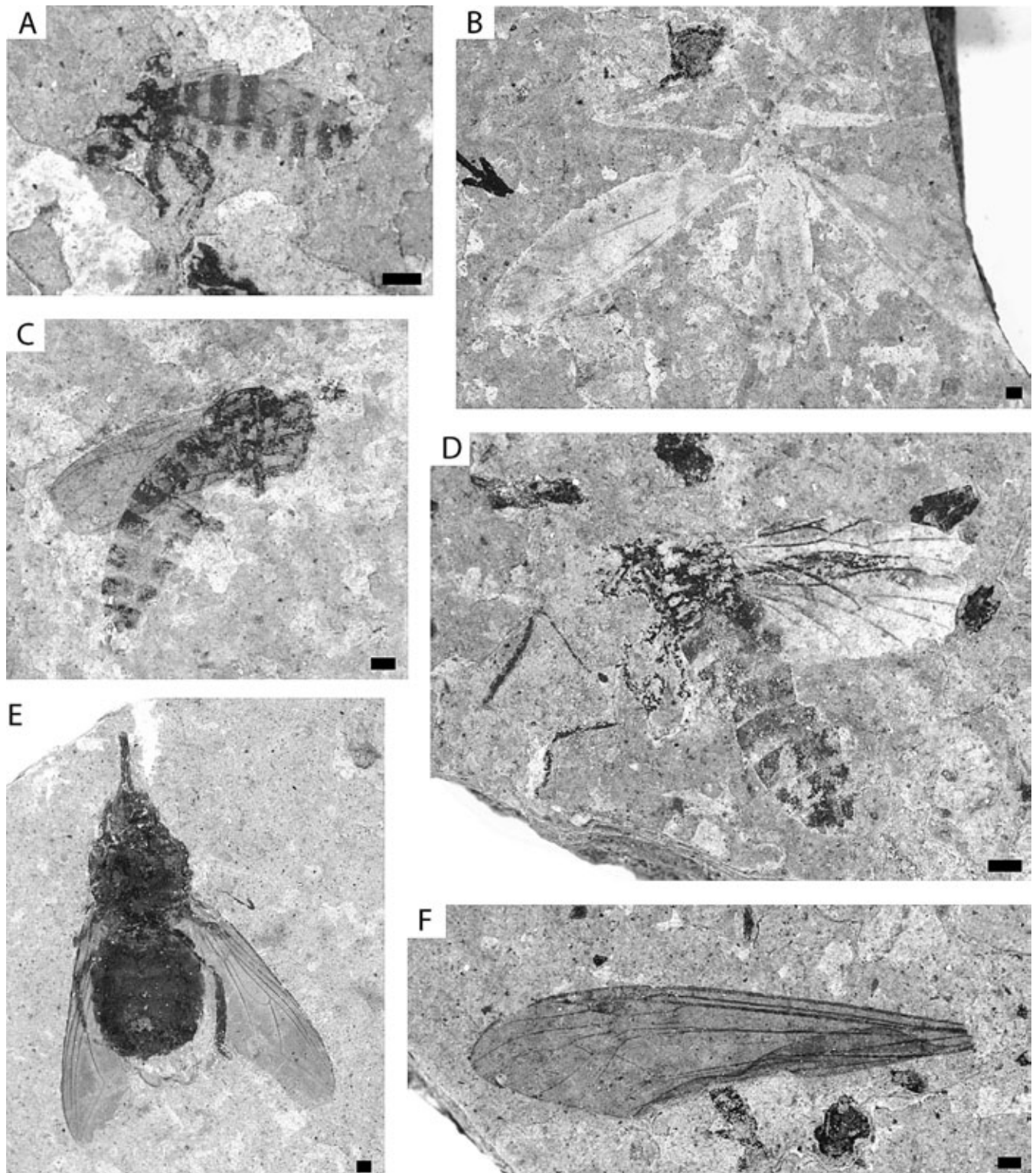


FIGURE 3—Examples of fossil Diptera specimens of various taphonomic grades. Scale bar = 1 mm. A) UCM 33692, *Bibio* sp., taphonomic grade 1. B) UCM 33602, *Tipula* sp., taphonomic grade 1. C) UCM 33543, *Bibio wickhami*, taphonomic grade 3. D) UCM 33546, *Bibio wickhami*, taphonomic grade 3. E) UCM 31594, *Glossina oligocena*, taphonomic grade 5. F) UCM 30011, *Tipula heilprini*, taphonomic grade 5.

lated. Disarticulation is usually considered to be a facet of preservation, but it is considered separately here. As the high grading of collections often leads to the removal of disarticulated specimens, it is important to examine the effects of disarticulation on both the taphonomic grade assignment of a specimen (quality) and the effect of disarticulation on whether a specimen was identified to the family, genus, or species level.

