THE TACHINID TIMES Issue 33

Can a tachinid save Portugal's eucalypts?

NEW STUDIES ON THE Voriini, Tachinini and Dexiinae

Exploring the Ozark Plateau

FEBRUARY 2020

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OFFICE ADDRESS

Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada Tel: 613-759-1795

E-MAIL ADDRESSES

james.ohara@canada.ca shannon.henderson@canada.ca

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This newsletter is distributed near the end of February each year. It is published simultaneously in hardcopy and online, both based on the same PDF generated from an InDesign file. Hardcopies are distributed to several libraries and to a few readers who request them.

INSTRUCTIONS TO AUTHORS

This newsletter accepts submissions on all aspects of tachinid biology and systematics. It is intentionally maintained as a non-peer-reviewed publication so as not to relinquish its status as a venue for those who wish to share information about tachinids in an informal medium. All submissions are subjected to careful editing and some are (informally) reviewed if the content is thought to need another opinion. Some submissions are rejected because they are poorly prepared, not well illustrated, or excruciatingly boring.

Authors should try to write their submissions in a style that will be of interest to the general reader, in addition to being technically accurate. This is a newsletter, not *Science* or *Nature*. Try to illustrate submissions with high quality images sent to the editor as separate files at the same time as the text. Text files sent with embedded images will not be considered for publication. All content should be original; if copyrighted material (online or in print) is used then permission from the copyright holder is needed. Submitted pictures of tachinids in the field will be considered for the cover, table of contents, or a special section in the newsletter.

Student submissions are particularly welcome. Writing about a thesis study or a side project involving tachinids is a good way to inform others about a study that is underway before it has generated formal publications.

Please send submissions for the 2021 issue of *The Tachinid Times* to the editor by the end of January 2021.

FRONT COVER A female *Gymnosoma* sp. visits a flower in Fergus, southern Ontario, Canada. Photo: S.A. Marshall, 19 October 2014

TABLE OF CONTENTS A female Winthemia sp.rests on a leaf in Point Pelee National Park,southern Ontario, Canada.Photo: S.A. Marshall, 25 July 2014

BELOW Three wild burros in Horseshoe Canyon, Canyonlands National Park, southern Utah, USA. Photo: J.E. O'Hara, 26 September 2017





by Catarina I. Gonçalves¹, Carlos Valente¹, Catarina Afonso², Cátia Martins¹, Ana Raquel Reis³, André Garcia², and Manuela Branco²

 ¹ RAIZ, Instituto de Investigação da Floresta e Papel, Eixo, Aveiro, Portugal. E-mails: catarina.goncalves@thenavigatorcompany.com, carlos.valente@thenavigatorcompany.com, catia.martins@thenavigatorcompany.com
 ² Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal. E-mails: afonso.catarina@gmail.com, andregarcia@isa.ulisboa.pt, mrbranco@isa.ulisboa.pt
 ³ Altri Florestal, Olho Marinho, Peniche, Portugal. E-mail: ana.reis@altri.pt

Introduction

Eucalypts (*Eucalyptus* L'Hér., Myrtaceae) are among the most commonly introduced tree species in plantations worldwide (Wingfield *et al.* 2008). In Portugal, eucalypts were introduced in the mid 19th Century, but rapid expansion did not take place until the 1950s. Currently, the Tasmanian blue gum, *Eucalyptus globulus* Labill., is the most extensively planted forest species in the country, and it is the main source of raw material for the pulp and paper industry (Alves *et al.* 2007).

The Australian eucalypt snout beetles, *Gonipterus* spp. (Coleoptera: Curculionidae) are among the major pests of eucalypts wherever they have been introduced. *Gonipterus platensis* Marelli (Fig. 1) is the most widespread species found outside Australia, including New Zealand, eastern and western South America, southwestern North America, and southwestern Europe (Mapondera *et al.* 2012).

One of the curiosities regarding the management of snout beetles is that a single parasitoid species, *Anaphes nitens* (Girault) (Hymenoptera: Mymaridae) (Fig. 2), has been responsible for keeping these pests mostly under control in the majority of their current distribution. First released in South Africa almost a century ago, the success of this tiny egg parasitoid was so spectacular that a monument was erected to it in 1995 in that country (Londt 1996).



Figure 2. Anaphes nitens female parasitizing Gonipterus platensis egg capsule.

In southwestern Europe, *G. platensis* was detected in 1991 in Spain, from where it quickly dispersed to Portugal and became the main pest of eucalypts. Biological control with *A. nitens* quickly ensued and, like elsewhere in the world, satisfactory control was obtained in most of the country (Pérez Otero *et al.* 2003, Valente *et al.* 2004). However, in cooler regions of Portugal and Spain, *G. platensis* attacks remain high. In these regions, parasitism rates by *A. nitens* are low during peak oviposition periods of *G. platensis*, resulting in severe defoliation (Fig. 3) of eucalypt trees (Reis *et al.* 2012, Valente *et al.* 2018b).

For decades, the eucalypt snout beetle was considered to be a single species, *Gonipterus scutellatus* Gyllenhal, but it is in fact a complex of cryptic species (Mapondera *et al.* 2012). This realization led us to wonder if there was partial mismatch between the Tasmanian native *G. platensis* and *A. nitens*, which is native to southern mainland Australia. In addition, *E. globulus*, which is highly susceptible to *G. platensis*, is also originally from Tasmania. We then hypothesized that Tasmanian native parasitoids might be a better fit to control *G. platensis* or add to the control already exerted by *A. nitens*.



Figure 3. Severe defoliation by Gonipterus platensis in Eucalyptus globulus plantation, in Barcelos, Portugal.

Early surveys (2008-2012) - Egg parasitoids

The journey for alternative natural enemies of *G. platensis* in Portugal began in 2008, when one of us, Carlos Valente, travelled to Australia to collect and identify prospective species. He was aided by several people along the way, most notably Australian researchers David de Little, Jane Elek, Mamoru Matsuki, and Rolf Oberprieler. In Tasmania, Carlos surveyed 30 locations, collecting egg capsules and larvae of *Gonipterus* spp. From 800 egg capsules, 235 parasitoids emerged, of which 94% were *Anaphes tasmaniae* Huber & Prinsloo and 4% were *A. inexpectatus* Huber & Prinsloo (unpublished

data). This was a very exciting finding, as *A. tasmaniae* showed great promise, but we did not yet know if it was well adapted to *G. platensis*. It is important to note that, at this point, clarification on the identity of the species composing the *G. scutellatus* complex was not yet fully available.

In addition to the egg parasitoids, several *Gonipterus* larvae were found to be parasitized by tachinid flies. At the time, however, and given that very little was known about this group of insects, further research on the tachinids was placed on hold.

The following year, we obtained authorization to import parasitized egg capsules and larvae of Gonipterus spp. and to study the emerging parasitoids under confinement, in Portugal. Between 2009 and 2012, more than 5100 egg capsules and 1250 larvae were collected in thirteen locations in Tasmania (Fig. 4) and imported into quarantine. Unsurprisingly, the majority of emerging egg parasitoids were A. tasmaniae, followed by A. inexpectatus. Three other parasitoids were recovered from egg capsules: Centrodora damoni (Girault) (Hymenoptera: Aphelinidae), Cirrospilus sp. (Hymenoptera: Eulophidae), and Euderus sp. (Hymenoptera: Eulophidae), but were rare. In 2012, we were surprised to find a few specimens of A. nitens in Tasmania, which seems to be a recent invasion. In addition, at least three parasitoid species were recovered from the larvae, namely Entedon magnificus (Girault & Dodd) (Hymenoptera: Eulophidae),



Figure 4. Collection sites for egg capsules and larvae of *Gonipterus* species in Tasmania in 2012.

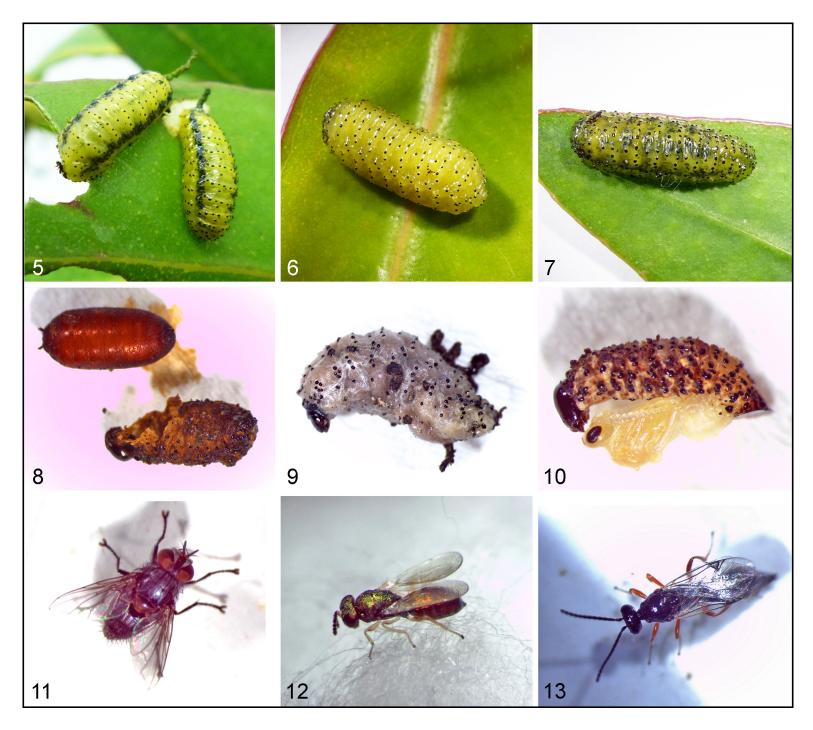
Anagonia cf. lasiophthalma (Malloch) (Diptera: Tachinidae), and Oxyserphus sp. (Hymenoptera: Proctotrupidae) (Valente et al., 2017b).

While *A. tasmaniae* was initially the most promising candidate for a biological control program against the snout beetle, it was *A. inexpectatus* that most readily accepted *G. platensis* eggs and became established under laboratory conditions. After several unsuccessful attempts to rear *A. tasmaniae*, we therefore focused on *A. inexpectatus*. Following a set of studies on its biology and risk assessment (Valente *et al.*, 2017a, b), *A. inexpectatus* has now been widely released in Portugal. Seven years after the initial releases, this parasitoid seems to have established, but field monitoring indicates it is still rare (unpublished data). Competition studies (Valente *et al.* 2018a) suggest that *A. inexpectatus* and *A. nitens* should be able to coexist, but whether the former species will eventually help to reduce pest levels in a significant way is still uncertain.

Recent surveys (2016-2017) - Larval parasitoids

A fter the biological control programs with *A. nitens* and *A. inexpectatus*, our focus shifted to larval parasitoids, as this life stage of the snout beetle is currently free of natural enemies outside its native range. Our results, which have been partly published in Valente *et al.* (2017b) and Garcia *et al.* (2019), can be summarized here as follows. In 2016 and 2017,

over 3500 *Gonipterus* spp. larvae were imported from Tasmania. At least four *Gonipterus* species were present in the imported material: *G. notographus* Boisduval, *G. platensis*, *G. pulverulentus* Lea, and *Gonipterus* sp. n. 1 (*sensu* Mapondera *et al.* 2012, Garcia *et al.* 2019) (Figs. 5–7). The same three larval parasitoids that were identified in 2012 emerged from this material; i.e., *E. magnificus*, *A.* cf. *lasiophthalma* and *Oxyserphus* sp. (Figs. 8–13). Larval parasitism rates were 12.0% in 2016 and 14.5% in 2017 (Fig. 14). It is worth noting that more species may have emerged, as these three parasitoid groups may in fact be cryptic species complexes.



Figures 5–13. 5. Larva of Gonipterus platensis. 6. Larva of Gonipterus pulverulentus. 7. Larva of Gonipterus sp. n. 1. 8–13. Parasitoid species that emerged from the Gonipterus larvae imported from Tasmania. 8. Puparium of Anagonia cf. lasiophthalma and host remains.
9. Larva of Gonipterus sp. parasitized by Entedon magnificus. 10. Larva of Gonipterus sp. parasitized by Oxyserphus sp. 11. Anagonia cf. lasiophthalma. 12. Entedon magnificus. 13. Oxyserphus sp.

The next step was establishing laboratory populations of the larval parasitoids. Although *E. magnificus* females accepted *G. platensis* larvae, residual numbers of female progeny emerged. In 2016, the parental generation started with more than 750 adults (40% females) that successfully parasitized 91 *G. platensis* hosts and originated 427 progeny. However, only 3% were female, and the population went extinct in the second laboratory generation. To this day, we have not been able to understand what conditions were missing to trigger female production. A similar situation occurred with *Oxyserphus* sp. A total of 39 individuals (60% females) were offered *G. platensis* larvae. Thirty-three larvae were parasitized, from which 13 male and no female *Oxyserphus* sp. emerged. After an initially failed attempt to rear the tachinid *A.* cf. *lasiophthalma*, in 2017 this species reproduced successfully and has been continuously reared for six generations.

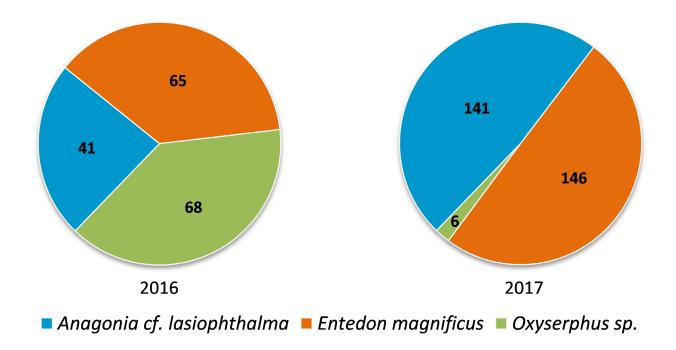


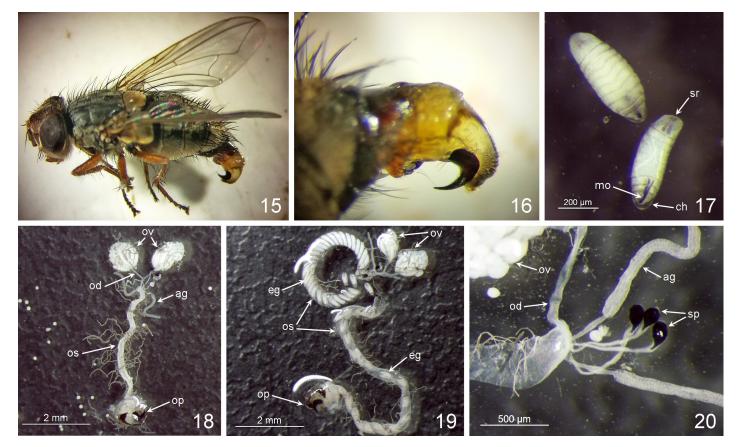
Figure 14. Number of imported larvae parasitized by each parasitoid species, in 2016 and 2017.

Besides the lack of appropriate stimuli under laboratory conditions, as was likely the case in our *E. magnificus* rearing attempt, parasitoid-host mismatch may also explain why some parasitoids were successfully reared on *G. platensis* while others were not. It was more often than not difficult to assign a larval type to the emerging parasitoid. As larvae develop, their exterior characteristics change. For instance, the characteristic lateral stripes of *G. platensis* only become visible on third instar larvae. However, as larvae begin to show evidence of being parasitized, their distinguishing features fade, often before positive identification of the host larva is made. Molecular studies were used to provide insight into the association between *Gonipterus* spp. and their egg parasitoids (Garcia *et al.* 2019), but such methods have not yet been successfully used for larval parasitoids. Because our aim has been to retrieve as many parasitoids as possible, DNA analyses of the hosts were attempted only on larval remains, after parasitoids had emerged. It is possible that fresh tissue from parasitized larvae, prior to parasitoid emergence, would have to be used. However, our records indicate that most *A.* cf. *lasiophthalma* emerged from the *G. platensis* morphotype (as illustrated in Fig. 5), suggesting that this species may very well be a preferred host in the wild.

Anagonia cf. lasiophthalma as a biological control agent

In our efforts to initiate a biological control program with A. cf. *lasiophthalma*, we started by devising a rearing protocol in the laboratory. The initial steps were empirical, as we did not know the reproductive strategy of this poorly studied genus, which led us to study its basic biology. In addition to the pragmatic need to maintain A. cf. *lasiophthalma* populations under confinement, understanding the life history of this potential biological control agent is paramount for a sound risk/ benefit analysis. It is widely accepted that the ideal natural enemy to be used in classical biological control (*sensu* Eilenberg *et al.* 2001¹) should be host specific, well adapted to the climatic conditions of the target habitat and to the pests' life cycle, and have good host searching ability and mobility, among other traits.

While biological studies are still underway and unpublished, we have clarified some characteristics. The first major trait of the species is that the females insert their eggs into the host larvae, a mechanism that is common to some members of the Blondeliini (Stireman *et al.* 2006). The female terminalia are equipped with a conspicuous, sharp-pointed, curved piercer (Figs. 15, 16), which it uses to penetrate the host. We have determined that females will mostly mate within 48 hours after emergence and require an additional week (at 20°C) before they start parasitizing hosts. Dissections revealed that the species is ovolarviparous; i.e., after mating, the eggs are incubated in the uterus, with the distal portions of the ovisac containing fully embryonated eggs (Figs. 17–20). What we have gathered so far was valuable to developing a rearing protocol for *A*. cf. *lasiophthalma*, and populations have thrived (Figs. 21, 22–30).



Figures 15-20. 15. Female *Anagonia* cf. *lasiophthalma*. **16**. Terminalia of female *A*. cf. *lasiophthalma* with conspicuous, sharppointed, thorn-like piercer. **17**. Embryonated eggs. **18**. Reproductive system of unmated female. **19**. Reproductive system of mated female, 12 days after copulation. **20**. Detail of the reproductive trait of mated female, 6 days after copulation (eggs removed from ovisac). Abbreviations: ag, accessory gland; ch, chorion; mo, mouthparts; od, oviduct; op, ovipositor; os, ovisac; ov, ovary; sp, spermatheca; sr, spiracle.

¹"The intentional introduction of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control".

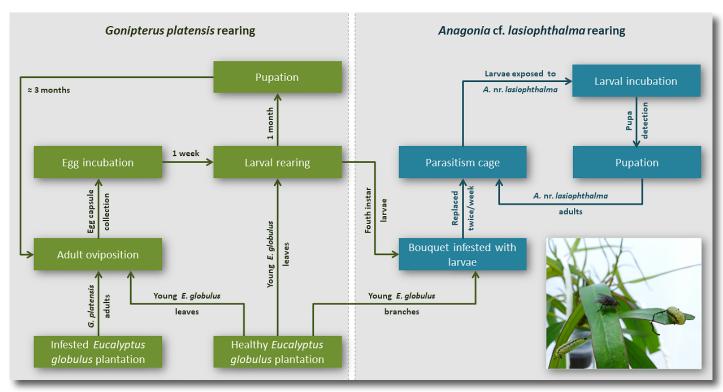


Figure 21. Rearing scheme of Anagonia cf. lasiophthalma and its host Gonipterus platensis.

There is still much information to be gathered on *A*. cf. *lasiophthalma* and its possible use as a biological control agent against *G. platensis*. Because many tachinid species have a wide range of hosts, the major deal-breaker will likely be potential non-target effects, particularly host specificity. The suitability of non-target organisms for the development of *A*. cf. *lasiophthalma* offspring will need to be tested. Furthermore, we will need to ascertain if females may kill unsuitable non-target species when attempting to parasitize them. In fact, we have observed that the largest fourth (and final) instar larvae of *G. platensis* are more likely to produce viable offspring, while smaller third or fourth instar larvae will often die before the *Anagonia* larva is mature.

