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# Using pre-Quaternary Diptera as indicators of paleoclimate

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## Abstract

Many researchers have used fossilized insects to determine Quaternary climates with great success. However, pre-Quaternary insect fossils have not been utilized as indicators of climate with the same frequency, despite levels of preservation that are often equal to that of Quaternary fossils. In this study we use the Mutual Climate Range (MCR) approach with fossil Diptera from the Florissant Formation to examine the accuracy with which pre-Quaternary insect fossils can be used to determine paleoclimate.

A database of extant Dipteran climate ranges was compiled and MCR analyses were performed on all fossil Dipteran genera from Florissant with extant representatives. The analyses were performed using all fossil Dipteran genera and then again with only non-host-specific taxa. The estimates of paleoclimate from our analyses were then compared to previous estimates obtained from various paleobotanical studies of the Florissant Formation. The paleobotanical studies utilize a variety of methods to determine paleoclimate, including nearest living relative (NLR), modern analogues, CLAMP, palynanalysis, and leaf margin analysis.

We found that using a MCR approach with fossil Diptera can provide an estimate of paleoclimate for pre-Quaternary assemblages that is consistent with estimates made by paleobotanists. The analysis that included all Diptera gave a less precise climate estimate (12–18 °C) than the analysis in which host-dependent taxa were omitted. Our climate estimate, based on only non-host-specific taxa, was 12–14 °C, which is well within the range of estimates for Florissant derived from floral material. Although approaches that use modern analogs are sometimes viewed with concern because of the necessary assumption that fossil taxa share the same environmental tolerances as their modern counterparts, we believe that fossil insect assemblages, especially when used in MCR analyses, can be quite informative in estimating pre-Quaternary paleoclimate.

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## 1. Introduction

Over the past 30 years researchers have become more aware of the benefits of using fossilized insects in climatic reconstructions. Insects often have distinct ecological tolerances that can be used to estimate the

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climatic ranges of past environments (Atkinson et al., 1986; Coope, 1970; Elias, 1994). There have been three main approaches used to reconstruct paleoclimates using fossil insects; the modern analog approach, the nearest living relative (NLR) approach, and the Mutual Climatic Range (MCR) approach. All three approaches use methods that emphasize the ecological tolerances of modern taxa to infer past climate. The modern analog approach relies on a few extant indicator species (those insects with distinct, modern ecological tolerances), the NLR approach uses the environmental tolerances of a non-specified number of extant relatives of fossil taxa, and the MCR approach utilizes the overlap of temperature ranges of all non-phytophagous, extant species from a fossil assemblage (Elias, 1994).

The modern analog approach uses the distribution of a handful of extant indicator species within a fossil assemblage to infer paleoclimate (Williams and Morgan, 1977). Typically, the composition of extant indicator taxa within a fossil assemblage is compared to the composition in modern communities to estimate the climate of the ancient community. The number of specimens available for use in modern analog studies is generally very low, and decreases with geologic time, since the number of extant taxa decreases with time. This qualitative approach to the determination of paleoclimate does not make use of the entire assemblage and as such, the climatic determination relies heavily on taxa surveyed in the study (Mosbrugger and Utescher, 1997). The lack of an a priori method for determining which taxa to incorporate into modern analog studies may also introduce researcher biases.

The NLR approach is similar to the modern analog approach. It is still assumed that the distribution of fossil species is analogous to modern species. The main difference is that no species used in the study are extant (Mosbrugger, 1999). The environmental tolerances of what are believed to be the closest living relatives of the taxa from the assemblage are used to infer paleoclimate, thus, the results of the study rely completely on accuracy of the systematic relationships of the taxa used in the study. As with the modern analog approach, there is no specified number or method for selecting taxa to use in a study and as such the results can vary depending on the specific taxa and number of taxa chosen by the researcher. In addition, fossil and extant

taxa that have been incorrectly interpreted as relatives can provide an invalid climate estimate.