The area of specimens was calculated to determine factors that might influence a specimen's taphonomic grade. The area of each specimen was calculated by multiplying specimen length and width, measured using digital calipers. Length was measured from the distal tip of the mouthparts to the distal end of the abdomen, including any protruding appendages, such as genitalia or ovipositors. The width was measured across the

TABLE 1—Detailed description of basis for designation of specimens to the various taphonomic grades. Identifying characters = characters used for taxonomic identification of specimens.

Taphonomic grade	Preservation description
1	General body shape or body parts distinguishable; identifying characters not present. Wings, if present, lack apparent venation and are preserved as a fragment or numerous fragments
2	At least one identifying character present or wings, if present, are not entire or have incomplete venation (<75% complete)
3	At least two identifying characters present or wings, if present, have apparent but incomplete venation ($\geq 75\%$ complete)
4	At least three identifying characters present, or wings, if present, have apparent and nearly complete venation ($\geq 90\%$ complete)
5	Greater than three identifying characters present or wings, if present, have apparent and complete venation

middle of the thorax. If a specimen lacked a head, thorax, and abdomen, it was not used in body-size analyses. The orientation of each specimen, dorsoventral or lateral positioning, was documented also to determine if this affected a specimen's taphonomic grade.

Specimens from sites 13 and 14 were compared to determine whether there were differences in the taphonomic grade or size of specimens found from each site. In addition, the frequency of specimen disarticulation between sites was determined. Finally, the species richness of both sites was compared, as was the degree to which their species compositions overlapped.

Statistical Analyses

A chi-square contingency test was used to determine whether the level of taxonomic determination of a given fossil (family, genus, or species level) was dependent on its taphonomic grade or whether it was disarticulated. To determine whether larger specimens were more likely to receive higher taphonomic grades, a one-way analysis of variance with a Tukey-Kramer test for pairwise comparisons was conducted. To establish whether a specimen's taphonomic grade was dependent on its orientation (preserved laterally or dorsoventrally), a chi-square contingency analysis was used. A chi-square contingency analysis was used also to determine whether being disarticulated determined a specimen's assigned taphonomic grade. All fossil fly specimens found at sites 13 and 14 were pooled for the above analyses.

Two separate chi-square contingency analyses were conducted to ascertain whether there were differences between the taphonomic grades and orientation patterns of specimens at sites 13 and 14. A Student's *t*-test was performed to determine whether there was a difference in specimen sizes between sites 13 and 14. A chi-square analysis was conducted to resolve whether the sites differed in the proportion of specimens found

to be disarticulated. All analyses were performed using JMP software (SAS Institute, 1989–2000).

RESULTS

Taxonomic Determination, Taphonomic Grade, and Disarticulation

Eighty-three percent of the 326 specimens were identifiable to the family level; this was not dependent on taphonomic grade ($\chi^2 = 8.77$, $df = 4$, $p = 0.07$). For the most part, even specimens considered to be relatively poor quality (grades 1–2) were identified to the family level. In contrast, only 49% of all specimens received a genus-level designation. The trend for specimens of higher taphonomic grades to be more likely to be identified at the genus-level was only marginally significant ($\chi^2 = 9.12$, $df = 4$, $p = 0.05$). Only 38% of all specimens had been identified to species-level. Species-level determination was highly dependent on that specimen's taphonomic grade ($\chi^2 = 19.26$, $df = 4$, $p = 0.0007$). In contrast, while 12% of all specimens not given a species-level determination were given a grade of 4 or 5, 27% of all specimens that were given a species-level determination had a grade of 4 or 5 (Fig. 4).

Two hundred and eighty-eight articulated and 38 disarticulated specimens were in the sample. Specimen articulation did not influence whether a specimen was identified to genus ($\chi^2 = 0.217$, $df = 1$, $p = 0.64$) or species-level ($\chi^2 = 2.472$, $df = 1$, $p = 0.1159$). Counter to expectation, disarticulated specimens were actually more likely to be identified to family level than articulated specimens ($\chi^2 = 6.042$, $df = 1$, $p = 0.0140$). That is, while 82% of articulated specimens were identified to the family level, 97% of disarticulated specimens were identified to the same level.