At this point, it is impossible to predict how host-specific *A*. cf. *lasiophthalma* may be. If testing under confinement reveals that it is not strictly monophagous, risk analysis may take into account mitigating factors. For instance, we suspect that *A*. cf. *lasiophthalma* females respond to stimuli from the environment to find and parasitize their hosts. While it is not yet clear which cues may be relevant, such as chemical stimuli from the host plants or the hosts themselves, or visual cues, this may impact the probability of *A*. cf. *lasiophthalma* dispersing outside of the target environment (i.e., eucalypt plantations) and physically encountering putative non-target organisms.

The aim of a classical biological control program is for natural enemies to establish and sustain permanent populations, but whether *A*. cf. *lasiophthalma* populations will (or will not) adapt to the target environment is unknown at this point. Notably, *G. platensis* populations typically have one or two population peaks each year, in spring and fall, alternating with periods of low populations that can last several months. How *A*. cf. *lasiophthalma* will survive such fluctuations is unclear, but there are several possibilities. Specifically, some laboratory-reared insects have been found to live for over three months at 20°C, as long as they are honey-fed. In the wild, food sources may be provided by both eucalypt flowers and understory vegetation. It is also possible that *A*. cf. *lasiophthalma* may have developed ways to synchronize its life cycle with that of its host through such mechanisms as diapause or aestivation.



Figures 22–30. 22. Arrival of *Eucalyptus globulus* branches to the laboratory. **23**. *Gonipterus platensis* adults and egg capsules in rearing cages. **24**. Larvae maintenance. **25**. *Anagonia* sp. maintenance. **26**. Eucalypt bouquet with *G. platensis* larvae. **27**. *Anagonia* cf. *lasiophthalma* female parasitizing *G. platensis* larva. **28**. Unparasitized *G. platensis* larvae. **29**. Parasitized *G. platensis* larvae. **30**. *Anagonia* cf. *lasiophthalma* puparium. Pictured are RAIZ employees Rui Gomes (Fig. 22), Sofia Simões (Fig. 24) and Cátia Martins (Fig. 25).

The identity of Anagonia cf. lasiophthalma (Malloch)

A swe unraveled the life history characteristics of *A*. cf. *lasiophthalma* that suggest it may indeed be a good biological control agent against the snout beetle, we began working towards giving it a name. In fact, until a few weeks ago, we were referring to this tachinid as *Anagonia* sp. We are indebted to Bryan Cantrell for providing a genus identification in an earlier stage, and to he and Jim O'Hara for narrowing the possibilities to *A. lasiophthalma*, *A. dayi* Colless, or perhaps an unidentified species. The late Donald H. Colless' review of the *Froggattimyia-Anagonia* genus group (Colless 2012) is the best available identification guide to members of this group, but a more reliable identification would involve direct comparisons between specimens of our species and specimens identified by Donald Colless (J. O'Hara, pers. comm.). We are

currently pursuing this with the help of the Australian National Insect Collection (ANIC) team in Canberra (Australia). To date, a morphological comparison by James Lumbers, a Ph.D. student at ANIC studying Tachinidae, has revealed a close similarity between our specimens and *A. lasiophthalm*a. However, our specimens are not an exact match and therefore could be either the same or a different species. James suggested we use the name *A.* cf. *lasiophthalma* for now and should use molecular data to resolve this species problem. ANIC has recently provided us with reliably identified specimens of *A. lasiophthalma* that we can use for DNA extraction and comparison with our specimens. This molecular work is currently being performed at the Research Center in Biodiversity and Genetic Resources (CIBIO) in Porto (Portugal) by Vanessa Mata.

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Study of a possibly new Ecuadorian *Trichopoda* Berthold species (Diptera: Tachinidae)

by Roberto Andreocci

Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Piazzale A. Moro 5, 00185, Rome, Italy. E-mail: roberto.andreocci@libero.it

I became interested in flies while pursuing an undergrad degree in Natural Sciences at Sapienza University in Rome. One of my courses was taught by dipterist Pierfilippo Cerretti, who is well known for his systematic research on Tachinidae and related families. Under his encouragement and supervision I undertook an undergrad thesis on the Rhinophoridae that I completed in the summer of 2018.

During my undergrad studies I heard about Diego Inclàn, a former Master's student with John Stireman at Wright State University in the United States and former Ph.D. student with Pierfilippo at Padova University in northern Italy. Diego studied tachinid flies for both degrees and returned to his native country of Ecuador with a background in both systematic and ecological research. He is now the Director of the Instituto Nacional de Biodiversidad (INABIO, http://www.biodiversidad.gob.ec/) and a professor at the Universidad Central del Ecuador in Quito. In addition to his other duties, Diego oversees a growing collection of Ecuadorian tachinids originating from some of the most biologically diverse areas of Ecuador, from the lowland rainforests of the Chocó region to the high elevation grasslands of the Andean páramo.

I contacted Diego about opportunities for graduate research on Tachinidae and he told me about a potential project involving an unstudied host-parasitoid association in Ecuador. He had stumbled upon some *iNaturalist* observations near Quito of a leaf-footed bug, *Leptoglossus zonatus* (Dallas) (Hemiptera: Coreidae), with tachinid eggs on an antenna (Fig. 1). This raised questions about the identity of the parasitoid. The study of this host and its tachinid parasitoid became the subject of my Master's thesis under the joint supervision of Pierfilippo and Diego.

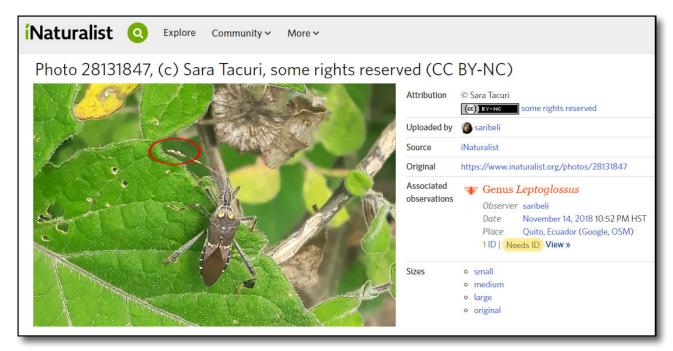


Figure 1. One of the *iNaturalist* observations of tachinid eggs (circled in red) on the antenna of a *Leptoglossus zonatus* bug near Quito, Ecudaor, that led to this project (https://www.inaturalist.org/photos/28131847).

My thesis project includes an internship of three months in Ecuador, from December 2019 to February 2020, under Diego's guidance in an INABIO laboratory. My first task was to collect live *L. zonatus* in the field and rear them in the lab for the possible emergence of tachinid parasitoids. A population of *L. zonatus* was found feeding on *Solanum betaceum* Cav. ("tomate de arbol", a popular juicy fruit in Ecuador) near the Agronomy Faculty of the Universidad Central del Ecuador. Both nymphs and adults were collected including many individuals with tachinid eggs glued to their antennae (Fig. 2). An adult tachinid belonging to the genus *Trichopoda* Berthold was also collected at the same time. This genus was later confirmed by our rearings to be the tachinid parasitizing *L. zonatus* (Fig. 3).

Trichopoda is an easily recognized genus even by non-dipterists due to its striking yellow and black patterns on the thorax, wing and abdomen, and the row of feathery black setae on its hind tibia. The best-known species, *Trichopoda pennipes* (Fabricius), is native to the New World and has been introduced to other parts of the world for biological control of bug pests, especially the southern green stink bug (*Nezara viridula* (L.)). Other species of *Trichopoda* are often mistaken for the more widely known *T. pennipes*, in part because this species is variable in size and coloration and has been difficult to characterize by morphology and host use.

In a Master's thesis on the Neotropical species of *Trichopoda* and *Ectophasiopsis* Townsend, Dios (2014) recognized 37 species of *Trichopoda*, including over a dozen new species. The known hosts of Neotropical *Trichopoda* species belong to the heteropteran families Alydidae, Coreidae, Pentatomidae and Scutelleridae (Guimarães 1977, Santos & Panizzi 1997). *Trichopoda* was not recorded from *Leptoglossus zonatus* until Souza & Amaral Filho (1999) reported on the parasitism of adults by *T. pennipes* in Brazil. This is the only record of *Trichopoda* parasitizing *L. zonatus*, although Tarango Rivera & González (2009) reported on *T. nr. pennipes* parasitizing a related species, *Leptoglossus clypealis* Heidemann, in Mexico.

We are looking closely at Rodrigo Dios' thesis on

Figure 2. Eggs of *Trichopoda* sp. attached to an antenna of a *L. zonatus* bug collected near the Agronomy Faculty of the Universidad Central del Ecuador in Quito.

Neotropical *Trichopoda* to determine if our specimens reared from *L. zonatus* represent a new species. We suspect that it might be new given its host, its peculiar behavior of ovipositing on its host's antennae, its morphological features, and its geographical location in Ecuador at 2500m. However, as pointed out by Dios in his study, *Trichopoda* taxonomy is difficult because the striking body and wing coloration, which is a fundamental characteristic for species identification, may be misleading due to intraspecific variation. This makes species boundaries less clear than in other genera.

When I return to Rome, my thesis will focus on the morphological description of the larval instars, puparium and adult of this Ecuadorian *Trichopoda* species and on the analysis of its parasitism rates in *L. zonatus*. I will also compare my results with previously published information on other *Trichopoda* species. At the end, I will submit my results to a journal for publication. This project will hopefully contribute to the knowledge of Andean tachinids, a peculiar fauna not yet as studied as it deserves to be.

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Figure 3. A Trichopoda specimen reared from a L. zonatus bug during this study.

Acknowledgements

I thank *iNaturalist* and the many users whose observations led to this project. The observation reproduced here (Fig. 1) is in compliance with the Creative Commons guidelines given at https://creativecommons.org/licenses/by-nc/4.0/. The information in Fig. 1 has been modified to fit the space available but no content has been altered. Pierfilippo Cerretti (Sapienza Università di Roma, Italy) and Diego Inclàn (Instituto Nacional de Biodiversidad, Quito) are thanked for making this project possible and for their guidance and support. Jim O'Hara (Agriculture and Agri-Food Canada, Ottawa) kindly assisted with the revision of the text. I also thank Alex Pazmiño for his help and support during my work at INABIO.

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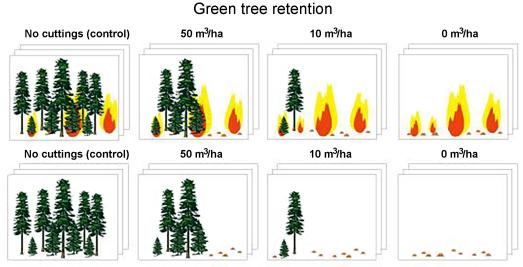
FUNCTIONAL DIVERSITY OF TACHINID PARASITOIDS IN MANAGED BOREAL FORESTS

by Antonio Rodríguez

Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), SE-90183 Umeå, Sweden. E-mail: incamyia@gmail.com

INTENSIVE FOREST MANAGEMENT is characterized by clear-cut harvesting, artificial regeneration, short rotation cycles, and fire suppression. This management poses a threat to forest multi-functionality and biodiversity, leading to forest simplification and reducing the provision of ecosystem services other than the steady supply of wood for fuel, pulp and timber (Bengtsson *et al.* 2000, Puettmann *et al.* 2009). Although negative effects of intensive forestry are widely acknowledged for saproxylic species diversity (species dependent on dead or decaying wood, Niemelä 1997), much less is known about its effects on other groups. There is especially a dearth of information about the effect of intensive forest management on insect parasitoid diversity and function, despite their staggering diversity (Heraty 2009), and their key role on the maintenance of forest biological control (Peralta *et al.* 2014).

In this contribution, I outline the main findings from Rodríguez *et al.* (2019), in which we assessed the effect of diversifying forest management practices on tachinid diversity and functional composition (the organization of groups of species according to traits related to ecosystem functioning and response to disturbances). We take advantage of a large-scale and replicated ecological experiment established in 2000 in Eastern Finland, where forest structure was manipulated with several harvesting regimes and prescribed fire according to a factorial design (Fig. 1).



Experimental design

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Figure 1. Experimental design. No cuttings (control) refers to old-growth forests, 50 m³/ha of tree retention, 10 m³/ha of tree retention, and 0 m³/ha refers to clear-cut. Flames in the upper row refer to prescribed burning. Number of replicates in each treatment combination was three. Reproduced here with permission from J. Kouki.

We sampled 750 individuals of 59 tachinid species parasitizing herbivorous insects with pan-traps (Appendix 1) and documented the understory vegetation functional diversity (trait diversity) as a measure of vegetation complexity for each study site, 13 years after the onset of the experiment. Tachinid species were identified by Jaakko Pohjoismäki (University of Eastern Finland). We compiled tachinid traits related to dispersal ability (body size), resource use (host taxonomic order, degree of specialization, host micro-habitat, host concealed or exposed habit), phenology and life-history (oviposition strategy, oviposition location, gregariousness) for the calculation of tachinid functional diversity and mean trait value in relation to forest habitats defined by forest management.

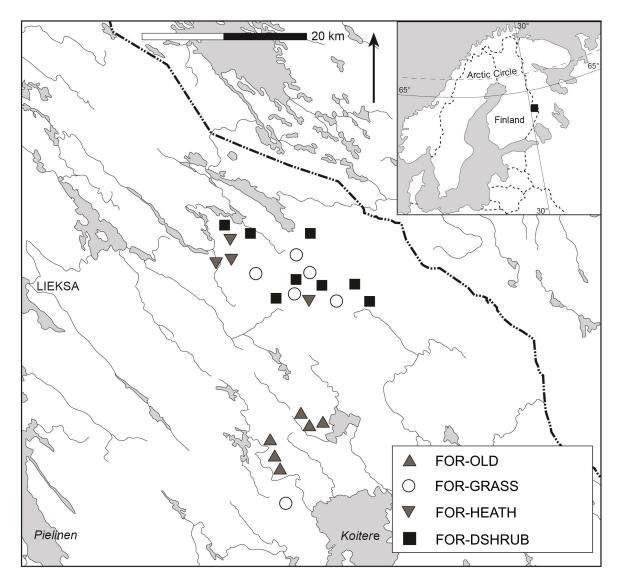
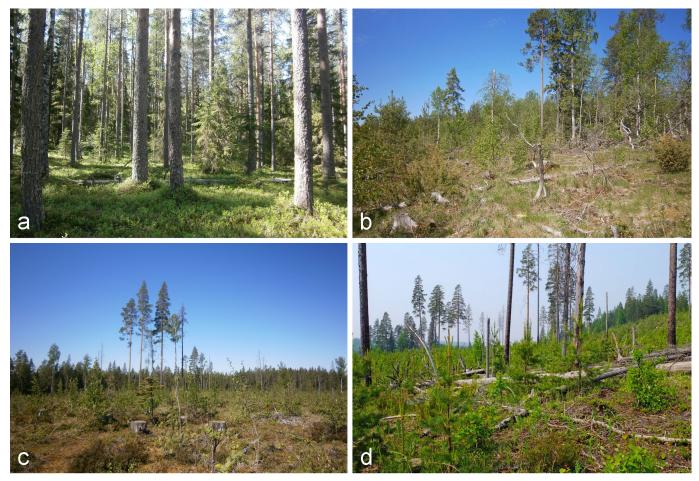
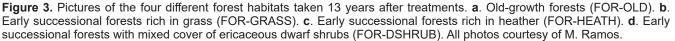


Figure 2. Map of the experimental area. The location of study sites is indicated by grey-filled triangles (oldgrowth forests), white-filled circles (early successional forests rich in grass), inverted grey-filled triangles (early successional forests rich in heather), and black-filled squares (early successional forests with mixed cover of ericaceous dwarf shrubs).

The combination of different levels of tree retention (retention of individual trees or forest patches at the time of clear-cut harvesting) and prescribed burning gave rise to four distinct vegetation communities (Figs. 2, 3): old-growth forests (FOR-OLD, Fig. 3a), early successional forests rich in grass (FOR-GRASS, Fig. 3b), early successional forests rich in heather (FOR-HEATH, Fig. 3c), and early successional forests with mixed cover of ericaceous

dwarf shrubs (FOR-DSHRUB, Fig. 3d). At the local scale, FOR-DSHRUB habitats contained higher tachinid diversity than most habitats, in connection with their higher level of understory vegetation complexity.





FOR-DSHRUB habitats correspond to burnt harvested forest stands with high levels of tree retention, which show high levels of heterogeneity caused by variability in fire intensity and augmented structural heterogeneity from retention trees. Enhanced vegetation complexity has profound implications for parasitoid behavior and development, providing diversity of physical and chemical oviposition cues (Kaiser et al. 2017), structural refuges for herbivores against parasitoids (Lill *et al.* 2002), refuge for parasitoids against predators (Murphy *et al.* 2014), and higher niche diversity and insect host availability.

At the landscape scale, diversity of forest management, involving prescribed fire, variable tree retention and the preservation of old-growth forest, increased habitat diversity, diversifying parasitoid trait composition (Figs. 4, 5). FOR-HEATH habitats contained on average the largest tachinid species (Fig. 4a), including *Tachina grossa* (Fig. 5a), attacking large caterpillars on heather and deciduous trees. Open areas from early successional boreal forests (FOR-GRASS, FOR-HEATH & FOR-DSHRUB) have higher vegetation functional diversity than old-growth forests, enabling higher herbivore host diversity for tachinid parasitoids. These early successional habitats contain more

specialized tachinids (Fig. 4b), like *Staurochaeta albocingulata* (Fig. 5c), and tachinids attacking a great diversity of host herbivores on herbs, grasses, shrubs and tree saplings (Figs. 4c, 4d, 5b, 5d, 5e).

Boreal old-growth (FOR-OLD), Scots pine dominated forests (Fig. 3a) provide a stable environment for generalist caterpillars feeding on bilberry (*Vaccinium myrtillus*), which is exploited by generalist tachinids attacking caterpillars on woody vegetation, like *Oswaldia muscaria* (Fig. 5f). These tachinid species may spill over to neighboring habitats (Inclán *et al.*, 2015), providing potential biological control services to forest plantations.

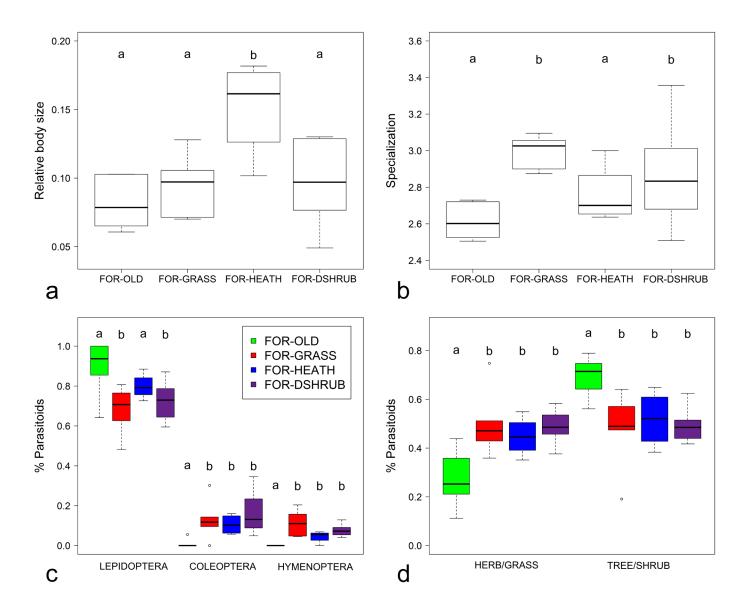


Figure 4. Relationship between mean trait values and habitats defined by forest management: **a**. Relative body size in reference to the largest species, which was scored as 1.0. **b**. Specialization (coded as 1, host species in several orders; 2, host species within one order; 3, host species within one family; 4, host species within one genus; and 5, species specific). **c**. Percentage of parasitoids attacking different host orders. **d**. Percentage of parasitoids known to attack herbivores associated with a particular plant type (herb/grass or tree/shrub). Significant differences indicated by letters relative to old-growth forest as the baseline habitat for comparison with other habitats. Habitat labels as in Fig. 2.