Atkinson et al. (1986) devised the MCR approach for determining paleoclimate by using the climatic ranges of all identifiable, non-phytophagous beetle species present in a fossil assemblage. In addition to being robust and relatively easy to recover from Quaternary sediments, beetle taxa are used in MCR studies because their fragments can often be determined to the species level (Elias, 1994; Walkling and Coope, 1996). Species level identification allows for the determination of ecological requirements that may lead to a more precise estimate of geographical distribution for a particular taxon than a genus level identification would. Phytophagous beetles are not used in MCR analyses because they are thought to skew the results of climatic studies due to their dependence on their host plants (Coope, 1970). As plants may respond more slowly to climate change, the presence of phytophagous beetles may reflect the distribution of their host plants as opposed to the true paleoclimate (Atkinson et al., 1986, 1987; Elias, 1994). Non-phytophagous beetles, on the other hand, may have more generalized diets and thus the ability to move rapidly in response to climate change.

In the MCR method, it is assumed that fossil and extant beetle species have the same climatic tolerances. The temperature ranges of the extant species are determined by gathering data from weather stations found within their current geographic distributions. The temperature ranges of all extant taxa are plotted, and the temperature at which the ranges overlap signifies the paleotemperature of the assemblage. By focusing on the climatic ranges of all extant taxa, rather than using a small number of taxa as indicators of a geographic area, and hence climate (as in the modern analog and NLR approaches), the MCR method minimizes the problems associated with the subjectivity of researcher decisions regarding which taxa were used in an analysis.

Although most of the MCR analyses of the past have focused on Quaternary beetles (Aalbersberg and Litt, 1998; Coope, 1994, 2000; Coope and Böcher, 2000; Coope and Lemdahl, 1995; Coope et al., 1998; Horton et al., 1992; Kasse et al., 1998; Keen et al., 1999; Lowe et al., 1999; Walkling and Coope, 1996; Witte et al., 1998), recent studies have begun to test the applicability of the MCR method on late Tertiary

beetle assemblages (Elias and Matthews, 2002). Other insect orders have also been used to estimate paleoclimate in the Quaternary, using other methods. For example, Chironomid (Diptera) larvae are excellent indicators of surface water temperature, and lake cores containing Chironomid head capsules and other fossils have been used to determine fine scale climatic changes (Levesque et al., 1994; Walker et al., 1991).

A modified version of the MCR approach has also been devised for fossil plants (Sinka and Atkinson, 1999). Several climatic variables important to the distribution of plant species such as light competition, leaf area, and avoidance of desiccation were used in a factor analysis to define climate ranges based on modern plant distributions. The method was further refined through an examination of two modern sites and then tested on two Quaternary sites. Using an MCR approach with plants appeared to be promising and the authors found that they were able to accurately determine the paleoclimate of the fossil sites. However, using a factor analysis approach introduced a great amount of variance and they found that they could not obtain the level of precision for which they were hoping (Sinka and Atkinson, 1999).

With the exception of a few studies (for example, Archibald and Mathewes, 2000; Elias and Matthews, 2002), nearly all insect-based paleoclimatic reconstructions have focused on relatively recent Quaternary sediments containing sub-fossilized insects. There are many insect lagerstätten (i.e. Green River, USA; Messel, Germany; Liaoning, China) that contain exquisitely preserved fossils of an older age that may also be useful for paleoclimatic reconstructions. In this study we use fossilized adult Diptera to determine whether they can provide a climatic signal for pre-Quaternary environments that is consistent with climatic signals obtained using other paleontological methods; specifically paleobotanical methods. We conducted this study on the Late Eocene, Florissant Fossil assemblage, where Diptera are well preserved and abundant.

Florissant is an ideal setting for testing the utility of insects as paleoclimate indicators, as there has been a great amount of research on the climate of the late Eocene Florissant Formation using various paleobotanical approaches (Axelrod, 1997; Forest et al., 1995; Gregory, 1994a,b; Gregory and Chase, 1992; Gregory

and McIntosh, 1996; Leopold and Clay-Poole, 2001, Meyer, 1986, 1992, 2001; Wolfe et al., 1998; Wolfe, 1992, 1994). These studies provide an excellent basis for comparison with the results of the present study.

The purpose of this study is to determine if the MCR approach can be used with pre-Quaternary insects to estimate paleoclimate. In order to test the utility of this method, we compiled a comprehensive database of modern climatic tolerances for extant genera of Diptera preserved in the Florissant Formation. The climate signals obtained using the MCR approach were then compared to previous climate estimates for Florissant based on fossil plants.