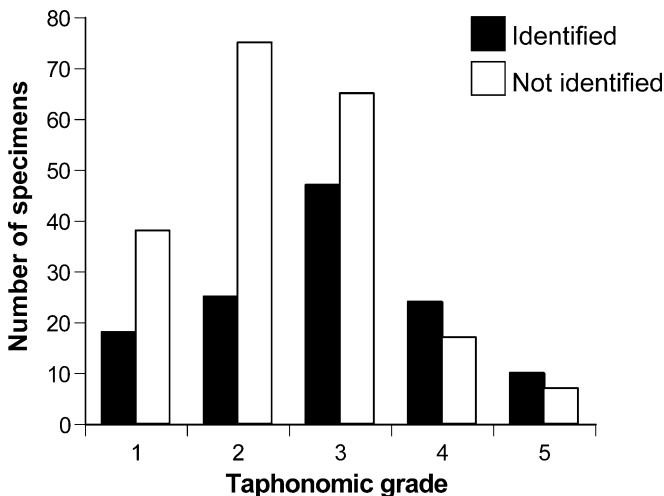
Size, Orientation, and Taphonomic Grade

Specimens that received different taphonomic grades were not of similar size ($F_{4, 301} = 21.71$, $p < 0.0001$, Fig. 5). Although there were no differences between the sizes of fossil specimens that received a grade of 1, 2, 3, or 4 (Tukey-Kramer, $p > 0.05$), specimens that received a grade of 5 were significantly larger than specimens from all other categories (Tukey-Kramer, $p < 0.05$). Large specimens were more likely to receive the highest grade because key characters were much more apparent, not because larger specimens were less damaged.

There was no difference between the orientation of a specimen and its taphonomic grade ($\chi^2 = 4.41$, $df = 4$, $p = 0.35$). This suggests that a specimen's orientation did not affect whether its key characteristics were more apparent or whether it was more or less likely to be damaged during the preservation process.

Locality Comparisons

Larger specimens were on average more likely to be preserved offshore than nearshore ($t_{1, 305} = 2.18$, $p < 0.03$; Fig. 6). While specimen size differed between the sites, there was no difference between the taphonomic grade assigned to nearshore versus offshore specimens ($\chi^2 = 3.33$, $df = 4$, $p = 0.50$). The orientation (dorsoventral or lateral) of preserved specimens was also not significantly different between the sites ($\chi^2 =$

**FIGURE 4**—Number of specimens in each taphonomic grade identified to species level compared to those not identified to species level.

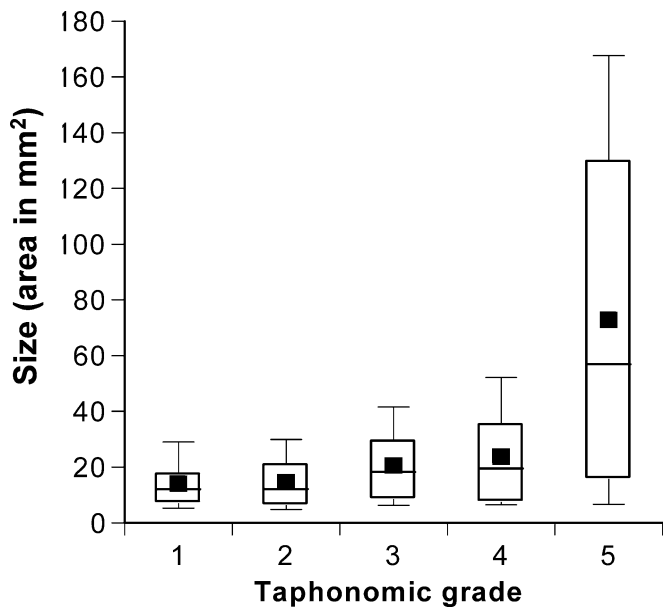


FIGURE 5—Size of specimens found in each taphonomic grade. ■ = mean size of specimens for each taphonomic grade. Specimens of taphonomic grade 5 were significantly larger than all other taphonomic grades.

1.06, $df = 1$, $p = 0.30$). Proportionally, it did not appear that more specimens were disarticulated at site 13 (16% of 111) than at site 14 (10% of 215; $\chi^2 = 3.398$, $df = 1$, $p = 0.065$).

The proportion of fly specimens relative to all insect specimens collected at sites 13 and 14 were examined to understand better how sampling influenced nearshore-offshore trends. The proportion of flies to all insect specimens differed between the sites ($\chi^2 = 8.15$, $df = 1$, $p = 0.0043$). While 41% of the 481 insect specimens from site 13 were flies, nearly 59% of the 702 insect specimens from site 14 were flies. Although the number of fly specimens was greater at site 14, there was no difference in the total number of fly species found at each site (23 vs. 34 from sites 13 and 14, respectively; $\chi^2 = 0.55$, $df = 1$, $p = 0.46$). Interestingly, while species richness did not differ between the two sites, only 9 out of the 48 species (19%) were found at both sites (Table 2).

