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IMPORTANCE OF FALLEN COARSE WOODY DEBRIS TO THE DIVERSITY OF SAPROXYLIC DIPTERA IN THE BOREAL MIXEDWOOD FORESTS OF EASTERN NORTH AMERICA

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L'IMPORTANCE DU DÉBRIS LIGNEUX GROSSIERS AU SOL POUR LA DIVERSITÉ DES DIPTÈRES SAPROXYLIQUES DANS LA FORÊT BORÉALE MIXTE DE L'EST DE L'AMÉRIQUE DU NORD

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RÉSUMÉ

L'information de base concernant la réponse des espèces saproxyliques aux propriétés des débris ligneux grossiers est nécessaire au raffinement des stratégies de conservation et d'aménagement basées sur l'approche du filtre brut en forêt boréale. Afin de vérifier si les besoins des insectes saproxyliques reflètent également ceux d'un plus large spectre d'espèces, nous avons mesuré l'utilisation des débris ligneux grossiers par les diptères saproxyliques, un groupe abondant mais peu étudié. Pour décrire les assemblages de diptères saproxyliques en forêt boréale mixte de l'est de l'Amérique du nord, des pièges d'émergence ont été installés sur des bûches de peuplier faux-tremble (*Populus tremuloides* Michaux; N=46) et d'épinettes noires (*Picea mariana* (Miller); N=47). La campagne d'échantillonnage s'est échelonnée sur deux étés de terrain (2006-2007) de mai à août. Nous avons mesuré les effets du diamètre, du stade de décomposition (densité) et de l'espèce de l'arbre hôte sur la composition et la structure des assemblages de diptères saproxyliques. Un total de 6753 individus ont été capturés pour un total de 227 taxa. Un peu plus de la majorité des taxa capturés se sont avérés relativement rares puisque 121 de ceux-ci (53%) n'ont été représentés que par un seul individu. De plus, 2119 individus (51 taxa) était présents dans au moins 5% des bûches échantillonnées. Les cinq familles les plus abondantes furent les suivantes : Sciaridae (1850 individus), Cecidomyidae (1539 individus), Ceratopogonidae (816 individus), Phoridae (801 individus) et Mycetophilidae (749 individus). Les Mycetophilidae constituèrent la plupart de la richesse avec un total de 178 taxa. La richesse spécifique et l'occurrence des espèces de diptères étaient négativement liées à la densité du bois chez l'épinette noire, indiquant que l'importance du bois mort s'accroît au cours du processus de décomposition pour la plupart des espèces. Les mycétophages et saprophages étaient les guildes les plus communes et leurs abondances étaient positivement associées au diamètre des bûches ainsi qu'à leur stade de décomposition, bien que la proportion de la variance expliquée par ces facteurs étaient modeste. De plus, la densité du bois influençait les assemblages d'espèces en général, mais seulement pour l'épinette noire. Lorsqu'ils sont analysés séparément des autres guildes, les assemblages de mycétophages répondaient aussi à la densité du bois de l'épinette noire, tandis que les saprophages répondaient à la densité du bois des deux espèces-hôtes. La prépondérance des espèces rares et agrégées suggère que les diptères saproxyliques qui émergent du bois mort sont fortement liés à certains microhabitats.

MOTS-CLÉS : Biodiversité, débris ligneux grossiers, bois mort, diptères, saproxylique

ABSTRACT

Baseline data regarding the associations of saproxylic species with coarse woody debris (CWD) properties are needed to refine coarse-filter conservation efforts and management in the boreal forest. In order to verify whether our current understanding of saproxylic insect requirements reflect the needs of a wide spectrum of species, we measured the use of coarse woody debris by Diptera an abundant but less studied group. More specifically, we measured the effect of log diameter, wood decay (wood density g/cm^3) and tree host species on the abundance, species richness and community structure of saproxylic Diptera. We used emergence tents *in situ* to collect adult Diptera from 70 cm length portions of aspen (*Populus tremuloides* Michaux., N=46) and black spruce (*Picea mariana* (Miller.), N=47) logs of different diameters and stages of decay (wood density g/cm^3) in boreal mixedwood forests in eastern North America. Collection from late May to August in 2006 and early May to August in 2007 yielded a total of 6753 individuals and a total of 227 taxa. Most taxa were rarely collected as 121 taxa or 53% were represented by one individual over two years of collection. A total of 2119 individuals (51 taxa) were present in 5% or more of sampled logs. The five most abundant families collected were Sciaridae (1850 individuals), Cecidomyiidae (1539 individuals), Ceratopogonidae, (816 individuals), Phoridae (801 individuals) and Mycetophylidae (749 individuals). The Mycetophilidae was the most species rich family with a total of 178 taxa. Overall dipteran abundance and species richness was negatively related to wood density in spruce indicating that coarse woody debris (CWD) becomes increasingly valuable as decay progresses for most saproxylic Diptera. Mycetophages and saprophages were the most dominant guilds and we revealed that although the amount of variation explained by our variables was small, increasing diameter and increasing decay has a positive affect on their abundance in spruce. Overall, assemblages changed along with changes in wood density in spruce. The same pattern was revealed when the mycetophagous guild was analyzed separately. Saprophagous guild assemblages changed along with changes in wood density in both tree host species. The preponderance of rare and aggregated taxa and the high assemblage dissimilarity between individual logs in our study suggests' saproxylic Diptera emerging from fallen CWD may be highly microhabitat specific.

KEY WORDS: Biodiversity, coarse woody debris, dead wood, Diptera, saproxylic

INTRODUCTION

Historically, the presence of coarse woody debris (CWD) in a managed forest was regarded as a waste of resources attributed to wasteful management practices. In addition, CWD was often considered a potential source of pest populations affecting healthy trees (Martikainen et al., 1999; Schiegg, 2001). However, CWD is now regarded as a key component of boreal forest ecosystems, providing energy, nutrients and habitat to a number of organisms (Schiegg, 2001; Grove, 2002; Hovemeyer and Schauermann, 2003; Hammond, Langor and Spence, 2001).

Widespread interest in the role of CWD in forest ecosystems stems from concerns over species richness and abundance loss resulting from reductions of dead wood and habitat fragmentation in Europe and Fennoscandia (Berg et al., 1994; Siitonen and Martikainen 1994; Edman et al., 2004). It has been estimated by IUCN (International Union for the Conservation of Nature and Natural Resources) that 50% of red listed species in Fennoscandia are threatened by forestry practices (Berg et al., 1994). In Sweden, species dependent on dead wood dominate threatened species lists (Jonsell, Weslien and Ehnström, 1998). In response to concerns over biodiversity loss, changes in forest management practices have occurred such as dead wood retention in the form of high-stumps in Fennoscandia (Jonsell, Nittérus and Stighall, 2004) and protection of forested land in many parts of Europe (Shiegg, 2001).

In Quebec, mechanized forestry has a much shorter history than Europe and Fennoscandia, therefore questions regarding CWD ecology and management have only recently begun to emerge (Drapeau, et al., 2002; Nappi, Drapeau and Savard, 2004; Saint-Germain, Drapeau and Buddle, 2007; Angers, 2009; Drapeau et al., 2009) and some objectives regarding its conservation have been outlined by decision makers (Ministère des ressources naturelles et de la faune (Ministère des ressources naturelles et de la faune et des parcs (MRNFP), 2005). For instance, moribund trees of no economic value should be left standing, 20% of the area within riparian boarders is to be subtracted from exploitation in perpetuity and tree patches of a few 100 m^2 on a minimum of 5% of harvested area should be left intact (MRNFP, 2005). There is no direct objective addressing fallen CWD and there is little addressing the quality or quantity of dead wood to be left in place.

Harvesting in Quebec is a major disturbance factor and has driven the boreal forest outside of its natural range of variability (Bergeron et al., 2002; Cyr et al., 2009). In some cases harvesting in Quebec has affected the proportion of old growth forests down to levels that were never reached during the entire post-glacial history of the boreal forest (Cyr et al., 2009). Older forests provide relatively constant inputs of coarse woody debris and a diversity of decay stages, tree species and size classes of standing and fallen wood (Martikainen et al., 1999; Hély, Bergeron and Flannigan, 2000) therefore changes in the proportion of old growth forests in Quebec have the potential to affect the natural continuity of dead wood over time and space.

In Quebec, the major harvesting technique used is CPRS (cutting with protection of regeneration and soils) (MRNF, 2009). This type of harvesting, like clear cutting disrupts the continuity of CWD input over time by removing live trees from the landscape (Siitonen, 2001; Grove, 2002; Jonsson, Kruys, and Ranius, 2005). In addition, a landscape harvested using CPRS is dominated by small classes of dead wood in the early stages of decomposition (Brais, Harvey and Bergeron, 2004) that are susceptible to rapid decomposition adding to the continuity gap (Grove, 2002). Large diameter dead wood in later stages of decay is presumably lost during harvesting through the crushing action of working machinery. Finally, harvesting is generally conducted before forests reach maturity limiting the size of tree growth and therefore the potential size of dead wood available (Angers, 2009).

Most recently, there have been concerns that increasing demands for fiber including use for biofuels will reduce long-term stocks of CWD (Jonsell, Hansson and Wedmo, 2007). In Quebec, the use of tree fiber for biofuel remains in the early developmental and experimental stages. This practice may be applied in the future through increased harvest intensities, such as whole-tree harvesting, or through operations that recover residual wood that remains after regular harvesting or after forest fire salvage logging operations.

Importance of coarse woody debris

Coarse wood debris (CWD) is involved in a number of biogeochemical process. Notably, it can serve as a temporary sink for carbon after large disturbances (Goodale et al., 2002) and serves as a source of nutrients, providing N and P to soil (Brais, Paré, Lierman, 2006). In addition, it likely regulates soil erosion and downward movement of water (Harmon and Hua, 1991; Hammond, Langor and Spence, 2001) Further, buried wood has been shown to indirectly affect site productivity by increasing cation exchange in the soil (Brais et al., 2005). A variety of animals are dependent on CWD for habitat (e.g.., as nesting sites for birds (Bunnell et al., 2002), denning sites for mammals (Moses and Boutin, 2001), and shelter for amphibians (Dupuis, Smith and Bunnell, 1995). Further benefits for birds are derived from CWD as it is used for perching, as a look out (Bunnell et al., 2002) and for drumming and foraging sites (Imbeau and Desrochers, 2002). Heterotrophs such as fungi and arthropods use CWD as a source of energy, nutrients and structure (Hammond, Langor and Spence, 2001).

Saproxylic insects

Saproxylic is the name given to the suite of organisms requiring dead or dying wood for a portion of their lifecycle (Speight, 1989). This functional group includes xylophagous wood and bark feeders, predators, parasites, parasitoids, detritivores and fungivores (Grove, 2002). Saproxylic insects are a popular topic of study as they account for a large proportion of diversity in forests and perform important functional roles in these ecosystems (Grove, 2002). For instance, they contribute to the dispersal of wood decomposing fungi (Beaver, 1989) and further promote decomposition through mechanical break up of woody tissues and the introduction of moisture (Speight, 1989). Decomposition of CWD is thought to be initiated and facilitated primarily by xylophagous beetles such as scolytid, buprestid and cerambycid beetles (Hammond, Langor and Spence, 2001). Invertebrates such as wood wasps and wood boring beetles help fungus establish often via introduction of fungus by specialized organs called mycangia (French and Roeper, 1972). After fungi have established, groups such as Collembola, Acari and Diptera appear, likely due to their saprophagous and fungivorous habits (Hammond, Langor and Spence, 2001). In Quebec, beetle activity (Cerambycidae activity) has been shown to be an important factor in snag mineralization for trembling aspen, jack pine and balsam fir (Angers, personal communication) and the amount of decay in branch-wood in Europe has been linked to the activity of arthropods (Swift, Boddy and Healey, 1984).

In addition to their role as decomposers, saproxylic insects are an important food source for woodpeckers in standing CWD (Murphy and Lenhaussen, 1998; Nappi et al., 2003; Drapeau et al., 2009) and potentially important for birds in fallen wood (Swift, Boddy and Healey, 1984; Bunnell et al., 2002). It has also been suggested that in old-growth forests where volumes of deadwood are relatively constant compared to managed forests saproxylic insects have the potential to control pest populations through predation, parasitism and competition (Martikainen et al., 1999).

Saproxylic insects and CWD properties

Dead wood properties affecting saproxylic insect species include: tree host, decay stage, diameter, sun exposure, type of wood-rotting basidiomycetes, and wood moisture content (Grove, 2002).

Tree host species is an important factor for xylophagous (wood feeding) insect species colonizing fresh dead wood (Grove, 2002). Different tree species become more similar with decomposition and saproxylic tree host specificity drops off (Grove, 2002). However, for reasons which remain unclear, the differences between dead conifer and deciduous wood appear to remain irrespective of the stage of decomposition as insect faunas differ between them (Grove, 2002). Special adaptations are required by insects inhabiting living wood to deal with different chemical components such as tannins and resins present in the bark, cambium and phloem (Haack and Slansky, 1987). It is not clear how long these characteristics play a role in specialization after decomposition. Fungi, an important food source for many saproxylic insects shows tree host preference (Lumley, Gignac and Currah, 2001; Heilmann-Clausen and Christensen, 2003; Heilmann-Clausen and Christensen, 2005) and many insects are host specific on large, long lasting polypores and mycelium (Kaila et al., 1994; Olsson, 2008) often resulting in an indirect relationship to tree host species.

Saproxylic beetles respond to CWD diameter with larger diameter debris having higher beetle richness and abundance than smaller pieces (Jonsell, Weslien and Ehnström, 1998). This is not surprising, as we would expect the probability of capturing more species and more individuals to increase as the volume of sampled area increases until the rarefaction asymptote is reached (Gotelli and Colwell, 2001). However, larger logs may have more microhabitats than smaller logs thus increasing the number of species beyond simple species volume relationships and making them potentially more valuable as habitat (Jonsson, Kruys, and Ranius, 2005). Other qualities of larger diameters may indirectly affect saproxylic insect preference. For instance, xylophagous species present in burned snags have been found to prefer larger diameters (Saint-Germain, Drapeau and Hébert, 2004). This was attributed to the thicker bark which provides protection during fire of the subcorticle layers on which beetle larvae feed (Saint-Germain, Drapeau and Hébert, 2004). Fallen logs of large diameter also provide greater water content and a more stable environment with less fluctuation in temperatures (Harmon et al., 1986).

Wood eating insects, particularly xylophagous Coleoptera, tend to specialize on particular tissues of a tree (phloem and cambium, xylem, including sapwood and heartwood, or bark) as evidenced by the differing types of digestive organs, development times and morphological characters among different species (Haack and Slansky, 1989). For example, Coleoptera larva in the family Cerambycidae often specialize on nutritionally poor xylem and have large bodies allowing for a long and complex digestive system which acquires nutrients more effectively than a shorter digestive system would allow (Haack and Slansky, 1989). When a tree dies changes in the availability of woody tissues are apparent as a succession of wood feeding Coleoptera can be found exploiting the wood throughout different stages of decomposition (Saint-Germain, Drapeau and Buddle, 2007). Early in the decay process phloem and cambium feeders are the first to exploit dead or dying wood. As this resource diminishes, other xylem (sapwood and heartwood) feeders emerge (Saint-Germain, Drapeau and Buddle, 2007). The bioavailability of proteins and minerals such as Ca, Zn, Fe and P are limited in wood with higher fiber and tannin content (Haack and Slansky, 1987) and are found in higher concentrations in later decay stages (Laiho and Prescott, 2004; Brais, Paré and Lierman, 2006) which may suggest that insects with greater nutritional needs or requiring rapid development may prefer wood in later stages of decomposition. Other factors important for insect growth and survival such as water content and N (Haak and Slansky, 1987) increase with decay and may play a role in the decay stage in which particular species are found (Hovemeyer and Schauermann, 2003; Laiho and Prescott, 2004; Brais, Paré, Lierman, 2006; Saint-Germain, 2006). Further contributions to saproxylic assemblage changes are likely driven by changes in fungal communities during decomposition (Allen et al., 2000; Lumley et al., 2001).

Diptera and coarse woody debris

In order to create sound guidelines regarding CWD conservation, information is required on the diversity it supports, notably saproxylic taxa. Although our knowledge of saproxylic Coleoptera ecology has expanded, more knowledge is required on the use of CWD by less studied taxa (Rotheray et al., 2001). Diptera, is one such group that is poorly known (Tesky, 1976; Schiegg, 2000; Schiegg, 2001) and may consequently be under-represented on threatened species lists in Europe and Fennoscandia (Jonsell, Weslien and Ehnström, 1998).Basic morphological and behavioral characteristics of saproxylic Diptera make them good candidates for comparison with Coleoptera and would help increase our knowledge on the functional role of CWD.

This thesis is comprised of one English chapter in the form of a scientific article. The article presents the results of a field study conducted on the importance of fallen CWD to the diversity of saproxylic Diptera in the boreal mixedwood forest of eastern North America. We captured emerging adult Diptera *in situ* from fallen aspen (*Populus tremuloides* Michaux.) and spruce (*Picea mariana* (Miller.)) logs of varying diameter and states of decay using emergence tents. We then measured the abundance, species richness and community structure of saproxylic Diptera and their associations with these wood properties. The article begins with an introduction which presents background information and current knowledge of saproxylic insects with particular attention paid to our current knowledge of saproxylic Diptera. We finish this section by presenting our hypothesis regarding Diptera response to the CWD properties: tree host species, decay stage and diameter. We follow by presenting our methods, statistical analyses, results and finish with a discussion on our findings.

Following the article a general conclusion provides a synthesis of the work and general discussion of the results. One reference section for the thesis is provided and combines references from the general introduction and chapter 1. Finally, four appendices are provided. Appendix A is a list of taxa collected during the study and includes information regarding abundance, year of capture, trophic guild designation and the frequency for each taxon. Logs from 2006 were re-sampled in 2007 however they were not included as part of the analysis or discussion of the thesis. A list of the species captured in these re-sampled logs is provided in Appendix B. Appendix C presents competing multiple linear regression models used in dipteran emergence analyses. Appendix D lists taxonomic literature that was used for species identification. Appendix E presents drawing from the authors personal notes which were used to classify Diptera in to morpho species. The drawings are not to scale and the author plans on having them re-drawn or photographed for a future work.

CHAPITRE 1

IMPORTANCE OF FALLEN COARSE WOODY DEBRIS TO THE DIVERSITY OF SAPROXYLIC DIPTERA IN THE BOREAL MIXEDWOOD FORESTS OF EASTERN NORTH AMERICA

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Annie Hibbert was responsible for the planning, field work, identification of specimens, compiling of data and analysis. Timothy T. Work and Pierre Drapeau contributed as co-directors throughout all stages and are co-authors of the article. Funding was provided in part by a CRSNG grant awarded to Suzanne Brais (Université du Québec à Abitibi-Témiscamingue). The final version of this thesis incorporates the comments and in some cases includes direct contributions by the co-authors.

1.1 Introduction

Throughout Northern and Western Europe long-term habitat fragmentation and a decrease in CWD due to tree harvesting have resulted in a decrease in saproxylic diversity (Siitonen and Martikainen, 1994; Siitonen, 2001; Grove, 2002). Recently, there have been concerns that increasing demands for fiber including use for biofuels will reduce long-term stocks of CWD (Jonsell, Hansson and Wedmo, 2007). Species in managed forests would benefit from a coarse-filter conservation approach which would take into account the amount of CWD on the ground (Work et al., 2004). However, an approach based solely on the quantity of CWD rather than its quality may overlook key habitat elements necessary for saproxylic conservation. For example, CWD in unmanaged landscapes can be found in a variety of sizes, decay stages and tree species which could represent varying wood qualities for saproxylic species. Baseline data regarding the associations of saproxylic species with dead wood properties in unmanaged stands are needed in order to refine conservation efforts in managed forests (Jonsell, Hansson and Wedmo, 2007).

Common ecological associations of saproxylic insects have been reviewed by Grove (2002). The Coleoptera which are by far the best studied saproxylic insect group have strong associations with the following dead wood properties: decay stage, tree host, diameter, sun exposure, type of wood-rotting basidiomycetes, and wood moisture content (Grove, 2002). Although our knowledge of saproxylic Coleoptera ecology has expanded, more knowledge is required on the use of CWD by less studied taxa to ensure that our current understanding of saproxylic requirements reflect the needs of a wider spectrum of species (Rotheray et al., 2001). Diptera are good candidates for comparison, as they may be more sensitive to desiccation and may have poorer dispersal capabilities than beetles (Okland, et al.1996; Jonsell, Nordlander and Jonsson, 1999). In addition, saproxylic Diptera have many other characteristics that make them good study subjects. They are very abundant (Swift, Boddy, and Healey, 1984; Irmler, Heller and Warning, 1996; Schiegg, 2000; Schiegg, 2001; Hovemeyer and Schauermann, 2003), diverse (Hovemeyer and Schauermann, 2003; Rotheray et al., 2001), and sensitive to changes in habitat such as clear-cutting and canopy-opening (Okland, 1994; Deans et al., 2007; Okland, Gotmark and Norden, 2008). In addition, they occupy a wide variety of microhabitats in dead wood (Rotheray et al., 2001) and can be grouped into trophic guilds (Hovemeyer, 1999) which can be used to analyze specialization or changes in community structure along wood property gradients.

Abundance and species richness of saproxylic Diptera in Europe have been found to increase with decomposition in fallen logs of alder, spruce and beech (Irmler, Heller and Warning, 1996; Shiegg, 2001) and in fallen branch wood of beech (Hovemeyer and Schauermann, 2003). Alternatively, abundance and richness were negatively correlated with bark cover, C:N ratio, and relative wood density in fallen beech branches (Hovemeyer and Schauermann, 2003). Saproxylic Diptera in Europe also show positive responses to water content and moss cover within fallen beech branches (Shiegg 2001; Hoveymeyer and Schauermann, 2003). Studies on saproxylic Diptera and their associations with wood properties in fallen CWD at the species level in North America have yet to be published.

As sampled volume increases we would expect the probability of capturing more species and more individuals to increase until the rarefaction asymptote is reached (Gotelli and Colwell, 2001). It has also been argued that larger logs have more microhabitats than smaller logs thus increasing the number of species beyond simple species volume relationships and making them potentially more valuable as habitat (Jonsson, Kruys, and Ranius, 2005). In addition, fallen logs of large diameter also provide greater water content and a more stable environment with less fluctuation in temperatures (Harmon et al., 1986).