## 2. Locality studied

We examined fossil Diptera from the Late Eocene Florissant Formation, in central Colorado, USA (Fig. 1). The exceptional preservation

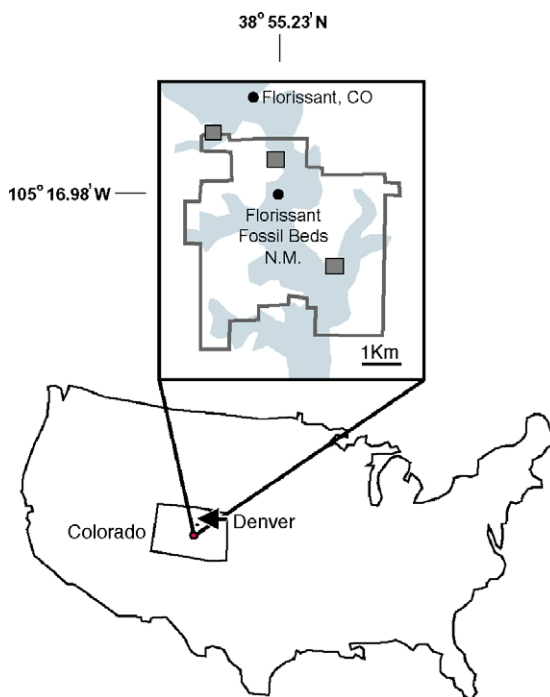


Fig. 1. Location of the Florissant Formation, Colorado, USA. Inset shows the boundary of the Florissant Fossil Beds National Monument and the large shaded area represents the boundary of the fossiliferous lake shale. All published Diptera have been collected from multiple sites within the boundaries of the National Monument, indicated by gray squares.

exhibited at Florissant has made it an ideal deposit for paleobotanical (Gregory-Wodzicki, 2001; Leopold and Clay-Poole, 2001; Lesquereux, 1883; MacGinitie, 1953; Manchester, 2001; Wheeler, 2001; Wingate and Nichols, 2001), paleoentomological (Bequaert, 1930; Bequaert and Carpenter, 1936; Cockerell, 1907b, 1926, 1927; Emmel et al., 1992; James, 1939; Melander, 1949; Scudder, 1874, 1880) and paleoaltitudinal studies (Axelrod, 1997; Forest et al., 1995; Gregory, 1994a,b; Gregory and Chase, 1992; Gregory and McIntosh, 1996; Meyer, 1986, 1992, 2001; Wolfe et al., 1998; Wolfe, 1992, 1994).

The Florissant Formation consists of a series of shales, mudstones and conglomerates comprised of volcanic sediments derived from an eruptive source to the southwest of present day Florissant Fossil Beds National Monument (Evanoff et al., 2001; Scudder, 1880; Wobus and Epis, 1978). Recent  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of sanidine crystals within pumice clasts in the Formation have yielded an age of  $34.07 \pm 0.10$  Ma, which places the formation in the Latest Eocene (Evanoff et al., 2001). All three shale units in the formation are fossiliferous, and all three contain insect and plant fossils. The insects are preserved as compression fossils in fine-grained, tuffaceous–diatomaceous shale (Evanoff et al., 2001).

MacGinitie (1953) utilized a floristic approach to determine that the Florissant flora was most similar to modern floras found in the Sierra Madre of northeastern Mexico and a palynological study (Leopold and Clay-Poole, 2001) using the NLR approach, yielded results similar to those determined by MacGinitie. These studies have supported the idea that the environment surrounding ancient Lake Florissant was dry during the winter and wet in the spring and summer. The discovery of one palm frond strengthened paleobotanists' arguments that it was necessary for Florissant to have warm winters with few, if any, days below freezing (Leopold and Clay-Poole, 2001).

A myriad of paleoclimate analyses have been performed using the climate-leaf analysis multivariate program (CLAMP) method (Wolfe, 1993) for the Florissant Formation, resulting in Mean Annual Temperatures (MATs) that range from  $10.7 \pm 1.5$  to  $15.5$  °C (Table 1; Axelrod, 1997; Gregory, 1994a,b;

Table 1

Paleobotanically derived estimates of paleotemperature for Florissant

Temperature estimated (MAT)	Citation
9.2–13.9 °C	Gregory and Chase, 1992
9.2–12.2 °C	Gregory, 1994a
10.8 °C	Wolfe, 1994
11.3–14.3 °C	Gregory, 1994b
12 °C	Wolfe, 1992
12.8 °C	Gregory and McIntosh, 1996
13.1–15.1 °C	Meyer, 1986, 1992
17 °C	Leopold and Clay-Poole, 2001
>18 °C	MacGinitie, 1953

All estimates are derived from taxon-free approaches, except for the estimates of Leopold and Clay-Poole (2001) and MacGinitie (1953).