In conclusion, the conservation of old-growth forests, together with the diversification of harvesting practices within the forest plantation matrix, generate forest heterogeneity at the landscape scale. Within forest stands, the application of practices based on natural disturbance (fire and increased tree retention), increases heterogeneity at the local scale. Both strategies increase functional heterogeneity at several spatial scales (Odion & Sarr 2007), leading to the conservation of Tachinidae functional diversity and the maintenance of biological control in managed boreal forests.

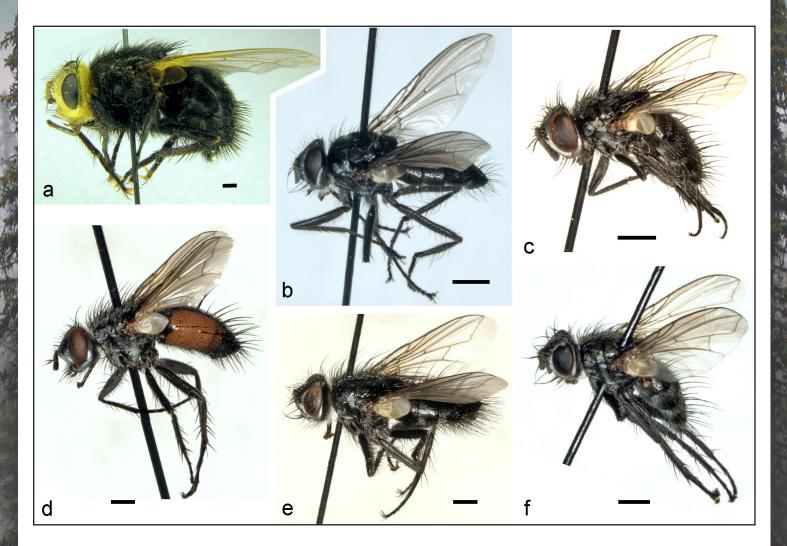


Figure 5. Examples of Tachinidae species from this study illustrating morphological, taxonomic, resource use and life-history trait diversity of tachinid parasitoids. **a**. *Tachina grossa* (Tachininae, Tachinini), the largest European tachinid (15–18 mm), ovolarviparous parasitoid of Lasiocampidae caterpillars. **b**. *Medina luctuosa* (Exoristinae, Blondeliini), the most abundant tachinid parasitoid on Coleoptera (oviparous on Chrysomelidae larvae) in our study sites. **c**. *Staurochaeta albocingulata* (Exoristinae, Blondeliini), oviparous parasitoid species-specific on *Monoctenus juniperi* (L.) larvae (Hymenoptera, Diprionidae). **d**. *Eriothrix rufomaculata* (Dexiinae, Voriini), the most abundant tachinid parasitoid in early successional forests rich in grass in our study sites; an ovolarviparous parasitoid attacking concealed Crambidae caterpillars in grasses. **e**. *Belida angelicae* (Exoristinae, Blondeliini), one of the most abundant tachinid parasitoids on Hymenoptera (oviparous on Argidae larvae) in our study sites. **f**. *Oswaldia muscaria* (Exoristinae, Blondeliini), the most abundant tachinid parasitoid sites; an oviparous generalist parasitoid attacking Geometridae and Noctuidae caterpillars. For all pictures, scale bar represents 1 mm.

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Appendix 1. Tachinid species abundances in different habitats (sum of observations). Habitat names as in Figure 2.

Species*	FOR-OLD	FOR-GRASS	FOR-HEATH	FOR-DSHRUB
SUBFAMILY DEXIINAE				
Tribe Dexiini				
<i>Trixa conspersa</i> (Harris)	1	0	0	1
Tribe Dufouriini				
<i>Microsoma exiguum</i> (Meigen)	0	1	0	4
Tribe Voriini				
<i>Athrycia impressa</i> (van der Wulp)	0	3	0	6
<i>Athrycia trepida</i> (Meigen)	0	2	7	14
Blepharomyia piliceps (Zetterstedt)	1	0	0	0
Campylocheta inepta (Meigen)	3	1	0	1
Eriothrix rufomaculata (De Geer)	1	57	3	9
<i>Klugia marginata</i> (Meigen)	0	0	0	1
<i>Ramonda prunaria</i> (Rondani)	0	0	0	1
Ramonda ringdahli (Villeneuve)	1	0	0	1
SUBFAMILY EXORISTINAE				
Tribe Blondeliini				
<i>Admontia blanda</i> (Fallén)	0	0	1	0
<i>Belida angelicae</i> (Meigen)	0	9	1	2
Blondelia nigripes (Fallén)	0	0	0	5
<i>Medina collaris</i> (Fallén)	1	6	0	5
<i>Medina luctuosa</i> (Meigen)	0	29	12	28
Oswaldia eggeri (Brauer & Bergenstamm)	0	0	0	1
Oswaldia muscaria (Fallén)	57	10	6	18
<i>Oswaldia spectabilis</i> (Meigen)	0	0	0	1
Staurochaeta albocingulata (Fallén)	0	3	0	2
Trigonospila ludio (Zetterstedt)	3	0	0	0
Tribe Eryciini				
Aplomya confinis (Fallén)	16	22	18	44
Carcelia atricosta Herting	3	0	0	1
Carcelia bombylans Robineau-Desvoidy	1	0	0	0
<i>Hubneria affinis</i> (Fallén)	0	0	0	1
Nilea hortulana (Meigen)	7	7	10	20
Nilea innoxia Robineau-Desvoidy	0	0	0	1
Phebellia strigifrons (Zetterstedt)	0	1	0	0
Senometopia pollinosa Mesnil	0	0	0	1
<i>Tlephusa cincinna</i> (Rondani)	0	8	0	8
Paratryphera barbatula (Rondani)	17	14	4	23
Paratryphera bisetosa (Brauer & Bergenstamm)	9	1	0	1

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Species*	FOR-OLD	FOR-GRASS	FOR-HEATH	FOR-DSHRUB	
Tribe Exoristini					
<i>Exorista fasciata</i> (Fallén)	0	1	1	2	
Exorista rustica (Fallén)	0	3	0	0	
Exorista nr. tubulosa Herting	0	4	2	7	
Parasetigena silvestris (Robineau-Desvoidy)	0	0	0	1	
Tribe Goniini					
Allophorocera ferruginea (Meigen)	3	3	1	9	
<i>Cyzenis jucunda</i> (Meigen)	2	0	0	0	
<i>Gonia picea</i> (Robineau-Desvoidy)	0	1	0	1	
Onychogonia flaviceps (Zetterstedt)	1	2	2	7	
Platymya fimbriata (Meigen)	0	13	1	12	
Tribe Winthemiini					
<i>Smidtia amoena</i> (Meigen)	1	2	2	6	
SUBFAMILY PHASIINAE					
Tribe Catharosiini					
<i>Catharosia pygmaea</i> (Fallén)	0	1	0	0	
Tribe Cylindromyiini					
<i>Cylindromyia interrupta</i> (Meigen)	0	6	0	15	
<i>Cylindromyia pusilla</i> (Meigen)	0	0	1	3	
Phania thoracica Meigen	1	0	0	0	
SUBFAMILY TACHININAE					
Tribe Linnaemyini					
Appendicia truncata (Zetterstedt)	0	1	0	1	
<i>Cleonice callida</i> (Meigen)	0	0	0	3	
Eurithia vivida (Zetterstedt)	0	3	0	2	
<i>Gymnocheta viridis</i> (Fallén)	0	1	0	0	
<i>Linnaemya haemorrhoidalis</i> (Fallén)	1	1	0	0	
<i>Linnaemya rossica</i> Zimin	1	2	4	3	
Panzeria rudis (Fallén)	5	0	2	1	
Tribe Polideini					
<i>Lydina aenea</i> (Meigen)	0	4	0	0	
<i>Lypha dubia</i> (Fallén)	5	2	3	0	
Tribe Siphonini					
Actia nigroscutellata Lundbeck	0	0	0	1	
<i>Ceromya silacea</i> (Meigen)	1	0	0	0	
Tribe Tachinini					
Nowickia marklini (Zetterstedt)	2	2	4	2	
<i>Tachina fera</i> (Linnaeus)	1	3	3	3	
<i>Tachina grossa</i> (Linnaeus)	0	2	3	5	
Totals	145	231	91	283	

* Tachinidae names and classification follow Pohjoismäki & Kahanpää (2014).

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A brief survey of tachinids from the Ozark Plateau of Missouri, USA

Figure 1. Oak-hickory woodland of the Drury-Mincy Conservation Area on a foggy morning,

by John O. Stireman III¹, James E. O'Hara² and Juan M. Perilla López¹

¹Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, Ohio 45435, USA. E-mails: john.stireman@wright.edu, jmperillal@gmail.com ² Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada. E-mail: james.ohara@canada.ca

Introduction

In 2019, the North American Dipterists Society (NADS) field meeting was held from 3–7 June at the Bull Shoals Field Station in the Ozark Mountains of southern Missouri. This informal meeting is held every two years at varying locations in North America and primarily consists of field collecting and socializing with old and new dipterist colleagues, along with an evening of short presentations (e.g., see O'Hara & Stireman 2016, Stireman *et al.* 2018). The 2019 meeting was organized by Greg Courtney (Iowa State University) and David Bowles (Missouri State University), and an overview of the meeting was given in their report in the November 2019 issue of *Fly Times* (Courtney & Bowles 2019). Here, we describe and report results from our brief, but intensive, tachinid collecting efforts during the meeting, where as a group we were able to collect more than 1000 tachinid flies of a wide diversity of species over a six-day period.

The state of Missouri is somewhat centrally located in the "Midwest" region of the United States (Fig. 2). It occupies a transition zone of habitats, where temperate deciduous forest to the east and south transitions to tall grass prairie to the north and west. About two thirds of the state was historically forested and about half that area, mostly in the Ozark Highlands, remains forested (Raeker *et al.* 2011). The Ozark highland region of Southern Missouri is characterized by highly dissected forested hills and plateaus. The "Ozark mountains" are not truly mountains, but rather the remains of

an ancient dome or plateau that has been eroding for many millions of years (McNab & Avers 1994), and even the highest points are less than 1000 m in elevation. Yet, they still represent the most extensive region of highlands in the United States between the Rocky Mountains to the west and the Appalachian Mountains to the east. The southern Ozark region that we visited was dominated by oak/hickory woodland (Fig. 1), with some areas of more open oak savanna, and occasional open grassy glades where bedrock is exposed and soils are thin. Apparently, during the last interglacial xerothermic period of high global temperatures (the Holocene Climate Optimum) about four to eight thousand years ago, many desert-adapted plants and animals invaded the Ozarks from the Southwest. Relict populations of a number of these species have persisted in the open sunny glades that are characteristic of the Ozarks (e.g., collared lizards, Templeton *et al.* 2001). Another notable characteristic of the area that we learned about is that it is a center of tick borne diseases, and the density of ticks was truly impressive. A short 20 m stroll through the underbrush would inevitably lead to 10, 20, or more unwelcome passengers. Luckily we were warned, and prepared ourselves with permethrin-treated clothing, which repelled the little arachnids quite effectively.

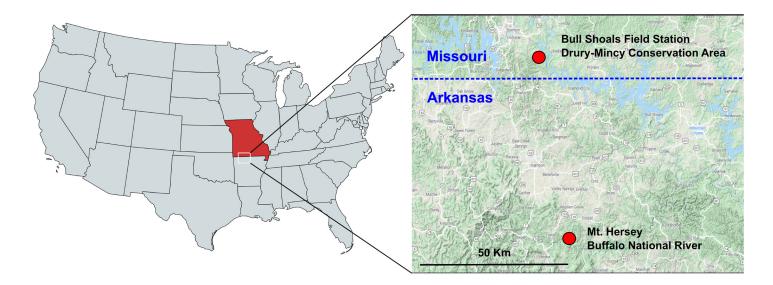


Figure 2. Map showing our collecting locations. On the map of the United States, the state of Missouri is indicated in red and the enlarged area of southern Missouri and northern Arkansas is outlined in white. Most collecting occurred in Missouri at the Bull Shoals Field Station/Drury-Mincy Conservation area, but some hand collecting was done near Mt. Hersey along the Buffalo National River in Arkansas.

Methods

Most of our collecting was focused around the Bull Shoals Field Station (BSFS; Taney County, Missouri) where the meeting was held and where many of us stayed. This field station, operated by the Missouri State University, is a small fiveacre site surrounded by the Drury section of the much larger Drury-Mincy Conservation Area (5600 acres [2266 ha]). This conservation area is managed for hunting, recreation, and conservation and consists of forest/woodland, oak savanna, open glades and managed "wildlife food plots." Collecting permits for this conservation area (and for Buffalo National River, see below) were arranged by David Bowles.



Figures 3–6. 3. O'Hara's 6m Malaise trap, situated at a forest edge in an open wildlife food plot. **4**. Dahlem's 6m Malaise trap, situated in a semi-open area near the Bull Shoals Field Station's "Drury House". **5**. A view of the Buffalo National River in northern Arkansas where we spent a morning collecting tachinids. **6**. The "tachinid team" alongside the Buffalo National River in Arkansas. Left to right: Sarah Workman, Greg Dahlem (honorary member), John Stireman, Juan Manuel Perilla López and Jim O'Hara.

The primary collectors of Tachinidae (Fig. 6) included the authors (JOS, JMPL, JEOH) as well as undergraduate student Sarah Workman (Wright State University) and Greg Dahlem (sarcophagid specialist, Northern Kentucky University). Collecting in this area consisted of hand netting (primarily along gravel roads and trails) and Malaise traps, sometimes with the assistance of a sugaring solution sprayed on leaves. Four 6m Malaise traps were erected near the BSFS: one was located in the open at a forest edge and facing into a wildlife food plot (operated 2–5 June, JEOH; Fig. 3), a second was located about 1.2 km from the first beside a stream and was semi-shaded by trees for a good portion of the day (2–7 June, Cumming), a third was located in a semi-open area surrounded by woods near the field station's "Drury House" (3–5 June, JOS, JMPL & SW), and a final trap was located in the same area as the last (4 June and part of 5 June, Dahlem; we did not acquire all specimens from this trap; Fig. 4). All were operated with dry heads that were taken off nightly to prevent fouling of samples with moth scales except for the Cumming trap, which had alcohol-filled heads that were left on continuously. In addition, we were able to extract tachinids from collections of three 2m Townes-style Malaise traps with "wet" (alcohol) heads operated by D. Bowles from 27 May to 3 June 2019. These were located in a forest glade, woodland, and woodland near a small pond (Buttonbush pond). All traps were within the Drury section of the Drury-Mincy CA and within 3 km of the field station. One late afternoon (4 June) and one morning (5 June) were spent hand collecting in the Bear Mountain area of the Mincy section of the Drury-Mincy CA about 7 km west of the BSFS. Our collecting here was mostly focused on a broad forested bluff that acted, to some degree, as a hilltop. In addition, a 6m Malaise trap (Dahlem's) was operated for a day in an open glade/savanna area in this area on 5 June. For the purposes of comparison, these Malaise trap samples are lumped with the hand collected samples from Bear Mountain.

We also spent half a day (4 June) collecting at a somewhat more distant site (about 65 km south of the BSFS) along the Buffalo National River in northern Arkansas (Hersey Mountain area; Searcy County, AR; Figs. 2, 5, 6). Collecting at this site consisted of hand netting, mostly along edges of a fallow field and in patches of sunlit vegetation adjacent to the Buffalo River. A number of species were collected from flowers and/or by sugar spraying vegetation in this area.

Specimens collected by or given to JEOH are housed in the Canadian National Collection of Insects (CNC) in Ottawa and those collected by or given to JOS are in the J.O. Stireman Collection (JOSC) at Wright State University in Dayton.

Specimen Identification

About half of the specimens were identified by JEOH with reference to specimens in the CNC and using DNA sequence data from COI gene "barcodes," which were generated for 190 specimens. This included specimens from the Malaise trap samples of G. Dahlem and J. Cumming. The remainder were identified by JOS, with assistance from JMPL. These were identified using available keys, comparison with specimens in the JOSC, comparison with images of specimens collected by JEOH, and with reference to the DNA sequencing results of JEOH. This included the wet trap samples collected by D. Bowles. Because specimens were not sorted and identified together (i.e., JEOH and JOS identified species separately), there may be errors in matching up specimens between collectors even with the exchange of images and information. However, the more likely source of error is that we assumed that similar but distinct species were the same rather than inferring that members of the same species were different. Thus, our results are likely conservative with respect to the total richness of species as well as to differences in species collected by different methods and collectors. We were unable to definitively match a number of our species with a named species either due to lack of available specimens of species in our collections or because the specimens do not appear to match any named species in the genus. Some of these appear to be undescribed species (see Appendix 1).

Analysis

A species rarefaction curve and extrapolated species richness were estimated using iNEXT (Chao *et al.* 2016). The R programming environment (R core team 2018) was used to examine and visualize species abundance distributions and overlap among collecting methods, traps, and sites (particularly the package *VennDiagram* (Chen 2018)).

Results and Discussion

Together we collected, sorted, and identified 1091 tachinid specimens belonging to an estimated 161 species over a six day period (Appendix 1). Most of the species were represented by only one or a few individuals with a handful of abundant species (Fig. 7a), including *Cylindromyia binotata* (N=77), *Siphona illinoiensis* (N=65), *Myiopharus* sp. nr. *infernalis* (N=59), and *Copecrypta ruficauda* (N=50). The lack of an obvious asymptote of the individual-based rarefaction curve indicates that many more species likely occur in this area at this time of the year (Fig. 7b). Indeed, when extrapolated to twice the observed sample size of 1091 individuals, over 200 species of tachinids would be expected to be collected.

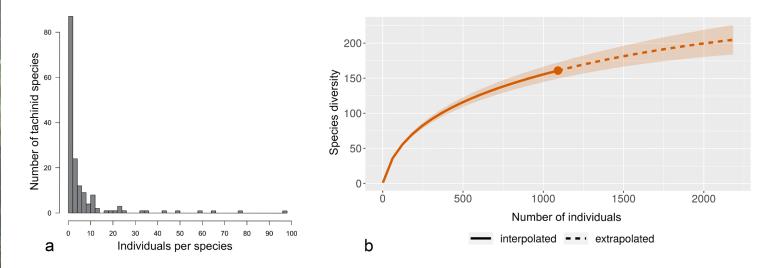


Figure 7. a. The distribution of abundances of all the tachinid species collected illustrating the large number of species represented by only one or two individuals with a few common species. **b**. A rarefaction curve of species accumulation relative to number of individuals with extrapolation to twice the observed sample size.