Structural and chemical characteristics of fallen wood, including wood density, minerals and water content change as decomposition proceeds (Hovemeyer and Schauermann, 2003; Laiho and Prescott 2004; Brais, Paré and Lierman, 2006). These factors may affect the nutritional quality of the substrate for saproxylic Diptera. For example, fungi, an important resource for mycetophagous Diptera,, will change in community structure along with decreasing wood density (Allen et al., 2000; Lumley, Gignac and Currah, 2001). Potential food sources for Diptera such as phloem-feeding beetle larvae, including *Ips* species (McAlpine et al., 1981), will decrease along with the degradation of phloem. The value of logs as an oviposition site should increase with decay as decreases in wood density could affect the ease with which saproxylic females oviposit and improve larval movement in the substrate. Further, increasing water content with decay (Haack and Slansky, 1987) could affect female choice of logs for oviposition as many species are thought to be drought sensitive (Okland, Gotmark and Norden, 2008) and water content has been found to affect the survival and growth of insects in wood (Haack and Slasky, 1987). Finally, decaying organic matter such as leaf litter cover, insect feces and bacteria of particular interest to the saprophagous Diptera may increase with decay.

Diptera may have less affinity for tree host species as compared to other groups like Coleoptera (Saint-Germain, Drapeau and Buddle, 2007) and fungi (Heilmann-Clausen and Chritensen, 2005). Unlike Coleoptera, few saproxylic Diptera species feed directly on wood (Teskey, 1976) and many rely on other food sources whose availability is not necessarily affected by tree host species. However, many factors which could vary among tree species, particularly between deciduous and coniferous hosts such as the rate of decay, colonization patterns of fungi, secondary chemical compounds or even saproxylic Coleoptera species (dipteran prey or food resources i.e., feces) could potentially drive an indirect tree host preference for Diptera (Saint-Germain, 2006; Saint-Germain, Drapeau and Buddle, 2007). For example, we would expect Diptera that specialize on particular species of fungi to have and indirect relationship to tree species as most fungi prefer particular species of tree (Lumley, Gignac and Currah, 2001 Heilmann-Clausen and Christensen, 2005).

In this study, we measure the abundance, species richness and community composition of saproxylic Diptera assemblages with regards to varying diameters and wood decay stages of two important host species in the eastern boreal forest of North America, aspen (*Populus tremuloides* Michaux.) and black spruce (*Picea mariana* (Miller.)). We ask how Diptera assemblages will change with diameter, decay stage and tree species. We predict: (1) overall saproxylic Diptera abundance and species richness will increase with log diameter and (2) overall saproxylic Diptera abundance and species richness will increase along with increasing wood decay.

1.2 Methods

1.2.1 Sampling sites

Our study sites were located in the Lake Duparquet Research and Teaching Forest (LDRTF) (48°86′N–48°32′N, 79°19′W–79°30′W) in the Abitibi region of northern Quebec, Canada. These sites are permanent unmanaged stands which are studied as part of the SAFE experiment (Sylviculture et Aménagement Forestier Écosystémique) (Brais, Harvey and Bergeron, 2004) (Figure 1.1). They are characterized as boreal-mixedwood forests on clay soils. Climate is cool with an average annual temperature of 2.5°C and has a relatively short growing season of 160 days (Robitaille and Saucier, 1998). Annual precipitation is 800mm to 900mm (Robitaille and Saucier, 1998).

We classified fallen aspen and spruce logs within six forest stands into 1 of 5 visual decay classes, 1 being the least decayed and 5 being the most decayed (modified from Waddell (2002) and Stokland and Kauserud, (2004)) (Table 1.1). Logs in decay class 2 and 4 were used for the study as they could be found in sufficient quantities for analysis. A total of 12 logs for each tree species / decay combination were randomly selected for sampling in the spring of 2006 for a total of 48 logs (Table 1.2). In the field, we used emergence tents similar to Shiegg (2001), made from quick drying, light weight nylon mesh that encircled 70 cm length sections of each log. We used urine cups filled with 30ml of 50%/50% water and propylene glycol to trap and preserve all emerging insects. Two young aspen and one young spruce were disturbed by animals throughout the summer of 2007 and had to be removed from the study leaving a total of 93 logs sampled (Table 1.2).

Forest stands differed in stand composition and time since fire and insect outbreak. Three of the six stands defined by Brais, Harvey and Bergeron (2004) as mixed forest, were dominated by trembling aspen (*Populus tremuloides* Michaux), black spruce (*Picea mariana* (Miller)) B.S.P.), and white spruce (*Picea glauca* [Moench] Voss). Aspen represented 70% of the basal area, and spruce represented 13-23% basal area (Brais, Harvey and Bergeron, 2004). The average fallen spruce deadwood volume was 2m^3/hectare and 6m^3/hectare for aspen. The last fire event in these stands occurred in 1919 (Brais, Harvey and Bergeron, 2004; Dansereau and Bergeron, 1993). Young aspen (decay 2), advanced aspen (decay 4) and young spruce (decay 2) logs were sampled in these stands (Table 1.2). Advanced decay classes of spruce were limited and therefore not sampled in these stands as much of this component was either likely consumed by the 1919 fire or long-since decayed.

The other three forest stands defined by Brais, Harvey and Bergeron (2004) as balsam fir-birch forest were dominated by white birch (*Betula papyrifera* Marsh.), (43-66% basal area), white spruce (*Picea glauca* [Moench] Voss), (13-43% basal area), balsam fir (*Abies* *balsamea* (L.) (Miller)), (13% basal area), and had an average fallen spruce deadwood volume of 8m^3/hectare (Brais, Harvey and Bergeron, 2004). This area was affected by a spruce budworm outbreak that occurred between the years 1970 and 1987 (Brais, Harvey and Bergeron, 2004) and the last fire event was 1720 (Dansereau and Bergeron, 1993). Only old spruce logs (decay 4) were sampled in these stands (Table 1.2).

We measured the diameter and wood density of each log. To measure wood density we cut a 10cm length wedge in 2007 from the sampled area of each log and split it in to two sections. The first section was weighed (fresh) and coated in paraffin before measuring volume by water displacement. The second section was weighed (fresh) and dried at 60°C to constant mass (after 4 days). The difference between fresh mass and dried constant mass was taken and the percentage humidity calculated. The first wood section was then corrected for moisture content giving the final mass used for wood density estimation: d=m/v. Four wood density measures (3 old aspen logs and 1 old spruce log) were not included in analyses due to erroneous measures.

1.2.2 Diptera sampling

We sampled insects once a month (4 collections) for a total of 88 days of continuous trapping. Tents were first erected over three days (May 28- 31, 2006). Collection dates were as follows: June 19-20, July 11-12, July 31-August 1 and August 24-25. In 2007, Diptera were again sampled once a month (4 collections). Trapping began earlier than the previous year giving a total of 104 sampling days. Tents were erected over three days (May 5-7, 2007) and collections dates were as follows: May 27-28, June 29-30, July 28-29 and the last collection was completed on August. 18. The last collection of one aspen-spruce forest block in 2007 took place two weeks later (September 4) due to site inaccessibility.

All Diptera families were identified to species or morpho species except for the Cecidomyiidae, Ceratopogonidae, Chironomidae and Psychodidae which were left at the family level. Identifications were determined to the genus level using McAlpine and others (1981) and McAlpine and others (1987) and the most recent taxonomic literature available for species identification (see Appendix C for full list of literature used). Identifications of Chloropidae and Mycetophilidae were verified by T.A. Wheeler and Chris Borkent, McGill

University. Species that could not be named were sorted into morpho species which were determined by detailed examination of genitalia (see Appendix E). We placed individuals into one of 5 trophic guilds based on information of known larval feeding habits at the species level when possible. When species level data were unavailable feeding habits were defined at the genus level and on occasion at the family level using McAlpine and others (1981) and McAlpine and others (1987) and Hovemeyer and Schauermann (2003). We defined the trophic guilds as (1) mycetophagous (MYT); species feeding on fungi, (2) saprophagous (SAP); species feeding on detritus including decaying plant material and insect waste, (3) parasitic (PAR); species that parasitize other insects, (4) xylophagous (XYL); wood-feeding, and (5) zoophagous (ZOO); feeding on insects and other animals. Very few xylophagous species were captured therefore they could not be used in analyses. Voucher specimens were deposited at McGill University's Lyman Entomological Museum and Université du Québec à Montréal.

1.3 Statistical analysis

A preliminary analysis of frequency distribution of wood density measures across our visual decay classes showed that wood density overlapped considerably among early and advanced decay stages (Figure 1.2). Thus, throughout all analyses we used wood density (g/cm^3) as a more direct measure of the decay gradient instead of the visual decay classes that were used for log selection.

Although efforts were made to sample logs that were within the commercial timber size classes of 10 to 20 cm, a range of diameters was sampled. The range of diameters we sampled differed between tree hosts with spruce logs having the widest range. Most spruce logs were in the lower range between 10 and 15 cm while most aspen were between 15 and 20 cm (Figure 1.3). We statistically controlled for differences in Diptera abundance related to differences in log volume by including diameter as a factor in general linear models.

All analyses were conducted in R (R Development Core Team, 2009)

1.3.1Dipteran emergence

In order to assess whether wood density, wood diameter and tree species were useful predictors of Diptera abundance at the order, guild and species level, we used the following procedure:

Abundance data was standardized to an emergence rate of flies per day to account for uneven sampling effort as a result of periodic disturbance of some traps. This was done for a data set including all Diptera (6753 indv.) and for 2 guilds (saprophagous (3663 indv.) and mycetophagous (2288 indv.). Emergence patterns were modeled with negative bionomial regression. The list of regression models are presented in Appendix D. The dispersion was corrected when necessary. For all data sets the sample size (89 logs after removal of logs with erroneous density) was small relative to the number of parameters, therefore the second-order Akaike's information criterion (AIC_c) was used to select the best model, which is expressed by:

$$AIC_c = -2(\text{log-likelihood}) + 2K + 2K\ (K+1) / (n\text{-}K\text{-}1)$$

where K is the number of parameters in the model (including intercept and variance), (Burnham and Anderson, 2002).

Multimodel inference was used when several models competed for top rank ($\Delta\ AIC_c < 2$), (Burnham and Anderson, 2002). This was done by computing a weighted average of the regression coefficients of a given variable for all models including that variable. Then, a model-averaged estimate and unconditional standard error were generated and used to build a 95% confidence interval, enabling us to assess the magnitude of the effect of the specific variable (Burnham and Anderson, 2002).

The abundance of individual species was converted to incidence (presence/absence) data. Multiple regression for species that were present in less than 15% of logs suffered from under dispersion and could not be corrected, therefore we assessed whether the probability of occurrence was related to variables using binomial regression for species that were present in 15% or more of the sampled logs which included the following 7 taxa: *Corynoptera sp.3* (257 indv.), *Corynoptera sp.5* (78 indv.), *Scatopsciara hastata* (378 indv.), *Neophylomyza* *quadripunctata* (271 indv.), *Ula* sp. (42 indv.), *Tachypeza* sp.1 (72indv), *Bradysia jucunda* (110 indv.). The zoophagous (305 indv) and parasitic (72 indv) guilds were treated in the same manner. The list of regression models are presented in Appendix D. Tree host was not included in a model alone when species occurrence was fairly equal between tree hosts. In such cases, it was placed in models as a potential factor interacting with diameter and density.

1.3.2 Dipteran species richness

Species richness analyses used a smaller data set which included taxa with positive species or morpho species identification (227 taxa, 2579 individuals). See Appendix A for species included in the data set. Since many of the Diptera species can only be distinguished on the basis of male genitalic characters these analyses were dominated by males. The following families proved difficult to resolve to morpho species because of a lack of good identification tools and were therefore not represented in this data set: Cecidomyiidae (n=1539), Ceratopogonidae (n=816) and Psychodidae (n=78). The genus *Megaselia* (family: Phoridae; n=721) was excluded because it proved too difficult for the authors to resolve into morpho species. Other authors have referred to *Megaselia* as "the Diptera enfant terrible" due to the difficulties in determining species even when male genitalia are compared (Disney, 1999).

Species richness between tree hosts (aspen and spruce) and estimates of richness were obtained from raw abundance data and used the rarefaction function by Jacobs (2009). Individual-based rarefaction was used to correct for uneven catches. Rarefaction provides unbiased estimates of species richness for samples with different numbers of individuals and therefore allows accurate comparisons among a number of treatments (Gotelli and Colwell, 2001).

Spearman's rank correlation (r_s) was used to evaluate the relationship between species richness and wood properties: log diameter and wood density for each tree species.

1.3.3 Community composition

Dipteran assemblage similarity was analyzed using a smaller data set that excluded taxa that were not present in 5% or more of sampled logs (51 taxa, 2119 individuals). This reduced the sample size from n=93 to n=88 because some logs did not produce any frequently occurring species. See Appendix A for species included in the data set. Compositional similarity was analyzed between logs using Bray-Curtis distance with nonmetric multidimensional scaling (NMS) ordination procedures. Multiresponse permutation procedure (MRPP) was used to measure the within and between group differences of the community for the categorical variable tree species (aspen and spruce).

Mantel's test (Mantel, 1967) was used to evaluate the correlation of the community matrix with CWD decay gradient (wood density g/cm^3), (n=84 logs) and diameter (n=88 logs). Wood density data were missing for 4 logs as they could not be accessed in the field when this measure was conducted. The correlation of the community matrix was tested against the Euclidean distance of each variable (wood density g/cm^3, diameter cm) independently. Significance was evaluated against a Monte-Carlo test with 1000 permutations. Mantel's test was also used to evaluate the correlation of trophic guild separately with wood density g/cm^3, and diameter.

1.4 Results

1.4.1 General trends in emergence

Overall, we collected 6753 adult Diptera, representing 227 taxa from 34 families (Appendix A). Most taxa were rarely collected as 121 taxa or 53% were represented by one individual over two years of collection. A total of 2119 individuals (51 taxa) were present in 5% or more of sampled logs. The most abundant families (100 or more individuals) were: Sciaridae (1850), Cecidomyidae (1539), Ceratopogonidae (816), Phoridae (801), Mycetophylidae (749), Milichiidae (271), Tipulidae (107), Dolichopodidae (110) (see Appendix A for details). The most species rich family was the Mycetophilidae with 179 species.

1.4.2 Factors associated with Dipteran emergence

Model selection with AICc approach is presented in Appendix D. Overall Diptera emergence increased with decomposition (decreasing wood density) in spruce logs ($p=0.01$, $R^2 = 0.45$, Table 1.3) and emergence was greater in 2006 compared to 2007 ($p=<0.01, R^2 = 0.45$, Table 1.3).

Mycetophagous and saprophagous guild emergence increased with decomposition (decreasing wood density) in spruce ($p=0.03$ $R^2 = 0.11$, Table1.4; $p=<0.01$, $R^2= 0.23$, Table 1.5) and positively affected by log diameter in spruce ($p= 0.01$, $R^2 = 0.11$, Table 1.4; $p=<0.01$, $R^2 = 0.23$, Table 1.5). For zoophagous and parasitic guild occurrences AICc scores suggested that many models shared high strength of evidence (Δ $AIC_c< 2$) therefore the multi-model inference approach (model-averaging) was used in order to select the most important variables. For an explanation of model-averaging please see the analysis section (1.3.1 Dipteran emergence) on page 15. After multi-model inference, no variables were found to affect emergence as 95% confidence intervals did not exclude zero (Burnham and Anderson, 2002).

1.4.3 Species richness

A negative relationship between species richness and wood density (decreasing wood decay) was observed for spruce logs ($p<0.001$, $r_s= -0.48$) (Figure 1.4). No relationship between species richness and wood density was found for aspen logs ($p= 0.49$, $r_s=0.11$). We did not detect any significant relationship between Diptera species richness and log diameter for either tree species (spruce: $p=0.62$, $r_s=0.08$; aspen: $p= 0.96$, $r_s=-0.01$).

Estimated species richness was higher in spruce logs than aspen logs. We were unable to observe an asymptote in either rarefaction curve (Figure 1.5 (b)). Estimated species richness for the entire data set is presented in Figure 1.5 (a).

1.4.4 *Community composition*

High assemblage dissimilarity between sampled logs was observed using nonmetric multidimensional scaling (NMS). The final solution consisted of 3 dimensions with a stress of 20 (Figure 1.6). This stress value is relatively high (McCune and Grace, 1999).

Differences between aspen and spruce groups evaluated with MRPP were statistically different however, the chance-corrected within group agreement (measure of homogeneity within groups) was low (A= 0.0044, p=0.02) indicating large variation in species assemblages within a given tree species. Although the homogeneity within groups was about equivalent to group membership by chance, a total of 8 taxa present in 5% or more of sampled logs emerged exclusively from one tree species. Those collected exclusively from aspen were: *Medetera crassivenis* (n=6, frequency (freq.) 4), *Acadia polypori*, (n=16, freq. 10), *Limonia sp.2* (n=36, freq. 6), *Mycetophila procera* (n=4, freq. 4), and *Stilpon sp.1* (n=8, freq. 5). Those collected exclusively from spruce were: *Eremomyioides* sp. (n=10, freq. 8), *Leptomorphus* sp. 4 (n=4, freq. 4), and *Trichonta pulchra* (n=7, freq. 5).

There was a significant correlation between variations in the overall saproxylic dipteran assemblages and wood density in spruce logs (R^2= 0.18 p=< 0.001) (Table 1.6). Wood density was also significantly correlated with variations in the composition of mycetophage assemblages (R^2= 0.15 p= 0.008) in spruce and for saprophage assemblage composition and wood density in both tree species (R^2= 0.27, p= 0.004; R^2=0.16, p=0.001) (Table 1.6).

1.4.5 Responses of individual taxa

AIC_c scores for species specific observations suggested that many models shared high strength of evidence (Δ AIC_c< 2) therefore we used the multi-model inference approach (model-averaging). For an explanation of model-averaging please see the analysis section (1.3.1 Dipteran emergence) on page 15. Occurrences for the species *Scatopsciara hastata* increased with decomposition (decreasing wood density) (model-averaged estimate= -10.96, SE= 3.56). The occurrences however for other species could not be associated with any factors with confidence (95% confidence intervals did not exclude zero).

1.5 Discussion

Our results suggest some saproxylic Diptera use CWD based on tree species, log diameter and wood density. Results followed our predictions that overall saproxylic Diptera abundance and richness would increase along with increasing wood decay (decreasing wood density) however, this pattern was significant only in spruce logs. When measured separately, the two most dominant guilds (mycetophagous and saprophagous) had the same response. The lack of patterns associated with decay in aspen may be due to the difficulties in obtaining representative wood density measures across a given volume for this tree species. Work by Saint-Germain, Buddle and Drapeau (2010), has demonstrated significant within-snag variation in wood density for aspen. When 5cm disks were taken along 1-m sections of snags, measurements within disks often revealed densities that ranged from 0.08-0.38 g/cm^3 within the same 1-m section (Saint-Germain, Buddle and Drapeau, 2010). Our wood samples therefore may not have been large enough to account for wood density variability within our aspen logs. It has been demonstrated that decay selection by beetle larvae can occur at a small scale within variable aspen hosts (Saint-Germain, Buddle and Drapeau, 2010) therefore we cannot conclude that a lack of patterns in our study confirms a lack of selection for decay by Diptera in aspen. Snag dissections of spruce revealed less variation in wood density (Saint-Germain, personal communication) and could explain our ability to observe stronger relationships with Diptera and wood decay in spruce logs. The bioavailability of proteins and minerals such as Ca, Zn, Fe and P are limited in wood with higher fiber and tannin content (Haack and Slansky, 1987) and most of these minerals have been found in higher concentrations in later stages of decomposition (Laiho and Prescott, 2004; Brais, Paré and Lierman, 2006). Diptera, especially the Sciaridae, develop rapidly (Nielson and Nielson, 2004) and may not find the adequate nutrients in earlier stages of decay in the time frame they require. Other factors important for insect growth and survival such as water content and N (Haak and Slansky, 1987) increase with decay and may further contribute to Diptera preference for well decomposed wood (Hovemeyer and Schauermann, 2003; Laiho and Prescott, 2004; Brais, Paré, Lierman, 2006).

We expected overall saproxylic dipteran abundance and richness to increase with diameter not only because increased volume should translate to a larger sample but also because we presumed that bigger logs have more microhabitats and contain a more stable microclimate (Grove, 2002). When analyzed by guild, the overall emergence of mycetophages and saprophages increased with increasing wood decay in spruce logs however little of the variation for either guild was explained by our models. It was surprising in this study that diameter was not more strongly associated with the emergence or species richness of Diptera at the order level, for other guilds or individual taxa. Most studies indicate a positive relationship between dead wood diameter and abundance and richness of beetles (Grove, 2002; Saint-Germain, Drapeau and Hébert, 2004).

Estimated richness in spruce logs was higher compared to aspen logs. Clear differences exist in the degradation pathways between spruce and aspen (Angers, Drapeau and Bergeron, 2010). Spruce decomposes more slowly than aspen (Brais, Paré and Lierman, 2006) and therefore persists in the environment longer (Angers, Drapeau and Bergeron, 2010). It is possible that the longer degradation pathway of spruce provides greater time for more chance colonization events of species to be successful. In addition, the longer persistence in the environment of spruce logs may provide greater connectivity on the forest floor between insect populations that disperse poorly.

We observed a difference in dipteran species composition between aspen and spruce however there was extremely high assemblage dissimilarity within each tree host which may be due to differences in microhabitat characteristics of each log. Dipteran assemblages at the order and guild level changed along with changes in wood density (mycetophages in spruce and saprophages in both host species) however little of the variation could be explained by this factor alone.

Studies by Irmler, Heller and Warning (1996), and Rotheray and others (2001), have observed little tree host specificity for saproxylic Diptera species therefore it was not surprising most species collected in our study emerged from both tree hosts. *Scatopsciara hastata,* family: Sciaridae, was the only species in this study in which density was observed to predict occurrence. We do not have any specific life history information available on this species however we do know that larva in the family Sciaridae develop rapidly (Nielson and Nielson, 2004) and may benefit from higher water content and greater concentrations of minerals in well decomposed wood compared to early stages.

Overall, it proved very difficult to identify relationships between occurrence of dipteran species and wood characteristics in this study. We attribute the difficulties in part, to the distributional inconsistencies of the species. The emerging Diptera were highly aggregated and rare. For example, of the 179 species of Mycetophilidae we captured, 139 were represented by only one individual and only 14 of these species were present in 5% or more of sampled logs. Hovemeyer and Schauermann (2003) also observed highly aggregated and rare species during their 10 year long study of beech branches. They controlled for many possible sources of variation by using branches cut from only two trees. Rarity and aggregated populations in their study was attributed to the high variability of decomposition between branches (Hovemeyer and Schauermann, 2003).