Gregory and Chase, 1992; Gregory and McIntosh, 1996; Meyer, 1986, 1992; Wolfe, 1992, 1994). Early paleoentomological studies of Florissant, all of which used a modern analog approach, have indicated climates most similar to those of the south-eastern United States, described as warm temperate (James, 1939; Scudder, 1880). However, the identification of two species of tse-tse flies (Cockerell, 1907a, 1909) suggest a hot and dry, subtropical environment for Florissant (Bequaert, 1930; Bequaert and Carpenter, 1936) because modern tse-tse flies are only found in the sub-Saharan deserts of Africa.

### 3. Methods

We compiled a comprehensive database of Florissant Diptera and information on the ecological tolerances of their extant relatives. We used the original taxonomic designations and corrected these designations based on revisions from the literature (Evenhuis, 1994; McAlpine et al., 1981). Although species-level identification of Florissant Diptera is often questionable, generic and family level identifications are much more reliable. While previous paleoclimate analyses of Quaternary insects have only been conducted at the species level (Elias, 1994), we believe that genus-level analyses should be appropriate as many Diptera have climate tolerances that are consistent across all taxa within a genus and sometimes within families. In addition, there are no extant species of Diptera in the Florissant assemblage;

therefore the data in this study were analyzed at the genus level.

Climate data for extant taxa from Florissant were compiled from the literature, through personal communication with experts on modern Dipteran ecology (see Acknowledgements), and from numerous online Diptera databases (Table A1). We recorded climate ranges, biogeographical ranges, altitudinal restrictions, larval and adult diet and habitat. The climate data were divided into five categories (tropical, subtropical, warm temperate, temperate, and arctic) based on a modified version of the Köppen climate classification system. Although the Köppen model combines annual and monthly averages of temperature and precipitation (Köppen, 1923, 1931), each of our climate categories is defined by an approximation of its mean annual temperature. We chose the Köppen model because of its broad use among researchers, its simplicity, and the ease with which it could be applied to our dataset.

We estimated paleoclimate of the Florissant Formation using two separate methods. First, we estimated the paleoclimate by determining the range of climate overlap of all extant Diptera in the assemblage. Second, we estimated the paleoclimate of Florissant by using only the non-phytophagous and non-blood feeding Diptera. Phytophages and sanguivores (even if only for one stage of development) were removed because, as is the case with Quaternary MCR analyses, it is assumed that the range of the host is what is reflected in the analysis, rather than the range of the insect. Sanguivores were also removed from the second analysis because it was unclear whether Eocene Diptera had host-specific relationships with their prey, which would have the potential to skew the results of an analysis as well. The range of climate overlap of the non-phytophages and non-sanguivores was then used as the estimate of paleoclimate for Florissant. Both MCR derived estimates were compared to the results of previous paleoclimate studies based on fossil plants from Florissant.

#### 4. Results

One hundred sixteen genera from 39 families of Diptera have been described from Florissant. Of those

genera, 94 are extant and 22 are extinct. There are no extant species of Diptera described from the Florissant Formation. There were 69 extant genera for which we could find modern climate information. These taxa are included in our database (Table A1) and used in the MCR analyses.

The majority (64%) of Diptera in the database belong to groups that require either forested or open areas, in close proximity to freshwater for one or more stages of their development. Some of the families require fast-moving freshwater environments while others require stagnant water for their development. Many of these groups have aquatic larval stages and a wide range of larval and adult diet-types are found in the assemblage. The remaining Diptera in the database consisted of taxa that were strictly aquatic or did not need water at any point in their development but, instead, used decaying wood, leaves and bark, carrion, or soil at different stages in their development. Most of the Diptera are Holarctic or Nearctic in their modern distributions, but some are currently restricted to the Afrotropics (Glossinids and Nemestrinids) and the Neotropics (Richardiids).