In terms of species richness, the tachinid fauna was dominated by Exoristinae, with 96 species, followed by Tachininae (32), Dexiinae (19), and Phasiinae (14) (Fig. 8a). However, several genera of Tachininae were quite abundant (e.g., *Archytas, Copecrypta, Siphona, Paradidyma*) as well as the phasiine genus *Cylindromyia*. Representive species from each subfamily are illustrated in Figure 9. Among the Exoristinae, the tribe Blondeliini was best represented, followed by the Goniini and Eryciini (Fig. 8b).

A slight majority of all the specimens were male (57.4%), but sex ratios of collected specimens varied widely among species. Considering only species with N≥10, sex ratios ranged from all or nearly all male (e.g., *Phebellia curriei*, *Aplomya theclarum*, *Masiphya confusa*), approximately even (e.g., *Ginglymia* nr. *acrirostris*, *Archytas* nr. *instabilis*), to >80% female (e.g., multiple species of *Lespesia*, *Paradidyma singularis* complex). Malaise traps might be expected to catch more host-searching females moving through the landscape, but we saw no clear evidence of this. Both hand and trap samples were similarly slightly male biased.

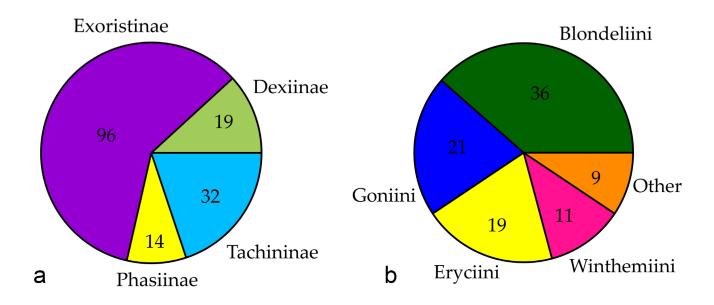


Figure 8. a. Proportions and numbers of species collected belonging to each of the four subfamilies of Tachinidae. b. Proportions and numbers of species collected belonging to various tribes of the subfamily Exoristinae.

Overlap among methods, sites, and traps

Nearly half (519) of all individuals were collected by hand netting, however the four large 6m Malaise traps collected more total species (117 versus 98 by hand; Fig. 10a). The three smaller Malaise traps collected the smallest number of species (28). A comparison of the overlap in species by collecting methods indicates that many species were collected only by hand or only with Malaise traps, with only about half of species (57) being collected by both methods. These results highlight the importance of using multiple collecting methods to obtain a representative sample of the tachinid fauna in an area. In particular, smaller taxa, like *Siphona*, tend to be under-represented by hand collecting. On the other hand, certain species appear to avoid traps in some way. For example, *Euhalidaya genalis* (Fig. 9b), a parasitoid of Phasmida, was only collected by hand (N=12). *Winthemia rufopicta* was also underrepresented in Malaise traps. We collected 98 individuals of this abundant species, however about 86% of them were collected by hand. These apparent biases suggest that we should use caution in inferring community composition and relative abundances of species from trap samples or hand collecting.

We also found a lot of variation in abundance and species composition among Malaise traps. Traps varied in the size of their catch, with JEOH's trap, which was located in a sunny location, catching many more individuals and correspondingly more species than the other two traps we compared (Fig. 10b). Each of the four 6m Malaise traps collected appreciable numbers of species that none of the other traps collected (Fig. 10b; Dahlem's trap is omitted for ease of visualization). Less than 10% of species collected by Malaise traps were found in all of the three traps compared. Part of this variation among traps is likely due to small sample sizes (i.e., catch numbers), such that if traps were run longer and more effective-ly sampled the communities at the trap sites there would be more overlap in species among them. However, some of the variation may be due to the different placement/microhabitat of the traps (e.g., sun versus shade, forest edge versus forest interior). Interestingly, when comparing just flies that were hand collected among individual collectors who were generally collecting in the same sites at the same times, we found similar patterns. For example, collectors JOS, JMPL and S. Workman each hand collected from 16–23 species that none of the other two collected, representing over 40% of the total species collected by each of them. This may reflect "sampling error" (as above), but also different search and collecting strategies, different attention to microhabitats in the same area (e.g., ground verses forest understory), and some differences in exactly where in an area each of us was collecting (e.g., different sides of the same hilltop).

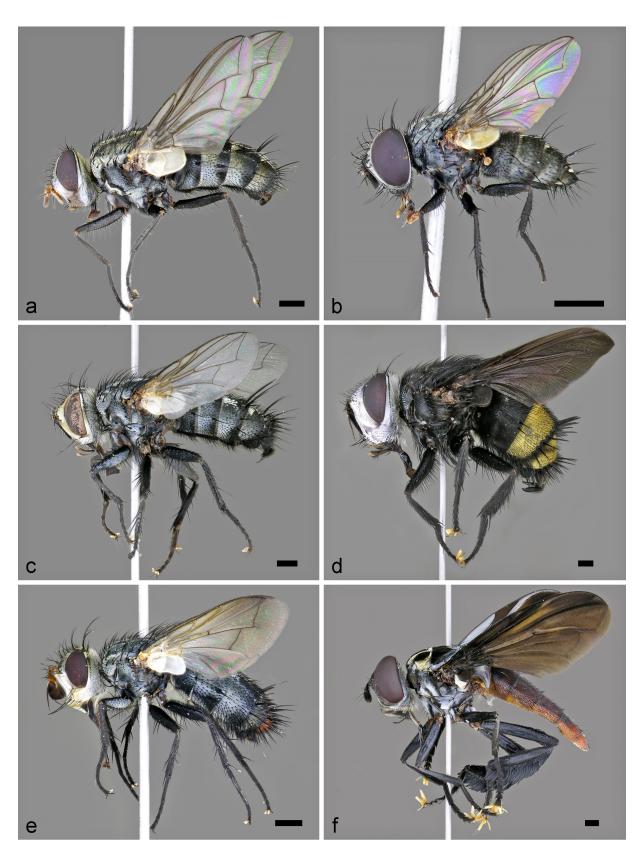


Figure 9. Representative tachinid species collected in the southern Ozark Plateau. **a**. *Billaea sibleyi* (West) (Dexiinae: Dexiini). **b**. *Euhalidaya genalis* (Coquillett) (Exoristinae: Blondeliini), a parasitoid of walking sticks. **c**. *Gueriniopsis* sp. MO1 (Exoristinae: Exoristini). **d**. *Belvosia borealis* Aldrich (Exoristinae: Goniini), among the largest tachinids we collected. **e**. *Copecrypta ruficauda* (van der Wulp) (Tachininae: Tachinini), one of the more abundant tachinines in the area. **f**. *Trichopoda lanipes* (Fabricius) (Phasiinae: Gymnosomatini), a colorful species of bug-killing flies that can reach impressive size. Right legs of specimens in **a**, **b** and **d** removed for DNA preservation. Scale bars = 1.0 mm.

Finally, we found that though there was some overlap in species among the three major sites where we collected, many species were only collected at a single site (Fig. 10c). By far the most species (127) were collected around the BSFS. where almost all the trapping and much of the hand collecting was done. Collecting at Bear Mountain and Buffalo River was mostly by hand, which may explain some of the variation in species collected, but local habitat may also play a role. The Buffalo River site was lowland, with collecting focused on herbaceous plants growing near the river and along the edges of an open mowed field nearby. Flowers at this site attracted relatively large numbers of Phasiinae and other anthophilous taxa. In contrast, most collecting at Bear Mountain was focused on a wooded hilltop/bluff favoring forest species and those that visit hilltops for mating.

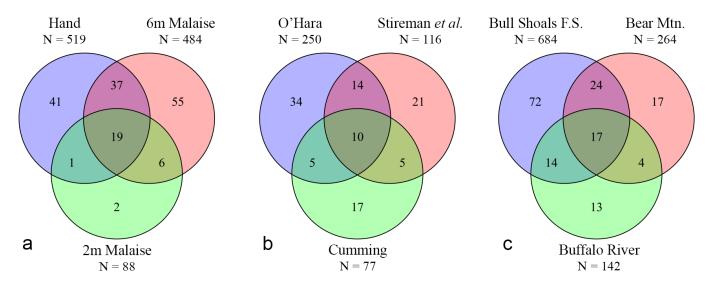


Figure 10. a. Comparison of the overlap in species by collecting method (hand netting, 6m Malaise traps, and 2m Malaise traps). N=total number of individuals collected using each method. **b**. Comparison of the overlap in species from three of the four Malaise traps, all in the vicinity of the Bull Shoals F.S. N=total number of individuals from each trap. Dahlem's Malaise trap, from which only 18 specimens were acquired from the Bull Shoals F.S., is omitted for clarity. **c**. Comparison of the overlap in species from the three major sites where we collected. Values indicate the combined totals from hand collecting and Malaise traps. N=total number of individuals from each site.

Notes on certain taxa

Several of the species we collected were rare or at least rarely collected, and as mentioned previously, a number of them may represent undescribed species (e.g., in *Celatoria, Neoethilla, Ceromya* and possibly other genera). Below, we provide notes on a few of the taxa that we collected.

- *Archytas* nr. *instabilis*. This species was abundant in the area. Its CO1 barcode places it close to, but distinct from, *A. instabilis*, but morphologically, it appears more similar to *A. aterrimus* (Rob.-Des.). It may represent a new species that was hidden within the latter.
- *Anoxynops aldrichi* is a common tachinid in eastern North America, but apparently has not been previously recorded from Missouri.
- *Aplomya theclarum.* This species is certainly a complex of multiple, morphologically similar species based both on genetic sequence data and morphology. At least three morphospecies were present in our collections.

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- *Billaea sibleyi* (Fig. 9a), which we collected resting on tree trunks on the Bear Mountain hilltop, was only recorded from New York and Quebec in O'Hara & Wood (2004) but has since been recognized from Ohio and Ontario (JEOH, unpubl. data).
- *Carcelia* **n. sp.** belongs to subgenus *Euryclea* Robineau-Desvoidy. This subgenus has 14 species in the Old World and was not known from the New World until an undescribed species was discovered in the Gila National Forest in New Mexico (O'Hara 2012). This species has since been found in Arizona and our Missouri specimens belong to it as well, further expanding its known range. The basal setae on the postpronotum are arranged in a triangle in this species and in other members of the subgenus, but form a nearly straight line in other North American *Carcelia* species. Because of the positioning of these setae and the presence of one or more setae on the posteroapical margin of the hind coxa, *Carcelia* n. sp. keys to *Hyphantrophaga* Townsend in Wood (1987).
- *Ceromya* n. sp. One male specimen of this species was caught in Cumming's Malaise trap. There is one female of this species in the CNC, coincidentally caught in G. Dahlem's 6m Malaise trap while it was operating in his backyard on the outskirts of Cincinnati, Ohio in 2015. This species is close to the Holarctic *C. bicolor* (Meigen), and these two species differ from other Nearctic *Ceromya* in having wing veins R_1 and CuA_1 bare. The abdomen of *C. bicolor* is entirely yellow (or yellow with a black median vitta, although this might indicate another undescribed species) whereas the abdomen of *Ceromya* n. sp. has a black band on the posterior third of syntergite 1+2 to segment 5 and a black median vitta.
- *Gueriniopsis* **sp. MO1** (Fig. 9c) is a relatively rarely collected genus and our two specimens appear to differ morphologically from the one described species, *G. setipes*.
- *Hypertrophomma opacum*. This small, widespread, goniine species is infrequently collected. The specimen is a first for JOS.
- *Lespesia* **spp.** We collected an apparent seven species of this genus. Reliable identifications are difficult in this genus despite relatively recent taxonomic attention (e.g., Sabrosky 1980). There are undoubtedly cryptic species complexes and other undescribed species.
- *Myiopharus* spp. We collected eight apparent species of this morphologically diverse genus. These small, beetle-attacking, blondeliines are represented by many species in the New World, and it is apparent that at least several undescribed species exist in America north of Mexico. They can be difficult to identify, due in part to the sexual dimorphism wherein males may look quite different from females. Interestingly, the genus contains species in which females may possess or lack piercing ovipositors.
- *Paradidyma singularis* appears to be a complex of multiple species based on COI barcode data and the specimens included within the complex here probably represent two species. A number of additional undescribed species in the genus are known from North America.
- *Trichopoda lanipes* and *T. pennipes*. These flower-visiting, bug-parasitizing tachinids are conspicuously colored with varying amounts of yellow and black. Larger specimens that are mostly black with yellow along the wing base are generally identified as *T. lanipes* (Fig. 9f) and smaller specimens with a mostly yellow abdomen and entirely black wing are regarded as *T. pennipes*. There is, however, variation in size and color between these extremes and COI barcodes are virtually the same for all morphotypes. More sophisticated molecular analyses are needed to explain why coloration is so varied and barcodes so similar, and whether there is one species or two.
- *Vibrissina* cf. *leibyi*. We collected several specimens of what appear to be *V. leibyi*, but the one sequenced specimen is genetically quite distant from other sequenced *Vibrissina* species. This, along with some previous genetic studies (Burington 2017) suggest the possibility that the genus *Vibrissina* may be paraphyletic.
- *Winthemia* spp. Of the 11 species of Winthemiini we collected, nine belong to the genus *Winthemia*. Despite multiple revisions of North American species (e.g., Reinhard 1931, Guimarães 1972), this genus is one of the most difficult in

which to make practical identifications. Several of the named species appear to represent species complexes (e.g., one or more of our unidentified species likely corresponds to *W. quadripustulata* (Fabricius)) and there appear to be several undescribed species. Even with keys and comparisons with "reliably" identified specimens it can be difficult to assign a name and male genitalia of this genus are notably homogenous with relatively little apparent variation. This problem becomes even more severe as one moves towards the tropics where a multitude of species exist. There are undoubtedly multiple species hidden within named species, and other undescribed species as well, as in *Lespesia*. Both of these genera have likely experienced recent bursts of speciation in the New World with relatively little associated morphological diversification.

Zelia spp. We collected four species of *Zelia*, only one of which we can definitively match to a named species. This is yet another genus that we know includes several undescribed species in North America (e.g., see O'Hara & Stireman 2016).

Acknowledgments

We would like to thank Sarah Workman (Wright State University, Dayton), Greg Dahlem (Northern Kentucky University, Highland Heights), Jeff Cumming (CNC, Ottawa) for sharing their tachinid specimens with us. (Sarah Workman, who is an undergraduate student and has limited collecting experience, was especially impressive, catching a number of specimens and species that was on par with veteran collectors.) At least two specimens were donated by Jon Gelhaus (Academy of Natural Sciences of Drexel University, Philadelphia), and we thank him for those. We would also like to thank and acknowledge Greg Courtney (Iowa State University, Ames) and David Bowles (Missouri State University, Springfield) for planning and organizing the 2019 NADS meeting, and David additionally for setting up the three smaller Malaise traps and allowing us to extract tachinids from the samples.

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Appendix 1. Table of species

Tachinid species and morphospecies collected from the southern Ozark Plateau, 2–7 June 2019. Tentative identifications are indicated by "cf.", species that are similar to named taxa but appear distinct are indicated by "nr.", species that we are unsure of are left as "sp." or "sp. MO#", and species that are clearly undescribed (i.e., new) are indicated by "n. sp." Note however, that each of these categories may include undescribed species. M=males, F=females, Total=total specimens. Site occurrences are given in the right columns: BS-T=Bull Shoals Field Station, Malaise traps, BS-H=Bull Shoals Field Station, hand netted, Bear=Bear Mountain area, Mincy section of the Drury-Mincy Conservation Area, and AR=Mt. Hersey area, Buffalo National River, Arkansas.

Species	м	F	Total	BS-T	BS-H	Bear	AR
SUBFAMILY DEXIINAE							
Tribe Dexiini							
Billaea sibleyi (West)	10	1	11	х		х	
Prosenoides sp. MO1	1	0	1			х	
<i>Ptilodexia</i> nr. <i>conjuncta</i> (van der Wulp)	0	1	1			х	
Zelia metalis (Reinhard)	0	1	1	х			
Zelia sp. MO1	0	2	2	х		х	
Zelia sp. MO2	0	1	1	х			
Zelia sp. MO3	1	0	1		х		
Tribe Epigrimyiini							
<i>Beskia aelops</i> (Walker)	2	0	2	х		х	
Epigrimyia illinoensis Robertson	23	2	25	х			х
Tribe Sophiini							
Cordyligaster septentrionalis Townsend	0	1	1			х	
Tribe Voriini							
<i>Campylocheta</i> sp. MO2	1	0	1	х			
<i>Campylocheta plathypenae</i> (Sabrosky)	0	4	4	х		х	
<i>Campylocheta semiothisae</i> (Brooks)	2	0	2	х			
Chaetonopsis spinosa (Coquillett)	2	0	2	х			
Chaetoplagia atripennis Coquillett	3	1	4	х			
<i>Periscepsia</i> sp. MO1	2	1	3	х			
<i>Spathidexia</i> sp. MO1	0	1	1	х			
Thelaira americana Brooks	2	1	3	х	х		
Voria ruralis (Fallén) complex	0	2	2		х	х	
SUBFAMILY EXORISTINAE							
Tribe Acemyini							
<i>Ceracia dentata</i> (Coquillett)	1	0	1	x			
Tribe Blondeliini							
Admontia sp. MO1	1	0	1	х			
Anisia nr. gilvipes (Coquillett)	7	4	11	х			
Anisia optata (Reinhard)	4	7	11	х	х		
Anisia serotina (Reinhard)	6	5	11	х		х	х

N

Species	М	F	Total	BS-T	BS-H	Bear	AR
Anisia nr. optata (Reinhard)	3	0	3	х			
Anoxynops aldrichi (Curran)	1	0	1		х		
Blondelia hyphantriae (Tothill)	1	0	1			х	
<i>Blondelia</i> sp. nr. <i>polita</i> (Townsend)	1	7	8	х	х		
Blondelia sp. MO2	0	2	2	х			
Celatoria diabroticae (Shimer)	10	1	11	х			х
<i>Celatoria</i> n. sp.	0	1	1	х			
Chaetonodexodes vanderwulpi (Townsend)	0	2	2	х			
Cryptomeigenia demylus (Walker)	0	1	1				х
Cryptomeigenia dubia Curran	0	1	1		х		
Eucelatoria dimmocki (Aldrich) grp.	0	7	7	х		х	х
Euhalidaya genalis (Coquillett)	5	7	12		х	х	
Lixophaga cf. diatraeae (Townsend)	1	0	1		х		
Lixophaga fasciata Curran	0	1	1			х	
Lixophaga mediocris Aldrich	0	4	4	х			
<i>Lixophaga</i> sp. MO3	0	1	1	х			
Lixophaga variabilis (Coquillett)	2	2	4	х	х		
<i>Medina barbata</i> (Coq.)/ <i>quinteri</i> (Tnsd.)	1	6	7	х	х	Х	
<i>Medina</i> sp. MO2	1	0	1	х			
Myiopharus ancilla (Walker)	1	1	2	х			х
Myiopharus cf. dorsalis (Coquillett)	0	3	3	х			
Myiopharus doryphorae (Riley)	1	2	3	х	х		
<i>Myiopharus</i> sp. MO3	0	1	1			х	
Myiopharus nr. aberrans (Tnsd.)/sedulus (Rnh.)	0	2	1	х			х
Myiopharus nr. americanus (Bigot)	0	1	1	х			
<i>Myiopharus</i> sp. MO5	0	1	1	х			
Myiopharus nr. infernalis (Townsend)	26	33	59	х	х	х	
<i>Opsomeigenia</i> (cf.) sp. MO1	0	1	1			х	
Oswaldia conica (Reinhard)	1	7	8	х	х		
Thelairodoria setinervis (Coquillett)	0	1	1	х			
Vibrissina cf. leibyi (Townsend)	0	3	3	х			
Vibrissina nr. aurifrons (Curran)	0	1	1				х
Tribe Eryciini							
Aplomya theclarum (Scudder) complex	32	2	34	х	х	х	
Aplomya theclarum (Scudder) complex sp. 2	4	1	5	х		х	
Aplomya theclarum (Scudder) complex sp. 3	0	1	1	х			
Carcelia cf. yalensis Sellers	1	0	1		х		
Carcelia formosa (Aldrich & Webber)	2	1	3	х			
Carcelia inflatipalpis (Aldrich & Webber)	1	2	3	х		х	
<i>Carcelia</i> n. sp.	1	2	3	х			
Drino bakeri (Coquillett)	1	2	3	х		х	х
Drino sp. MO2 (cf. incompta (van der Wulp))	3	0	3			х	
Drino sp. MO4	0	1	1	х			
Eunemorilla alearis (Reinhard)	2	0	2	х			