DISCUSSION

Collect Everything

Having the appropriate storage space to accommodate large collections of fossil shale material is always a concern for museum curators. Researchers, therefore, often focus their search for specimens of the highest quality. Specimens that appear to be preserved poorly, or only preserved partially, are often left aside. Clearly, all specimens should be collected, and researchers should avoid the tendency to high-grade their collections, as even poorly preserved specimens (taphonomic grades 1 or 2) can be identifiable to family and genus levels. Some may argue that identifications not made to the species level are of no value; however, it has been shown that Diptera and other insects that are identified only to genus-level still provide valuable information regarding paleoenvironments (Coope, 1994; Elias, 1994; Moe and Smith, 2005). These types of specimens also have the potential to provide valuable information about first and last appearances of insect groups (Labandeira and Sepkoski, 1993; Farrell, 1998; Smith and Cook, 2001). For example, many of the large-scale, macroevolutionary analyses of fossil taxa have used occurrence data from fossil assemblages as their primary data set and have focused on recognizing and analyzing patterns at the generic and family levels (Sepkoski et al., 1981; Raup and Sepkoski, 1982; Alroy, 2000; Kiessling and Baron-Szabo, 2004).

Size, orientation, and disarticulation should also not factor into col-

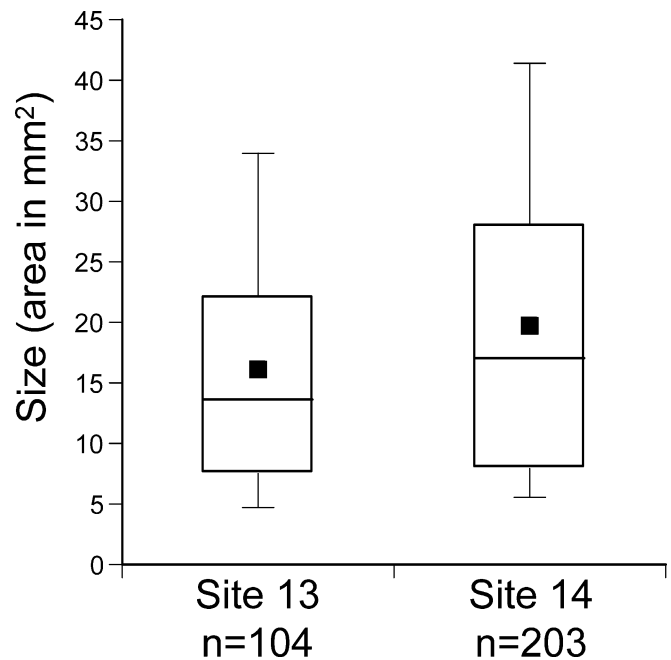


FIGURE 6—Size of specimens found nearshore (site 13) compared to the size of specimens found offshore (site 14). ■ = mean size of specimens for each site.

lecting decisions. Identifiable specimens are found in all size classes, although larger specimens tend to have characters that are easier to view and easier to identify. Removing smaller specimens may also affect diversity estimates and inferences about past paleoenvironments. Orientation is not a hindrance to identification as suites of characters are used for identification.

Disarticulated specimens are usually considered to be low-quality specimens by paleontologists. In this study it was found that disarticulated specimens often have high preservation quality (taphonomic grades 4 and 5) and that even disarticulated parts of specimens can be identified to the species level when they have the appropriate combination of characters (see Fig. 3F). Disarticulated parts are not usually obscured by overlapping body parts, making characters used for identification easier to view. In addition, some disarticulated specimens can be referred to previously diagnosed articulated specimens, at least for taxa that are common, for example, many of the crane flies (Tipulidae) and march flies (Bibionidae) found at Florissant. Further support for the importance of disarticulated specimens include the finding that disarticulated specimens were more likely to be identified to the family level than articulated specimens.

Depositional Environment Matters

The depositional environment of fossil insect occurrences is rarely described in the paleoentomologic literature, which primarily focuses on the taxonomic description of new fossil specimens. It is clear from this study, however, that subtle differences in the depositional environment lead to dramatic differences in the composition of an assemblage.

In this study, larger specimens were preserved offshore more often than nearshore. In addition, significantly more fly specimens were collected from the offshore site compared to the nearshore site. What does this mean in terms of the fly taxa sampled? Different depositional settings sampled different aspects of the overall fly assemblage. Sixty-one percent of the species are found only at site 13, and 74% of the species are found only at site 14 (Table 2). Collecting from only one locality, thus, appears to severely underestimate overall diversity; and this outcome considers only two of the many Florissant localities. A similar pattern of differential sampling can be found when global trends in insect diversity are examined and lacustrine and amber deposits are compared, each of which

TABLE 2—List of Diptera species from UCM 83013 (Cockerell site 13) and UCM 83014 (Cockerell site 14). Asterisks indicate species found in both sites.