Diptera may be highly microhabitat specific and therefore may be responding to finer level characteristics of individual logs not measured in this study. The genus *Phronia* spp. (Mycetophilidae) collected in our study (8 morpho species, and 68 individuals) provides one of many possible examples of habitat specialization that are likely contributing to the rare and patchy nature of our dataset. Most of the known larvae of *Phronia* spp. are free living and graze on slime moulds (Myxomycetes) and other fungi growing on the surface of sodden, barkless logs (Gagné, 1975). The presence of *Phronia spp.* may be determined indirectly by the presence of their hosts. Feeding specialization within beetles that feed on slime-mould can be extreme, as they have been known to specialize even on particular stages of development within particular species (Laaksonen et al., 2010). For instance, some *Agathidium* species specialize on the plasmodial phase only and still others only on their fruiting bodies (Laaksonen et al., 2010). The plasmodial phase of slime mould feeds on bacteria and other micro-organisms on dead wood and the formation of fruiting bodies by slime mould is dependent on microclimatic conditions, especially moisture (Laaksonen, et al., 2010).

In the context of saproxylic insect conservation studies, CWD is considered an important microhabitat for species at the scale of a stand (Work et al. 2004). However, important microhabitats also occur at the scale of a single log. Barbour, Storer and Potts (2009), found that the fungal community structure, species richness and individual species of fungi, colonizing fallen *Eucalyptus* logs are affected by microhabitats such as the presence of bark, newly exposed wood and north and south facing surfaces. In that particular study, high fungal richness in bark compared with exposed areas of wood was believed to be related to the greater surface area of bark. Higher richness of fungi on south facing surfaces was attributed to higher moisture and shade compared to north surfaces (Barbour, Storer and Potts, 2009). Fine scale characteristics of logs such as those mentioned above and additional physical and biological aspects of the logs (ie. number of cracks and crevices, thickness of bark, water fluctuation, ground evenness, aspect of logs, and presence of particular fungi or bacteria) may be important factors directly or indirectly affecting Diptera.

Many Diptera like the Sciaridae are opportunists, exploiting small food sources that occur by chance and are short lived (Papp, 2002). They are able to do this because of their rapid larval development and adult flight which allows them to disperse to new sources of food (Papp, 2002). For example, many species of forest dwelling Diptera specialize on animal feces, dead snails or sap holes (Papp, 2002). Saproxylic Diptera, like other forest Diptera, may be responding to unpredictable food sources which could make predicting species occurrence difficult.

1.6 Conclusion

This study provides the first replicated study on CWD use by saproxylic Diptera in aspen and spruce logs in eastern North America. This study has highlighted the importance of studying a wide variety of saproxylic taxa, as Diptera were found to respond differently to CWD properties than other better studied groups such as the saproxylic Coleoptera. For instance, beetle communities and individual species are tree host specific in early stages of decay (Grove, 2002). In later stages, tree specificity may decrease but differences between coniferous and deciduous hosts remain (Grove, 2002). In this study, few individual Diptera species were specific to tree host.

Our observations of low dipteran assemblage similarity between logs, high species rarity and patchiness are consistent with other studies conducted on saproxylic Diptera. These findings indicate that Diptera may be highly microhabitat specific. In order to have a more complete picture of the factors affecting CWD use by saproxylic Diptera, more study is required on fine scale characteristics of logs that may play a larger role. Particularly useful avenues of research would include associations between Diptera and saproxylic fungi (ie. Basidiomycetes and Myxomycetes).We were able to reach a rather fine scale of saproxylic Diptera identification using a morpho species approach, however, in order to fully understand observed patterns, more tools for the identification of saproxylic Diptera and knowledge on their associated life history is required.

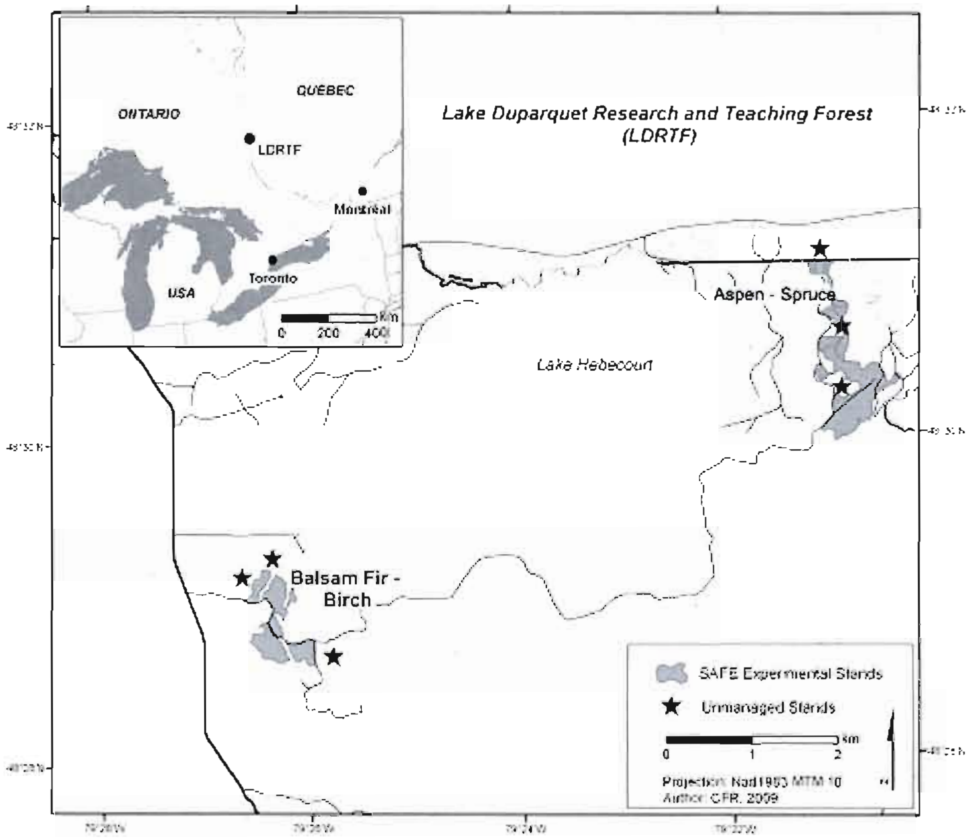
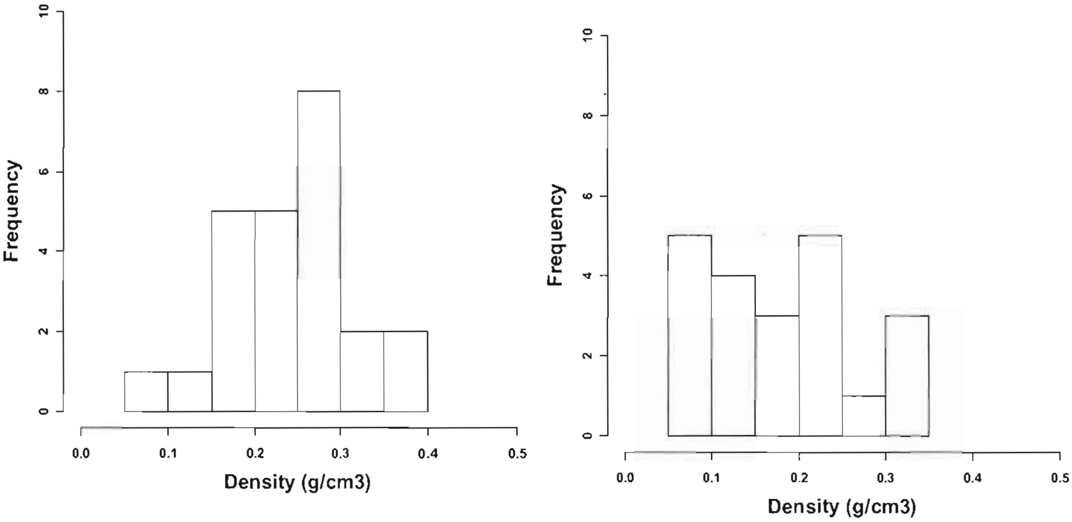
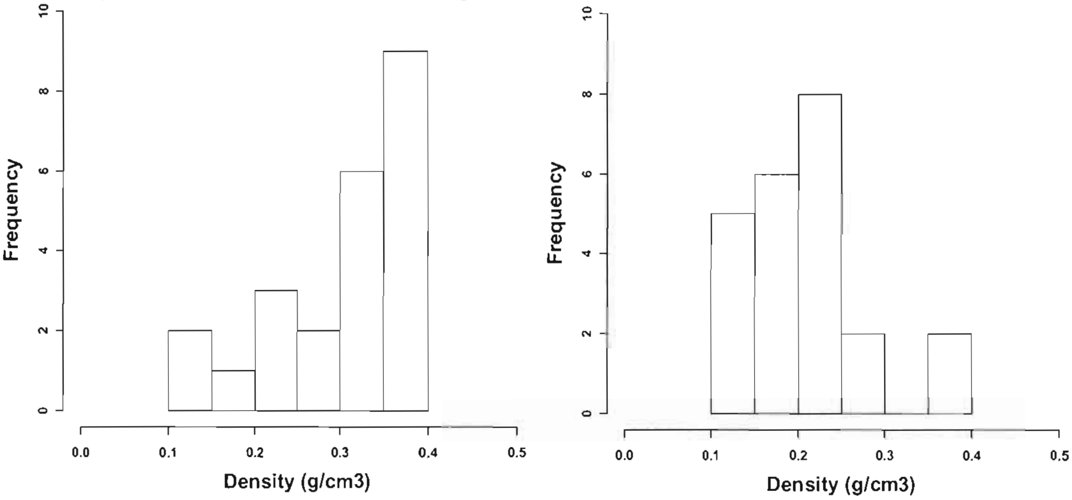


Figure 1.1 Map depicting general location of study in eastern North America and general location of unmanaged stands where logs were sampled for saproxylic Diptera using emergence tents within two forest types (balsam fir-birch and aspen-spruce forest).

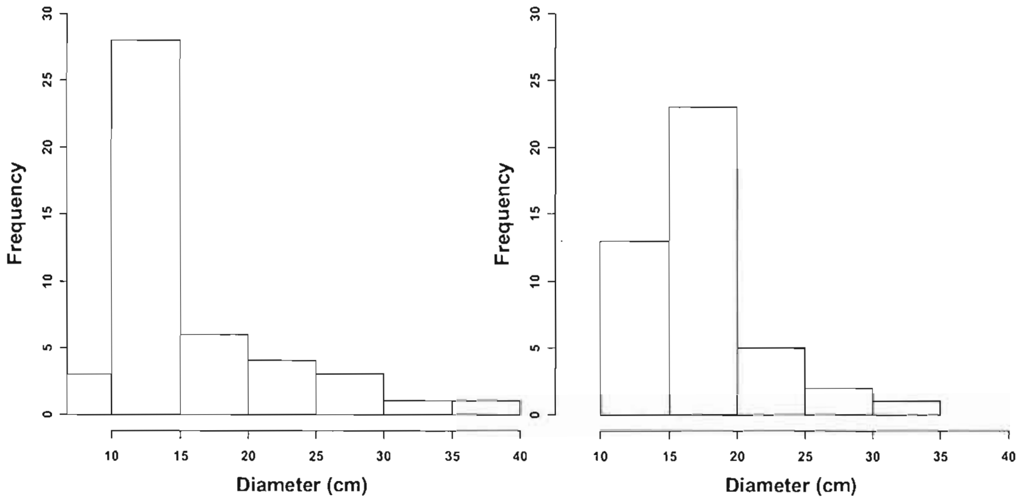


a) Young aspen b) Old aspen



c) Young spruce d) Old spruce

Figure 1.2 Frequency of wood densities for young aspen (a), old aspen (b), young spruce (c), and old spruce logs (d).


a) Spruce logs

b) Aspen logs

Figure 1.3 Frequency of log diameters for spruce (a) and frequency of log diameters for aspen (b).

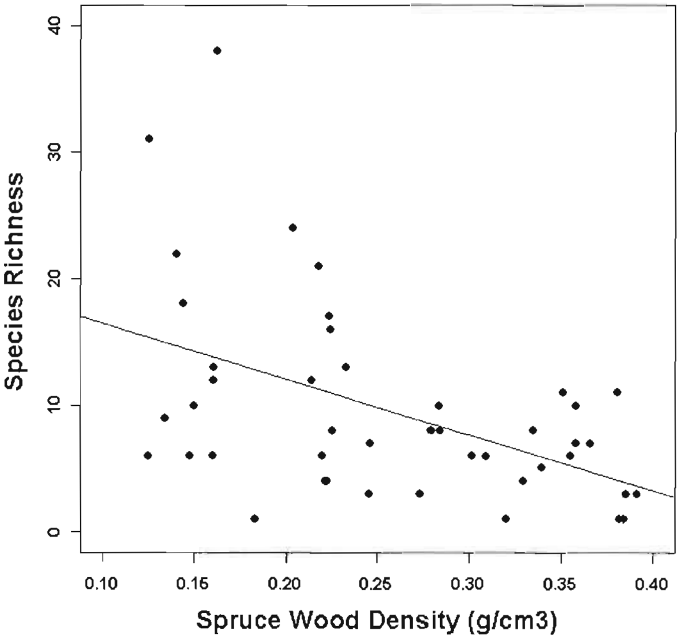


Figure 1.4 Scatter plot of species richness and spruce wood density (g/cm^3). Spearman's coefficient of rank correlation (r_s): -0.48, $p<0.001$.

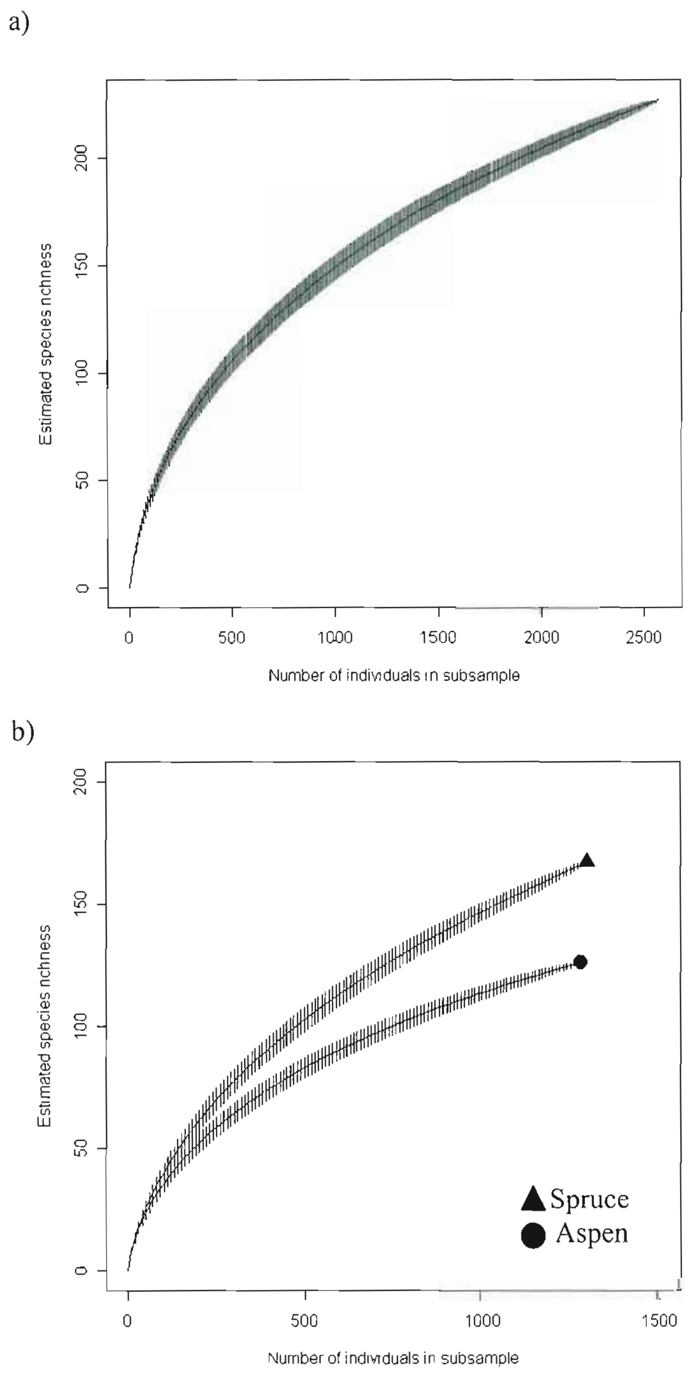


Figure 1.5 Rarefied species richness curves with positive species identification or morphospecies designation including 227 taxa from a pool of 2579 individuals sampled in one season. Measures of variance (±1 SD), a) all species, all log types and b) species accumulation for aspen (1281 individuals) and spruce (1298 individuals).

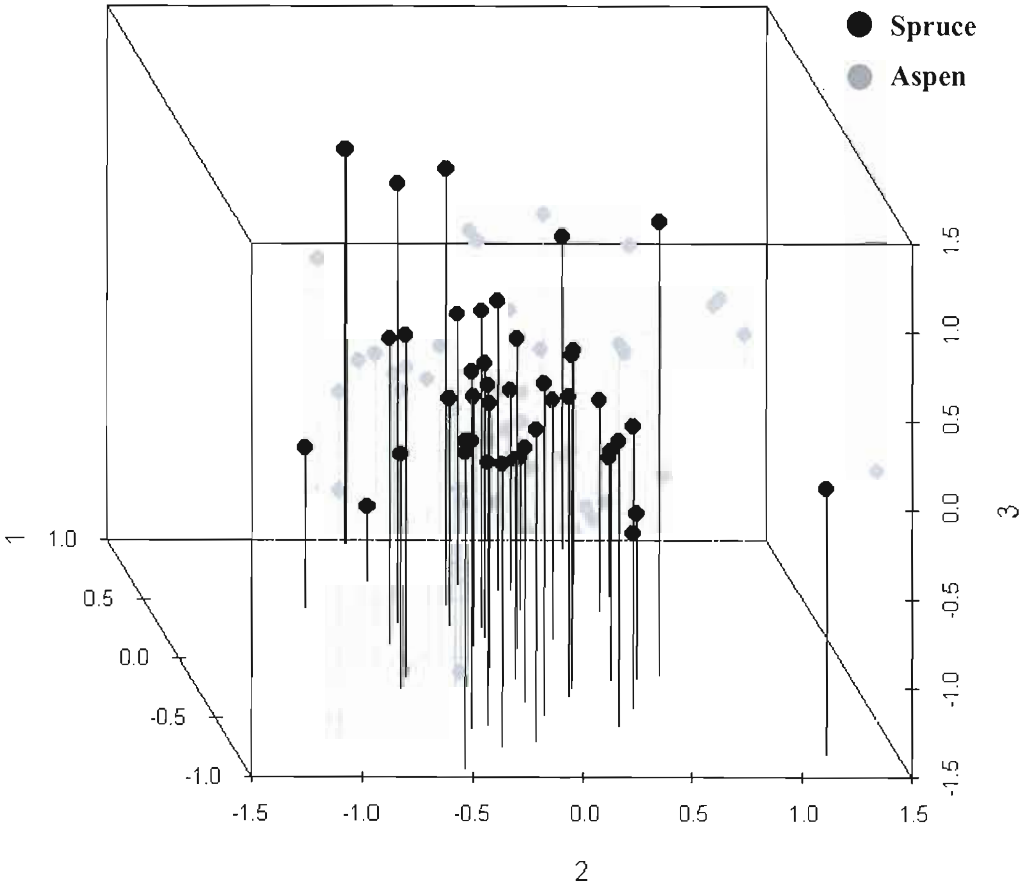


Figure 1.6 Three-dimensional NMS ordination illustrating saproxylic dipteran assemblage similarity between 88 logs and 51 taxa (species present in 5% or more of sampled logs) from 1-year emergence data. Different colours represent different tree species (aspen and spruce).

Table 1.1 Classification that was used for determination of decay stage for logs (modified from Waddell 2002 and Stokland and Kauserud 2004).

Decay class	Structural integrity	Wood texture	Condition of branches and twigs	Presence of fungi and rot
1	Sound	Intact, no rot; conks on stem absent	If branches present, fine twigs still attached with tight bark	Hardly any fungus mycelium developed under patches of loose bark
2*	Heartwood sound; sapwood somewhat decayed	Mostly intact; sapwood partly soft and starting to decay. Wood cannot be pulled apart by hand	If branches present, many fine twigs gone; fine twigs still present have peeling bark	Well-developed mycelium between bark and wood, rot extends less than 3 cm radially into the wood
3	Heartwood sound; log supports its weight	Large, hard pieces sapwood can be pulled apart by hand	Large branch stubs will not pull out	Rot extends more than 3 cm into the wood
4*	Heartwood rotten; log does not support its weight, but shape is maintained	Soft, small, blocky pieces; metal pin can push apart heartwood	Large branch stubs will not pull out easily	Rotten throughout the log
5	No structural integrity; no longer maintains shape	Soft, powdery when dry	Branch stubs and pitch pockets have rotted away	The log is section wise completely decomposed

* indicates decay classes used in this study.

Table 1.2 Sampling design illustrating the number of fallen logs (n=93) of each tree species and decay stage used to measure emergence, species richness and community composition of saproxylic Diptera.

	2006					2007			
Log type	rep. 1	2	3	subtotal		1	2	3	subtotal
Aspen class 2	4	4	4	12		2	4	4	10
Aspen class 4	4	4	4	12		4	4	4	12
Spruce class 2	4	4	4	12		3	4	4	11
Spruce class 4*	4	4	4	12		4	4	4	12
Total logs				48					45

*Logs sampled in balsam fir-birch forest blocks. The other logs were sampled in aspen-spruce forest blocks.

Table 1.3 Multiple linear regression results predicting overall dipteran emergence*.

Overall Dipteran Emergence n=89	Estimate	Std.Error	z	P
Intercept	1288.56	386.82	3.33	<0.01
Year	-0.64	0.19	-3.33	**<0.01**
Diameter	-0.03	0.03	-0.85	0.39
Density	-1.29	1.64	-0.79	0.43
Treespruce	0.59	0.93	0.64	0.52
Density:Treespruce	-5.68	2.26	-2.51	**0.01**
Diameter:Treespruce	0.05	0.04	1.37	0.17

*Best model according to Δ AICc (Appendix D): Year + Diameter + Density + Tree + Density:Tree + Diameter:Tree. AIC: 109.61. Residual deviance: 59.27 on 82 degrees of freedom. Null deviance: 86.289 on 88 degrees of freedom. Dispersion parameter for gamma distribution was taken to be: 0.79

Table 1.4 Multiple linear regression results predicting Mycetophagous emergence*.

Mycetophagous guild n= 89	Estimate	Std. Error	z	P
Intercept	-1.28	0.5	-2.55	**0.01**
Diameter	-0.01	0.03	-0.52	0.06
Density	0.34	1.64	0.21	0.84
Density:Treespruce	-4.07	1.91	-2.13	**0.03**
Diameter:Treespruce	0.07	0.03	2.64	**0.01**

*From best model according to Δ AICc (Appendix D):Diameter + Density + Density:Tree + Diameter:Tree. R^2=0.11. AIC: 728.77. Null deviance: 116.48 on 88 degrees of freedom. Residual deviance: 97.94 on 84 degrees of freedom. The dispersion parameter for negative binomial taken to be 1.27.