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Species	м	F	Total	BS-T	BS-H	Bear	AR
Lespesia aletiae (Riley) sp. MO1	2	11	13	х	х	х	х
<i>Lespesia aletiae</i> (Riley) sp. MO2	2	10	12	x		х	х
Lespesia anisotae (Webber)/datanarum (Tnsd.)	2	2	4		х	х	
<i>Lespesia</i> cf. <i>pholi</i> (Webber)	0	1	1	x			
<i>Lespesia</i> cf. <i>sabroskyi</i> Beneway	0	1	1			х	
<i>Lespesia</i> nr. <i>aletiae</i> (Riley) sp. MO3	1	0	1	x			
Lespesia schizurae (Townsend)	1	1	2			х	
Phebellia curriei (Coquillett)	19	0	19	х			
Siphosturmia melampyga (Coquillett)	0	3	3		х	х	
Tribe Ethillini							
<i>Neoethilla</i> n. sp.	0	1	1	x			
Tribe Euthelairini							
Neomintho celeris (Townsend)	7	2	9	x		х	
Tribe Exoristini							
Chetogena sp. MO2	2	3	5			х	х
<i>Chetogena scutellaris</i> (van der Wulp)	3	2	5	x	х		х
Exorista cf. dydas (Walker)	0	1	1			х	
<i>Gueriniopsis</i> sp. MO1	1	1	2				х
Tachinomyia variata Curran	1	1	2	x			
Tribe Goniini							
Allophorocera celeris (Coquillett)	0	3	3	x			
Allophorocera sp. MO2	0	1	1	x			
Atacta brasiliensis Schiner	1	1	2	x			
Atacta crassiceps Aldrich	0	1	1			х	
Belvosia bifasciata (Fabricius)	4	2	6	x		х	х
Belvosia borealis Aldrich	7	0	7	x		х	
Belvosia unifasciata (Robineau-Desvoidy)	12	1	13	x	х		х
Blepharipa fimbriata (van der Wulp)	3	1	4	x	х	х	х
Euceromasia spinosa Townsend or sp. nr.	3	2	5	x	х		х
Eumea caesar (Aldrich)	2	8	10	x		х	х
Gonia sp. MO1	1	0	1		х		
Houghia coccidella (Townsend)	0	1	1	x			
Houghia setipennis Coquillett	2	3	5	x	х		х
Hypertrophomma opacum Townsend	1	0	1			х	
Hyphantrophaga cf. euchaetiae (Sellers)	3	1	4	x		х	
<i>Hyphantrophaga</i> sp. MO2	0	3	3				х
<i>Hyphantrophaga</i> sp. nr. <i>virilis</i> (Ald. & Web.)	0	1	1				х
Hyphantrophaga virilis (Ald. & Web.) complex	1	6	7	x		х	х
Leschenaultia reinhardi Toma & Guimarães	0	2	1			х	х
Leschenaultia nr. reinhardi Toma & Guimarães	0	1	1			х	
Spallanzania hesperidum (Williston)	0	1	1		х		
Tribe Masiphyini							
Masiphya confusa Aldrich	21	2	23	х	х	х	

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Tribe Winthemini Image: Vertical Struture	Species	м	F	Total	BS-T	BS-H	Bear	AR
Nemorilla cf. insolens Aldrich & Webber 0 1 1 × Winthernia nr. rulopicta (Bigot) 0 1 1 2 X X Winthernia nr. rulopicta (Bigot) 65 33 98 X X X X Winthernia sinuata Reinhard complex sp. 1 9 0 8 X X X Winthernia sinuata Reinhard complex sp. 2 8 0 8 X X X Winthernia sp. MO3 0 1 1 X X X Winthernia sp. MO4 0 1 1 X X X SUBFAMILY PHASINAE Tibe Cylindromylini Tibe Cylindromylini fumipennis (Bigot) 0 1 1 X <td>Tribe Winthemiini</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>	Tribe Winthemiini							
Nemorilla cf. insolens Aldrich & Webber 0 1 1 × Winthernia nr. rulopicta (Bigot) 0 1 1 2 X X Winthernia nr. rulopicta (Bigot) 65 33 98 X X X X Winthernia sinuata Reinhard complex sp. 1 9 0 8 X X X Winthernia sinuata Reinhard complex sp. 2 8 0 8 X X X Winthernia sp. MO3 0 1 1 X X X Winthernia sp. MO4 0 1 1 X X X SUBFAMILY PHASINAE Tibe Cylindromylini Tibe Cylindromylini fumipennis (Bigot) 0 1 1 X <td>Hemisturmia parva (Bigot)</td> <td>0</td> <td>1</td> <td>1</td> <td>х</td> <td></td> <td></td> <td></td>	Hemisturmia parva (Bigot)	0	1	1	х			
Winthemia nr. rufopicta (Bigot) sp. 2 1 1 1 2 x x x Winthemia sinuata Reinhard complex sp. 2 8 0 9 . x x x Winthemia sinuata Reinhard complex sp. 2 8 0 8 x x x Winthemia sp. MQ3 0 1 1 . x x Winthemia sp. MQ4 0 1 1 . .x x Winthemia sp. MQ5 0 2 2 x .x x SUBFAMILY PHASIINAE . . .x .x .x .x .x Cylindromyla binolata (Bigot) 0 1 1 2 .x .x .x .x Cylindromyla binolata (Bigot) 0 1 1 2 .x .x .x .x Cylindromyla binolata (Bigot) 0 1 1 2 .x .x .x Gymnoclylia inmaculata (Macquart) 2 <td< td=""><td>Nemorilla cf. insolens Aldrich & Webber</td><td>0</td><td>1</td><td>1</td><td></td><td></td><td>х</td><td></td></td<>	Nemorilla cf. insolens Aldrich & Webber	0	1	1			х	
Winthemia rufopicta (Bigot) 65 33 98 x x x x x Winthemia sinuata Reinhard complex sp. 2 8 0 8 x x x Winthemia sinuata Reinhard complex sp. 2 8 0 8 x x x Winthemia sp. MO3 0 1 1 x x Winthemia sp. MO4 0 1 1 x x Winthemia sp. MO5 0 2 2 x x x SUBFAMILY PHASIINAE Tribe Cylindromyini 1 1 x	<i>Winthemia</i> nr. <i>rufopicta</i> (Bigot)	0	1	1			х	
Winthemia sinuata Reinhard complex sp. 1 9 0 9 x x x Winthemia nr. sinuata Reinhard complex sp. 2 8 0 8 x x x Winthemia nr. sinuata Reinhard complex sp. 2 8 0 1 1 x x Winthemia sp. MO3 0 1 1 x x x Winthemia sp. MO4 0 1 1 x x x SUBFAMILY PHASIINAE Tribe Cylindromyia binotata (Bjot) 49 28 77 x x x x Cylindromyia binotata (Bjot) 49 28 77 x x x x Cylindromyia propusilla Sabrosky & Amaud 14 10 24 x x x Hemyda aurata (Robineau-Desvoidy) 1 1 2 x x x Gymnoclytia immaculata (Macquart) 2 3 5 x x x Gymnoclytia unicolor (Brooks) 1 1 2	<i>Winthemia</i> nr. <i>rufopicta</i> (Bigot) sp. 2	1	1	2	х		х	
Winthemia sinuata Reinhard complex sp. 2 8 0 8 x x Winthemia sp. MO3 0 1 1 x x Winthemia sp. MO3 0 1 1 x x Winthemia sp. MO3 0 1 1 x x Winthemia sp. MO4 0 1 1 x x Winthemia sp. MO5 0 2 2 x x x SUBFAMILY PHASINAE Tribe Cylindromyia binotata (Bigot) 49 28 77 x x x x Cylindromyia binotata (Bigot) 0 1 1 x x x x Cylindromyia propusilla Sabrosky & Amaud 14 10 24 x x x Hemyda aurata (Robineau-Desvoidy) 1 1 2 x x x Gymnoclytia unicolor (Brooks) 1 0 1 x x x Gymnosoma par Walker 1 1 2	<i>Winthemia rufopicta</i> (Bigot)	65	33	98	х	х	х	х
Winthemia nr. sinuata Reinhard 2 4 6 x x x Winthemia sp. MQ3 0 1 1	<i>Winthemia sinuata</i> Reinhard complex sp. 1	9	0	9			х	х
Winthemia sp. MO3 0 1 1 × × Winthemia sp. MO5 0 2 2 X X SUBFAMILY PHASINAE Tribe Cylindromyiain - - - Cylindromyia binotata (Bigot) 49 28 77 X X X Cylindromyia binotata (Bigot) 0 1 1 x - - Cylindromyia binotata (Bigot) 0 1 1 X X X X X Cylindromyia binotata (Bigot) 0 1 1 X X X X X Cylindromyia binotata (Macquart) 2 3 5 X X X Cylindromyia binotata (Macquart) 1 1 2 X X X Gymnochylia immaculata (Macquart) 1 1 2 X X X Gymnochylia unicolor (Brooks) 1 1 2 X X X Gymnochylia unicolor (Brooks) <td< td=""><td><i>Winthemia sinuata</i> Reinhard complex sp. 2</td><td>8</td><td>0</td><td>8</td><td>х</td><td>х</td><td></td><td></td></td<>	<i>Winthemia sinuata</i> Reinhard complex sp. 2	8	0	8	х	х		
Winthemia sp. MO4 0 1 1 x x Winthemia sp. MO5 0 2 2 x x x SUBFAMILY PHASIINAE	<i>Winthemia</i> nr. <i>sinuata</i> Reinhard	2	4	6	х		х	х
Winthemia sp. MO5 0 2 2 x x SUBFAMILY PHASIINAE Tribe Cylindromyiani -	<i>Winthemia</i> sp. MO3	0	1	1				х
SUBFAMILY PHASIINAE Tribe Cylindromyiai (Cylindromyia binotata (Bigot)) 49 28 77 x x x x x Cylindromyia binotata (Bigot) 0 1 1 x </td <td><i>Winthemia</i> sp. MO4</td> <td>0</td> <td>1</td> <td>1</td> <td></td> <td></td> <td></td> <td>х</td>	<i>Winthemia</i> sp. MO4	0	1	1				х
Tribe Cylindromylini 49 28 77 x x x x x Cylindromyla binotata (Bigot) 0 1 1 x x x x Cylindromyla propusilla Sabrosky & Arnaud 14 10 24 x x x x Hemyda aurata (Robineau-Desvoidy) 1 1 2 x x x x Gymnoclytia immaculata (Macquart) 2 3 5 x x x Gymnoclytia unicolor (Brooks) 1 0 1 x x x Gymnoclytia unicolor (Brooks) 1 0 1 x x x Gymnoclytia unicolor (Brooks) 1 1 2 x x x Gymnosoma par Walker 1 1 2 x x x Trichopoda pennipes (Fabricius) 1 1 2 6 x x x Thibe Phasiini	<i>Winthemia</i> sp. MO5	0	2	2	х		х	
Cylindromyia binotata (Bigot) 49 28 77 x x x x Cylindromyia fumipennis (Bigot) 0 1 1 x <	SUBFAMILY PHASIINAE							
Cylindromyia fumipennis (Bigot) 0 1 1 x Cylindromyia propusilla Sabrosky & Arnaud 14 10 24 x x x x x Hemyda aurata (Robineau-Desvoidy) 1 1 1 2 x<	Tribe Cylindromyiini							
Cylindromyja propusilla Sabrosky & Arnaud 14 10 24 x x x x x Hemyda aurata (Robineau-Desvoidy) 1 1 2 x x x x x Tribe Gynnoclytia immaculata (Macquart) 2 3 5 x x x x Gymnoclytia onciolra (Walker) 14 3 17 x x x Gymnoclytia onciolor (Brooks) 1 0 1 x x x Gymnosoma par Walker 1 1 2 x x x Trichopoda lanipes (Fabricius) 8 3 11 x x x Xanthomelanodes arcuatus (Say) 4 2 6 x x x Tribe Phasiini 7 7 x x x x x Phasia aeneoventris (Williston) 0 3 3 6 x x x SUBFAMILY TACHININAE 7 7 x x x x x Phytomyptera melissopodis (Coquillett)	Cylindromyia binotata (Bigot)	49	28	77	х	х	х	х
Hemyda aurata (Robineau-Desvoidy) 1 1 2 x x Tribe Gymnosomatini	Cylindromyia fumipennis (Bigot)	0	1	1	х			
Tribe Gymnosomatini Image: Constraint of the second se	Cylindromyia propusilla Sabrosky & Arnaud	14	10	24	х	х	х	х
Gymnoolytia immaculata (Macquart) 2 3 5 x x x Gymnoolytia occidua (Walker) 14 3 17 x x Gymnoolytia unicolor (Brooks) 1 0 1 x x Gymnoolytia unicolor (Brooks) 1 0 1 x x Gymnoolytia unicolor (Brooks) 1 1 2 x x Trichopoda lanipes (Fabricius) 8 3 11 x x x Tribe Phasiini 0 3 3 X x x x Phytomyptera melissopodis (Coquillett) 1 8 9 x x x	Hemyda aurata (Robineau-Desvoidy)	1	1	2	х	х		
Gymnoclytia occidua (Walker) 14 3 17 x x Gymnoclytia unicolor (Brooks) 1 0 1 x x Gymnosoma par Walker 1 1 2 x x Trichopoda lanipes (Fabricius) 1 1 2 x x Trichopoda pennipes (Fabricius) 8 3 11 x x Xanthomelanodes arcuatus (Say) 4 2 6 x x x Tribe Phasiini x x x Phasia aeneoventris (Williston) 0 3 3 x x x Tribe Phasiini x x x Phasia aeneoventris (Williston) 0 1 1 x x x Tribe Strongygasterini x x x SUBFAMILY TACHININAE x x x Phytomyptera sp. MO1 1 1 8 9 x x x	Tribe Gymnosomatini							
Gymnoclytia unicolor (Brooks) 1 0 1 x Gymnosoma par Walker 1 1 2 x x Trichopoda lanipes (Fabricius) 1 1 2 x x Trichopoda pennipes (Fabricius) 8 3 11 x x Xanthomelanodes arcuatus (Say) 4 2 6 x x x Tribe Phasiini 7 7 6 x x x x Phasia aeneoventris (Williston) 0 3 3 x x x Phasia purpurascens (Townsend) 0 1 1 x x x Strongygaster triangulifera (Loew) 3 3 6 x x x SUBFAMILY TACHININAE 7 7 7 x x x x Phytomyptera melissopodis (Coquillett) 1 8 9 x x x x Phytomyptera sp. MO3 0 1 1 x x x x Clausicella geniculata (Townsend) 0	<i>Gymnoclytia immaculata</i> (Macquart)	2	3	5	х	х	х	
Gymnosoma par Walker 1 1 2 x x Trichopoda lanipes (Fabricius) 1 1 2 x x Trichopoda pennipes (Fabricius) 8 3 11 x x Xanthomelanodes arcuatus (Say) 4 2 6 x x x Tribe Phasiini	<i>Gymnoclytia occidua</i> (Walker)	14	3	17	х			х
Trichopoda lanipes (Fabricius) 1 1 1 2 x Trichopoda pennipes (Fabricius) 8 3 11 x x Xanthomelanodes arcuatus (Say) 4 2 6 x x x Tribe Phasiini 0 3 3 x x x Phasia aeneoventris (Williston) 0 3 3 x x x Phasia aeneoventris (Williston) 0 1 1 x x x Phasia purpurascens (Townsend) 0 1 1 x x x Strongygaster triangulifera (Loew) 3 3 6 x x x SUBFAMILY TACHININAE	<i>Gymnoclytia unicolor</i> (Brooks)	1	0	1	х			
Trichopoda pennipes (Fabricius)8311xxXanthomelanodes arcuatus (Say)426xxxTribe Phasiini033xxxPhasia aeneoventris (Williston)033xxxPhasia aeneoventris (Williston)011xxPhasia purpurascens (Townsend)011xxTribe Strongygastrini336xxStrongygaster triangulifera (Loew)336xxSUBFAMILY TACHININAE	<i>Gymnosoma par</i> Walker	1	1	2	х	х		
Xanthomelanodes arcuatus (Say)426xxxxTribe Phasiini033xxxPhasia aeneoventris (Williston)033xxxPhasia purpurascens (Townsend)011xxTribe Strongygastrini336xxxStrongygaster triangulifera (Loew)336xxxSUBFAMILY TACHININAE	Trichopoda lanipes (Fabricius)	1	1	2				х
Tribe Phasiini033xxPhasia aeneoventris (Williston)011xPhasia purpurascens (Townsend)011xTribe Strongygastrini0336xxStrongygaster triangulifera (Loew)336xxSUBFAMILY TACHININAE336xxPhytomyptera melissopodis (Coquillett)189xxPhytomyptera sp. MO1112xxPhytomyptera sp. MO3011xxClausicella geniculata (Townsend)011xxClausicella nr. opaca (Coquillett)101xxClausicella setigera (Coquillett)101xxOl usicella turmalis (Reinhard)022xx	Trichopoda pennipes (Fabricius)	8	3	11	х			х
Phasia aeneoventris (Williston)033xxPhasia purpurascens (Townsend)011xxTribe Strongygastrini336xxStrongygaster triangulifera (Loew)336xxSUBFAMILY TACHININAETribe GraphogastriniPhytomyptera melissopodis (Coquillett)189xxxPhytomyptera sp. MO1112-xPhytomyptera sp. MO3011xClausicella geniculata (Townsend)011xClausicella setigera (Coquillett)1011x-Clausicella setigera (Coquillett)022x	Xanthomelanodes arcuatus (Say)	4	2	6	х	Х		Х
Phasia purpurascens (Townsend)011xTribe Strongygastrini Strongygaster triangulifera (Loew)336xxSUBFAMILY TACHININAE Tribe Graphogastrini Phytomyptera melissopodis (Coquillett)189xxxPhytomyptera sp. MO1112xx1Phytomyptera sp. MO30112xxClausicella geniculata (Townsend)011x1Clausicella setigera (Coquillett)011x1Clausicella setigera (Coquillett)022x1	Tribe Phasiini							
Tribe Strongygastrini Strongygaster triangulifera (Loew)336xxSUBFAMILY TACHININAE	Phasia aeneoventris (Williston)	0	3	3	х			х
Strongygaster triangulifera (Loew)3336xxSUBFAMILY TACHININAE <td< td=""><td>Phasia purpurascens (Townsend)</td><td>0</td><td>1</td><td>1</td><td></td><td>х</td><td></td><td></td></td<>	Phasia purpurascens (Townsend)	0	1	1		х		
SUBFAMILY TACHININAETribe GraphogastriniPhytomyptera melissopodis (Coquillett)189xxxPhytomyptera sp. MO1112xxPhytomyptera sp. MO3011xxTribe Leskiini011xxClausicella geniculata (Townsend)011xClausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella setigera (Coquillett)022x	Tribe Strongygastrini							
Tribe GraphogastriniPhytomyptera melissopodis (Coquillett)189xxxPhytomyptera sp. MO1112xxPhytomyptera sp. MO3011xxTribe Leskiini011xxClausicella geniculata (Townsend)011xClausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Strongygaster triangulifera (Loew)	3	3	6	х			х
Phytomyptera melissopodis (Coquillett)189xxxPhytomyptera sp. MO11112xxPhytomyptera sp. MO3011xxxTribe Leskiini011xxxClausicella geniculata (Townsend)011xxClausicella nr. opaca (Coquillett)011xxClausicella setigera (Coquillett)101xxClausicella turmalis (Reinhard)022xx	SUBFAMILY TACHININAE							
Phytomyptera sp. MO1112xPhytomyptera sp. MO3011xTribe Leskiini	Tribe Graphogastrini							
Phytomyptera sp. MO3011xTribe Leskiini011xClausicella geniculata (Townsend)011xClausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Phytomyptera melissopodis (Coquillett)	1	8	9	х	х	х	
Tribe Leskiini011xClausicella geniculata (Townsend)011xClausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Phytomyptera sp. MO1	1	1	2			х	
Clausicella geniculata (Townsend)011xClausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Phytomyptera sp. MO3	0	1	1	х			
Clausicella nr. opaca (Coquillett)011xClausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Tribe Leskiini							
Clausicella setigera (Coquillett)101xClausicella turmalis (Reinhard)022x	Clausicella geniculata (Townsend)	0	1	1	х			
Clausicella turmalis (Reinhard) 0 2 2 x	<i>Clausicella</i> nr. <i>opaca</i> (Coquillett)	0	1	1	х			
		1	0	1	х			
Genea aurea James 0 3 3 x	Clausicella turmalis (Reinhard)	0	2	2	х			
	<i>Genea aurea</i> James	0	3	3	х			