Locality	Family	Species
83013	Asilidae	<i>Ceraturgus praecursor</i>
83013	Asilidae	<i>Cophura antiquella</i>
83013	Athericidae	<i>Atrichops hesperius</i>
83013	Bibionidae	<i>Bibio cockerelli</i> *
83013	Bibionidae	<i>B. wickhami</i> *
83013	Bibionidae	<i>Bibiodes intermedia</i> *
83013	Bombyliidae	<i>Megacosmus secundus</i>
83013	Bombyliidae	<i>Melanderella glossalis</i> *
83013	Bombyliidae	<i>Verrallites cladurus</i>
83013	Empididae	<i>Progloma rohweri</i>
83013	Empididae	<i>Rhamphomyia sepulta</i>
83013	Ptychopteridae	<i>Bittacomorpha miocenica</i>
83013	Rhagionidae	<i>Rhagio mystaceaeformis</i>
83013	Sciomyzidae	<i>Sciomyza florissantensis</i> *
83013	Tipulidae	<i>Limnocema mortoni</i>
83013	Limoniidae	<i>Dicranomyia saxetana</i>
83013	Tipulidae	<i>Tipula clauda</i> *
83013	Tipulidae	<i>T. florissanta</i> *
83013	Tipulidae	<i>T. heilprini</i> *
83013	Tipulidae	<i>T. limi</i> *
83013	Tipulidae	<i>T. rigens</i>
83013	Tipulidae	<i>T. picta</i>
83013	Xylomidae	<i>Xylomya moratula</i>
83014	Asilidae	<i>Asilus florissantinus</i>
83014	Asilidae	<i>A. peritulus</i>
83014	Asilidae	<i>Lestomyia miocenica</i>
83014	Asilidae	<i>Microstylus wheeleri</i>
83014	Asilidae	<i>Taracticus contusus</i>
83014	Bibionidae	<i>Bibio cockerelli</i> *
83014	Bibionidae	<i>B. vetus</i>
83014	Bibionidae	<i>B. wickhami</i> *
83014	Bibionidae	<i>Bibiodes intermedia</i> *
83014	Bibionidae	<i>Plecia explanata</i>
83014	Bibionidae	<i>P. melanderi</i>
83014	Bombyliidae	<i>Geronites stigmalis</i>
83014	Bombyliidae	<i>Lithocosmus coquilletti</i>
83014	Bombyliidae	<i>Megacosmus mirandus</i>
83014	Bombyliidae	<i>Melanderella glossalis</i> *
83014	Glossinidae	<i>Glossina oligocena</i>
83014	Mycetophilidae	<i>Lasiosoma mirandula</i>
83014	Mydidae	<i>Mydas miocenicus</i>
83014	Nemestrinidae	<i>Neorhynchocephalus occulator</i>
83014	Rhagionidae	<i>Dialysis revelata</i>
83014	Sciomyzidae	<i>Sciomyza florissantensis</i> *
83014	Stratiomyidae	<i>Cyphomyia rohweri</i>
83014	Tipulidae	<i>Cyrtaromyia cancellata</i>
83014	Tipulidae	<i>Tipula fmartinbrownii</i>
83014	Tipulidae	<i>T. carolinae</i>
83014	Tipulidae	<i>T. carpenteri</i>
83014	Tipulidae	<i>T. clauda</i> *
83014	Tipulidae	<i>T. florissanta</i> *
83014	Tipulidae	<i>T. heilprini</i> *
83014	Tipulidae	<i>T. lethaea</i>
83014	Tipulidae	<i>T. limi</i> *
83014	Tipulidae	<i>T. maclurei</i>
83014	Tipulidae	<i>T. subterjacens</i>
83014	Tipulidae	<i>T. consumpta</i>

sample different aspects of an overall insect assemblage (Smith and Cook 2001; Smith 2004).

Why is there a pattern of size and, therefore, taxonomic sorting in the Florissant Diptera? It may be that size has an influence on the sinking time of flies, as has been demonstrated for beetles (Smith et al., 2006). Using an experimental approach, Smith et al. (2006) demonstrated that the interaction of both the size and robustness of beetles affects their sinking times, with large, robust beetles have faster sinking times. If smaller flies do not sink as fast as larger flies, then smaller flies may be

more likely to raft to the shoreline, as has been observed in some modern environments (Smith, 2000a). Such accumulations of fossil insect remains are observed commonly at Florissant and in other Cenozoic lake deposits (D.M. Smith, personal observations, 2005–present; Smith and Cook, 2001; C.C. Labandeira, personal communication, 2006). This could create a distribution with more small fly specimens at nearshore sites and more large specimens at offshore sites.