Table 1.5 Multiple linear regression results predicting Saprophagous emergence*.

Saprophagous guild n= 89	Estimate	Std.Error	z	P
Intercept	-0.01	0.42	-0.01	0.99
Diameter	-0.03	0.02	-1.36	0.17
Density	-1.47	1.36	-1.08	0.28
Density:Treespruce	-5.40	1.60	-3.37	**<0.01**
Diameter:Treespruce	0.08	0.02	3.50	**<0.01**

*From best model according to Δ AICc (Appendix D): Diameter + Density + Density:Tree + Diameter:Tree. R^2=0.23. AIC: 828.6. Null deviance: 131.30 on 88 degrees of freedom. Residual deviance: 97.48 on 84 degrees of freedom. The dispersion parameter for negative binomial taken to be 1.51.

Table 1.6 Results of mantel tests revealing correlations between variations in dipteran species assemblages and variations in wood properties.

Dipteran species distance matrix	Wood property distance matrix	Tree	*p-value*	*Pearson's* R^2
All species	Wood density	Aspen	0.136	
		Spruce	< 0.001	0.180
	Diameter	Aspen	0.989	
		Spruce	0.152	
Mycetophages	Wood density	Aspen	0.155	
		Spruce	0.008	0.151
	Diameter	Aspen	0.552	
		Spruce	0.326	
Saprophages	Wood density	Aspen	0.004	0.268
		Spruce	< 0.001	0.167
	Diameter	Aspen	0.997	
		Spruce	0.362	
Parasites	Wood density	Aspen	0.362	
		Spruce	0.996	
	Diameter	Aspen	0.872	
		Spruce	0.108	
Zoophages	Wood density	Aspen	0.890	
		Spruce	0.174	
	Diameter	Aspen	0.550	
		Spruce	0.659	

GENERAL CONCLUSION

Coarse woody debris is widely acknowledged as an essential component of boreal forest ecosystems providing habitat and nutrients to a number of organisms. In Quebec, reduction of mature and old-growth forests, widespread clear-cutting and future harvesting of woody residue for biofuel have the potential to disrupt CWD continuity in space and time. This may have negative affects on saproxylic species diversity and abundance.

Species in managed forests would benefit from a coarse-filter conservation approach which would take in to account the quantity of CWD (Work et al., 2004). However, an approach based solely on quantity may overlook key habitat elements necessary for saproxylic conservation. Saproxylic insects particularly beetles have been found to have strong associations with the following dead wood properties: decay stage, tree host, diameter, sun exposure, type of wood-rotting basidiomycetes, and wood moisture content (Grove, 2002).

This study used saproxylic Diptera, an abundant but less studied group to verify whether our current understanding of saproxylic requirements reflect the needs of a wider spectrum of species. More specifically, we measured the abundance, species richness, and community structure of saproxylic Diptera with regards to varying diameters and wood decay stages of two important host species in the eastern boreal forest of North America, aspen (*Populus tremuloides* Michaux.) and black spruce (*Picea mariana* (Miller.)) using on site emergence traps.

The species richness of fallen logs of spruce and aspen in the mixedwood forests of the Abitibi region was impressive with >227 taxa from 6753 specimens collected over two summer seasons. Many of the genera collected in our study have closely related species on threatened species lists in Europe. We can not provide the exact number of new species records represented for Quebec but we can be certain many species are new to the province and new to science. For example, from one of the most morpho species rich genera we identified (*Phronia* (Mycetophilidae)) we believe 14 have not been described in the literature (Gagné, 1975).

Our results suggest that some patterns of saproxylic Diptera use of CWD can be explained using tree host species, diameter and wood density. Increased wood decay, measured as decreasing wood density, appears to be the most important factor, as positive affects were revealed on dipteran species richness and abundance at the order, guild (mycetophagous and saprophagous) and species level (*Scatopsciara hastata*) for spruce and the guild level (saprophagous) in aspen. The preference for later stages of decay may be indicative of their need for high water content and their rapid development.

This study has highlighted the importance of studying a wide variety of saproxylic taxa as Diptera were found to respond differently to CWD properties than other better studied taxa such as the saproxylic Coleoptera. For instance, beetle species are generally tree host specific in early stages of decay (Grove, 2002). In later stages, tree specificity may decrease but differences between coniferous and deciduous hosts remain. In this study, irrespective of decay stage, few individual Diptera species were specific to coniferous or deciduous host. Saproxylic beetle species richness and abundance are generally positively affected by increasing diameter however, in this study only a small amount of variation was explained by models including this factor. No affects of diameter were observed for dipteran species richness, assemblages or species occurrence. More quantitative data on biotic variables from the logs sampled in this study such as species richness of fungi, bacteria would be useful.

Long-term forest utilization can decrease forest floor microhabitat diversity including the amount and quality of decayed wood (Kuuluvainen and Laiho, 2004). The resulting habitat continuity gap in time and space can have a negative impact on saproxylic species (Grove, 2002). Conservation strategies could incorporate some of the log characteristics analyzed in this study however, given the high variability of dipteran assemblages among logs irrespective of host type, size or decay stage, decision makers should aim on the side of caution and work to conserve mature and overmature forest where a diversity of CWD types and their associated microhabitats are made available for this diverse group of organisms.

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APPENDIX A

SPECIES LIST FOR DIPTERA REARED FROM FALLEN ASPEN AND SPRUCE LOGS.

Freq = frequency: number of logs species emerged from.
TG = Trophic guild: when defined, included in guild emergence and community data sets.
• Species used for individual species response data and all other data sets.
* Species included in all data sets with the exception of individual species response data.
~ Not defined to species: females and genera excluded from nms and species richness data sets.
◘ Families excluded from all data sets except for order and guild level emergence data sets.
No symbol- Species excluded from nms and species level emergence data sets.

Family	**Species**	**TG**	**2006**	**2007**	**sum**	**freq**
Anthomyiidae	*Eremomyioides sp.**	SAP	10	0	10	8
	Fucellia sp.	SAP	0	2	2	1
Anthomyziidae	*Mumetopia sp.*	SAP	1	0	1	1
	Laphria ?sericea Say, 1823	ZOO	2	0	2	2
Asteiidae	*Leiomyza sp.*	SAP	0	3	3	1
Calliphoridae	*Cynomya sp.1*	SAP	3	0	3	2
Cecidomyiidae	◘	MYT	1042	497	1539	87
Ceratopogonidae	◘	SAP	502	314	816	75
Chironomidae	◘	SAP	2	3	5	5
Chloropidae	*Elachiptera costata* Loew, 1863	SAP	1	0	1	1
	*Gaurax dorsalis_dark** Loew, 1863	SAP	38	4	42	13
	Gaurax dorsalis_light Loew, 1863	SAP	2	0	2	2
	Gaurax dorsalis Loew, 1863	SAP	1	1	2	2
	Thaumatomyia glaba Meigen, 1830	ZOO	2	0	2	2
	*Tricimba brunnicollis** (Becker, 1912)	SAP	25	9	34	17
	*Tricimba spinigera** Malloch, 1913	SAP	8	3	11	8
Clusiidae	*Clusiodes unknown sp.*		2	1	3	2

Family	Species	TG	2006	2007	sum	freq
Clusiidae cont'd	_Clusiodes johnsoni_* Malloch, 1922		24	4	28	7
	Clusiodes orbitalis Malloch, 1922		3	0	3	1
	Clusiodes sp.1		0	2	2	2
	Clusiodes sp.2		1	0	1	1
	Clusiodes sp.3		0	1	1	1
	Clusiodes sp.4		1	1	2	2
	~_Clusiodes_ females		0	2	2	2
Diastatidae	_Diasta sp._		0	2	2	2
Dolichopodidae	_Dolichopus canadensis_* VanDuzee, 1921	ZOO	14	5	19	12
	Dolichopus dasypodus Coquillett, 1910	ZOO	1	0	1	1
	Medetera unknown sp.	ZOO	0	1	1	1
	_Medetera crassivenis_* Curran, 1928	ZOO	6	0	6	4
	_Medetera sp.1_*	ZOO	0	4	4	4
	Medetera females~	ZOO	44	4	48	21
	_Medetera vittata_* Van Duzee, 1919	ZOO	21	8	29	11
	Neurigona sp.	ZOO	2	0	2	2
	_Drosophila sp.1_*	SAP	5	24	29	12
	_Drosophila sp.2_*	SAP	1	9	10	6
	Drosophila sp.3	SAP	1	1	2	2
	Drosophila sp.4	SAP	2	1	3	3
	Drosophila females~	SAP	3	6	9	8
	Mycodrosophila sp.	SAP	5	0	5	3
	Stegana sp.	SAP	2	7	9	2
Empididae	_Chelipoda sp.1_	ZOO	1	0	1	1
	Allanthalia pallida Zetterstedt, 1838	ZOO ZOO	2	0	2	1
	Chelipoda females~	ZOO	1	0	1	1
	_Euthyneura sp.1_*	ZOO	5	9	14	8
	Iteaphila sp.	ZOO	0	3	3	1
	Leptopeza sp.1	ZOO	3	0	3	3
	Micrempis sp.	ZOO	1	0	1	1
	Oedalea sp.1	ZOO	0	1	1	1

Family	Species	TG	2006	2007	sum	freq
Empididae cont'd	*Oedalea sp.2*	ZOO	1	2	3	2
	Oedalea females~	ZOO	11	0	11	5
	Rhamphomyia sp.1	ZOO	0	1	1	1
	Rhamphomyia sp.10	ZOO	1	0	1	1
	Rhamphomyia sp.11	ZOO	1	0	1	1
	Rhamphomyia sp.3	ZOO	0	2	2	1
	Rhamphomyia sp.4	ZOO	0	1	1	1
	Rhamphomyia sp.5	ZOO	0	2	2	2
	Rhamphomyia sp.7	ZOO	1	0	1	1
	Rhamphomyia sp.8	ZOO	1	0	1	1
	Rhamphomyia sp.9	ZOO	1	0	1	1
	Rhamphomyia females~	ZOO	3	1	4	4
	*Stilpon sp.1**	ZOO	7	1	8	4
	Syneches sp.2	ZOO	0	1	1	1
	*Tachypeza sp.1**	ZOO	46	26	72	39
	Trichina sp.	ZOO	0	1	1	1
Ephydridae	*Eutaenionotum guttipennis* Stenhammar, 1844	SAP	1	0	1	1
Heleomyzidae	*Amoebaleria sp.*	SAP	0	1	1	1
	Heleomyza sp.	SAP	2	0	2	1
	Suillia loewi Garrett, 1925	MYT	1	0	1	1
Lauxaniidae	*Homoneura homoneura sp.* *	SAP	1	3	4	4
	Lauxania sp.	SAP	0	1	1	1
	Minettia sp. Robineau & Desvoidy, 1830	SAP	2	0	2	2
	Sapromyza rotundicorus Loew, 1863	SAP	1	0	1	1
Lonchaeidae	*Lonchaea spp.* ~	SAP	6	12	18	9
Milichiidae	*Neophyllomyza quadricornis* Melander, 1913*	SAP	166	105	271	33
Muscidae	*Fannia sp.* *	SAP	6	5	11	11
	Fannia females~	SAP	0	2	2	2
	Paregle sp.		1	2	3	2

Family	Species	TG	2006	2007	sum	freq
Muscidae cont'd	*Pentacricia aldrichii* Stein, 1898		0	1	1	1
	Phaonia sp. *	ZOO	2	9	11	8
	Thricops sp.		4	1	5	1
Mycetophilidae	*Acadia polypori* * *Vockeroth, 1980*	MYT	8	8	16	5
	Acnemia sp.1	MYT	0	1	1	1
	Acomoptera ?plexipus (Garrett, 1925)	MYT	0	1	1	1
	Allocotocera pulchella (Curtis, 1837)	MYT	0	1	1	1
	Anatella sp.1	MYT	0	1	1	1
	Apolephthisa unnamed (Grzegorzek, 1885)	MYT	31	0	31	1
	Boletina sp.2	MYT	1	0	1	1
	Boletina females~	MYT	3	0	3	3
	Brachypeza females~	MYT	1	0	1	1
	Brevicornu sp.9	MYT	0	2	2	2
	Brevicornu females~	MYT	3	7	10	5
	Coelophthinia curta (Johannsen, 1912)	MYT	6	0	6	1
	Diadocidia ?borealis Coquillett, 1900	MYT	1	0	1	1
	Docosia sp.1	MYT	1	0	1	1
	Dynatosoma sp.	MYT	0	1	1	1
	Dynatosoma sp.1	MYT	1	0	1	1
	Dynatosoma sp.2	MYT	1	0	1	1
	Dynatosoma sp.4	MYT	32	0	32	1
	Dynatosoma sp.5	MYT	2	0	2	1
	Dynatosoma females~	MYT	12	1	13	3
	Dziedzickia sp.1	MYT	1	0	1	1
	Ectrepesthoneura sp.	MYT	1	0	1	1
	Epicypta helvopicta Chandler, 1981	MYT	4	0	4	3
	Epicypta limnophila * *Chandler, 1981*	MYT	2	5	7	7
	Exechia sp.1	MYT	0	2	2	2

Family	Species	TG	2006	2007	sum	freq
Mycetophilid cont'd	*Exechia sp.10*	MYT	1	0	1	1
	Exechia sp.2	MYT	1	0	1	1
	Exechia sp.3	MYT	1	0	1	1
	Exechia sp.4	MYT	5	0	5	2
	Exechia sp.6	MYT	1	1	2	2
	Exechia sp.9	MYT	1	1	2	2
	Exechia females~	MYT	35	15	50	21
	Exechiopsis females~	MYT	1	0	1	1
	Impleta polypori (Vockeroth, 1980)	MYT	1	0	1	1
	Keroplatus clausus Coquillett,1901	ZOO	2	0	2	2
	Keroplatus females~	ZOO	2	0	2	2
	Leia sp.1	MYT	2	2	4	3
	Leia sp.2	MYT	0	1	1	1
	Leia sp.4	MYT	0	1	1	1
	Leia sp.5	MYT	1	0	1	1
	Leia females~	MYT	5	3	8	8
	Leptomorphus sp. 1	MYT	1	0	1	1
	Leptomorphus sp. 2	MYT	1	0	1	1
	Leptomorphus sp. 3	MYT	3	0	3	1
	*Leptomorphus sp. 4**	MYT	4	0	4	4
	Leptomorphus females~	MYT	0	4	4	3
	Macrobrachius productus (Johannsen, 1912)	MYT	8	0	8	1
	Macrocera insignis Vockeroth, 1976	MYT	1	0	1	1
	Macrocera sp.	MYT	1	0	1	1
	Megalopelma sp.1	MYT	1	0	1	1
	Megalopelma females~	MYT	1	0	1	1
	Monoclona furcata Johannsen,1910	MYT	10	1	11	2
	Mycetophila ?ruficolis Meigen, 1818	MYT	0	1	1	1
	Mycetophila unknown	MYT	1	0	1	1
	Mycetophila fungorum De Geer, 1776	MYT	2	0	2	2

Family	Species	TG	2006	2007	sum	freq
Mycetophilid cont'd	*Mycetophila procera** (Loew, 1869)	MYT	4	0	4	4
	*Mycetophila sp. 1**	MYT	94	4	98	8
	*Mycetophila sp. 10**	MYT	15	135	150	6
	Mycetophila sp. 11	MYT	0	1	1	1
	Mycetophila sp. 12	MYT	1	1	2	2
	Mycetophila sp. 15	MYT	0	3	3	1
	Mycetophila sp.17	MYT	0	1	1	1
	Mycetophila sp.18	MYT	0	2	2	1
	Mycetophila sp.2	MYT	2	0	2	2
	Mycetophila sp.4	MYT	1	0	1	1
	Mycetophila sp.5	MYT	1	0	1	1
	Mycetophila sp.6	MYT	1	0	1	1
	Mycetophila sp.7	MYT	1	0	1	1
	Mycetophila sp.8	MYT	16	0	16	3
	Mycetophila sp.9	MYT	1	0	1	1
	Mycetophila females~	MYT	2	0	2	1
	Mycomya circumdata (Staeger, 1840)	MYT	1	2	3	2
	Mycomya dentate Fisher, 1937	MYT	1	0	1	1
	Mycomya hirticollis * (Say, 1824)	MYT	3	2	5	5
	*Mycomya ostensackeri** Vaisanen, 1984	MYT	3	2	5	5
	Mycomya females~	MYT	1	0	1	1
	*Orfelia sp.2**	MYT	1	4	5	4
	*Orfelia sp.3**	MYT	3	2	5	5
	Orfelia females~	MYT	1	2	3	3
	Phronia sp.10	MYT	0	2	2	2
	Phronia sp.13	MYT	1	0	1	1
	Phronia sp.14	MYT	1	0	1	1
	Phronia sp.15	MYT	0	1	1	1
	Phronia sp.16	MYT	2	0	2	2
	Phronia sp.17	MYT	1	0	1	1
	Phronia sp.3	MYT	5	0	5	1
	Phronia sp.8	MYT	0	1	1	1

Family	Species	TG	2006	2007	sum	freq
Mycetophilid cont'd	*Phronia* females~	MYT	39	15	54	22
	Phthinia miranda Zaitzev, 1984	MYT	3	0	3	3
	Phthinia females~	MYT	0	3	3	2
	Polylepta sp.1	MYT	1	0	1	1
	Polylepta females~		1	0	1	1
	*Pseudobrachypeza bulbosa** (Johannsen, 1912)	MYT	3	8	11	6
	Rondaniella dimidiata (Meigen, 1804)*	MYT	1	16	17	4
	Rymosia sp.	MYT	1	0	1	1
	Sceptonia sp.1	MYT	0	1	1	1
	Sciophila unknown	MYT	3	0	3	3
	*Sciophila sp.1**	MYT	4	2	6	4
	Sciophila sp.2	MYT	0	3	3	2
	Sciophila females~	MYT	4	0	4	3
	Syntemna sp.1	MYT	0	1	1	2
	Syntemna females~	MYT	0	2	2	1
	Tetragoneura sp.1	MYT	0	2	2	2
	Tetragoneura sp.2	MYT	0	1	1	1
	Tetragoneura sp.3	MYT	3	0	3	3
	Tetragoneura sp.4	MYT	1	0	1	1
	Tetragoneura sp.5	MYT	2	2	4	3
	Tetragoneura sp.6	MYT	1	0	1	1
	Tetragoneura sp.7	MYT	1	0	1	1
	Tetragoneura females~	MYT	10	6	16	10
	*Trichonta pulchra ** Gagné, 1981	MYT	6	1	7	4
	Zygomyia sp.1	MYT	2	0	2	2
	Zygomyia females~	MYT	3	1	4	5
Phoridae	*Xanionotum sp.*		0	1	1	1
	Anevrina sp.	SAP	1	1	2	2
	Apocephalus sp.1	PAR	3	0	3	1
	Beckerina sp.1	SAP	2	0	2	1
	Beckerina sp.3	SAP	1	0	1	1

Family	Species	TG	2006	2007	sum	freq
Phoridae cont'd	*Borophaga sp.1*	SAP	1	0	1	1
	*Chaetopleurophora sp.1**	SAP	12	0	12	6
	Citrago sp.		1	0	1	1
	Conicera sp.		0	1	1	1
	*Gymnophora sp.1**	PAR	9	9	18	12
	*Lecanocerus compressiceps** Borgmeier, 1962	PAR	21	6	27	11
	Megaselia spp. ~	SAP	484	237	721	85
	*Phora sp.1**	SAP	14	4	18	14
	*Pseudacteon sp.1**	PAR	3	13	16	8
Piophilidae	*Mycetaulus sp.*	MYT	2	0	2	2
Pipunculidae	*Pipunculus sp.*	PAR	1	0	1	1
Platypezidae	*Agathomyia sp.*	MYT	4	0	4	1
Psychodidae	◘		28	22	50	32
Rhagionidae	*Chrysopilus quadratus* (Say, 1823)	ZOO	1	0	1	1
Sarcophagidae	*Senotarnia sp.*	PAR	0	1	1	1
Scathophagidae	*Gonarcticus sp.*	SAP	1	1	2	2
Sciaridae	*Metangela toxoneura* (Osten Sacken, 1862)	SAP	2	0	2	1
	Phytosciara sp.	SAP	0	1	1	1
	*Bradysia ?jucunda** (Johannsen, 1912)	SAP	84	26	110	41
	*Bradysia ?mutua** (Johannsen, 1912)	SAP	4	42	46	18
	Bradysia ?trifurca (Pettey, 1918)	SAP	0	1	1	1
	*Bradysia sp.2**	SAP	0	38	38	7
	Bradysia sp.3	SAP	0	1	1	1
	*Bradysia sp.4**	SAP	0	10	10	4
	Bradysia sp.5	SAP	0	2	2	1
	Bradysia females~	SAP	148	193	341	68
	Chaetosciara joffrei (Petty, 1918)	SAP	2	0	2	1
	*Corynoptera sp.1**	SAP	7	34	41	11

Family	Species	TG	2006	2007	sum	freq
Sciaridae cont'd	*Corynoptera sp.2*	SAP	0	16	16	2
	Corynoptera sp.3•	SAP	103	154	257	62
	Corynoptera sp.4	SAP	1	2	3	2
	Corynoptera sp.5•	SAP	27	51	78	28
	Corynoptera sp.8	SAP	2	1	3	2
	Corynoptera females~	SAP	148	200	348	71
	Scatopsciara hastata• (Johannsen, 1912)	SAP	164	214	378	62
	Scatopsciara females~	SAP	12	0	12	10
	Sciara sp.1	SAP	3	0	3	1
	Sciara sp.2	SAP	0	5	5	1
	Sciara sp.4	SAP	4	0	4	2
	Sciara females~	SAP	28	14	42	20
	*Zygoneura sp.1**	SAP	3	2	5	5
	Zygoneura sp.3	SAP	0	1	1	1
	Zygoneura females~	SAP	2	5	7	5
Sphaeroceridae	*Leptocera sp.1*	ZOO	1	3	4	3
	Leptocera sp.3	ZOO	0	1	1	1
	Leptocera sp.4	ZOO	0	2	2	1
	Leptocera sp.5	ZOO	2	0	2	2
	Leptocera sp.6	ZOO	0	8	8	1
	Leptocera sp.7	ZOO	0	0	1	1
	Leptocera females~	ZOO	6	3	9	8
Syrphidae	*Platycheirus sp.*	ZOO	1	0	1	1
	Sphegina lobata Loew, 1863	ZOO	1	0	1	1
	Temnostoma balyras (Walker, 1849)	XYL	1	0	1	1
	Temnostoma vespiforme (Linnaeus, 1758)	XYL	2	0	2	2
	Trichopsomyia sp.	ZOO	1	0	1	1
Tachinidae	*Phytomyptera sp.1**	PAR	6	0	6	4
	Archytas sp.		0	1	1	1
Tipulidae	*Atarba sp.*	SAP	0	1	1	1
	Dactylolabis sp.	SAP	0	1	1	1
	Dolichopeza oropeza sp.	SAP	0	1	1	1

Family	Species	TG	2006	2007	sum	freq
Tipulidae cont'd	*Epiphragma sp.1**	SAP	15	0	15	4
	*Epiphragma sp.2**	SAP	8	5	13	7
	Gnophomyia sp.	SAP	8	0	8	1
	*Limonia sp.2**	SAP	26	10	36	4
	Limonia sp.3	SAP	3	0	3	1
	Limonia sp.4	SAP	10	0	10	1
	Tipula sp.1	SAP	0	1	1	1
	Tipula females~	SAP	0	3	3	2
	Ula sp. *	SAP	17	25	42	17
Otitidae	*Pseudotephritis vau* Say, 1830	SAP	1	1	2	2
Xylophagidae	*Xylophagus reflectens* Walker, 1848	ZOO	1	2	3	3
Total Diptera			3955	2798	6753	

APPENDIX B

SPECIES LIST FOR DIPTERA REARED FROM RESAMPLED FALLEN ASPEN AND SPRUCE LOGS.