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Species	М	F	Total	BS-T	BS-H	Bear	AR
Genea brevirostris (James) or nr.	0	1	1	х			
Genea pavonacea (Reinhard)	1	5	6	х		х	
Ginglymia nr. acrirostris (Townsend)	12	10	22	х	х	х	х
Tribe Megaprosopini							
<i>Microphthalma disjuncta</i> (Wiedemann)	1	0	1	х			
Tribe Minthoini							
Paradidyma affinis Reinhard	0	2	2	х			
Paradidyma cf. apicalis Reinhard	1	0	1		х		
<i>Paradidyma</i> sp. MO2	0	1	1	х			
Paradidyma petiolata Reinhard	5	3	8	х			
Paradidyma singularis (Townsend) complex	6	29	35	х	х		х
Tribe Polideini							
Chromatocera cf. setigena (Coquillett)	0	1	1	х			
Chrysotachina alcedo (Loew)	1	1	2		х	х	
Euscopolia dakotensis Townsend	0	1	1				х
Tribe Siphonini							
Ceromya americana (Townsend)	5	2	7	х			
<i>Ceromya</i> n. sp.	1	0	1	х			
<i>Siphona</i> (unknown subgenus) sp. MO1	0	1		1	х		
Siphona illinoiensis Townsend	48	17	65	х			х
Tribe Tachinini							
Archytas apicifer (Walker)	16	8	24	х	х	х	х
Archytas metallicus (Robineau-Desvoidy)	1	0	1				х
Archytas nr. instabilis Curran	23	20	43	х	х	х	х
<i>Copecrypta ruficauda</i> (van der Wulp)	38	12	50	х	х	х	х
Deopalpus nr. torosus (Reinhard)	3	0	3	х	х		
<i>Juriniopsis adusta</i> (van der Wulp)	0	1	1				х
<i>Peleteria</i> sp. MO1	6	0	6	х			
Totals	626	465	1091				

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Announcing...

Preliminary Checklist of the Tachinidae (Diptera) of the World. Version 2.

Preliminary checklist of the **TACHINIDAE** (Diptera) of the world

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VERSION 2 2020

James E. O'Hara hannon J. Henderson D. Monty Wood

by James E. O'Hara, Shannon J. Henderson & D. Monty Wood

Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada. E-mails: james.ohara@canada.ca, shannon.henderson@canada.ca

Introduction

Last year marked the introduction of our first *Preliminary Checklist of the Tachinidae (Diptera) of the World* (O'Hara *et al.* 2019a), with a concurrent explanation of its history and development in this newsletter (O'Hara *et al.* 2020). A revised and expanded version of the Checklist has been prepared and will be available online on the same day as this newsletter. Changes in this version compared with the last are discussed below.

Names and distributions

Each year new taxa are described and new distributional records are published and sometimes changes to the higher level classification of the family are proposed. We do our best to collect all the literature on these subjects throughout the year and continuously update our two databases accordingly: 1) a customized FileMaker Pro database of tachinid names, classification and species distributions, and 2) an EndNote database of tachinid literature. The yearly literature is listed at the end of each issue of *The Tachinid Times* and all literature since 1980 is listed online and updated on a yearly basis (O'Hara & Henderson 2020; about 4500 references as of February 2020).

The process of incorporating new taxa and distributions into our database – and outputting data for the *Checklist* – is relatively straightforward because the *Code* (ICZN 1999) governs how such names should be treated. Authors can disagree about whether a new species name is valid or invalid (i.e., a junior synonym) but the name itself is nomenclaturally "available" and cannot be ignored. At the present time the *Checklist* lists only valid names of species, without lists of synonyms.

Unlike new names, there are no rules regarding the classification of species into a hierarchy of genera, tribes and subfamilies. These are subjective categories and authors are governed by their own perceptions of how best to classify tachinids. In the past, authors favouring large genera were termed "lumpers" and those preferring small groups were "splitters" but in modern times there is less of a division into these two extremes. Our purpose with the *Checklist* is not to lead the way in revising the classification of world Tachinidae but to reflect its current status, bearing in mind there is no single agreed-upon or "official" classification of the Tachinidae.

The traditional four subfamilies are recognized in the *Checklist* along with a conservative approach towards tribes and problematic taxa. This arrangement of higher categories is expected to change as a clearer understanding of tachinid evolution emerges. Phylogenetic studies like those of Cerretti *et al.* (2014), Blaschke *et al.* (2018) and Stireman *et al.* (2019) are suggesting that the current classification mirrors the phylogenetic history of the family in many respects but their findings also question the current number and composition of subfamilies and tribes. There is a renewed interest in tachinid phylogenetics and more researchers are getting involved in this field of study. In fact, in this issue of *The Tachinid Times* there are reports by three graduate students about their current studies on relationships within the Voriini (Torres 2020), Dexiinae (de Santis 2020) and Tachinini (Gudin 2020).

Generic names

Version 1 of the *Checklist* listed only valid generic names along with author(s) and year of publication. Version 2 provides lists of all generic synonyms and expands on the basic information given previously to consist of the following: genus name in italics and capital letters (in bold if valid), author, year (with suffix to match a publication listed in accompanying references), page(s), note in parentheses if applicable (e.g., junior homonym or proposed as subgenus), type species with author and date, form of type fixation, and country (or region, such as Europe, if country unknown) of the type locality of the type species in square brackets. Each type species is cited in its original binomen (Recommendation 67B of the *Code*, ICZN 1999), and if that name is a synonym then it is followed by the valid name of the species in parentheses.

Article 70.3.2 of the *Code* was invoked in previous catalogues (e.g., O'Hara & Cerretti 2016) to fix the type species of a generic name as the intended species in instances where the type species was misidentified. We have avoided doing this in the Checklist but have indicated where such actions are needed using the following format:

PACHYMYIA Macquart, 1844 α : 115 [also 1844 β : 272]. Type species: [to be fixed under Article 70.3.2 of the Code (ICZN 1999) as *Pachymyia macquartii* Townsend, 1916, misidentified as *Stomoxys vexans* Wiedemann, 1830 in the fixation by monotypy of Macquart (1844 α)] [Brazil].

Species names

Species information in Version 1 consisted of a valid name, author(s), date, distribution, and original combination (original genus name and original spelling of species name). Version 2 has one addition: a citation for the publication and page number of the original description. Information about synonymy and name-bearing types is not provided because we have not yet entered all of the relevant data into our database.

References

Literature cited in the *Checklist* is now listed in the References. This section also includes most of the literature pertaining to information not yet given in the *Checklist*, such as species synonyms and name-bearing type data. The list of over 3000 references contains a substantial proportion of the systematic literature on Tachinidae.

A problem we faced in synchronizing reference citations between our FileMaker Pro nomenclatural database and EndNote references was to uniquely identify each paper published by an author in a given year. The standard method for doing this is to add a Roman letter suffix to the year of publication. For example, the 18 papers of C.H.T. Townsend we cite for 1915 would normally be given as 1915a to 1915r. However, this is problematic when subsets of references are extracted from our database for various purposes; e.g., the species of a country, the genera of a region, or the taxa belonging to a tribe. This inevitably results in a reference list with gaps in the Roman letter suffixes. It is easy to change a series from "1915b, 1915e, 1915g, 1915i, 1915a, 1915b, 1915c, 1915d, when a reference list is short but is more challenging when hundreds or thousands of references are involved. For this reason and others Roman letter suffixes were the bane to our databasing and cataloguing efforts.

We solved the problems associated with Roman letter suffixes by replacing them with a different character set, namely the Greek alphabet. This was chosen because the characters are easy to recognize, they are cross-platform compatible (FileMaker Pro, EndNote, MS Word, Adobe Acrobat, etc.), and they are not apt to appear in our products except as a suffix to a date. We treat the order of these as "unordered" when associated with a date; *no offense to the classically trained intended*!

As an example of our system for uniquely identifying publications, the 18 Townsend papers mentioned above are cited in Version 2 of the *Checklist* as follows:

Townsend 1915α, 1915β, 1915γ, 1915δ, 1915ε, 1915ζ, 1915η, 1915θ, 1915λ, 1915μ, 1915π, 1915σ, 1915ζ, 1915τ, 1915φ, 1915ψ, 1915ω, 1915Ω.

Switching from unordered Greek suffixes to ordered (i.e., chronological) Roman suffixes is easier and less subject to error when producing various outputs from our database compared to switching from unordered Roman suffixes to ordered ones. There is less chance of error using the former method and the presence of Greek suffixes in a manuscript after the conversion is completed is a clear indication that an error has occurred during the process. Errors are far more difficult to spot when converting from unordered to ordered Roman letter suffixes.

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Messy but worthy! An overview of the systematics of Neotropical Tachinini (Diptera: Tachinidae)

by Filipe Macedo Gudin

Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Laboratório de Sistemática e Biogeografia de Insecta, Rua do Matão, Travessa 14, nº 101, São Paulo, SP, CEP 005508-090, Brazil. E-mail: filipe.gudin@gmail.com

Since I began my studies with tachinids as an undergrad student in 2010 at the Universidade de São Paulo, my attention was instantly drawn to the large, bristly and colorful specimens of the tribe Tachinini. Under the supervision of Dr. Silvio Nihei in the Departamento de Zoologia, I chose to revise the taxonomy of a small genus of Tachinini, *Xanthozona* Townsend (Fig. 1). This was the beginning of my career in the taxonomy and systematics of Tachinidae. Although the task was initially small, I had no idea at the time of how challenging the study of Neotropical tachinids would be, especially within this tribe.

First of all, the tribe Tachinini is part of the controversial subfamily Tachininae, whose classification has been the subject of debate for many decades (Mesnil 1966, Crosskey 1973, 1976, 1980, O'Hara & Cerretti 2016). The monophyly of Tachinini was confirmed by morphological and molecular characters (Cerretti



Figure 1. Lateral view of a male *Xanthozona melanopyga* (Wiedemann) from São Carlos, SP, Brazil.

et al. 2014, Stireman *et al.* 2019), but the classification of the polyphyletic subfamily Tachininae and its tribes has still to be clearly defined. The classification of Tachinini, however, was subjected to considerable rearrangement during the last century. Townsend (1936) divided Tachinini into seven tribes, namely the Cuphocerini, Dejeaniini, Juriniini (also known as Epalpini), Microtropesini, Macromyini, Schineriini and Tachinini. Later, Mesnil (1966) provided some diagnostic characters for the tribe Tachinini (subtribe Tachinina in his classification) and lumped all of Townsend's tribes into it with the exception of Macromyini (now incorporated into the tribe Nemoraeini). Mesnil's concept of Tachinini has been accepted without much debate since then.

Despite some limitations of Townsend's classification there is, indeed, some degree of morphological heterogeneity among many of the taxa in the current Tachinini, especially when considering the development of palpi, antennae, head chaetotaxy, and wings. Furthermore, comparative studies of characters of the male and female terminalia of Tachinini remain very scarce, despite the significant phylogenetic signal that these character systems exhibit within the family (Herting 1957, Verbeke 1962, Thompson 1963, Tschorsnig 1985, Cantrell 1988, Cerretti *et al.* 2014).

Another layer of complexity in the taxonomy of Neotropical Tachinini is the historical legacy of splitting taxa into multiple monotypic genera, as was done also in other tribes of the family (O'Hara 2013). With a worldwide distribution, Tachinini are a large tribe, comprising 139 valid genera and a little more than 900 species (Guimarães 1971, Crosskey 1973, 1976,

Herting & Dely-Draskovits 1993, O'Hara & Wood 2004, O'Hara *et al.* 2009, 2019, O'Hara & Cerretti 2016). However, 71 genera (about 51%) of the tribe are monotypic, with 67 of them endemic to the Neotropical Region. Curiously, the majority of monotypic taxa (42 genera) is concentrated in the former New World tribe Juriniini, characterized by specimens with vestigial or absent palpi. These numbers clearly reflect an over-splitting of the lineages comprising the Tachinini in the Neotropics, and this situation needs to be reassessed and revised.

In light of the challenges found in the classification of Tachininae and in the taxonomic problems of Tachinini that I found during my undergrad research and Master's degree, I decided to focus my Ph.D. project on the phylogeny and historical biogeography of the New World Tachinini. Therefore, the main objectives of my Ph.D. project are to infer the phylogeny of Tachinini with morphological characters and molecular data, focusing on New World taxa, and to reconstruct the biogeographic history of the New World Ineages of Tachinini. With a phylogenetic perspective, I intend to propose an updated classification of New World Tachinini, providing diagnostic characters for the genera. Additionally, with a biogeographic reconstruction it will be possible to better understand the diversification of tachinine lineages in the New World, especially in such important biogeographic areas as the Amazon rainforest, the Atlantic Forest, the Cerrado (also known as the Brazilian savanna) and the Andean mountains.



Figures 2-3. Itatiaia National Park in the Atlantic Forest (state of Rio de Janeiro, Brazil). **2**. Author at an overlook in the park after collecting many tachinids and before heading back to São Paulo. **3**. Female of a probable new species of *Rhachoepalpus* Townsend collected in the rupestrian grasslands of the park. Photo taken by Thalles P. L. Pereira.

To sample genetic data, I traveled with Dr. Silvio Nihei and my colleagues at the Laboratório de Sistemática e Biogeografia de Insecta to several field sites in Brazil to collect fresh specimens. One amazing site where we collected a great diversity of species of Tachinini was the Itatiaia National Park in the state of Rio de Janeiro (Figs. 2, 3). The park covers a large area of native Atlantic Forest with rupestrian grasslands at elevations above 2,400 m. One of the highest peaks in Brazil, known as Pico das Agulhas Negras, has an elevation of 2,790 m and is the main attraction for visitors, but the surrounding area is inhabited by many endemic species of flora and fauna. Another interesting and curiously unexplored site for tachinids is the Cantareira State Park on the northern edge of metropolitan São Paulo (Fig. 4). Despite being so close to the large city, the insect fauna of the park is not well known. We collected some species there described by Charles Townsend, who had lived in the nearby city of Itaquaquecetuba, the type locality of many of his species (Hansen & Toma 2004).

To obtain morphological and biogeographical data of species, I visited eight Brazilian collections dispersed throughout the country¹. I also had the opportunity to visit the Smithsonian National Museum of Natural History (Washington, D.C., USA) for six months, from late 2018 to early 2019, to study the type material of Tachinini (including many Townsend's types). While in North America I was also able to visit the collections of the American Museum of Natural History (New York, USA) and the Canadian National Collection of Insects (Ottawa, Canada).

My first phylogenetic analyses based on morphology included 115 characters for 192 taxa of Tachinini, covering about 79% of the genera of the tribe. Preliminary results indicate that Tachinini are a monophyletic group, with lineages of the Old World being the first divergences of the tribe. The old Juriniini were also reconstructed as monophyletic and nested within Tachinini, including other genera with vestigial palpi formerly classified in Cuphocerini. Several monotypic taxa share many morphological characters of the male terminalia with other broader genera, such as *Epalpus* Rondani, *Jurinia* Robineau-Desvoidy and *Trichophora* Macquart, which might result in new synonyms. Analyses with molecular data and the reconstruction of historical biogeography of this tribe are still in progress.

As part of my study, I hope to provide morphological diagnoses of the main generic groups of the New World Tachinini, and to compare the tribe with other related tribes of the subfamily. I am also willing to collaborate with other researchers interested in the taxonomy, host associations and phylogenetics of Tachinidae, especially in the Neotropical Region.

- CEIOC, Coleção Entomológica do Instituto Oswaldo Cruz, Instituto Oswaldo Cruz, Rio de Janeiro
- DZUP, Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba
- INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus
- MNRJ, Museu Nacional, Universidade Federal do Rio Janeiro, Rio de Janeiro
- MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo

MZUFBA, Museu de Zoologia da Universidade Federal da Bahia, Universidade Federal da Bahia, Salvador UFMG, Coleção Entomológica do Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Universidade Federal de Minas Gerais, Belo Horizonte

¹ The collections visited were:

VOBC, private collection of Vitor Becker, Camacan, Bahia.

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Morphology in the era of phylogenomics: a case for Dexiinae (Tachinidae) phylogeny

by Marcelo Domingos de Santis

Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Laboratório de Sistemática e Biogeografia de Insecta, Rua do Matão, Travessa 14, nº 101, São Paulo-SP, CEP 005508-0900, Brazil. E-mail: mrclsantis@gmail.com

The subfamily Dexiinae is a large and morphologically diverse group, with larvae that parasitize mainly immatures of Coleoptera and Lepidoptera. The subfamily is distributed worldwide (Guimarães 1971, Crosskey 1976, Cantrell & Crosskey 1989, Herting & Dely-Draskovits 1993, O'Hara & Wood 2004, O'Hara & Cerretti, 2016, O'Hara *et al.*, 2019) and contains 1375 species in 287 genera. Dexiinae have had a problematic history regarding their systematic position relative to the other tachinid subfamilies. The subfamily has been regarded as close to Tachininae (Herting 1983), Voriinae (Dexiinae, in part) (Mesnil 1966, Richter 1987), Dufouriinae (Dexiinae, in part), and Phasiinae (Shima 1989). Shima's (1989) proposition was partially recovered by Cerretti *et al.* (2014), because Dexiinae were considered as close to Phasiinae, but as paraphyletic with it. However, in the last phylogenetic hypothesis of Tachinidae, Stireman *et al.* (2019) considered it as monophyletic. Today Dexiinae appears to be established as having a sister group relationship with Phasiinae.