All Lacustrine Deposits Are Not Created Equal

Few studies have investigated insect preservation in lacustrine environments (Wilson, 1980, 1988; Martínez-Délclòs et al., 1991, 2004; Martínez-Délclòs and Martinell, 1993; Smith, 2000a; Smith et al., 2006). Until the present study, Wilson's work (1980, 1988) identified broad patterns in preservation and depositional environments, providing the only model of preservation within lake systems based on fossil insect specimens. Wilson examined different depositional settings at multiple Eocene lakes from British Columbia. These included lakes that had varved sediments and those that did not. He also studied multiple insect orders, including Coleoptera, Diptera, Hemiptera, Hymenoptera, and Trichoptera. Wilson found that nearshore sites had greater numbers of insect specimens and higher levels of species richness relative to offshore sites. He hypothesized that wind and water currents, as well as insect flying ability, were responsible for the accumulation of insects along ancient shorelines. In addition, specimens from offshore sites had higher preservation quality, illustrated by higher numbers of articulated specimens than those found in nearshore sites.

The patterns described in Wilson's earlier work were not found in our study. For example, greater numbers of specimens were found in the offshore site, and there was no difference in the number of fly species between the sites. There was no difference in preservation quality or in the proportion of disarticulated specimens between the two sites. Key in Wilson's (1980, 1988) model was the importance of wind, water currents, and insect flying ability. It is assumed that insect-flying ability was equivalent between this study and that of Wilson, but wind and water currents could have been very different in Lake Florissant compared to lakes in Wilson's study. In addition, Wilson examined multiple insect orders, instead of focusing on a single group like the flies. It is possible that an examination of other insect groups, in addition to flies from Florissant, would yield diversity and abundance results that are more similar to those found in Wilson's studies. Separating how these variables work to concentrate insects is best tested using an actualistic approach with several insect orders in modern lake environments and then testing the results using data from fossil assemblages with well-defined depositional data.

Despite these differences, the taxonomic composition of flies differed between the nearshore and offshore sites, which is consistent with Wilson's findings. It is difficult to evaluate, however, as Wilson (1980, 1988) examined multiple insect orders and this study focused on taxa within a single order. What is clear from both sets of studies is that there is differential sampling of assemblages depending on depositional environment. This has also been shown for plants (Roth and Dilcher 1978; Spicer, 1981; Ferguson, 1985; Spicer and Wolfe, 1987) and should clearly be considered by paleontologists as well.

Overall, we agree with Wilson's (1980, 1988) assessment that researchers studying insect evolution and ecology through geologic time need to be certain that they are examining true patterns of biologic change and not simply documenting sampling differences due to depositional environments.

SUMMARY

Specimen quality, size, orientation, and disarticulation should not be used to evaluate whether a fossil insect should be collected, as none of these factors strongly correlated with the identifiability of a specimen. Specimens that were considered to be of low quality were still identifiable to the family and genus levels. In addition, the influence of depositional

environment on the preservation of insect taxa is much less straightforward than previously thought, and even subtle differences in the setting within a lake environment can affect which groups are preserved. Care should be taken to document depositional environments, including both the sedimentologic and stratigraphic context of lacustrine deposits, especially if these data are to be used in larger analyses of evolutionary trends or in paleoenvironmental interpretations.

ACKNOWLEDGMENTS

We thank the CU Museum for the use of specimens, access to field notes, and additional information on Cockerell's localities. Thanks to C.R. Nufio for statistical advice and reviews of the earlier versions of the manuscript. Greatly appreciated is the feedback received from P. Allison, C.C. Labandeira, and S. T. Hasiotis.