Freq = frequency (number of logs each species emerged from). TG=Trophic guild.

Family	Species	TG	Year 2	freq
Acartophthalmidae	*Acartophthalmus nigrinus* (Zetterstedt, 1848)		1	1
Asilidae	*Lampria sp.*	ZOO	1	1
Axymyiidae	*Axymyia furcata* Mcatee,1921	ZOO	15	2
Bibionidae	*Hesperinus brevifrons* Walker, 1848	SAP	1	1
Cecidomyiidae		MYT	486	36
Ceratopogonidae		SAP	271	51
Chironomidae		SAP	4	2
Chloropidae	*Elachiptera costata* Loew, 1863	SAP	1	1
	Gaurax dorsalis_dark Loew, 1863	SAP	10	4
	Tricimba brunnicollis (Becker, 1912)	SAP	18	8
Clusiidae	*Clusiodes unknown sp.*	XLY	3	2
	Clusiodes johnsoni Malloch, 1922	XLY	18	6
	Clusiodes orbitalis Malloch, 1922	XLY	1	1
	Clusiodes sp.1	XLY	5	4
	Clusiodes sp.2	XLY	1	1
	Clusiodes sp.3	XLY	4	1
	Clusiodes sp.4	XLY	1	1
	Clusiodes sp.5	XLY	1	1
	Clusiodes females	XLY	1	1
Diastatidae	*Diasta sp.*		1	1
Dolichopodidae	*Dolichopus canadensis* VanDuzee, 1921	ZOO	3	3
	Medetera sp.1	ZOO	13	4

Family	Species	TG	Year 2	freq
Dolichopodid cont'	*Medetera* females	ZOO	11	7
	Medetera vittata Van Duzee, 1919	ZOO	3	2
Drosophilidae	*Drosophila* unknown sp.		1	1
	Drosophila sp.	SAP	1	1
	Drosophila sp.1	SAP	7	5
	Drosophila sp.2	SAP	1	1
	Drosophila sp.3	SAP	1	1
	Drosophila sp.4	SAP	1	1
	Drosophila sp.5	SAP	1	1
	Drosophila females	SAP	8	7
	Mycodrosophila sp.	SAP	68	4
	Stegana sp.	SAP	1	1
Dryomyzidae	dammaged specimens		1	1
Empididae	*Chelipoda sp.1*	ZOO	1	1
	Empis sp.1	ZOO	3	3
	Euthyneura sp.1	ZOO	5	3
	Iteaphila sp.	ZOO	8	1
	Megagrapha sp.	ZOO	1	1
	Oedalea sp.1	ZOO	4	2
	Oedalea sp.2	ZOO	3	1
	Oedalea sp.3	ZOO	1	1
	Rhamphomyia sp.2	ZOO	1	1
	Rhamphomyia sp.3	ZOO	5	5
	Rhamphomyia sp.5	ZOO	2	1
	Rhamphomyia sp.6	ZOO	1	1
	Rhamphomyia females	ZOO	2	2
	Stilpon sp.1	ZOO	1	1
	Syneches sp.1	ZOO	1	1
	Syneches sp.2	ZOO	1	1
	Syneches females	ZOO	4	4
	Tachypeza sp.1	ZOO	34	21
Heleomyzidae	*Allophyla atricornis* (Meigen, 1830)	SAP	1	1
	Trichochlamys borealis Czerny, 1924	SAP	1	1
Lauxaniidae	*Lyciella sp.*	SAP	1	1
	Poecilominettia sp.	SAP	1	1
	Homoneura homoneura sp.	SAP	3	3

Family	Species	TG	Year 2	freq
Lauxaniidae cont'd	*Minettia sp.* *Robineau & Desvoidy, 1830*	SAP	1	1
Lonchaeidae	*Lonchaea spp.*	SAP	28	12
Milichiidae	*Neophyllomyza quadricornis* Melander, 1913	SAP	67	11
Muscidae	*Fannia sp.*	SAP	1	1
	Fannia females	SAP	1	1
	Muscina sp.		1	1
	Phaonia sp.	ZOO	8	7
	Thricops sp.		1	1
Mycetophilidae	*Acadia polypori Vockeroth, 1980*	MYT	14	5
	Allodiopsis sp.1	MYT	1	1
	Allodiopsis females	MYT	1	1
	Anatella sp.1	MYT	3	3
	Apolephthisa unnamed (Grzegorzek, 1885)	MYT	6	1
	Boletina sp.1	MYT	1	1
	Boletina females	MYT	1	1
	Brachypeza sp.1	MYT	1	1
	Brevicornu sp.1	MYT	1	1
	Brevicornu sp.2	MYT	1	1
	Brevicornu sp.3	MYT	3	1
	Brevicornu sp.4	MYT	1	1
	Brevicornu sp.5	MYT	1	1
	Brevicornu sp.6	MYT	1	1
	Brevicornu sp.7	MYT	1	1
	Brevicornu sp.8	MYT	1	1
	Brevicornu females	MYT	13	5
	Diadocidia ?borealis Coquillett, 1900	MYT	1	1
	Docosia sp.1	MYT	1	1

Family	Species	TG	Year 2	freq
Mycetophilid cont'd	*Dynatosoma sp.1*	MYT	5	2
	Dynatosoma sp.2	MYT	7	1
	Dynatosoma sp.3	MYT	1	1
	Dynatosoma sp.4	MYT	1	1
	Dynatosoma females	MYT	3	3
	Dziedzickia sp.1	MYT	6	4
	Epicypta helvopicta Chandler, 1981	MYT	1	1
	Epicypta limnophila Chandler, 1981	MYT	31	13
	Epicypta sp.1	MYT	1	1
	Exechia sp.1	MYT	7	4
	Exechia sp.11	MYT	1	1
	Exechia sp.2	MYT	1	1
	Exechia sp.3	MYT	3	1
	Exechia sp.4	MYT	1	1
	Exechia sp.5	MYT	5	1
	Exechia sp.6	MYT	1	1
	Exechia sp.7	MYT	1	1
	Exechia sp.8	MYT	1	1
	Exechia sp.9	MYT	2	2
	Exechia females	MYT	32	7
	Exechiopsis sp.1	MYT	1	1
	Exechiopsis females	MYT	2	2
	Leia sp.1	MYT	10	7
	Leia sp.2	MYT	1	1
	Leia sp.4	MYT	1	1
	Leia females	MYT	12	10
	Monoclona furcata Johannsen,1910	MYT	6	1
	Mycetophila ?ocellus Walker, 1848	MYT	17	3

Family	Species	TG	Year 2	freq
Mycetophilid cont'd	*Mycetophila ?ruficolis Meigen, 1818*	MYT	3	1
	Mycetophila dammaged	MYT	1	1
	Mycetophila sp. 1	MYT	12	4
	Mycetophila sp. 10	MYT	26	3
	Mycetophila sp. 11	MYT	125	7
	Mycetophila sp. 12	MYT	19	4
	Mycetophila sp. 13	MYT	3	2
	Mycetophila sp. 14	MYT	1	1
	Mycetophila sp.16	MYT	2	1
	Mycetophila sp.2	MYT	2	2
	Mycetophila sp.4	MYT	10	1
	Mycetophila sp.5	MYT	5	1
	Mycetophila sp.8	MYT	4	1
	Mycomya biseriata (Loew, 1869)	MYT	1	1
	Mycomya circumdata (Staeger, 1840)	MYT	2	2
	Mycomya hirticollis (Say, 1824)	MYT	1	1
	Mycomya ostensackeri Vaisanen, 1984	MYT	3	3
	Orfelia sp.1	MYT	1	1
	Orfelia females	MYT	3	3
	Phronia sp.1	MYT	1	1
	Phronia sp.10	MYT	5	1
	Phronia sp.11	MYT	1	1
	Phronia sp.12	MYT	6	3
	Phronia sp.13	MYT	2	1
	Phronia sp.14	MYT	7	1
	Phronia sp.16	MYT	3	2
	Phronia sp.2	MYT	2	1

Family	Species	TG	Year 2	freq
Mycetophilid cont'd	*Phronia sp.3*	MYT	19	4
	Phronia sp.4	MYT	1	1
	Phronia sp.6	MYT	1	1
	Phronia sp.7	MYT	2	1
	Phronia sp.8	MYT	5	3
	Phronia females	MYT	53	24
	Phthinia miranda Zaitzev, 1984	MYT	1	1
	Pseudobrachypeza bulbosa (Johannsen, 1912)	MYT	11	2
	Rondaniella dimidiata (Meigen, 1804)	MYT	9	6
	Sceptonia females	MYT	1	1
	Sciophila sp.1	MYT	3	2
	Sciophila sp.3	MYT	2	2
	Sciophila females	MYT	1	1
	Stigmatomeria crassicornis (Stannius, 1831)	MYT	1	1
	Symmerus sp.1	MYT	1	1
	Syntemna sp.1	MYT	1	1
	Tarnania tarnanii (Dziedzicki, 1910)	MYT	1	1
	Tetragoneura sp.1	MYT	1	1
	Tetragoneura sp.3	MYT	2	1
	Tetragoneura sp.4	MYT	1	1
	Tetragoneura females	MYT	11	8
	Trichonta pulchra Gagné, 1981	MYT	2	1
	unknown genera		1	1
	Zygomyia sp.1	MYT	1	1
	Zygomyia females	MYT	1	1
Opomyzidae	*Anomalochaeta guttipennis*		1	1

Family	Species	TG	Year 2	freq
Phoridae	*Chaetopleurophora sp.1*	SAP	1	1
	Dohrniphora sp.		1	1
	Gymnophora sp.1	PAR	8	4
	Lecanocerus compressiceps Borgmeier, 1962	PAR	13	8
	Megaselia spp.	SAP	275	38
	Phora sp.1	SAP	7	7
	Pseudacteon sp.1	PAR	10	8
Psychodidae			50	11
Rhagionidae	*Rhagio sp.*	ZOO	1	1
Sarcophagidae	*Ptychoneura woodi Shewell, 1987*	PAR	1	1
Sciaridae	*Metangela toxoneura* (Osten Sacken, 1862)	SAP	57	2
	Bradysia ?jucunda (Johannsen, 1912)	SAP	51	19
	Bradysia ?mutua (Johannsen, 1912)	SAP	32	17
	Bradysia sp.2	SAP	23	9
	Bradysia sp.3	SAP	2	2
	Bradysia females	SAP	245	37
	Corynoptera sp.1	SAP	13	8
	Corynoptera sp.2	SAP	4	1
	Corynoptera sp.3	SAP	113	1
	Corynoptera sp.4	SAP	5	5
	Corynoptera sp.5	SAP	29	11
	Corynoptera sp.6	SAP	1	1
	Corynoptera females	SAP	237	37
	Scatopsciara hastata (Johannsen, 1912)	SAP	205	30
	Sciara sp.1	SAP	3	2
	Sciara sp.3	SAP	2	2

Family	Species	TG	Year 2	freq
Sciaridae cont'd	*Sciara sp.4*	SAP	4	3
	Sciara sp.5	SAP	1	1
	Sciara sp.6	SAP	1	1
	Sciara females	SAP	16	10
	Zygoneura sp.1	SAP	8	1
	Zygoneura sp.2	SAP	1	1
	Zygoneura females	SAP	17	4
	Leptocera sp.5	ZOO	1	1
	Leptocera sp.6	ZOO	5	1
	Leptocera sp.7	ZOO	1	1
	Leptocera females	ZOO	2	2
Stratiomyidae	*Actina viridis* (Say, 1824)	ZOO	1	1
	Beris sp.	ZOO	1	1
	Pachygaster sp.	ZOO	1	1
Syrphidae	*Sphegina lobata* Loew, 1863	ZOO	1	1
	Temnostoma vespiforme (Linnaeus, 1758)	XYL	4	1
	Trichopsomyia sp.	ZOO	1	1
Tachinidae	*Phytomyptera sp.1*	PAR	1	1
Tipulidae	*Epiphragma sp.2*	SAP	11	2
	Limonia sp.2	SAP	28	4
	Limonia sp.4	SAP	5	2
	Limonia females	SAP	1	1
	Ula sp.	SAP	50	7
Xylophagidae	*Rachicerus sp.*	ZOO	1	1
Total Diptera			3309	

APPENDIX C

LIST OF PUBLICATIONS USED FOR SPECIES IDENTIFICATION

Brochu C. and T. A. Wheeler. 2009. Systematics and Ecology of the Nearctic Species of Neophyllomyza (Diptera: Milichiidae).*The Canadian Entomologist*, vol 14, p. 103-111.

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Gagné, R. J. 1981. *A monograph of the genus Trichonta with a model for the distribution of Holarctic Mycetophilidae. Technical Bulletin of the U.S. Department of Agriculture.* p. 64.

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Johannsen, A. O. 1910. *The fungus gnats of North America, Part II. Maine Agricultural Experiment Station. Orono Bulletin No. 180.* p. 125-192.

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McAlpine, J. F., B. V. Peterson, G. E.Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. Manual of Nearctic Diptera: Volume 1. *In*: *Monograph of the Research Branch Agriculture Canada. Vol. 27.* Research Branch Agriculture Canada, Ottawa, Ontario. p.674.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M.Wood. 1987. *In*: *Monograph of the Research Branch Agriculture Canada. Vol. 28.* Research Branch Agriculture Canada, Ottawa, Ontario. p.1332.

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Sabrosky, C. W. 1948. A synopsis of the Nearctic species of *Elachiptera* and related genera (Diptera Chloropidae). *Journal of the Washington Academy of Sciences*, vol 38, p. 365-382.

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Vockeroth, J. R. 1990. Revision of the nearctic species of *Platycheirus* (Diptera, Syrphidae). *Canadian Entomologist*, vol 122, 659-766.

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Zaitsev, A. I. 1984. Holarctic species of the genus *Phthinia* Winn. (Diptera, Mycetophilidae). *Entomologicheskoe Obozrenie*, vol 63, p. 830-839 (*in Russian*).

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APPENDIX D

AICc PARAMETERS OF THE MULTIPLE LINEAR REGRESSION MODELS FOR DIPTERAN EMERGENCE.

Model*	Model ID	Log-likelihood	K	AICc	Δ AICc	wi
Bradysia jucunda (n=89)						
§Diameter	1	123.76	3	124.04	0.01	0.24
¦Density	2	123.74	3	124.03	0.00	0.25
§Diameter + Density	4	125.06	4	125.54	1.51	0.12
Density + Density:Tree	8	127.56	6	128.59	4.57	0.02
§Diameter + Diameter:Tree	9	123.76	3	124.04	0.01	0.24
§Diameter + Density + Tree + Density:Tree	12	125.06	4	125.54	1.51	0.12
§Diameter + Density + Tree + Diameter:Tree	13	124.07	4	124.55	0.52	0.19
Diameter + Density + Tree + Density:Tree + Diameter:Tree	14	127.03	5	127.76	3.73	0.04
Corynoptera sp.3 (n=89)						
¦Diameter	1	113.32	3	113.6	0.00	0.28
Density	2	115.54	3	115.82	2.22	0.09
Tree	3	115.42	3	115.7	2.09	0.10
Diameter + Density	4	115.31	4	115.79	2.19	0.09
§Diameter + Tree	5	114.82	4	115.3	1.69	0.12
Density + Tree	6	117.36	4	117.84	4.23	0.03
Diameter + Density + Tree	7	116.81	5	117.54	3.94	0.04
Density + Density:Tree	8	117.54	4	118.02	4.41	0.03
§Diameter + Diameter:Tree	9	114.81	4	115.29	1.69	0.12
Tree +Density:Tree	10	118.07	5	118.8	5.20	0.02
Tree +Diameter:Tree	11	116.81	5	117.54	3.93	0.04
Diameter + Density + Tree + Density:Tree	12	117.61	6	118.65	5.04	0.02
Diameter + Density + Tree + Diameter:Tree	13	118.8	6	119.84	6.23	0.01
Diameter + Density + Tree + Density:Tree + Diameter:Tree	14	119.61	7	121.01	7.40	0.01

K Number of parameters including intercept and variance.
wi Akaike weight.
§Models competing for best model according to Akaike model selection approach (Δ AICc<2).
¦Best model according to Akaike model selection approach.

Model*	Model ID	Log-likelihood	K	AICc	Δ AICc	wi
Corynoptera sp.5 (n=89)						
Diameter	1	110.14	3	110.43	0.90	0.18
§Density	2	109.85	3	110.13	0.60	0.21
Diameter + Density	4	111.39	4	111.87	2.34	0.09
§Density + Density:Tree	8	110.79	4	111.28	1.75	0.12
§Diameter + Diameter:Tree	9	112.13	4	112.62	3.09	0.06
Diameter + Density + Density:Tree	12	112.48	5	113.22	3.69	0.04
Diameter + Density + Diameter:Tree	13	113.32	5	114.05	4.52	0.03
¦Diameter + Density + Density:Tree + Diameter:Tree	14	108.49	6	109.53	0.00	0.28
Ula sp. (n=89)						
Diameter	1	84.36	3	84.65	6.59	0.00
Density	2	81.95	3	82.23	4.17	0.02
§Tree	3	78.75	3	79.03	0.97	0.09
Diameter + Density	4	81.97	4	82.45	4.39	0.01
§Diameter + Tree	5	78.75	4	78.85	0.78	0.10
¦Density + Tree	6	77.58	4	78.06	0.00	0.15
§Diameter + Density + Tree	7	77.80	5	78.53	0.47	0.11
Density + Density:Tree	8	80.01	4	80.50	2.43	0.04
§Diameter + Diameter:Tree	9	77.86	4	78.35	0.29	0.13
Tree +Density:Tree	10	78.13	5	78.86	0.80	0.10
Tree +Diameter:Tree	11	79.85	5	80.58	2.52	0.04
§Diameter + Density + Tree + Density:Tree	12	77.98	6	79.02	0.96	0.09
Diameter + Density + Tree + Diameter:Tree	13	79.20	6	80.24	2.17	0.05
Diameter + Density + Tree + Density:Tree + Diameter:Tree	14	79.59	7	80.99	2.93	0.03

K Number of parameters including intercept and variance.

wi Akaike weight.

§Models competing for best model according to Akaike model selection approach (Δ AICc<2).

¦Best model according to Akaike model selection approach.

Model*	Model ID	Log-likelihood	K	AICc	Δ AICc	wi
Neophylomyza quadricornis (n=89)						
Diameter	1	116.93	3	117.21	4.41	0.05
¡Density	2	112.52	3	112.80	0.00	0.43
Diameter + Density	3	114.37	4	114.85	2.05	0.15
Density + Density:Tree	4	115.75	4	114.96	2.16	0.15
Diameter + Diameter:Tree	5	114.48	4	119.20	6.39	0.02
Diameter + Density + Density:Tree	6	118.71	5	117.08	4.28	0.05
Diameter + Density + Diameter:Tree	7	117.34	5	116.23	3.43	0.08
Diameter + Density + Density:Tree + Diameter:Tree	8	116.86	6	116.40	3.60	0.07
Tachypeza sp.1 (n=89)						
Diameter	1	122.51	3	122.79	4.29	0.04
¡Density	2	118.22	3	118.50	0.00	0.36
§Diameter + Density	3	119.94	4	120.42	1.91	0.14
Density + Density:Tree	4	121.90	4	122.94	4.43	0.04
Diameter + Diameter:Tree	5	122.51	4	122.79	4.29	0.04
§Diameter + Density + Density:Tree	6	119.94	5	120.42	1.91	0.14
Diameter + Density + Diameter:Tree	7	123.94	5	124.42	5.91	0.02
Diameter + Density + Density:Tree + Diameter:Tree	8	120.44	6	121.17	2.67	0.10
Scatopsciara hastata (n=89)						
Diameter	1	114.99	3	115.28	14.24	0.00
¡Density	2	100.75	3	101.03	0.00	0.46
§Diameter + Density	3	102.69	4	103.17	2.14	0.16
Diameter + Density + Tree	4	104.01	4	104.74	3.71	0.07
Density + Density:Tree	5	105.97	4	107.01	5.97	0.02
Diameter + Diameter:Tree	6	114.99	5	115.28	14.24	0.00
Diameter + Density + Tree + Density:Tree	7	102.69	5	103.17	2.14	0.16
Diameter + Density + Tree + Diameter:Tree	8	116.37	6	116.85	15.82	0.00
Diameter + Density + Tree + Density:Tree + Diameter:Tree	9	104.00	3	104.74	3.70	0.07

K Number of parameters including intercept and variance.
wi Akaike weight.
§Models competing for best model according to Akaike model selection approach (Δ AICc<2).
¡Best model according to Akaike model selection approach.

Model*	Model ID	Log-likelihood	K	AICc	Δ AICc	wi
All Diptera (n=89)						
Year	1	129.30	3	129.58	18.17	0.00
Diameter	2	132.44	3	132.73	21.32	0.00
Density	3	126.02	3	126.30	14.90	0.00
Tree	4	136.61	3	136.89	25.49	0.00
Diameter + Density	5	124.69	4	125.17	13.76	0.00
Diameter + Tree	6	133.93	4	134.40	23.00	0.00
Density + Tree	7	127.36	4	127.83	16.43	0.00
Diameter + Density + Tree	8	126.06	5	126.79	15.38	0.00
Density + Density:Tree	9	128.00	4	128.48	17.07	0.00
Diameter + Diameter:Tree	10	132.86	4	133.33	21.93	0.00
Tree +Density:Tree	11	121.06	5	121.78	10.38	0.01
Tree +Diameter:Tree	12	131.70	5	132.42	21.01	0.00
Diameter + Density + Tree + Density:Tree	13	120.96	6	121.99	10.58	0.00
Diameter + Density + Tree + Diameter:Tree	14	124.53	6	125.55	14.14	0.00
Diameter + Density + Tree + Density:Tree + Diameter:Tree	15	119.84	7	121.22	9.81	0.01
¦Year + Diameter + Density +Tree +Density:Tree +Diameter:Tree	16	109.61	8	111.41	0.00	0.98

K Number of parameters including intercept and variance.

wi Akaike weight.