Our first MCR analysis included all 69 Diptera, 25 of which were found to range across all of the climate categories and were, therefore, uninformative in regards to climate (Fig. 2). The ranges of the remaining 44 taxa resulted in a broad climate signal. The range of overlapping climate was temperate to subtropical. This would be the equivalent of a MAT of 12–18 °C, a range that is so broad it spans three of the five climate categories (Fig. 2). Although this MAT includes values in the range of estimates derived from previous paleobotanical analyses, it also includes values that are higher (16–18 °C) than the paleobotanical estimates, which we consider too broad an estimate to be useful.

The second MCR analysis excluded climatic data associated with phytophagous and blood-feeding Diptera and 18 of the genera had climate tolerances that ranged through all of the climate categories. Removal of all phytophages, sanguivores and one genus for which we could find no ecological information (32 taxa) produced a much more narrow climate range of warm-temperate to temperate, which is equivalent to a MAT of 12 °C to 16 °C (Fig. 3). This estimate is well within the range, and the majority



(2/3), of climate estimates for Florissant derived from paleobotanical analyses.

## 5. Discussion

Our study provides strong support for the utility of the MCR approach and the use of adult Diptera for determining the climate of pre-Quaternary environments. Our paleoclimate estimate is consistent with most of the previous paleotemperatures estimated using taxon-free approaches with plant macrofossil data (Table 1; Gregory, 1994a,b; Gregory and Chase, 1992; Gregory and McIntosh, 1996; Meyer, 1986, 1992; Wolfe, 1992). Using the habitat preferences of the extant Diptera, we interpret the paleoenvironment of Florissant to have been forested with open areas near freshwater. This interpretation is also supported by work on the flora and other insect groups (Bequaert, 1930; Emmel et al., 1992; Hayden, 1890; Leopold and Clay-Poole, 2001; Lesquereux, 1883; MacGinitie, 1953; Melander, 1949; Scudder, 1874).

The MCR method is a tool that can be used with Diptera to estimate paleoclimate. Although the method provides an accurate measure of climate, the precision of the estimate is dependant on the ecology of taxa used in the study. Using all Diptera from the assemblage produced a climate range that was too broad to be useful. In accordance with the MCR method currently utilized with Quaternary beetle assemblages, host-specific taxa were removed from the study. This omitted all taxa that spanned all five of the climate ranges, and produced a second, more precise estimate of paleoclimate. We believe that the second MCR analysis, which excluded host-dependant Diptera (phytophages and sanguivores), provided a more reliable estimate. Host-dependant taxa are more likely to reflect the climate tolerances of their hosts. These hosts, be they plants or large mammals, may not be as informative regarding climate because they may represent a much larger geographical range, and therefore, a much greater range in climate tolerance. In addition, plant lag time, the time required for a plant assemblage to adjust to a change in climate, can be anywhere from 10 to 2000 years, depending on the severity and timing of climate change (Jackson and Overpeck,

2000). During this lag interval, a plant assemblage will reflect the former climate rather than the new climate. Mammalian hosts may not exhibit lag-time, but instead may reflect much broader geographic distributions and greater climate tolerances (Alroy et al., 2000). Removing host-dependant taxa removes the noise in the climate signal that is likely to be due to the hosts.

Perhaps the greatest concern in using an MCR approach with pre-Quaternary insects is that one must assume that the ecological tolerances of the taxa studied have changed very little over the time period being studied. We believe this is a reasonable assumption for pre-Quaternary insect assemblages that are analyzed at the generic level. This is because 1) there appears to have been little morphological change in insects since the Cenozoic, 2) insects, in general, appear to have low speciation rates and 3) it appears that insects move in response to climate change instead of adapting to new climate.

MacGinitie (1953) was the first to note the morphological similarity between Cenozoic and extant insects and the Diptera, specifically, were mentioned as a group that had undergone little to no evolutionary change. Numerous examples of fossil taxa that are morphologically indistinguishable from modern taxa have been cited in the literature, including the extant Strepsipteran, *Bohartilla megalognatha*, which has been found in both Dominican (25–35 Ma) and Baltic (35–40 Ma) ambers (Rasnitsyn and Quicke, 2002).