For a long time the Dexiinae were thought to be supported as a subfamily of Tachinidae by a putative synapomorphy in the male terminalia, that being a membranous and flexible connection between the basiphallus and distiphallus. However, this traditional putative synapomorphy was not confirmed by Cerretti *et al.* (2014). Instead, this character state was interpreted as having undergone a reversal, being secondarily lost in most Phasiinae. In contrast to previously hypotheses, this character state of a dexiine-type phallus was a synapomorphy of the clade Dexiinae + Phasiinae. The Dexiinae were paraphyletic in this reconstruction because the Dufouriini were not monophyletic and were more closely related to the Phasiinae than to the rest of Dexiinae. Santis (submitted) also found the Dexiinae to be paraphyletic in relation to Phasiinae, with evidence supporting a likely new subfamily, Dufouriinae (with Dufouriini and Freraeini), formerly in Dexiinae, as the sister group to Phasiinae.

Cerretti *et al* (2014) discussed three tribes of Dexiinae: Dexiini, Dufouriini and Voriini. Of these, only Dexiini was regarded as monophyletic. As more tribes and genera were sampled, Stireman *et al.* (2019) recovered some tribes as polyphyletic, leading the authors to suggest that the tribal classification is likely to need a major revision. For instance, Voriini and Dexiini were recovered as polyphyletic groups, the former appearing in five distinct places in the Dexiinae clade and having one genus in the Tachininae (*Microchaetina* van der Wulp), and the latter appearing in three places in the Dexiinae clade as well as having one genus in the Tachininae (*Eulasiona* Townsend). Both *Microchaetina* and *Eulasiona* were singled out as possibly misplaced in the Dexiinae.

The checklist of Tachinidae of O'Hara *et al.* (2019) was compiled on a world basis and followed some of the better-supported changes suggested by the recently published phylogenies (i.e., Cerretti *et al.* 2014, Blaschke *et al.* 2018, Stireman *et al.* 2019). Therefore it can be cited here for comparative purposes. In it, the Dexiinae are composed of 13 tribes: Dexiini, Doleschallini, Dufouriini, Epigrimyiini, Eutherini, Freraeini, Imitomyiini, Parerigonini, Rutiliini, Sophiini Telothyriini, Uramyini and Voriini. One of these,

the tribe Imitomyiini, is an ambiguous taxon, being considered as Phasiinae in Cerretti et al. (2014) and Blaschke et al. (2018), but as Dexiinae in Stireman et al. (2019). The checklist also reflects a big change in the interpretation of the Voriini, suppressing into it the former tribes Thelairini, Camplylochetini and Wagneriini. My study is favoring a different tribal composition within the Dexiinae, namely the following nine tribes: Dexiini, Doleschallini, Epigrimyiini, Eutherini, Rutiliini, Sophiini, Telothyriini, Uramyini and Voriini (along with tribes that were considered as Dufouriinae by Santis (submitted): Dufouriini, Freraeini and the currently invalid Oestrophasiini).

Certainly, Dexiinae systematics has recently undergone improvements in its knowledge and understanding. However, the Neotropical dexiines are still in great need of taxonomic and phylogenetic work. The Neotropical Region is recognized for its rich and diverse fauna and flora and different ecoregions. For instance, the Cerrado is the largest savanna formation in South America and is characterized by a ground layer of grasses and a mixture of small palms, shrubs, and trees (Fig. 2).



Figure 2. The Cerrado, a vast and heterogeneous savanna covering much of southcentral Brazil.

Regarding tachinids, the Neotropical Region is noteworthy for its high rates of endemic species. Of the 1073 species of Tachinidae in the world that are endemic to one region, 608 (57%) of them are in the Neotropics (O'Hara & Henderson 2018). But, at the same time, this highly endemic fauna holds serious taxonomic problems. These problems can be related to two issues: an excessive number of genera (many originally described without illustrations or with characters that currently do not aid in their recognition) and by the high number of undescribed species. The identification of Neotropical material requires cross-checking among existing identification keys and other resources, often prepared for other regions (e.g., Wood & Zumbado 2010) to reach an approximation of a particular group to which a taxon may belong. Even with the great contributions of authors like J.H. Guimarães (mainly Brazilian taxa), R. Cortés (Chile and Argentina), J.M. Aldrich (particularly Patagonia), W.R. Thompson (Trinidad), H.J. Reinhard, D.M. Wood and J.E. O'Hara, the progress has been small in relation to the immensity of the taxonomic problems still unresolved. In the Dexiinae for instance, of the 288 genera in the world, 162 occur in the Neotropics and of these 85 (or 52%) are monotypic. The main keys to these genera are still those in Townsend's (1934-1942) Manual of Myiology

The early 21th Century marked a new generation of tachinidologists, for instance, the revisions and new species of dexiine genera from Area de Conservación Guanacaste in northwestern Costa Rica by Fleming and coauthors (e.g., Fleming *et al.* 2015, 2017), and by Brazilian workers dealing with Neotropical taxa (e.g., Toma 2001, Nihei & Pansonato 2006, Santis 2018, Dios & Santis 2019). Only recently has all the Neotropical taxa of Dexiinae and the rest of Tachinidae been assembled together into a checklist of world Tachinidae (O'Hara *et al.*, 2019). While this is clearly an advance in comparison to Guimarães (1971), as a checklist it does not have descriptions or keys to genera or species and therefore does not help with the identification of the difficult Neotropical fauna of tachinids.

Given these problems with Neotropical Tachinidae, there is always room for more work and much that can be added. My Ph.D. project is being done at the Laboratório de Sistemática e Biogeografia de Insecta at the Universidade de São Paulo (Brazil) under the supervision of Dr. Silvio Shigueo Nihei. The general objective of this study is to propose a natural classification (i.e., containing only monophyletic groups) which represents the phylogeny of Dexiinae, based on adult and immature (egg and larval) stages, and with an emphasis on Neotropical taxa. With the resulting phylogenetic tree, I hope to determine if Phasiinae are the sister group of Dexiinae, and if Dexiinae are monophyletic or paraphyletic. My more specific objectives are to delimit the following ambiguous tribes in order to propose for each of them a well-supported systematic placement at the subfamily and tribal level:

- 1) are the Eutherini a clade of Dexiinae?
- 2) are the Imitomyini a clade of Phasiinae?
- are tribes Thelairini, Campylochetini and Wagneriini of Crosskey (1976) invalid and best placed within a large Voriini?
- 4) are the tribes Zeliini and Trichodurini of Townsend (1934–1942) invalid and best placed within Dexiini?
- 5) are the subtribes Rhamphinina, Stominina, Phyllomyina and Eriothrixina of Mesnil (1966) invalid and best placed within Voriini?

To answer the above questions in my Ph.D., I intend to include all the valid and invalid tribes of Dexiinae, and possible Dexiinae, from all over the world. I am trying to sample the greatest number of genera of Neotropical Dexiinae as possible, and by doing so I hope to understand the morphological disparity of this group. This will help with the identification and placement of long unrecognized taxa; e.g., *Tyreomma muscinum* van der Wulp, 1896 (Fig. 3).

It soon became clear that taxonomic revisions are needed, and some are being prepared. For example, the Dexiini with spine-like setae on the abdomen, like Hystrichodexia insolita (Walker, 1853) (Fig. 4). I am expanding my knowledge and sampling of Dexiinae by studying the collection of the Natural History Museum (London, England). At this museum I have been able to study the type material described by van der Wulp, Bigot and Walker, authors who famously described species using poorly defined characters and some trivial ones. Visiting this collection has also allowed me to include more terminal taxa in the analysis. My preliminary analyses recovered a tree for the Dexiinae that again is paraphyletic and the results are different from those proposed before. They are, however, preliminary and some changes will occur once more taxa are added to

the analysis. I expect to recognize synapomorphies for most or all of the tribes and for the subfamily itself, as well as discuss and try to interpret some important Dexiinae traits.

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Figures 3-4. Type specimens of Dexiinae in the Natural History Museum, London. 3. *Tyreomma muscinum* van der Wulp (female).4. *Hystrichodexia insolita* (Walker) (female).

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Revisionary study of the Argentine Voriini (Tachinidae: Dexiinae)

by Diana Torres

Grupo de Estudios sobre Sistemática y Ecología de Dípteros Caliptrados, División Entomología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" MACN, Buenos Aires, Argentina. E-mail: dianamarcela24@gmail.com

I am originally a biologist from Cali, Colombia (Fig. 1), but I am now a first-year doctoral student at Universidad Nacional de La Plata in Buenos Aires, Argentina. I have moved here to undertake a systematic study of the Argentinian Tachinidae belonging to the tribe Voriini (Dexiinae). I will do this using both morphological and molecular evidence. My study also involves collecting fresh material, examining specimens deposited in natural history collections, recording host data associated with reared specimens, and attempting to learn about the natural history of voriines that can be observed in the field.

My research is supervised by Dr. Pablo Mulieri, who is head of the Entomology Division at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), in the city of Buenos Aires. His research is focused on the systematics of the Calyptratae and particularly the Oestroidea, the superfamily to which the Tachinidae belongs. My other supervisor is Dr. Fabiana Gallardo, a specialist on parasitoid insects and a researcher associated with the Universidad Nacional de La Plata, in the city of La Plata just a short distance from Buenos Aires.

I am conducting my research at MACN, where I can be close to the voriine specimens I am studying. This museum houses one of the most complete collections of Argentinian Diptera, with about 50,000 pinned specimens. Among these is an outstanding collection of Tachinidae, with over 5000 specimens. This collection was largely accumulated over time by local dipterists, most notably Jean Brèthes (1871–1928) and Everard Blanchard (1895–1971) (Mulieri *et al.* 2013). Curation of this collection and identification of its holdings are an ongoing process that I hope to contribute to during my studies.



Figures 2–3. Argentine specimens of voriine flies that are under review. 2. *Voria* sp. 3. *Trichodischia* sp.

Currently, the Voriini have about 118 genera and 504 species in the world with 68 genera and 142 species known from the Neotropical Region (Guimarães, 1971, Valencia 1972, Cortés & González 1989, O'Hara *et al.* 2019). Within the Neotropics there are many voriines that are specially adapted to the temperate zones of South America and are found only in Andean and Patagonian environments (Guimarães 1971). The known hosts of voriines are mainly lepidopteran larvae of Noctuidae and Geometridae (Cortés & González 1989).

During the last century the Voriini were placed in the Tachininae by some authors (e.g., Guimarães 1971) and in the Dexiinae by others (e.g., Herting 1984) but today there is a consensus to classify the tribe in the latter. Recent support for this view has come from the morphological study of Cerretti et al. (2014) and molecular study of Stireman et al. (2019). Thompson (1961), who reviewed the voriines of Trinidad, mentioned that most systematists regard the voriines as a taxonomic unit that can be identified by two main characteristics: the retracted hind cross-vein and the long coiled phallus of the male genitalia. However, as pointed out by Fleming et al. (2017: 2), "while these characters prove useful to separate most of the voriines from other tribes, this minimalist approach is not a perfect fit, with some genera in the tribe having one but not both of these traits". This raises some questions about the limits of the tribe. Cortés & González (1989) characterized the tribe more broadly but their definition of it is not entirely satisfactory for the whole group.

In the molecular phylogeny of Tachinidae published by Stireman *et al.* (2019), the Voriini and also other groups

such as Blondeliini and Eryciini were of questionable monophyly, containing a wide diversity of forms that may overlap in appearance with other groups. Similarly at the generic level, Cerretti (2009) noted in his treatment of a new genus of Voriini that there are many groups of tachinids (Voriini included) where generic concepts overlap, making the assignment of species difficult. We can infer from such comments that the major morphological and ecological transitions between certain groups remain mostly unknown. This current knowledge provides an interesting perspective for addressing and initiating more detailed studies on these problematic and interesting flies.

I have found in my review of the literature that the descriptions of many South American Voriini, and particularly Argentinian voriines, do not include features of the male genital structures. The placement of such taxa in the tribe therefore remains tentative until the male genitalia can be studied. I would also like to mention that so far only 16 genera and 24 species of Voriini have been reported from Argentina, of which a high percentage, about 63% (10 genera) are represented by a single species. We believe that the actual fauna must be much greater and are motivated by this thought to continue exploring the fauna of Tachinidae in Argentina. We hope to contribute to the knowledge of the biology of voriines at the same time.

At this point in my study, I am working on the recognition of Argentine voriine genera, and searching for and examining type material and other specimens held in MACN, Museo de La Plata (MLP) in La Plata, and Fundación e Instituto Miguel Lillo (IFML) in Tucumán. I am also preparing a photographic record of representative specimens (Figs. 2, 3) and conducting a detailed morphological exploration of the Voriini to better understand the relationships within this interesting tribe of flies.

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Included here are references on the Tachinidae that have been found during the past year and have not appeared in past issues of this newsletter. This list has been generated from an EndNote 'library' and is based on online searches of literature databases, perusal of journals, and reprints or citations sent to me by colleagues. The complete bibliography, incorporating all the references published in past issues of *The Tachinid Times* and covering the period from 1980 to the present is available online at: http://www.nadsdiptera.org/Tach/WorldTachs/Bib/Tachbiblio.html. I would be grateful if omissions or errors could be brought to my attention.

Please note that citations in the online Tachinid Bibliography are updated when errors are found or new information becomes available, whereas citations in this newsletter are never changed. Therefore, the most reliable source for citations is the online Tachinid Bibliography.

I am grateful to Shannon Henderson for performing the online searches that contributed most of the titles given below and for preparing the EndNote records for this issue of *The Tachinid Times*.

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MAILING LIST

Telephone numbers and E-mail addresses are included where known.

- Acquisitions Section, Department of Library Services, Natural History Museum, Cromwell Road, London, SW7 5BD, UNITED KINGDOM
- Entomology Library, Peabody Museum, Yale University, New Haven, Connecticut 06511, USA
- Dr. Peter Adler, Department of Entomology, Clemson University, Long Hall, Box 340365, Clemson, South Carolina 29634-0365, USA [Tel: 864-656-5044, ext. 5070; Fax: 864-656-5069; E-mail: padler@clemson.edu]
- Evgeniy V. Aksenenko, Voronezh State University, Voronezh, 394006, RUSSIA [Tel: 7 4732 208884; Fax: 7 473 2208755; E-mail: entoma@mail.ru]
- Deivys M. Alvarez G., Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, nº 101, São Paulo-SP, CEP 005508-0900, BRAZIL [E-mail: deivysalvarez@gmail.com]
- Roberto Andreocci, Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Piazzale A. Moro 5, 00185, Rome, ITALY [E-mail: roberto.andreocci@libero.it]
- Mike Ashworth, 6 Farm Lane, Warrington WA4 3BZ, UNITED KINGDOM [Tel: +44 7710 482530; E-mail: mikeashworth1957@yahoo.co.uk]
- Dr. Turgut Atay, Plant Protection Central Research Institute, Ankara, TURKEY [E-mail: turgutatay60@hotmail.com]
- Dr. Susana Avalos, Zoología Agrícola, Facultad de Ciencias Agropecuarias, Avda Valparaíso, s/n Ciudad Universitaria, Universidad Nacional de Córdoba, Córdoba, ARGEN-TINA [E-mail: d-avalos@agro.unc.edu.ar]
- Mike Baldwin, 5340 Tudor Top Circle, Anchorage, Alaska 99507, USA [Tel: 907-222-0316; E-mail: akmrbaldwin@gmail.com]
- Dr. David Barraclough, School of Biological and Conservation Sciences, George Campbell Building, University of KwaZulu-Natal, Durban 4041, SOUTH AFRICA [Tel: 031-260-1612; E-mail: barracloughd@ukzn.ac.za]
- Dr. Maurizio Benelli, Research Officer, Department of Biological Sciences, Fauna Park, 205b Culloden Road, Macquarie University, NSW 2109, AUSTRALIA [Tel: +61 (2) 9850 4189; E-mail: maurizio.benelli@mq.edu.au]
- Mr. Christer Bergström, Säves väg 10, S-752 63 Uppsala, SWEDEN [E-mail: christer.bergstrom@zeta.telenordia.se]
- Dr. Prakash M. Bhoje, 26, Sarswati Patil Nagar, Padali Khurd, Tal. Karveer, Dist. Kolhapur, Maharashtra, INDIA [E-mail: pmb_bhoje@yahoo.co.in]
- Dr. Jeremy D. Blaschke, Department of Biology, Union University, 1050 Union University Drive, Jackson, Tennessee 38305, USA [Tel: 731-661-5768;
 E-mail: jblaschke@uu.edu]
- Mr. Jeff Boettner, Department of Plant, Soil and Insect Sciences, Fernald Hall, University of Massachusetts, Amherst, Massachusetts 01003, USA [E-mail: boettner@psis.umass.edu]

- Dr. Kai Burington, Department of Biological Sciences, 3640 Colonel Glenn Highway, Wright State University, Dayton, Ohio 45435, USA [E-mail: keroplatus@gmail.com]
- Dr. Cezary Bystrowski, Forest Research Institute, ul. Braci Lesnej nr 3, 05-090 Raszyn, POLAND [E-mail: C.Bystrowski@ibles.waw.pl]
- Dr. Hye-Woo Byun, Invertebrates Research Division, National Institute of Biological Resources, Environmental Research Complex, Gyoungseo-dong, Seo-gu, Incheon, 404-170, SOUTH KOREA [Tel: 82-32-590-7154; E-mail: hwbyun@korea.kr]
- Dr. Bryan K. Cantrell, 3 Wingarra Street, Yeerongpilly, Queensland, 4105 AUSTRALIA [Tel: 61 7 3848 7904; E-mail: bjlcantrell@ozemail.com.au]
- Dr. Ronald D. Cave, Indian River Research & Education Center, University of Florida, 2199 South Rock Road, Ft. Pierce, Florida 34945, USA [Tel: 772-468-3922 x 145; Fax: 772-460-3673; E-mail: rdcave@ifas.ufl.edu]
- Dr. Pierfilippo Cerretti, Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Piazzale A. Moro 5, 00185, Rome, ITALY [E-mail: pierfilippo.cerretti@uniroma1.it]
- Dr. D.E. Conlong, SASA Experiment Station, Private Bag X02, Mount Edgecombe, 4300, Natal, SOUTH AFRICA [Tel: (031) 593205; Fax: (031) 595406;
 E-mail: xentdc@sugar.org.za or conlong@iafrica.com]
- Heather Cumming, Plant Health Risk Assessment Unit, Canadian Food Inspection Agency, 1400 Merivale Road, Tower 1, Ottawa, Ontario K1A 0Y9, CANADA [E-mail: heather.cumming@canada.ca]
- Dr. Jeffrey Cumming, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [Tel: 613-759-1794; Fax: 613-759-1927; E-mail: jeff.cumming@canada.ca]
- Mr. Abhijit Somanrao Desai, Zoology Department, Shivaji University, Kolhapur, Maharastra, INDIA [E-mail: desai_abhi25@rediffmail.com]
- Prof. Maria Luisa Dindo, Dipartimento di Scienze e Tecnologie Agro-Alimentari (DISTAL), Alma Mater Studiorum Università di Bologna, Viale Fanin, 42, 40127 Bologna, ITALY [Tel: +39 051 2096288; Fax: +51 051 2096281; E-mail: marialuisa.dindo@unibo.it]
- Rodrigo de Vilhena Perez Dios, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, São Paulo - SP, CEP 005508-0900, BRAZIL [Tel: +55 11 3091 7511; E-mail: rodrigodios@gmail.com]
- John Dobson, 46 Elmwood Avenue, Kenton, Harrow, Middlesex, HA3 8AH, UNITED KINGDOM [Tel: 07800 869 579; E-mail: bugs@jdobson.co.uk]