§Models competing for best model according to Akaike model selection approach (Δ AICc<2).

¦Best model according to Akaike model selection approach.

Mycetophagous (n=86)	model	AIC	K	AICc	Δ AICc	wt
Diameter	1	732.67	3	732.96	3.13	0.09
Density	2	734.72	3	735.01	5.18	0.03
Diameter + Density	7	731.88	4	732.38	2.55	0.12
Density + Density:Tree	8	736.42	4	736.91	7.09	0.01
Diameter + Diameter:Tree	9	732.23	4	732.72	2.89	0.10
Diameter + Density + Density:Tree	12	733.51	5	734.26	4.42	0.05
Diameter + Density + Diameter:Tree	13	731.22	5	731.97	2.14	0.15
¦Diameter + Density + Density:Tree + Diameter:Tree	14	728.77	6	729.83	0.00	0.44
Parasitic (n=89)						
§Diameter	1	113.86	3	114.15	1.63	0.15
§Density	2	114.07	3	114.36	1.83	0.13
Diameter + Density	4	115.86	4	116.34	3.82	0.05
Density + Density:Tree	8	114.58	4	115.06	2.54	0.09
¦Diameter + Diameter:Tree	9	112.04	4	112.52	0.00	0.34
Diameter + Density + Density:Tree	12	116.20	5	116.93	4.41	0.04
Diameter + Density + Diameter:Tree	13	113.81	5	114.54	2.02	0.12
Diameter + Density + Density:Tree + Diameter:Tree	14	114.54	6	115.58	3.06	0.07

K Number of parameters including intercept and variance.
wi Akaike weight.
§Models competing for best model according to Akaike model selection approach (Δ AICc<2).
¦Best model according to Akaike model selection approach.

Model*	Model ID	Log-likelihood	K	AICc	Δ AICc	wi
Saprophagous (n=89)						
Diameter	1	848.72	3	849.00	19.37	0.00
Density	2	836.12	3	836.40	6.77	0.03
Diameter + Density	3	837.88	4	838.36	6.79	0.03
Density + Density:Tree	4	828.60	6	829.63	8.73	0.01
Diameter + Diameter:Tree	5	848.72	3	849.00	20.51	0.00
Diameter + Density + Density:Tree	6	837.88	4	838.36	8.83	0.01
Diameter + Density + Diameter:Tree	7	849.66	4	850.14	8.07	0.02
¦Diameter + Density + Density:Tree + Diameter:Tree	8	837.73	5	838.46	0.00	0.90
Zoophagous (n=89)						
§Diameter	1	102.28	3	102.57	1.10	0.17
¦Density	2	101.19	3	101.47	0.00	0.29
§Diameter + Density	3	102.82	4	103.31	1.83	0.12
Density + Density:Tree	4	104.39	6	105.43	3.95	0.04
§Diameter + Diameter:Tree	5	102.28	3	102.57	1.10	0.17
§Diameter + Density + Density:Tree	6	102.82	4	103.31	1.83	0.12
Diameter + Density + Diameter:Tree	7	104.03	4	104.52	3.04	0.06
§Diameter + Density + Density:Tree + Diameter:Tree	8	103.44	5	104.17	2.70	0.08

K Number of parameters including intercept and variance.

wi Akaike weight.

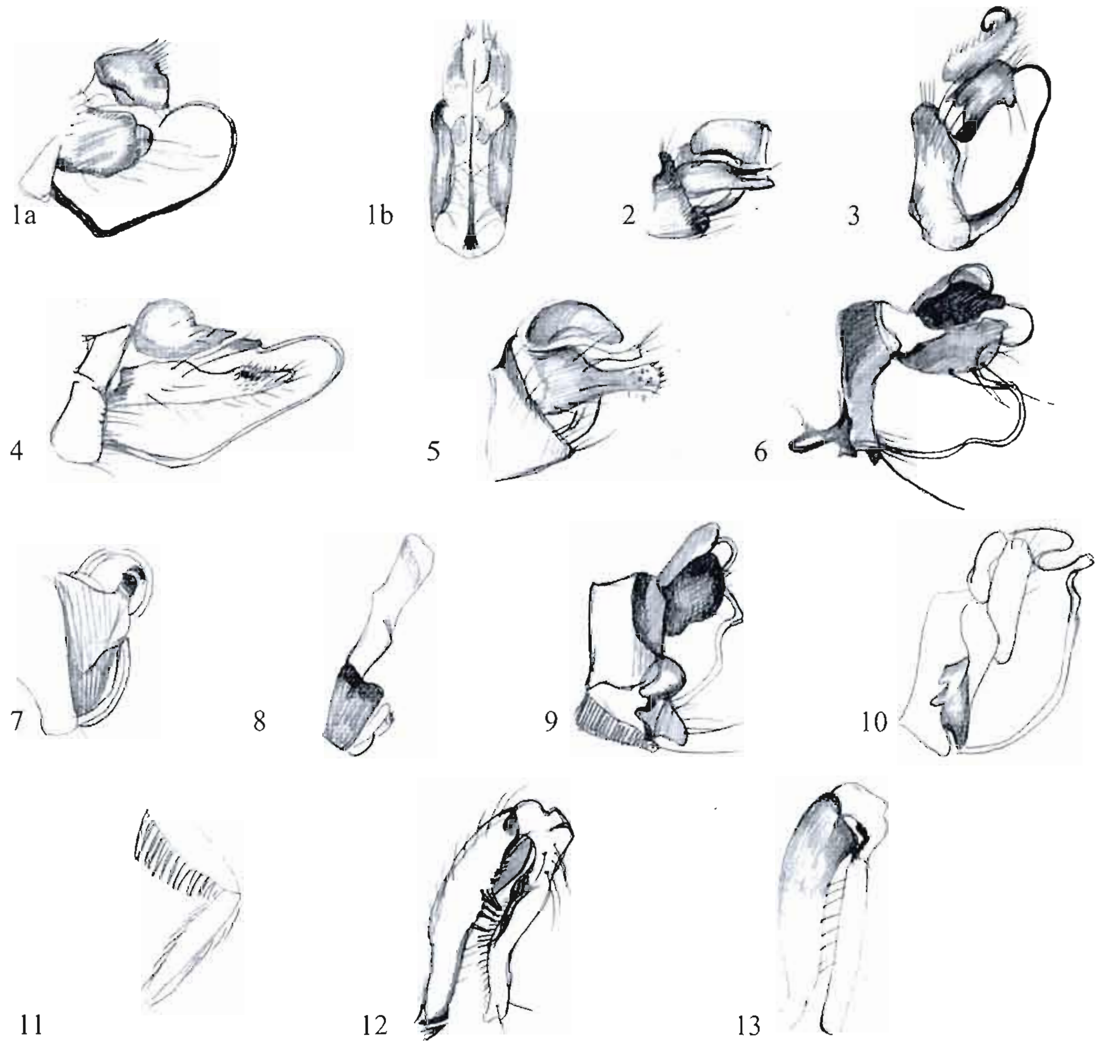
§Models competing for best model according to Akaike model selection approach (Δ AICc<2).

¦Best model according to Akaike model selection approach.

APPENDIX E

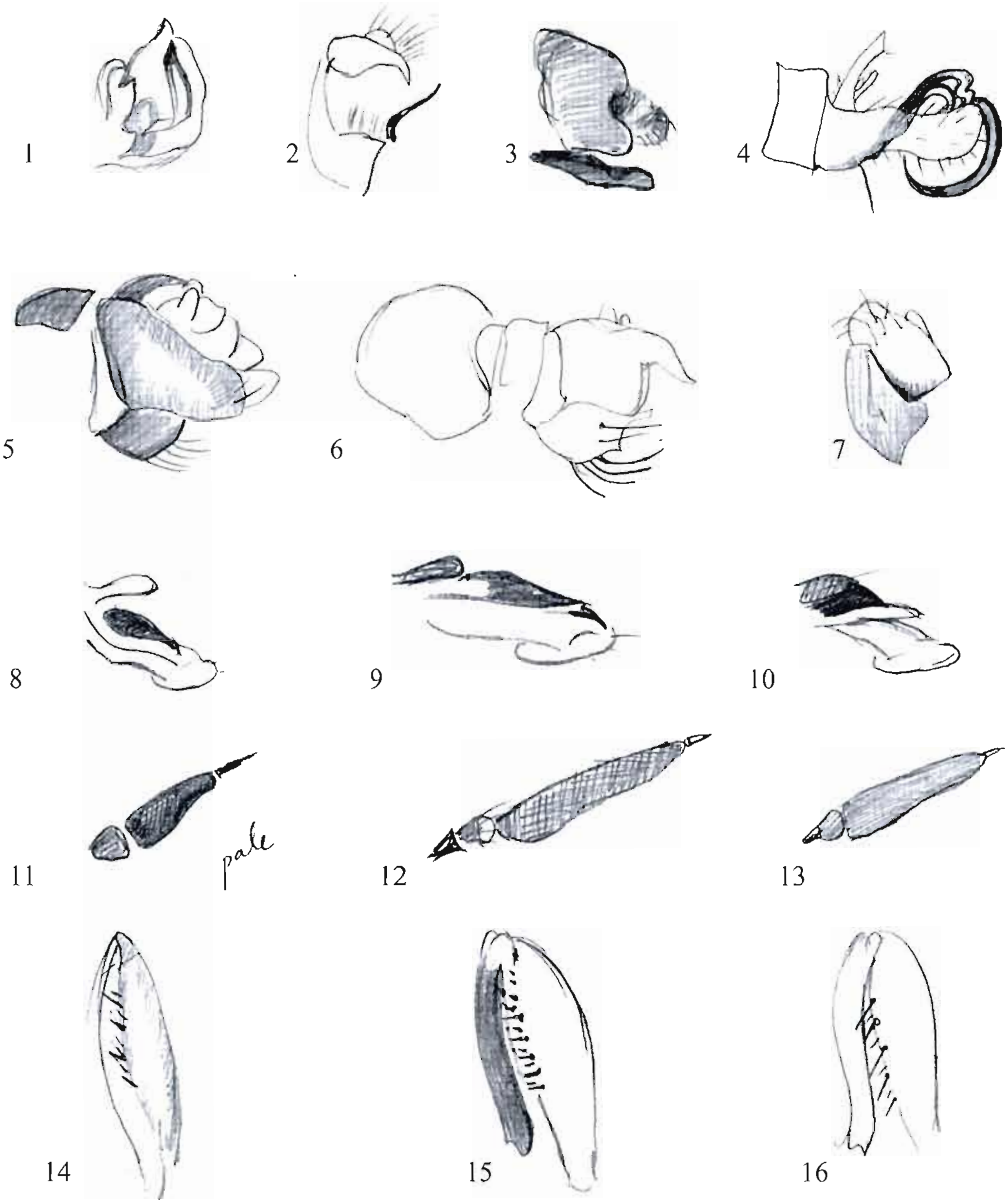
SELECTED DRAWINGS OF DIPTERA GENITALIA USED FOR MORPHO SPECIES DESIGNATION

Family: Empididae, Genus: *Rhamphomyia*. Drawings are not to scale.



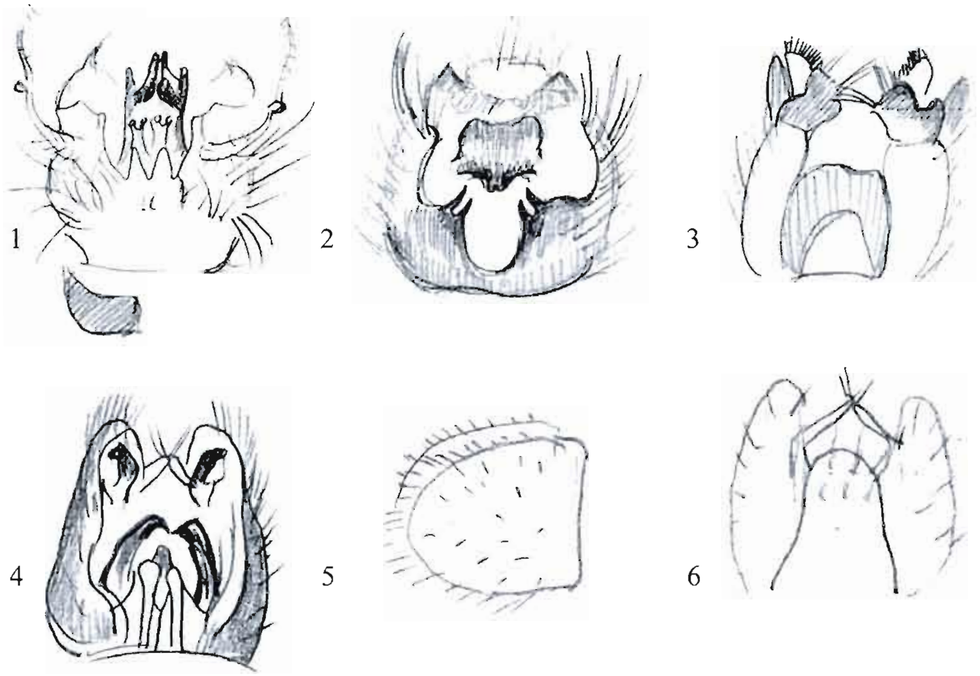
Figs. 1-13. Male genitalia and front legs: male genitalia, lateral (1a) and ventral (1b) of *Rhamphomyia* sp.1; male genitalia, lateral (2) of *Rhamphomyia* sp. 2, (3) *Rhamphomyia* sp.3, (4) *Rhamphomyia* sp. 4, (5) *Rhamphomyia* sp. 5, (6) *Rhamphomyia* sp. 6, (7) *Rhamphomyia* sp. 8, (8) *Rhamphomyia* sp. 9, (9) *Rhamphomyia* sp. 10, and (10) *Rhamphomyia* sp. 11; front leg of (11) *Rhamphomyia* sp. 7, (12) *Rhamphomyia* sp.5, and (13) *Rhamphomyia* sp.2.

Family: Empididae, Genera: mixed. Drawings are not to scale.



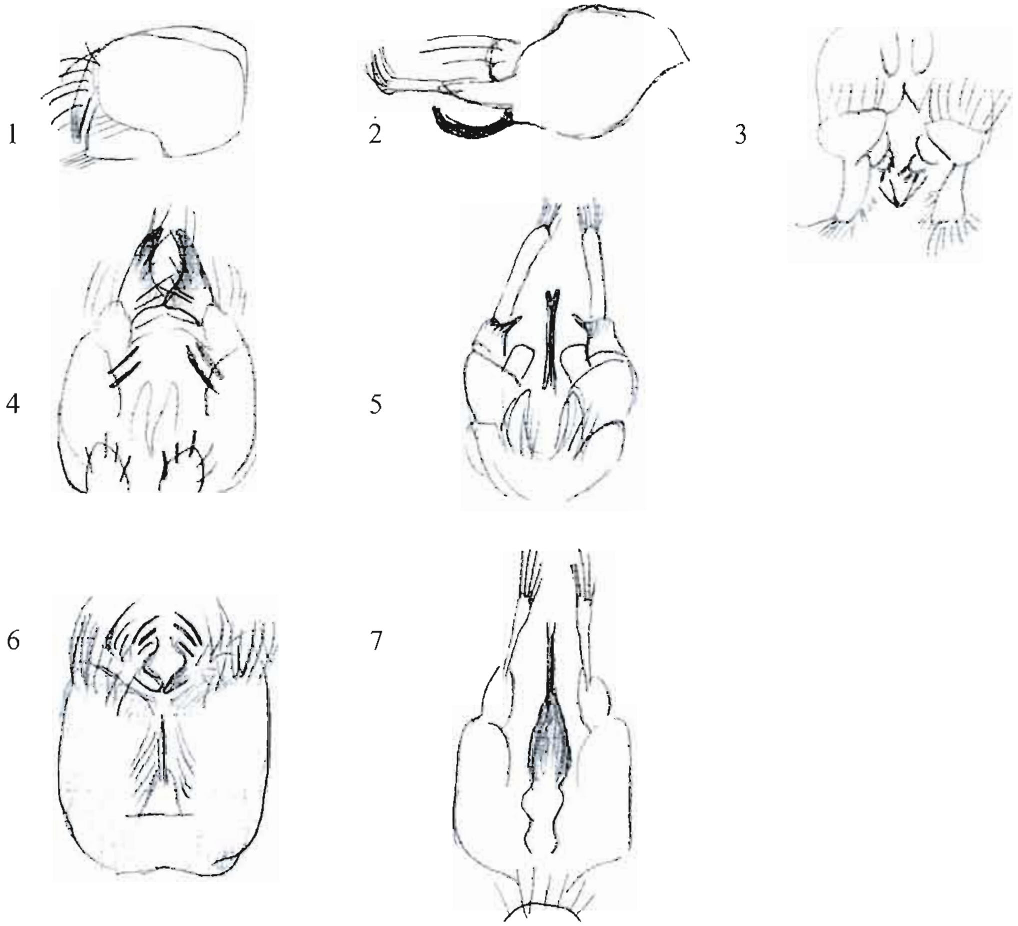
Figs. 1-16. Male genitalia, mouth parts, antennae and hind legs: male genitalia, lateral (1) of *Chilipoda* sp.1; male genitalia, posterior (2) of *Leptopeza* sp. 1; male genitalia, lateral (3) of *Stilpon* sp.1, (4) *Iteaphila* sp., (5) *Syneches* sp.1, (6) *Syneches* sp. 2 and (7) *Euthyneura* sp. 1; male mouth parts, of (8) *Odelea* sp. 1, (9) *Odelea* sp. 2 and (10) *Odelea* sp. 3; male antennae of (11) *Odelea* sp.1, (12) *Odelea* sp.2 and (13) *Odelea* sp. 3; male hind femurs of (14) *Odelea* sp.1, (15) *Odelea* sp. 2, and (16) *Odelea* sp. 3.

Family: Mycetophilidae, Genus: *Leia*. Drawings are not to scale.



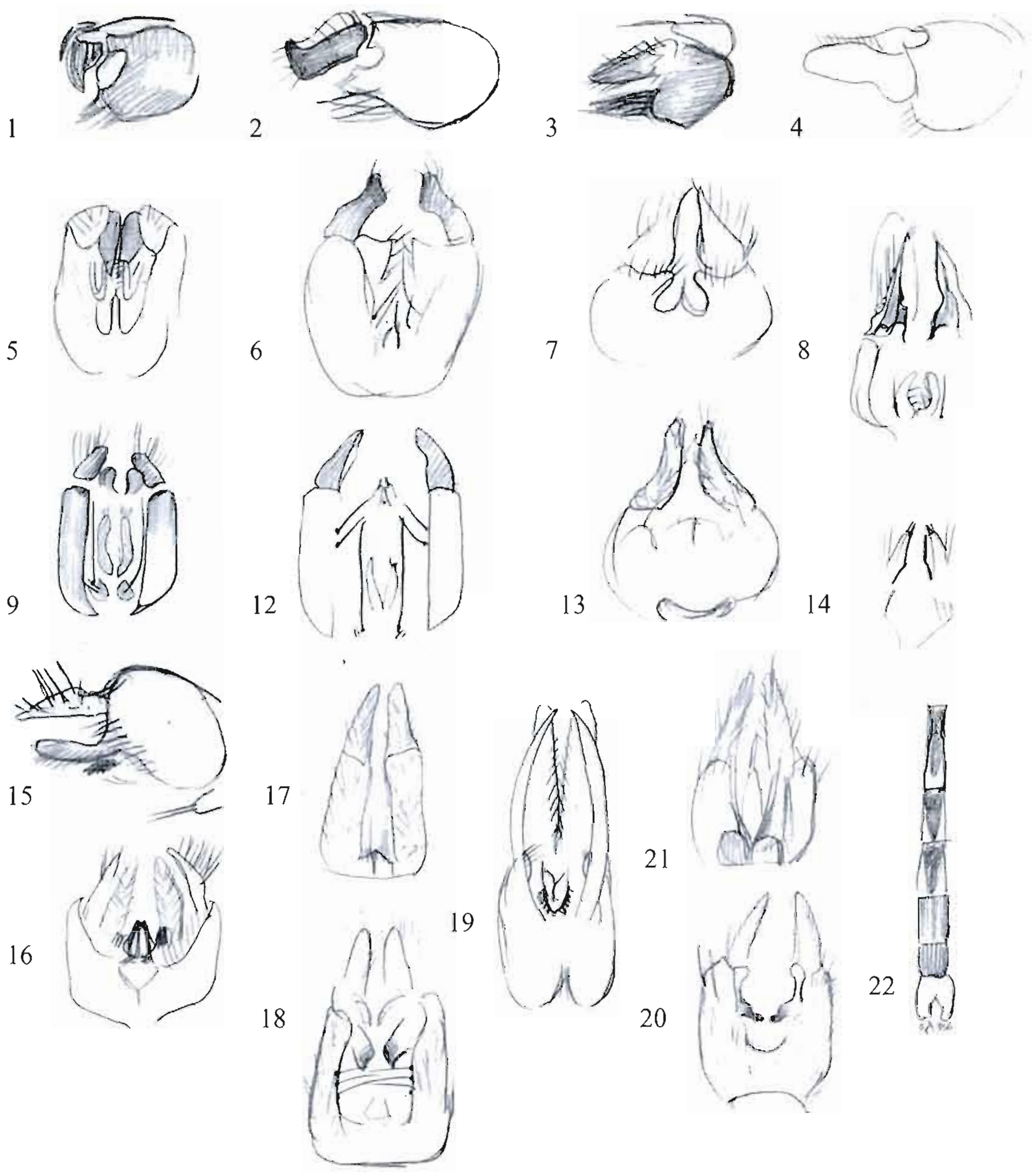
Figs. 1-6. Male genitalia: dorsal (1) of *Leia* sp.1, (2) *Leia* sp.2, (3) of *Leia* sp.4, (4) *Leia* sp. 5; lateral (5), and ventral (6) of *Leia* sp. 5.

Family: Mycetophilidae, Genera: mixed. Drawings are not to scale.