Low speciation rates are thought to account for the lack of morphological divergence between fossil and extant insect taxa. Many researchers have found evidence from the Quaternary supporting the idea that speciation rates for insects are very low (Böcher, 1989; Coope, 1970, 1994; Elias, 1994; Rasnitsyn and Quicke, 2002; Matthews, 1976a,b, 1977, 1979a,b). According to both Coope (1970) and Matthews (1976a), there has been no major beetle speciation since at least the middle to late Pleistocene. Furthermore, there is no evidence of any significant beetle extinction events during the climatically unstable Quaternary (Elias, 1994), and presumably no major Dipteran extinctions as well. In addition, geologically long-lived taxa have been documented in the literature. For example, Matthews (1977, 1979a,b)

described a Pliocene rove beetle from Alaska that was later discovered to be extant in Russia (Elias, 1994). Another example can be found in a Pliocene–Pleistocene insect assemblage from Greenland, in which nearly all of the fossil species were determined to be extant (Böcher, 1989). Although these examples are much more recent than the Eocene assemblage at Florissant, they demonstrate that insect species can persist, relatively unchanged, for great spans of geologic time.

Among other things, it is the high mobility of insects, and thus their ability to respond quickly to environmental changes, that is thought to have kept insect speciation rates low (Coope, 1978). Insects are extremely mobile and have the ability to track climate change as it moves across the landscape. As a result, fossil insect assemblages often have compositions that are similar to modern insect assemblages (Elias, 1994). However, those similarities do not mean that fossil insect assemblages directly reflect those that we see today. This is why we cannot rely solely on non-quantitative techniques like the modern analogue and NLR methods to determine paleoclimate.

Using an MCR approach with pre-Quaternary fossil insects provides researchers with a previously unused dataset of biological indicators. An MCR analysis of fossil insects can be used in combination with more traditional paleobotanical methods of climate inference. In addition, it is common to find abundant insect fossils in localities where few to no plants are available and we expect this method to be especially useful for estimating the climate of assemblages that have too few plant fossils to conduct a climate analysis (Wolfe, 1993).

In addition, conducting MCR analyses on a dataset that includes the non-phytophagous members of other insect orders, such as Coleoptera and Hymenoptera, will also provide useful paleoclimate estimates. These orders are commonly found at Florissant and in other Cenozoic fossil assemblages and often have very specific climatic tolerances. Using additional insect orders may provide more specific ecological data such as habitat preference (lake chemistry or surrounding vegetation) and seasonality. Using an MCR approach with a combination of insect orders and plant data is likely to provide the most reliable estimate of paleoclimate.

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## Appendix A

For a list of Florissant Diptera, their climate designations and host specificities see Table A1.

Table A1  
Florissant Diptera and their climate categories and host specificities

Family	Genus	Climate category	Host specificity
Agromyzidae	<i>Agromyza</i>	All	Yes
Agromyzidae	<i>Melanagromyza</i>	Warm Temperate– Tropical	Yes
Anthomyiidae	<i>Anthomyia</i>	All	Yes
<b>Anthomyiidae</b>	<b><i>Mecistoneuron</i></b>	<b>Unknown</b>	<b>Unknown</b>
Asilidae	<i>Asilus</i>	Temperate– Warm Temperate	No
Asilidae	<i>Ceraturgus</i>	All	No
Asilidae	<i>Cophura</i>	Warm Temperate	No
Asilidae	<i>Dioctria</i>	All	No
Asilidae	<i>Leptogaster</i>	All	No
Asilidae	<i>Lestomyia</i>	All	No
Asilidae	<i>Microstylum</i>	Warm Temperate	No
Asilidae	<i>Nicocles</i>	Warm Temperate	No
Asilidae	<i>Philonicus</i>	All	No
Asilidae	<i>Saropogon</i>	Warm Temperate	No
Asilidae	<i>Senobasis</i>	All	No
Asilidae	<i>Senoprosopis</i>	All	No
Asilidae	<i>Taracticis</i>	All	No
Athericidae	<i>Atrichops</i>	Unknown	No

Table A1 (continued)