REFERENCES

- ALROY, J., 2000a, Successive approximations of diversity curves: Ten more years in the library: *Geology*, v. 28, p. 1023–1026.
- BAAS, M., BRIGGS, D.E.G., VANHEEMST, J.D.H., KEAR, A.J., and DELEEUW, J.W., 1995, Selective preservation of chitin during the decay of shrimp: *Geochimica et Cosmochimica Acta*, v. 59, p. 945–951.
- BEQUAERT, J.C., 1930, Notes on American Nemestrinidae: *Psyche*, v. 37, p. 286–297.
- BIERSTEDT, A., STANKIEWICZ, B.A., BRIGGS, D.E.G., and EVERSLED, R.P., 1997, Application of a colorimetric method and flash pyrolysis GC/MS for the detection of chitin in fossil arthropod cuticles: *Abstracts of Papers of the American Chemical Society*, v. 214, p. 38.
- BRIGGS, D.E.G., 1999, Molecular taphonomy of animal and plant cuticles: Selective preservation and diagenesis: *Philosophical Transactions of the Royal Society of London, ser. B (Biological Sciences)*, v. 354, p. 7–16.
- BRIGGS, D.E.G., KEAR, A.J., MARTILL, D.M., and WILBY, P.R., 1993, Phosphatization of soft-tissue in experiments and fossils: *Journal of the Geological Society*, v. 150, p. 1,035–1,038.
- BRIGGS, D.E.G., STANKIEWICZ, B.A., MEISCHNER, D., BIERSTEDT, A., and EVERSLED, R.P., 1998, Taphonomy of arthropod cuticles from Pliocene lake sediments, Willershausen, Germany: *PALAIOS*, v. 13, p. 386–394.
- BRIGGS, D.E.G., and WILBY, P.R., 1996, The role of the calcium carbonate calcium phosphate switch in the mineralization of soft-bodied fossils: *Journal of the Geological Society*, v. 153, p. 665–668.
- CARPENTER, F.M., 1992, *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volumes 3 and 4, Superclass Hexapoda*: Paleontological Institute and the Geological Society of America, Lawrence, Kansas, and Boulder, Colorado, 655 p.
- COCKERELL, T.D.A., 1907a, A fossil tse-tse fly in Colorado: *Nature*, v. 1973, p. 414.
- COCKERELL, T.D.A., 1907b, An enumeration of the localities in the Florissant basin from which fossils were obtained in 1906: *Bulletin of the American Museum of Natural History*, v. 23, p. 127–132.
- COCKERELL, T.D.A., 1909, Another fossil tse-tse fly: *Nature*, v. 2,057, p. 128.
- COCKERELL, T.D.A., 1914, New and little-known insects from the Miocene of Florissant, Colorado: *Journal of Geology*, v. 22, p. 714–724.
- COCKERELL, T.D.A., 1917, Some fossil insects from Florissant, Colorado: *Proceedings of the United States National Museum*, v. 53, p. 389–392.
- COOPE, G.R., 1994, The response of insect faunas to glacial-interglacial climatic fluctuations: *Philosophical Transactions of the Royal Society of London*, v. 344, p. 19–26.
- DRUMMOND, B., 2004, Florissant fossil insects: Patterns of taxonomic diversity: *Geological Society of America, Abstracts with Programs*, v. 36, p. 40.
- ELIAS, S.E., 1994, *Quaternary Insects and Their Environments*: Smithsonian Institution Press, Washington, District of Columbia, 284 p.
- EVANOFF, E., MCINTOSH, W.C., and MURPHEY, P.C., 2001, Stratigraphic summary and ⁴⁰Ar/³⁹Ar geochronology of the Florissant Formation, Colorado, in *Evansoff, E., Gregory-Wodzicki, K.M., and Johnson, K.R., eds., Proceedings of the Denver Museum of Nature and Science: ser. 4, no. 1, p. 1–16.*
- EVENHUIS, N.L., 1994, *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*: Backhuys Publishers, Leiden, The Netherlands, 600 p.
- FARRELL, B.D., 1998, "Inordinate fondness" explained: Why are there so many beetles?: *Science*, v. 218, p. 555–559.
- FERGUSON, D.K., 1985, The origin of leaf-assemblages—New light on an old problem: *Review of Palaeobotany and Palynology*, v. 46, p. 117–188.
- GRIMALDI, D. and ENGEL, M.S., 2005, *Evolution of the Insects*: Cambridge University Press, New York, 755 p.
- HENWOOD, A., 1993a, Still life in amber: *New Scientist*: v. 137, p. 31–34.
- HENWOOD, A., 1993b, Ecology and taphonomy of Dominican Republic amber and its inclusions: *Lethaia*, v. 25, p. 237–245.
- JAMES, M.T., 1937, A preliminary review of certain families of Diptera from the Florissant Miocene beds: *Journal of Paleontology*, v. 11, p. 241–247.
- JAMES, M.T., 1939, A preliminary review of certain families of Diptera from the Florissant Miocene Beds II: *Journal of Paleontology*, v. 13, p. 49–51.
- KIESSLING, W., and BARON-SZABO, R., 2004, Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 214, p. 195–223.