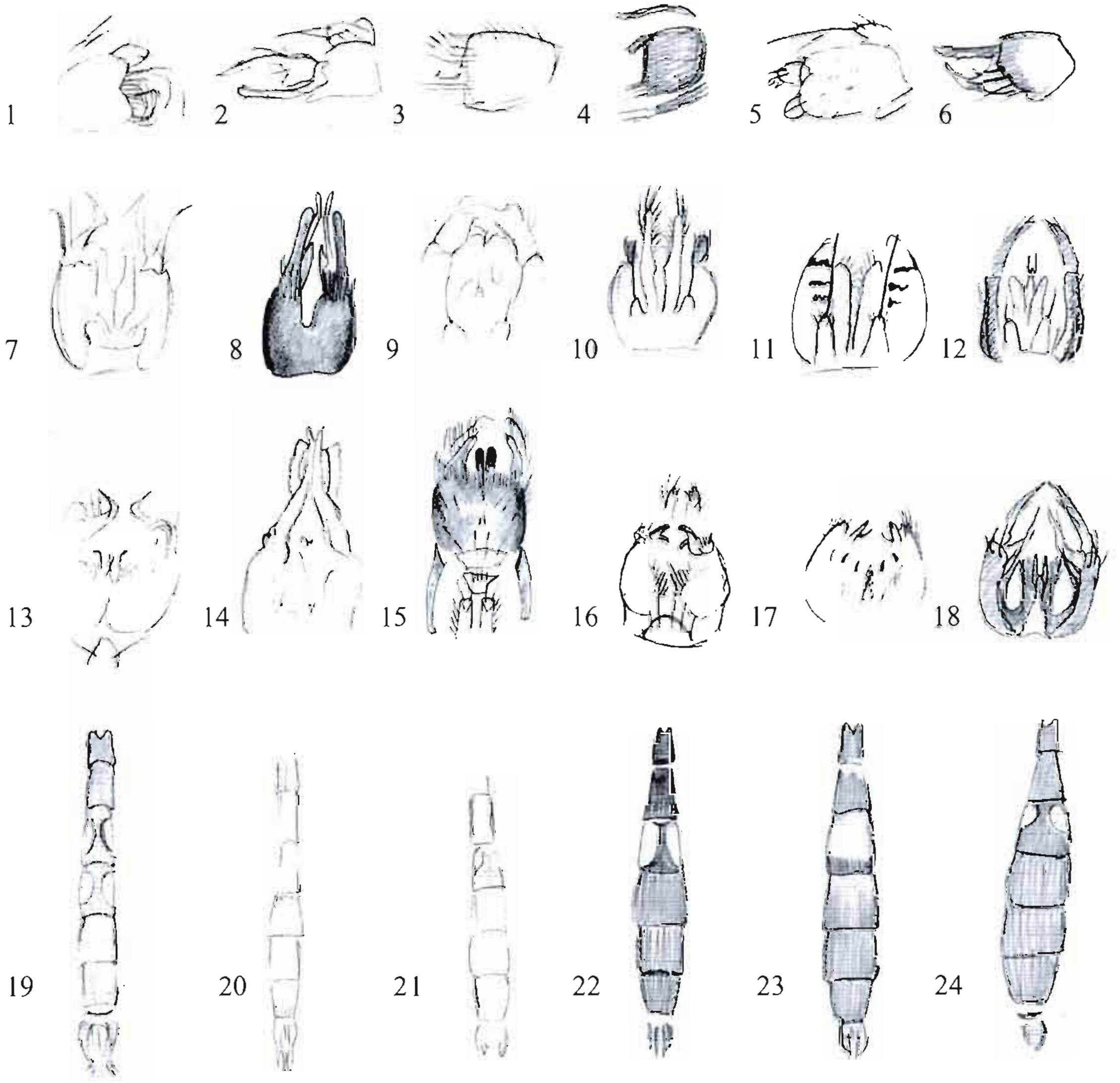
Figs. 1-7. Male genitalia: (1) lateral, (4) dorsal, (6) ventral of *Alodiopsis* sp.; (2) lateral, (5) dorsal,(7) ventral of *Exechiopsis* sp.1; male genitalia, posteroventral (3) of *Boletina* sp.1.

Family: Mycetophilidae, Genus: *Brevicornu*. Drawings are not to scale.



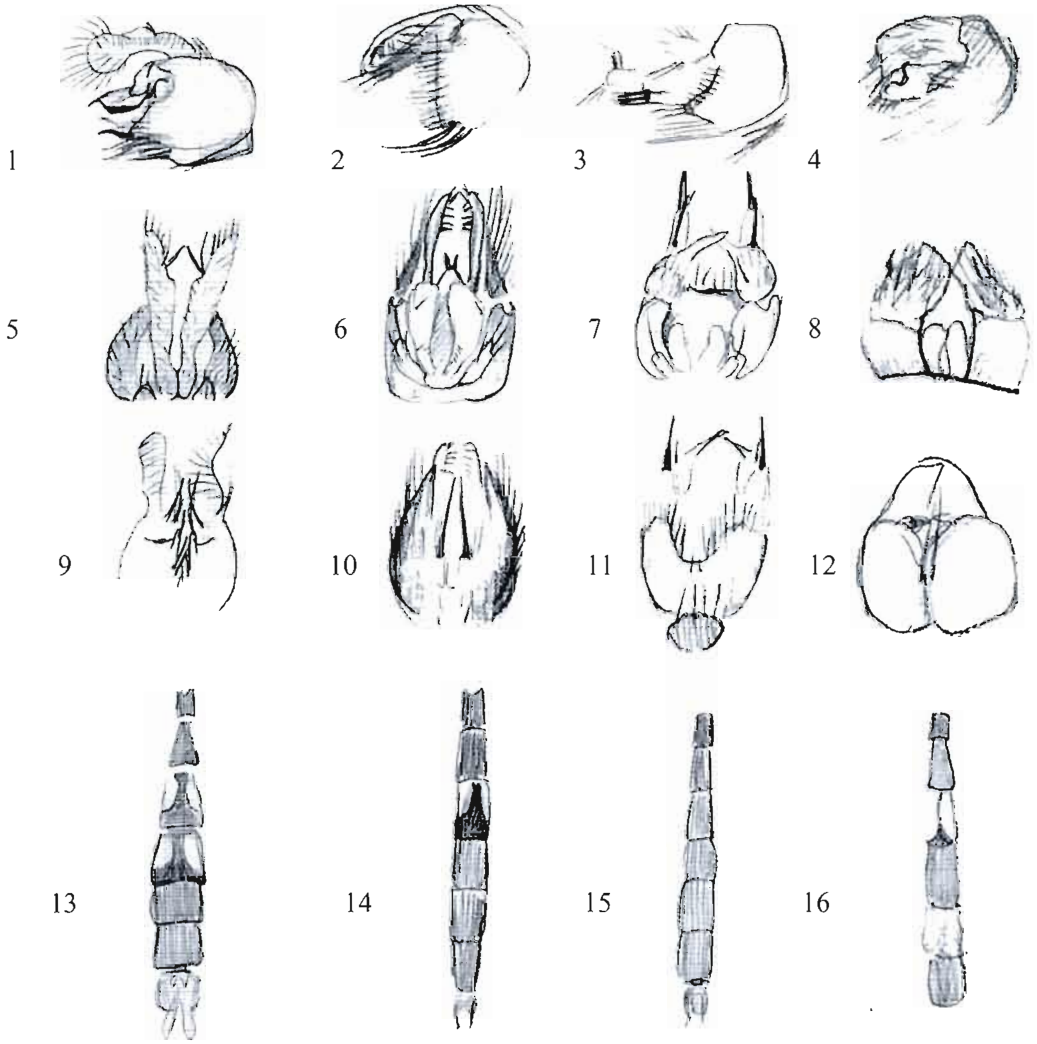
Figs. 1-22. Male genitalia and abdomen: lateral (1), ventral (5) and dorsal of (9) *Brevicornu sp.1*; lateral (2), ventral (6), and dorsal (12) *Brevicornu sp.2*; lateral (3), ventral (7), and dorsal (13) of *Brevicornu sp.3*; lateral (4), ventral (8) and dorsal (14) of *Brevicornu sp. 4*; lateral (15) and dorsal (16) of *Brevicornu* sp. 5; dorsal (17) and ventral (18) of *Brevicornu* sp.8; ventral (19) of *Brevicornu* sp. 6; dorsal (21), ventral (20), abdomen (22) of *Brevicornu* sp. 9.

Family: Mycetophilidae, Genus: *Exechia*. Drawings are not to scale.



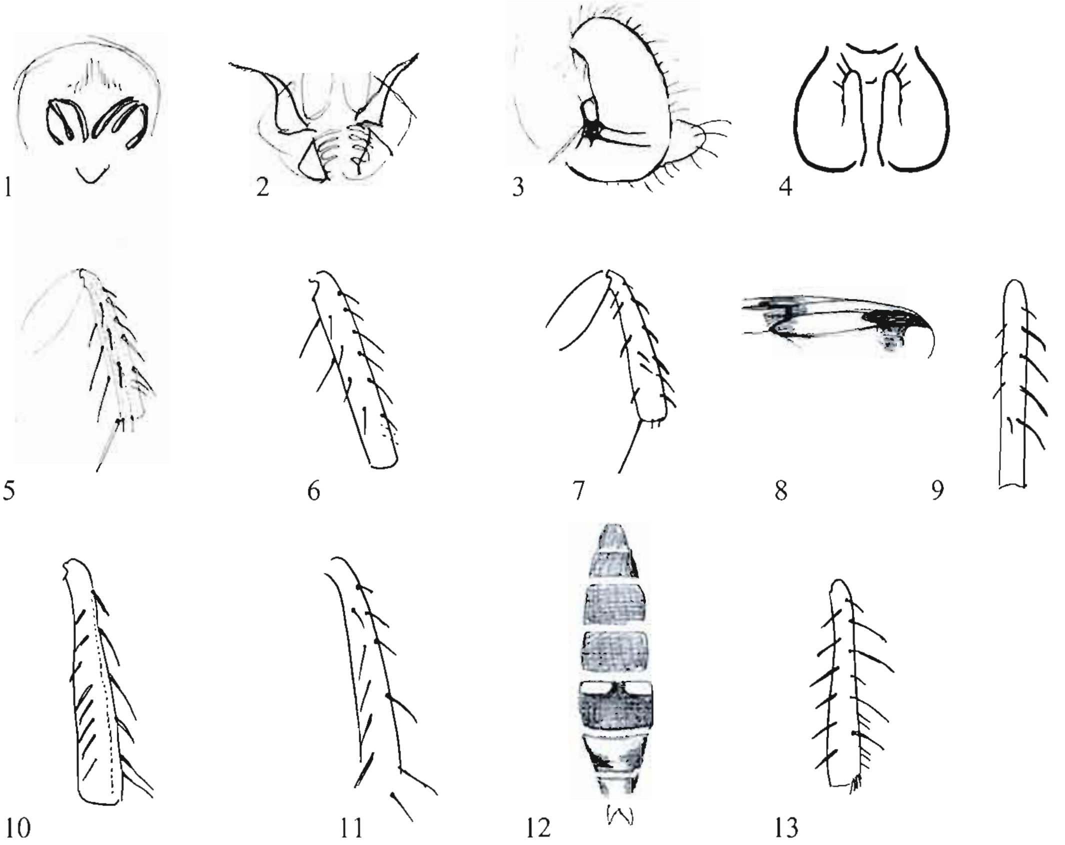
Figs. 1-24. Male genitalia and abdomens: lateral (1), dorsal(7), ventral (13), abdomen (19) of *Exechia* sp.1; lateral (2), dorsal (8), ventral (14), abdomen (20) of *Exechia* sp.2; lateral (3), dorsal (9), ventral (15), abdomen (21) of *Exechia* sp.3; lateral (4), dorsal (10), ventral (16), abdomen (22) of *Exechia sp. 4*; lateral (5), dorsal (11), ventral (17), abdomen (23) of *Exechia* sp. 5; lateral (6), dorsal (12), ventral (18), abdomen (24) *Exechia* sp.6.

Family: Mycetophilidae, Genus: *Exechia* continued. Drawings are not to scale.



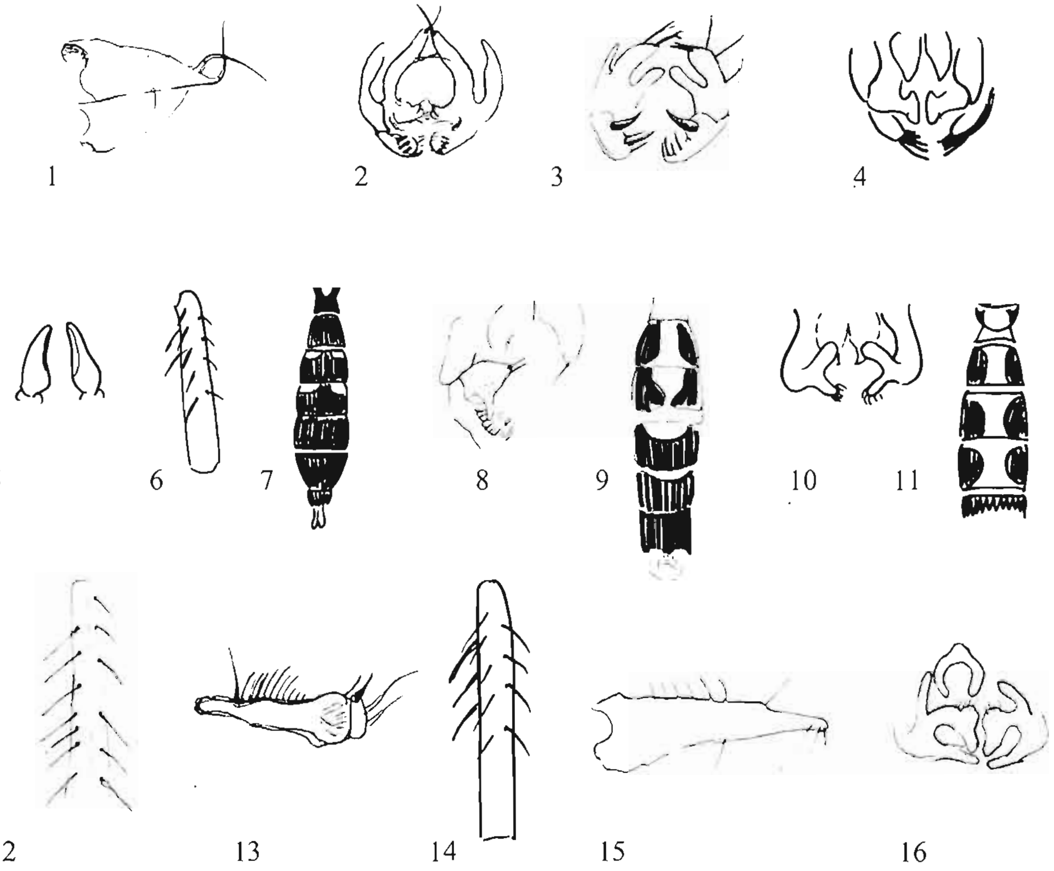
Figs. 1-16. Male genitalia and abdomens: lateral (1), dorsal (5), ventral (9), abdomen (13) of *Exechia* sp.7; lateral (2), dorsal (6), ventral (10), abdomen (14) of *Exechia* sp.8; lateral (3), dorsal (7), ventral (11), abdomen (15) of *Exechia* sp.9; lateral (4), dorsal (8), ventral (12), abdomen (16) of *Exechia sp.* 10.

Family: Mycetophilidae, Genus: *Mycetophila*. Drawings are not to scale.



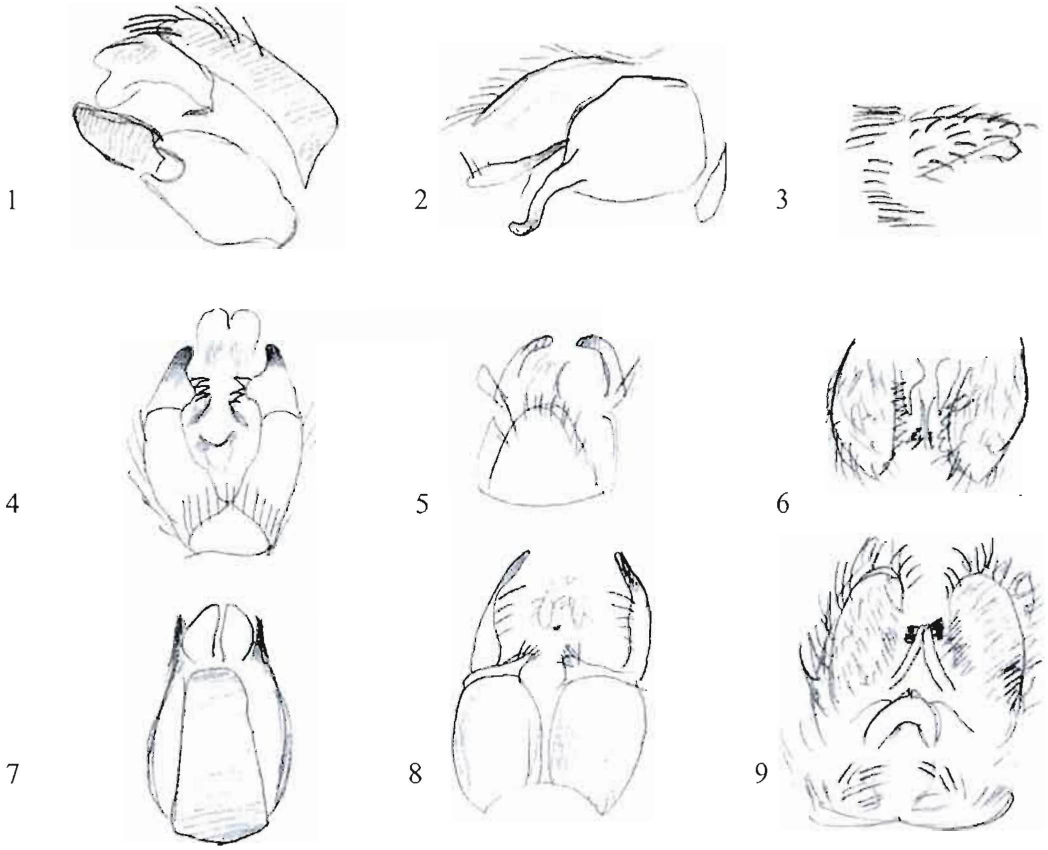
Figs. 1-13. Male genitalia, tibia, abdomens and wings: male genitalia, posteroventral (1), mid tibia (5), hind tibia (10) of *Mycetophila* sp.1; posteroventral (2), mid tibia (6), hind tibia (11) of *Mycetophila* sp. 2; lateral (3), mid tibia (7), abdomen (12) of *Mycetophila* sp.4; posteroventral (4), wing (8), hind tibia (13) of *Mycetophila* sp.5; mid tibia (9) of *Mycetophila* sp. 6.

Family Mycetophilidae, Genus: *Mycetophila* continued. Drawings are not to scale.



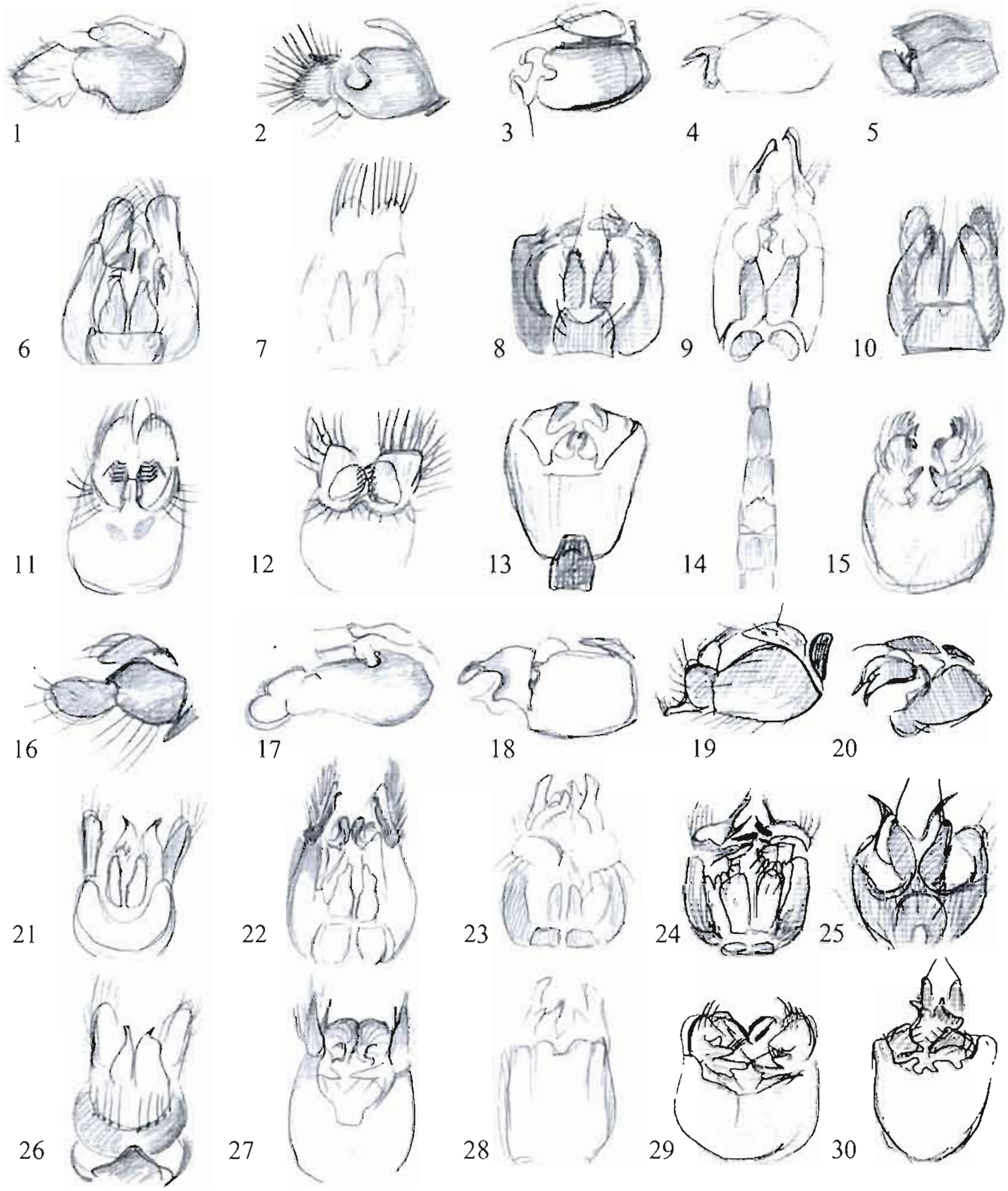
Figs. 1-16. Male genitalia, abdomens and tibia: male genitalia, dorsal (1) of Mycetophila sp.10; posteroventral (2) *Mycetophila* sp. 11, (3) *Mycetophila* sp.12, (4) *Mycetophila* sp.14; hypandrial arms (5), mid tibia (6), abdomen (7) of *Mycetophila* sp. 8; posteroventral (8), abdomen (9) of *Mycetophila* sp.13; posteroventral (10), abdomen (11) of *Mycetophila* sp.17; hind tibia (12) of Mycetophila sp.7; hypandrial arm (13) of *Mycetophila ?fungorum*; mid tibia (14) of *Mycetophila* sp. 9; hypandrial arm (15) of *Mycetophila ?ruficolis*; posteroventral (16) *Mycetophila ?ocellus*.