Family	Genus	Climate category	Host specificity
Bibionidae	<i>Bibio</i>	All	Yes
Bibionidae	<i>Bibiodes</i>	Temperate	Yes
Bibionidae	<i>Hesperinus</i>	All	Yes
Bibionidae	<i>Penthetria</i>	Tropical–Subtropical	Yes
Bibionidae	<i>Plecia</i>	Tropical–Subtropical	Yes
<b>Bombyliidae</b>	<b><i>Alepidophora</i></b>	<b>Unknown</b>	<b>Unknown</b>
<b>Bombyliidae</b>	<b><i>Alomatia</i></b>	<b>Unknown</b>	<b>Unknown</b>
Bombyliidae	<i>Amphicosmus</i>	Warm	Yes
Bombyliidae	<i>Apolysis</i>	Temperate	Yes
Bombyliidae	<i>Desmatomyia</i>	Warm	Yes
Bombyliidae	<i>Dolichomyia</i>	Temperate	Yes
Bombyliidae	<i>Geron</i>	Tropical	Yes
<b>Bombyliidae</b>	<b><i>Melanderella</i></b>	<b>Unknown</b>	<b>Unknown</b>
<b>Bombyliidae</b>	<b><i>Pachysystropus</i></b>	<b>Unknown</b>	<b>Unknown</b>
Bombyliidae	<i>Paracosmus</i>	Warm	Yes
Bombyliidae	<i>Phthiria</i>	Temperate–Subtropical	Yes
Bombyliidae	<i>Poecilognathus</i>	Warm	Yes
<b>Bombyliidae</b>	<b><i>Tithonomyia</i></b>	<b>Unknown</b>	<b>Unknown</b>
<b>Bombyliidae</b>	<b><i>Verrallites</i></b>	<b>Unknown</b>	<b>Unknown</b>
Bombyliidae	<i>Villa</i>	Unknown	Yes
Bombyliidae	<i>Ylasoia</i>	Unknown	Yes
Cecidomyiidae	<i>Cecidomyia</i>	Unknown	Yes
Chironomidae	<i>Chironomus</i>	All	Yes
Chironomidae	<i>Diamesa</i>	Warm	No
Chironomidae	<i>Diamesa</i>	Temperate	No
<b>Cylindrotomidae</b>	<b><i>Cyttaromyia</i></b>	<b>Unknown</b>	<b>Unknown</b>
Empididae	<i>Empis</i>	Temperate	No
<b>Empididae</b>	<b><i>Progloma</i></b>	<b>Unknown</b>	<b>No</b>
Empididae	<i>Rhamphomyia</i>	All	No
Empididae	<i>Tachypeza</i>	Unknown	No
Glossinidae	<i>Glossina</i>	Unknown	No
Heleomyzidae	<i>Heteromyza</i>	Tropical–Subtropical	Yes
<b>Keroplastidae</b>	<b><i>Proapemon</i></b>	<b>Unknown</b>	<b>Unknown</b>
Lauxaniidae	<i>Sapromyza</i>	Temperate	No
Limoniidae	<i>Antocha</i>	Tropical	No
<b>Limoniidae</b>	<b><i>Cladoneura</i></b>	<b>Unknown</b>	<b>Unknown</b>
Limoniidae	<i>Cladura</i>	All	No
Limoniidae	<i>Dicranomyia</i>	All	No
<b>Limoniidae</b>	<b><i>Limnocema</i></b>	<b>Unknown</b>	<b>Unknown</b>
Limoniidae	<i>Limnophila</i>	Unknown	No
<b>Limoniidae</b>	<b><i>Oryctogma</i></b>	<b>Unknown</b>	<b>Unknown</b>
Limoniidae	<i>Rhabdomastix</i>	All	No
<b>Limoniidae</b>	<b><i>Rhabdinobrochus</i></b>	<b>Unknown</b>	<b>Unknown</b>

Table A1 (continued)