- LABANDEIRA, C. C., 1999, Insects and other hexapods, in *Singer, R., ed., Encyclopedia of Paleontology (Volume 1, A–L)*: Fitzroy Dearborn, London, p. 603–624.
- LABANDEIRA, C.C., and SEPKOSKI, J.J., 1993, Insect diversity in the fossil record: *Science*, v. 261, p. 265–396.
- MARTÍNEZ-DÉLCLOS, X., BARALE, G., WENZ, S., DOMENECH, R., MARTINELL, J., MERCADE, L., and RUIZ DE LOIZAGA, M.J., 1991, The outcrops of lithographic limestones of Montsec (Catalonia, Spain), The Lower Cretaceous lithographic limestones of Montsec: Ten Years of Paleontological Expeditions: Institut d'Estudis Ilerdencs, Lleida, Spain, p. 101–106.
- MARTÍNEZ-DÉLCLOS, X., BRIGGS, D.E.G., and PENLAVER, E., 2004, Taphonomy of insects in carbonates and amber: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 203, p. 19–64.
- MARTÍNEZ-DÉLCLOS, X., and MARTINELL, J., 1993, Insect taphonomy experiments: Their application to the Cretaceous outcrops of lithographic limestones from Spain: *Kaupia: Darmstader Beitrage zur Naturgeschichte*, v. 2, p. 133–144.
- MCALPINE, J.F., PETERSON, B.V., SHEWELL, G.E., TESKEY, H.J., VOCKEROTH, J.R., WOOD, D. M., coordinators, 1981, *Manual of Nearctic Diptera, vols. 1 and 2: Monograph no. 27 of Research Branch Agriculture Canada, Biosystematics Research Institute, Ottawa, Canada, 1,332 p.*
- MEYER, H.W., 2003, *The Fossils of Florissant*: Smithsonian Institution, Washington, District of Columbia, 258 p.
- MILLER, R.F., 1991, Chitin paleoecology: *Biochemical Systematics and Ecology*, v. 19, p. 401–411.
- MOE, A.P., and SMITH, D.M., 2005, Using pre-Quaternary Diptera as indicators of paleoclimate: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 221, p. 203–214.
- RASNITSYN, A.P., and QUICKE, D.L.J., 2002, *History of Insects*: Kluwer Academic Publishers, Dordrecht, The Netherlands, 517 p.
- RAUP, D., and SEPKOSKI, J.J., 1982, Mass extinctions in the marine fossil record: *Science*, v. 215, p. 1,501–1,503.
- ROTH, J.L., and DILCHER, D.L., 1978, Some considerations in leaf size and margin analysis of fossil leaves: *Courier Forschungsinstitut Senckenberg*, v. 30, p. 165–171.
- SAS INSTITUTE, INC., 1998–2000, JMP 4.0.2: SAS Institute Inc., Cary, North Carolina.
- SCUDDER, S.H., 1890, *The Tertiary Insects of North America*: Publication of the Hayden Survey, U.S. Geological Survey, Washington, District of Columbia, 734 p.
- SCUDDER, S.H., 1893, Some insects of special interest from the Florissant and other points in the Tertiaries of Colorado and Utah: *American Naturalist*, v. 27, p. 558–559.
- SEPKOSKI, J.J., BAMBACK, R.K., RAUP, D.M., and VALENTINE, J.W., 1981, Phanerozoic marine diversity and the fossil record: *Nature*, v. 293, p. 435–437.
- SMITH, D.M., 2000a, Beetle taphonomy in a recent ephemeral lake, southeastern Arizona: *PALAIOS*, v. 15, p. 152–160.
- SMITH, D.M., 2000b, *The Evolution of Plant-Insect Interactions: Insights from the Tertiary fossil record*: Ph.D. dissertation, University of Arizona, Tucson, Arizona, 303 p.
- SMITH, D.M., 2004, Florissant is better than amber: A comparison of beetle preservation, diversity and ecological representation: *Geological Society of America Annual Meeting, Abstracts with Programs*, v. 36, p. 40.
- SMITH, D.M. and COOK, A., 2001, Beetle bias: How sedimentary environment influences patterns of Coleopteran diversity in the fossil record: *Geological Society of America Annual Meeting, Abstracts with Programs*, v. 33, p. 267.
- SMITH, D.M., COOK, A., and NUFIO, C.R., 2006, How physical characteristics of beetles affect their fossil preservation: *PALAIOS*, v. 21, p. 305–310.
- SPICER, R.A., 1981, The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England: *Geological Survey Professional Papers*, v. 1,143, p. 1–77.
- SPICER, R.A. and WOLFE, J.A., 1987, Plant taphonomy of late Holocene deposits in Trinity (Clair Engle) Lake, northern California: *Paleobiology*, v. 13, p. 227–245.
- STANKIEWICZ, B.A., BRIGGS, D.E.G., EVERSLED, R.P., FLANNERY, M.B., and WUTTKE, M., 1997, Preservation of chitin in 25-million-year-old fossils: *Science*, v. 276, p. 1,541–1,543.
- WILSON, M.V.H., 1980, Eocene lake environments: depth and distance-from-shore variation in fish, insect, and plant assemblages: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 32, p. 21–44.
- WILSON, M.V.H., 1988, Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 62, p. 609–623.