Family: Mycetophilidae, Genus: *Orfelia.* Drawings are not to scale.



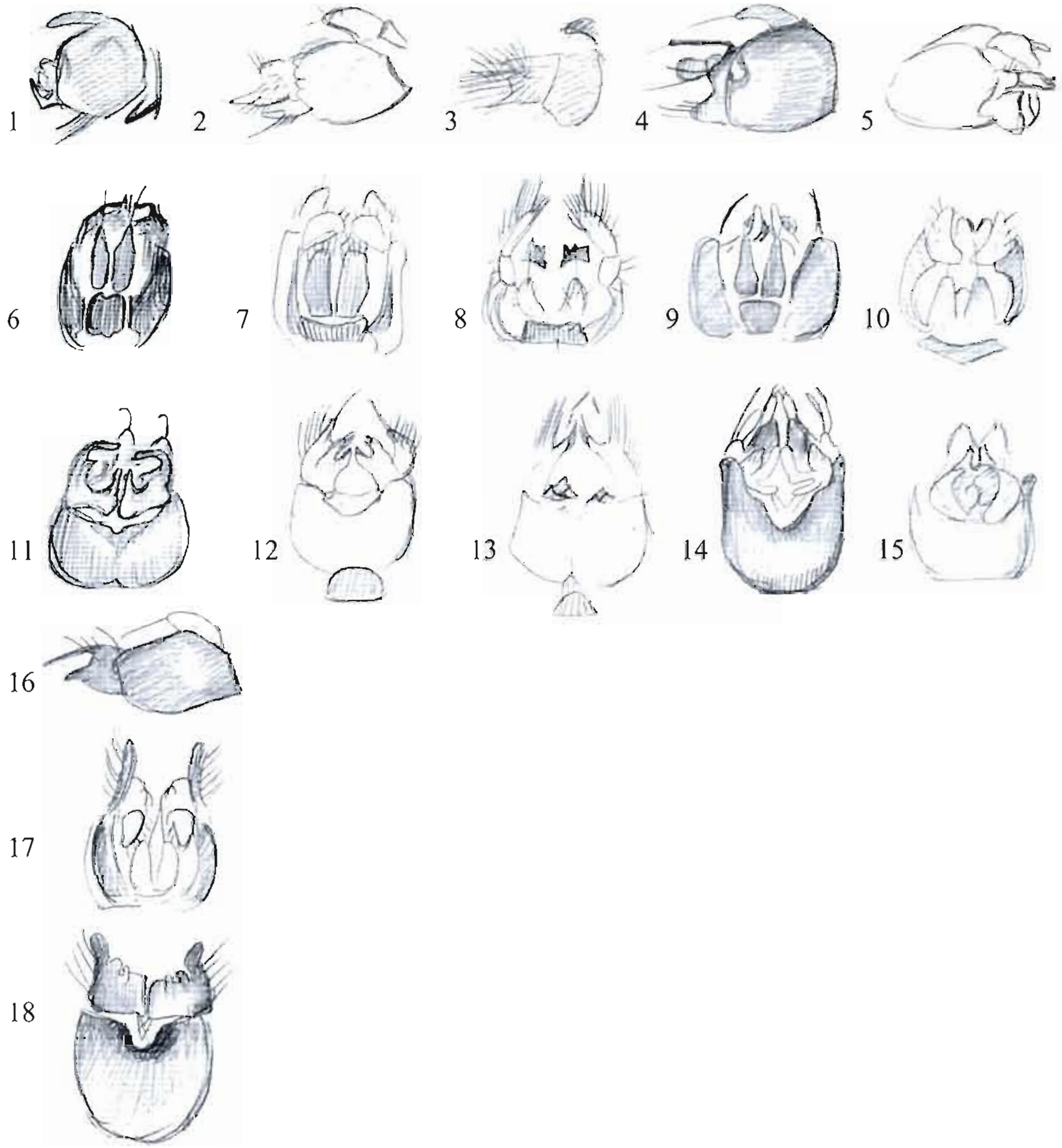
Figs. 1-9. Male genitalia: lateral (1), dorsal (4), ventral (7) of *Orfelia* sp.1; lateral (2), dorsal (5), ventral (8) of *Orfelia* sp.2; lateral (3), dorsal (6), ventral (9) of *Orfelia* sp.3.

Family: Mycetophilidae, Genus: *Phronia*. Drawings are not to scale.



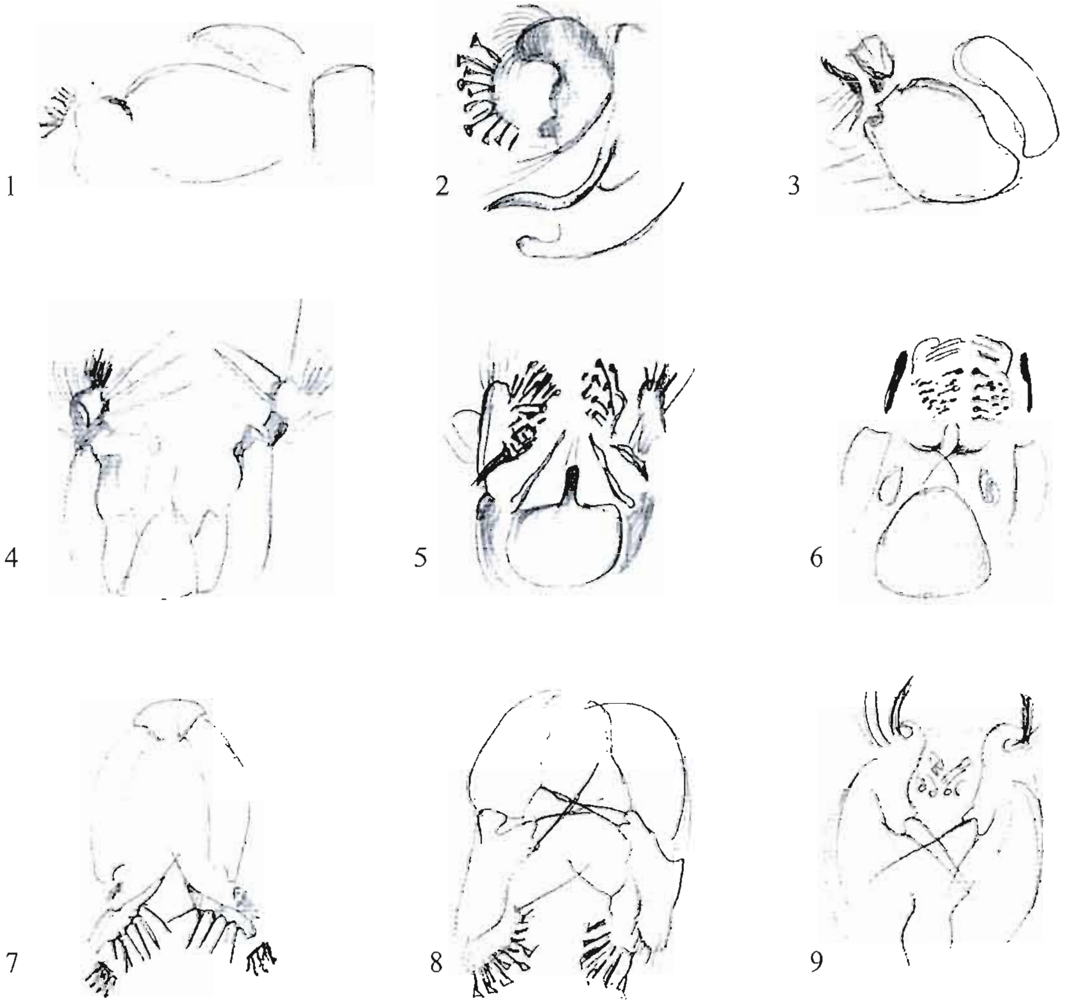
Figs. 1-30. Male genitalia and abdomens: male genitalia, lateral (1), dorsal (6), ventral (11) of *Phronia* sp.1; lateral (2), dorsal (7), ventral (12) of *Phronia* sp.2; lateral (3), dorsal (8), ventral (13) of *Phronia* sp.3; lateral (4), doral (9), abdomen (14) of *Phronia* sp.4; male genitalia, lateral (5), dorsal (10), ventral (15) of *Phronia* sp.6; lateral (16), dorsal (21), ventral (26) of *Phronia* sp.7; lateral (17), dorsal (22), ventral (27) of *Phronia* sp.8; lateral (18), dorsal (23), ventral (28) of *Phronia* sp.9; lateral (19), dorsal (24), ventral (29) of *Phronia* sp.10; lateral (20), dorsal (25), ventral (30) of *Phronia* sp.11.

Family: Mycetophilidae, Genus: *Phronia* continued. Drawings are not to scale.



Figs.1-18. Male genitalia: lateral (1), dorsal (6), ventral (11) of *Phronia* sp.12; lateral (2), dorsal (7), ventral (12) of *Phronia* sp.13; lateral (3), dorsal (8), ventral (13) of *Phronia* sp.14; lateral (4), dorsal (9), ventral (14) of *Phronia* sp.15; lateral (5), dorsal (10), ventral (15) of *Phronia* sp.16; lateral (16), dorsal (17), ventral (18) of *Phronia* sp.17.

Family: Mycetophilidae, Genus: *Sciophila*. Drawings are not to scale.



Figs. 1-9. Male genitalia: lateral (1), dorsal (4), dorsoventral (7) of *Sciophila* sp.1; lateral (2), dorsal (5), dorsoventral (8) of *Sciophila* sp.2; lateral (3), dorsal (6), dorsoventral (9) of *Sciophila* sp.3.

Family: Mycetophilidae, Genus: *Tetragoneura*. Drawings are not to scale.

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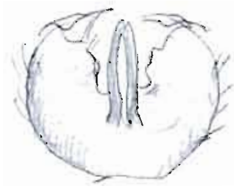

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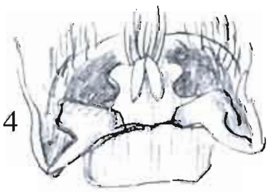

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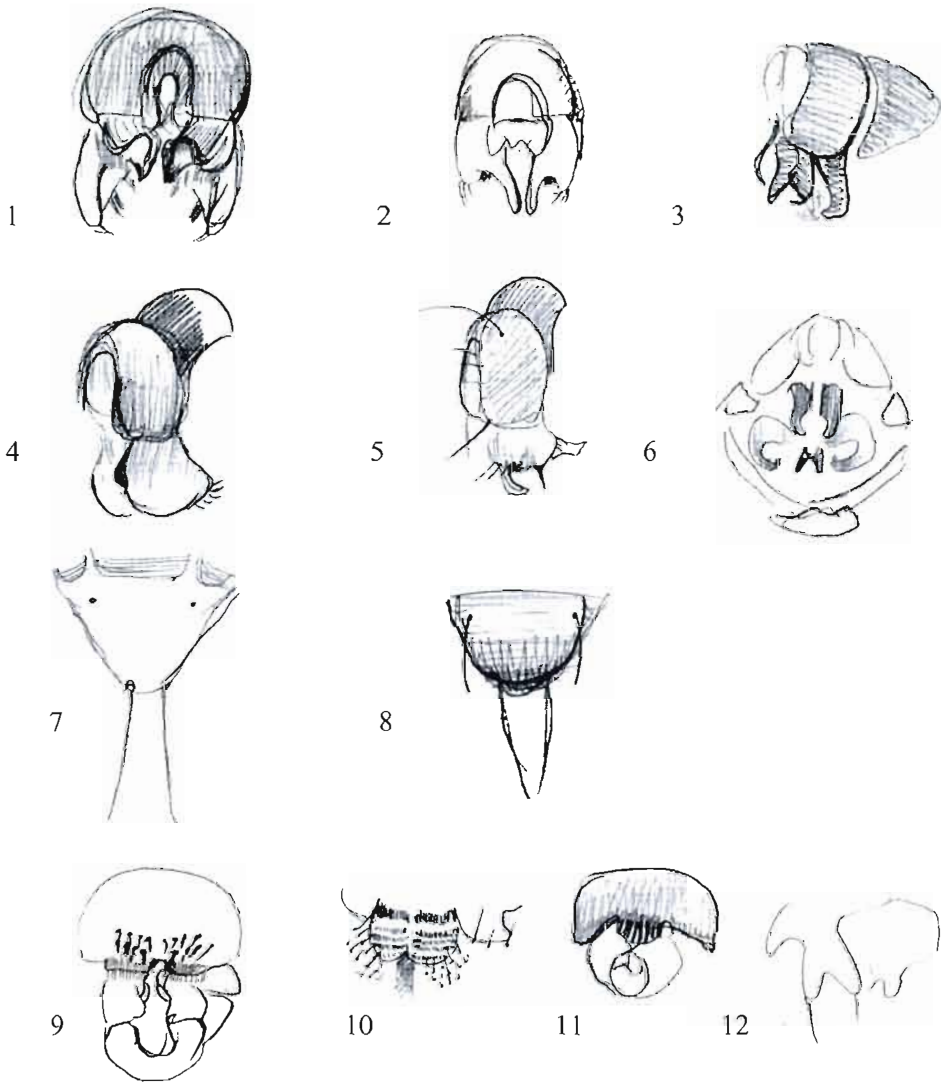
Figs. 1-15. Male genitalia: lateral (1), dorsal (3), ventral (8) of *Tetragoneura* sp.1; lateral (2),ventral (4), dorsoventral (9) of *Tetragoneura* sp.2; ventral (5), dorsal (10) of *Tetragoneura* sp.3; dorsal (6), ventral (11) of *Tetragoneura* sp. 4; lateral (7), dorsal (12) of *Tetragoneura* sp. 5; dorsoventral (13) of *Tetragoneura* sp. 6; dorsal (14), ventral (15) of *Tetragoneura* sp. 7.

Family: Sphaeroceridae, Genus: *Leptocera*. Drawings are not to scale.



Figs. 1-12. Male genitalia, scutella and sternites: male genitalia, posteroventral of (1) *Leptocera* sp. 1, (2) Leptocera sp.6; last sternite, lateral of (3) *Leptocera* sp.3; male genitalia, lateral (4) of *Leptocera* sp.1, (5) *Leptocera* sp.6; male genitalia, posteroventral of (6) *Leptocera* sp. 3; scutellum of (7) *Leptocera* sp.1, (8) *Leptocera* sp. 6, (9) *Leptocera* sp.6, (10) *Leptocera* sp. 4, (11) *Leptocera* sp. 5, (12) *Leptocera* sp. 7.

Family:Tipulidae, Genera: Mixed. Drawings are not to scale.

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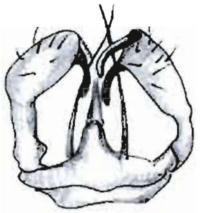

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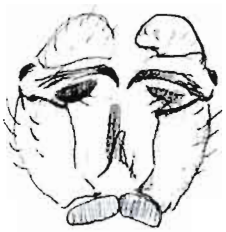

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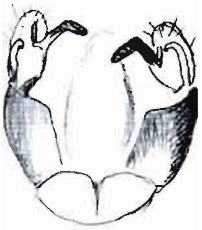

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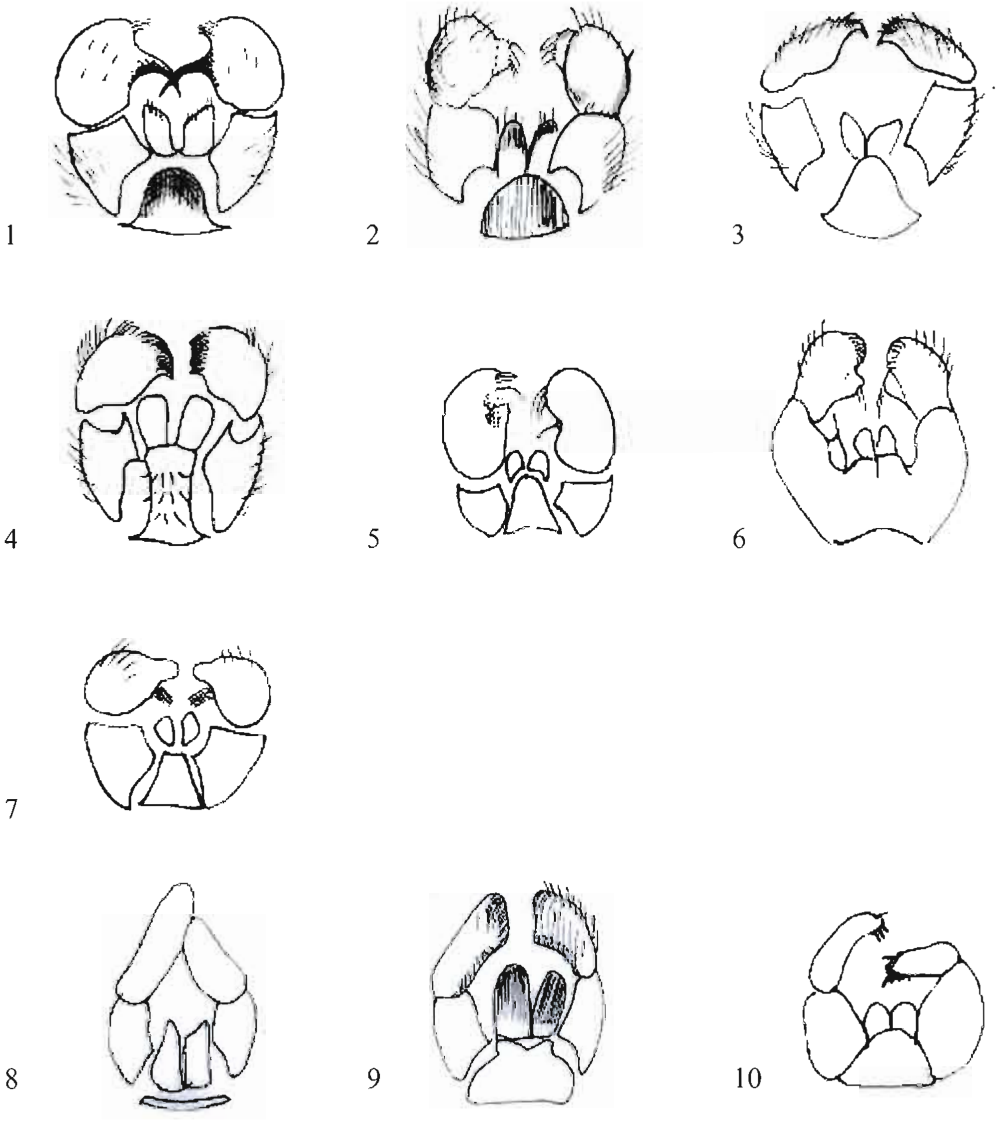
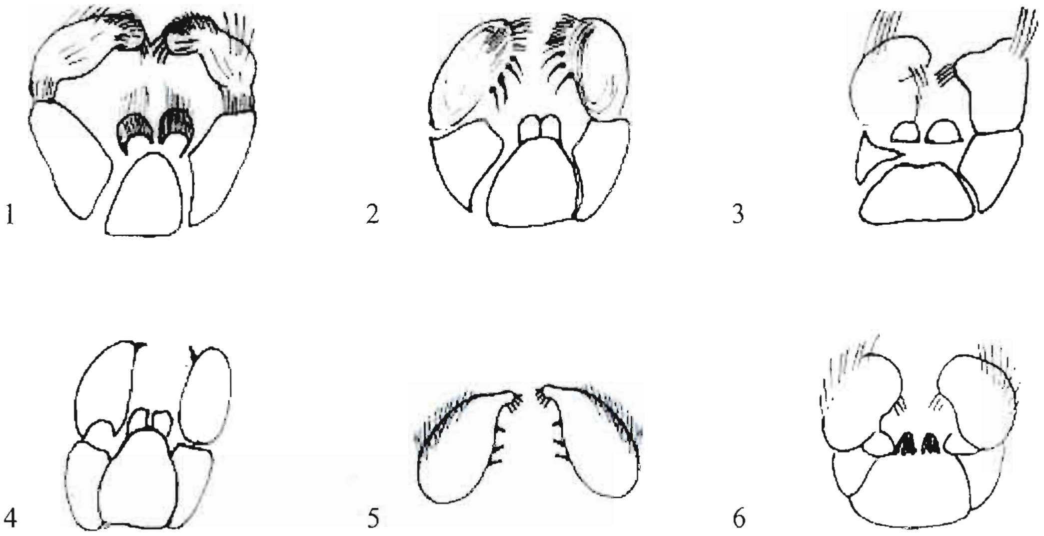
Figs. 1-7. Male genitalia and thorax: male genitalia, dorsal of (1) *Epiphragma* sp.1; male genitalia, dorsal (2) and ventral of (3) *Epiphragma* sp. 2; male genitalia, dorsal of (4) *Limonia sp.2*; male genitalia, posteroventral (5) and thorax (6) of *Limonia* sp. 4; male genitalia, posterodorsal of (7) *Ula* sp.1.

Family:Sciaridae, Genera: Mixed. Drawings are not to scale.



Figs. 1-10. Male genitalia (dorsal view): (1) *Corynoptera* sp.1; (2) *Corynoptera* sp. 2; (3) *Corynoptera* sp.3; (4) Corynoptera sp.4; (5) Corynoptera sp. 5; (6) Corynoptera sp. 6; (7) Corynoptera sp. 8; (8) Zygoneura sp. 1; (9) Zygoneura sp. 2; (10) Zygoneura sp. 3.

Family:Sciaridae, Genus: *Sciara*. Drawings are not to scale.



Figs. 1-6. Male genitalia (dorsal view): (1) *Sciara* sp.1; (2) *Sciara* sp. 2; (3) *Sciara* sp.3; (4) Sciara sp.4; hypandrial arms only (5) of Sciara sp. 5; (6) Sciara sp. 6.

Family : Drosophilidae, Genus : *Drosophila*. Drawings are not to scale.

Figs. 1-5. Abdomens and genitalia: male genitalia, posteroventral of (1) *Drosophila* sp.1, (2) *Drosophila* sp. 2, (3) *Drosophila* sp.3, (4) *Drosophila* sp.4, (5) *Drosophila* sp. 5.