Family	Genus	Climate category	Host specificity
<b>Muscidae</b>	<b><i>Ophyra</i></b>	<b>All</b>	<b>Unknown</b>
Mycetophilidae	<i>Boletina</i>	Temperate–Warm	No
Mycetophilidae	<i>Exechia</i>	Temperate	No
Mycetophilidae	<i>Leia</i>	Temperate–Warm	No
Mycetophilidae	<i>Mycetophila</i>	Temperate	No
Mycetophilidae	<i>Mycomya</i>	Unknown	No
Mycetophilidae	<i>Sciophila</i>	Temperate–Warm	No
Mydidae	<i>Mydas</i>	Temperate	No
Nemestrinidae	<i>Hirnoneura</i>	Warm	Yes
Nemestrinidae	<i>Neorhynchocephalus</i>	Temperate–Subtropical	Yes
Nemestrinidae	<i>Prosoeca</i>	Warm	Yes
Otitidae	<i>Meliera</i>	Temperate–Subtropical	No
Phoridae	<i>Chaetopleurophora</i>	Temperate	Yes
Phoridae	<i>Phora</i>	Unknown	Yes
Phoridae	<i>Spiniphora</i>	Unknown	Yes
Piophilidae	<i>Mycetaulus</i>	Unknown	No
Pipunculidae	<i>Protonephrocercus</i>	Temperate	Yes
Platypozidae	<i>Eucallimya</i>	Unknown	No
Ptychopteridae	<i>Bittacomorphella</i>	Unknown	No
Rhagionidae	<i>Dialysis</i>	Unknown	No
Rhagionidae	<i>Rhagio</i>	Unknown	No
Rhagionidae	<i>Symphoromyia</i>	Unknown	No
<b>Richardiidae</b>	<b><i>Pachysomites</i></b>	<b>Unknown</b>	<b>Unknown</b>
<b>Richardiidae</b>	<b><i>Urotalis</i></b>	<b>Unknown</b>	<b>Unknown</b>
Scathophagidae	<i>Cordilura</i>	Arctic–Temperate	No
Scatopsidae	<i>Rechertella</i>	Temperate–Warm	No
Sciaridae	<i>Sciara</i>	Temperate	No
Sciomyzidae	<i>Sciomyza</i>	All	No
Sepsidae	<i>Themira</i>	Temperate–Subtropical	Yes
Stratiomyidae	<i>Beris</i>	Unknown	No

(continued on next page)

Table A1 (continued)

Family	Genus	Climate category	Host specificity
Stratiomyidae	<i>Cyphomyia</i>	Unknown	No
Stratiomyidae	<i>Lasiopa</i>	Unknown	No
<b>Stratiomyidae</b>	<b><i>Moyamyia</i></b>	<b>Unknown</b>	<b>Unknown</b>
Stratiomyidae	<i>Nemotelus</i>	Unknown	No
Stratiomyidae	<i>Oxycera</i>	Unknown	No
Stratiomyidae	<i>Rhingiopsis</i>	Unknown	No
<b>Syrphidae</b>	<b><i>Archalia</i></b>	<b>Unknown</b>	<b>Unknown</b>
<b>Syrphidae</b>	<b><i>Cacogaster</i></b>	<b>Unknown</b>	<b>Unknown</b>
Syrphidae	<i>Cheilosia</i>	Temperate–Tropical	Yes
Syrphidae	<i>Chrysogaster</i>	Temperate–Tropical	Yes
Syrphidae	<i>Leucozona</i>	Temperate–Tropical	Yes
Syrphidae	<i>Pipiza</i>	Temperate–Tropical	Yes
Syrphidae	<i>Platycheirus</i>	Temperate–Tropical	Yes
<b>Syrphidae</b>	<b><i>Protochrysotoxum</i></b>	<b>Temperate–Tropical</b>	<b>Yes</b>
Syrphidae	<i>Rhingia</i>	Temperate–Tropical	Yes
Syrphidae	<i>Sphegina</i>	Temperate–Tropical	Yes
Syrphidae	<i>Syrphus</i>	Temperate–Tropical	Yes
Tabanidae	<i>Silvius</i>	Temperate–Tropical	Yes
Tabanidae	<i>Tabanus</i>	Warm Temperate–Subtropical	Yes
<b>Tachinidae</b>	<b><i>Lithexorista</i></b>	<b>Unknown</b>	<b>Unknown</b>
Therevidae	<i>Nebritus</i>	All	No
Therevidae	<i>Psilocephala</i>	All	No
Therevidae	<i>Ruepellia</i>	Unknown	No
<b>Tipulidae</b>	<b><i>Manapsis</i></b>	<b>Unknown</b>	<b>Unknown</b>
Tipulidae	<i>Tipula</i>	All	No
Xylomyiidae	<i>Solva</i>	All	No

Extinct genera are in boldface type. Taxa that are phytophagous, parasitic or sanguivorous have a yes for Host Specificity and are not used in the second MCR analysis. Taxa with unknown climate categories and/or host specificities are unknown either because the genus is extinct or because there was no literature available for that group.

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