Ms. Stephanie Erb, Lethbridge Research Centre, Agriculture and Agri-Food Canada, P.O. Box 3000, Lethbridge, Alberta T1J 4B1, CANADA [E-mail: stephanie.erb@agr.gc.ca]

Dr. Neal L. Evenhuis, Department of Natural Sciences, Bishop Museum, 1525 Bernice Street, Honolulu, Hawaii 96817-2704, USA [Tel: 808-848-4138; Fax: 808-847-8252; E-mail: neale@bishopmuseum.org]

Dr. Sheila Fitzpatrick, Agriculture and Agri-Food Canada Research Station, 6660 N.W. Marine Drive, Vancouver, British Columbia, V6T 1X2, CANADA [Tel: 604-224-4355; Fax: 604-666-4994; E-mail: sheila.fitzpatrick@agr.gc.ca]

Mr. Alan J. Fleming, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [E-mail: ajfleming604@gmail.com]

Mr. John P. Flynn, 274 Hainton Avenue, Grimsby, North East Lincolnshire, DN32 9LS, UNITED KINGDOM [E-mail: jpflynn100@hotmail.com]

Dr. Serge Gaponov, Voronezh State University, Voronezh, 394006, RUSSIA [Tel: 7 4732 208884; Fax: 7 473 2208755; E-mail: gaponov2005@yahoo.ca]

Dr. Mehdi Gheibi, Department of Plant Protection, Faculty of Agricultural Sciences, Shiraz Islamic Azad University, P.O. Box: 71993-4, Shiraz, Fars Province, IRAN [Telefax: +98 711 6410047; E-mail: mehgheibi@yahoo.com]

Dr. Ebrahim Gilasian, Insect Taxonomy Research Department, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran 19395-1454, IRAN [Tel: 0098 (21) 22418982; E-mail: gilasian@iripp.ir, egilasian@yahoo.com]

Dr. Marjolaine Giroux, Service des renseignements entomologiques, Collections entomologiques et recherché, Insectarium de Montréal, 4581, rue Sherbrooke E., Montréal, Québec H1X 2B2, CANADA [Tel: 514-872-0661; E-mail: marjolaine.giroux@ville.montreal.qc.ca]

Silvia Gisondi, Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Piazzale A. Moro 5, 00185, Rome, ITALY [E-mail: silvia.gisondi@uniroma1.it]

Dr. Catarina I. Gonçalves, RAIZ, Instituto de Investigação da Floresta e Papel, Eixo, Aveiro, PORTUGAL [E-mail: catarina.goncalves@thenavigatorcompany.com]

Dr. Christian González, Instituto de Entomología, Facultad de Ciencias Básicas, Universidad Ciencias de la Educación, Santiago, CHILE [E-mail: christian.gonzalez@umce.cl]

Dr. Simon Grenier, 6 rue des Mésanges, 69680 Chassieu, FRANCE [Tel: (0)4 78 90 46 51; E-mail: simon-grenier@orange.fr]

Dr. Horacio Grillo Ravelo, Laboratorio de Taxonomía, Centro de Investigaciones Agropecuarias, Universidad Central de Las Villas, Santa Clara, Villa Clara, CUBA [Tel: 53 042 281520; E-mail: hgrillo@agronet.uclv.edu.cu]

Filipe Macedo Gudin, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, São Paulo - SP, CEP 05508-0900, BRAZIL [Tel: +55 11 3091 7511; E-mail: filipe.gudin@gmail.com] Dr. Martin Hauser, Plant Pest Diagnostics Branch, California Department of Food & Agriculture, 3294 Meadowview Road, Sacramento, California 95832-1448, USA [Tel. 916-262-1190; E-mail: martin.hauser@cdfa.ca.gov]

Dr. Ho-Yeon Han, Department of Life Science, Yonsei University, 234 Maeji-ri, Wonju-si, Gangwon-do 220-710, SOUTH KOREA [E-mail: hyhan@yonsei.ac.kr]

Mr. Håkon Haraldseide, Ålavikvegen 4, 4250 Kopervik, NORWAY [E-mail: hharaldseide@gmail.com]

Dr. Martin Hauser, Plant Pest Diagnostics Branch, California Department of Food & Agriculture, 3294 Meadowview Road, Sacramento, California 95832-1448, USA [Tel. 916-262-1190; E-mail: martin.hauser@cdfa.ca.gov]

Shannon Henderson, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [Tel: 613-759-1794; Fax: 613-759-1927; E-mail: shannon.henderson@canada.ca]

Dr. Zdravko Hubenov, Institute of Zoology, Bulgarian Academy of Sciences, Boul. "Tsar Osvoboditel" 1, 1000 Sofia, BULGARIA

[E-mails: zkhubenov@abv.bg, zhubenov@nmnhs.com]
Dr. Ryoko Ichiki, Japan International Research Center for Agricultural Sciences, 1-1, Ohwashi, Tsukuba, Ibaraki

305-8686, JAPAN [E-mail: richiki22@gmail.com] Dr Diego I Inclán Instituto Nacional de Biodiversidad. Se

Dr. Diego J. Inclán, Instituto Nacional de Biodiversidad, Sección Invertebrados, Rumipamba 341 y Av. de los Shyris, Quito, ECUADOR [E-mail: djinclan@gmail.com]

Dr. Daniel H. Janzen, Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA [Tel: 215-898-5636; Fax 215-898-8780;
E-mail: djanzen@sas.upenn.edu]. When in Costa Rica, Dan can be reached at Guanacaste Conservation Area: tel and Fax 506-695-5598, best to call at night or on weekends.

Shin Komagata, Graduate School of Integrated Sciences for Global Society, Kyushu University, Fukuoka City, Fukuoka, 819-0395 JAPAN [E-mail: komagatashin@gmail.com]

Dr. Ulrich Kuhlmann, Executive Director, Global Operations, CABI Bioscience Centre Switzerland, Rue des Grillons 1, CH-2800 Delémont, SWITZERLAND [Tel: +41-32-421 4882; Fax: +41-32-421 4871; E-mail: u.kuhlmann@cabi.org]

Mr. A.R. Lahiri, Asst. Zoologist, Diptera Section, Zoological Survey of India, Prani Vigyan Bhavan, 'M' Block, New Alipur, Calcutta - 700 053, INDIA

Prof. Dr. Gerlind U.C. Lehmann, Humboldt University Berlin, Department of Biology, Evolutionary Ecology, Invalidenstrasse 110, 10115 Berlin, GER¬MANY [E-mail: gerlind.lehmann@t-online.de]

Alice Lenzi, Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Piazzale V. Massimo 6, 00162, Rome, ITALY [E-mail: alice.lenzi1996@gmail.com]

Dr. Gerardo Liljesthröm, Museo de La Plata, Paseo del Bosque S/N, 1900 La Plata, ARGENTINA [E-mail: gerardo@cepave.edu.ar]

Dr. John T. Lill, George Washington University, Department of Biological Sciences, 2023 G Street, NW, Suite 340, Washington, DC 20052, USA [Tel: 202-994-6989; Fax: 202-994-6100; E-mail: lillj@gwu.edu] Josh Lincoln, V.M.D., 107 Nannacher Road, Waterbury, VT 05676 USA [E-mail: Jkhlincoln@gmail.com]

Dr. Richard L. Lindroth, Department of Entomology, 1630 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706, USA [Tel: 608-263-6277; Fax: 608-262-3322 [E-mail: lindroth@entomology.wisc.edu]

James Lumbers, Australian National Insect Collection, CSIRO Black Mountain, 1 Clunies Ross Street, Acton ACT 2601, AUSTRALIA [E-mail: james.lumbers@csiro.au]

Dr. Erikas Lutovinovas, Lithuanian Entomological Society, Akademijos 2, LT-08412 Vilnius, LITHUANIA [E-mail: wohlfahrtia@gmail.com]

Dr. Jean-Michel Maes, Museo Entomologico, AP 527, Leon, NICARAGUA [Tel: 505-3116586; Fax: 505-3110126; E-mail: jmmaes@ibw.com.ni]

Dr. Steve Marshall, Department of Environmental Biology, Univer-sity of Guelph, Guelph, Ontario N1G 2W1, CANADA [Tel: 519-824-4120, ext. 2720; Fax: 519-837-0442; E-mail: samarsha@uoguelph.ca]

Dr. Peter G. Mason, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [Tel: 613-759-1908; Fax: 613-759-1927; E-mail: peter.mason@canada.ca]

Manuel Mejia, Entomólogo, Agencia de Regulación y Control de la Bioseguridad y Cuarentena para Galápagos, Puerto Ayora, Santa Cruz, Galápagos, ECUADOR 200350 [Tel: +583 958756580; E-mail: manuelmejiatoro@gmail.com]

Dr. Kevin Moulton, Department of Entomology and Plant Pathology, University of Tennessee, 2431 Joe Johnson Drive, 205 Ellington Plant Sciences Bldg., Knoxville, Tennessee 37996-4560, USA [Tel: 865-974-7950; Fax: 865-974-4744; E-mail: jmoulton@utk.edu]

Dr. Pablo Ricardo Mulieri, CONICET Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo 470, C1405DJR, Buenos Aires, ARGENTINA [E-mail: mulierii@yahoo.com]

Dr. Satoshi Nakamura, Japan International Research Centre for Agricultural Sciences, 1-2 Ohwashi, Tukuba, Ibaraki, 305, JAPAN [Tel: 0298-38-8318; Fax: 0298-38-6316; E-mail: tachinid@jircas.affrc.go.jp]

Dr. Vincent Nealis, Pacific Forestry Centre, Forestry Canada, 506 West Burnside Road, Victoria, British Columbia V8Z 1M5, CANADA [Tel: 250-363-0663; Fax: 250-363-0775; E-mail: vnealis@pfc.cfs.nrcan.gc.ca]

Dr. William C. Nettles, Jr., 25 Admiral Lane, Salem, South Carolina 29676, USA [Tel: 864-944-8401; E-mail: bill-29676net@yahoo.com or wcnettles@earthlink.net]

Dr. Silvio S. Nihei, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, São Paulo - SP, CEP 05508-900, BRAZIL [E-mail: silvionihei@gmail.com]

Dr. Enio Nunez, Secretaria de Estado de Agricultura do Rio de Janeiro,Núcleo de Defesa Agropecuária Vassouras, Rua Fernando Pedrosa Fernandes, 20, Sala 16, Centro, Vassouras - RJ - CEP 27.700-000, BRAZIL [Tel: 0055 24 2471 6841; E-mail: enionunez@engineer.com] Dr. James E. O'Hara, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [Tel: 613-759-1795; Fax: 613-759-1927; E-mail: james.ohara@canada.ca]

Dr. Michael Oraze, National Biological Control Institute, USDA, APHIS, OA, 4700 River Road, Unit 5, Riverdale, Maryland 20737-1229, USA [Tel: 301-734-4329; E-mail: moraze@aphis.usda.gov]

Marcelo Pansonato, Coleção de Entomologia – Diptera, Museu de Zoologia, Universidade de São Paulo, Avenida Nazaré, 481, Ipiranga, São Paulo-SP, CEP 04263-000, BRAZIL [E-mail: marcelopansonato@hotmail.com]

Dr. Thomas Pape, Zoological Museum, Entomology Department, Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen Ø, DENMARK [Tel: +45 3532 1106; Fax: +45 3532 1010; E-mail: tpape@snm.ku.dk]

Dr. Mehrdad Parchami-Araghi, Insect Taxonomy Research Department, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran 19395-1454, IRAN [E-mail: maraghi20@yahoo.ca]

Juan Manuel Perilla López, Department of Biological Sciences, 3640 Colonel Glenn Highway, 235A, BH, Wright State University, Dayton, Ohio 45435, USA [Tel: 1- 605-690-6185; E-mail: jmperillal@gmail.com]

Dr. Jaakko Pohjoismäki, Department of Biology, University of Eastern Finland, Room 340, P.O. Box 111, FI-80101 Joensuu, FINLAND [Tel. +358-2944-53052; E-mail: jaakko.pohjoismaki@uef.fi]

Dr. Bandekodigenahalli M. Prakash, Evolutionary Biology Laboratory, Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur Post Office, Bangalore – 560064, INDIA. E-mail: prakashbm@gmail.com

Prof. Hosagavi P. Puttaraju, Division of Biological Sciences, School of Natural Science, Bangalore University, Bangalore – 560056, INDIA [Tel: (R) +91-80-23284880; (O) +91-80-22961923; E-mail: puttarajuhp@hotmail.com]

Dr. S. Ramani, Project Directorate of Biological Control, Hebbal, Bangalore - 560 024, INDIA [Tel: 3511982; Fax: 341 1961; E-mail: s_ramani@vsnl.net]

Mr. Chris Raper, c/o Tachinid Recording Group, http://tachinidae.org.uk/ [E-mail: chris.raper@tachinidae.org.uk]

Marie Roche, European Biological Control Laboratory, USDA – ARS, Campus International de Baillarguet, 810, Avenue du Campus Agropolis, 34980 Montferrier-sur-Lez, France [Tel: 04 99 62 30 47; Fax: 04 99 62 30 49; E-mail: mroche@ars-ebcl.org]

Dr. Antonio Rodríguez, Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), SE-90183 Umeå, SWEDEN [E-mail: incamyia@gmail.com]

Dr. Knut Rognes, Alunsjøveien 30 C, NO-0957 Oslo, NOR-WAY [E-mail: knut@rognes.no] Dr. Jens Roland, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, CANADA [Tel: 403-492-1180; Fax: 403-492-9234;
E-mail: jroland@ualberta.ca]

Dr. Tomas Roslin, Spatial Foodweb Ecology Group, Department of Agricultural Sciences, University of Helsinki, FI-00014, Helsinki, FINLAND [E-mail: tomas.roslin@helsinki.fi]

Paul A. Rude, 1357 Addison Street, Berkeley, California 94702, USA [Tel: 510-644-3725; E-mail: paul.rude@berkeley.edu]

Marcelo Domingos de Santis, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, São Paulo - SP, CEP 005508-0900, BRAZIL [Tel: +55 11 3091 7511; E-mail: mrclsantis@gmail.com]

Dr. Franz-Rudolf (Rudi) Schnitzler, Manaaki Whenua-Landcare Research NZ Ltd., Private Bag 92170, Auckland Mail Centre, Auckland 1142, NEW ZEALAND [Tel: +64 9 574 4202; Fax: +64 9 574 4101; E-mail: schnitzlerr@landcareresearch.co.nz]

Prof. Dr. Ulrich Schulz, Fachhochschule Eberswalde, Fachbereich Landschaftsnutzung und Naturschutz, Fachgebiet Angewandte Tierökologie und Zoologie, Friedrich Ebertstr. 28, 16225 Eberswalde, GERMANY [E-mail: uschulz@fh-eberswalde.de]

Mr. Peter Sehnal, Internationales Forschungsinstitut für Insekten¬kunde, Naturhistorisches Museum Wien, Burgring 7, A-1014 Wien, AUSTRIA [E-mail: peter.sehnal@ nhm-wien.ac.at]

Miss Nilam N. Shendage, Zoology Department, Shivaji University, Kolhapur, Maharastra, INDIA [E-mail: nilomkar.shendage@gmail.com]

Dr. Hiroshi Shima, 2-11-1-406 Kusagae, Chuo-ku, Fukuoka 810-0045, JAPAN [E-mail: shimarcb@kyudai.jp]

Mr. Dnyaneshwar Shinde, Bhogawati College, Kurukali, Kolhapur, Maharashtra, INDIA [E-mail: dragonfly.2009@rediffmail.com]

Dr. Mike Singer, Department of Biology, Wesleyan University, Hall-Atwater Labs, Rm.259, Middletown, Connecticut 06459, USA [Tel: 860-685-2548; E-mail: msinger@wesleyan.edu]

Dr. Jeffrey Skevington, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA [Tel: 613-759-1647. Fax: 613-759-1927; E-mail: jhskevington@gmail.com]

Dr. John O. Stireman III, Department of Biological Sciences, 3640 Colonel Glenn Highway, 235A, BH, Wright State University, Dayton, Ohio 45435, USA [Tel: 1-937-775-3192; E-mail: john.stireman@wright.edu]

Dr. Teresa Stoepler, Postdoctoral Associate, Virginia Tech, AHS Jr. Agricultural Research and Extension Center, 595 Laurel Grove Rd., Winchester, Virginia 22602, USA [Tel: 540-869-2560 x42; E-mail: teresa.stoepler@gmail.com]

Dr. Xuekui Sun, 26 Courtney Cres, Richmond Hill, Ontario L4E 4B9, CANADA [Tel: 905-237-0240; E-mail: xuekuisun@hotmail.com] Dr. Takuji Tachi, Biosystematics Laboratory, Kyushu University, Motooka, Fukuoka 819-0395, JAPAN [E-mail: tachi@scs.kyushu-u.ac.jp]

Dr. Ronaldo Toma, Fiocruz-Mato Grosso do Sul, Rua Gabriel Abrão, S/N, Jardim das Nações, Campo Grande, Mato Grosso do Sul, Cep: 79081-746, BRAZIL [Tel: 55-67-91262772; e-mail: rtkuna@hotmail.com]

Diana Torres, Grupo de Estudios sobre Sistemática y Ecología de Dípteros Caliptrados, División Entomología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo 470, C1405DJR, Buenos Aires, AR-GENTINA [E-mail: dianamarcela24@gmail.com]

Dr. Luis Miguel Torres-Vila, Jefe de Sección de Protección Integrada, Servicio de Sanidad Vegetal, Consejería de Medio Ambiente y Rural PAyT, Avda. Luis Ramallo s/n, 06800 Mérida, Badajoz, SPAIN [Tel. +34 924 002530 or +34 924 002529; e-mail: luismiguel.torres@juntaex.es]

Dr. Hans-Peter Tschorsnig, (retired from) Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, GERMANY [Tel: (0711) 8 93 60; Fax: 49 711 8936100; E-mail: hanspeter.tschorsnig@smns-bw.de]

Mr. Godard Tweehuysen, Librarian, Library Netherlands Entomological Society, Plantage Middenlaan 45, NL-1018 DC Amsterdam, NETHERLANDS [Tel: + 31(0)20 5256246; E-mail: biblio@nev.nl]

Guy Van de Weyer, Pieter Breughellaan, 26, B-2840-Reet, BELGIUM [Tel: 003238889269; E-mail: guido.vandeweyer@skynet.be]

Prof. Jaromír Vaňhara, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlárská 2, 611
37 Brno, CZECH REPUBLIC [Tel: +420 532 146 323; Fax: 420 541 211 214; E-mail: vanhara@sci.muni.cz]

Dr. Gergely Várkonyi, Friendship Park Research Centre, Finnish Environment Institute, Lentiirantie 342B, FI-88900 Kuhmo, FINLAND [E-mail: gergely.varkonyi@ymparisto.fi]

Dr. Philippe Vernon, UMR 6553, CNRS, Université de Rennes 1, Station Biologique, 35380, Paimpont, FRANCE [Tel: +33 (0)2.99.61.81.69; Fax: +33 (0)2.99.61.81.87; E-mail: philippe.vernon@univ-rennes1.fr]

Natalia Vinasco [Arias], Ag. Eng. University of Caldas, Agricultural Science Faculty, Manizales, COLOMBIA [Tel: (57) 321-8739817; E-mail: vinasco.natalia@gmail.com]

Mr. Wang Qiang, College of Life Science, Nankai University, Tianjin 300071, P.R. CHINA [E-mail: wqmy_mvp@126.com]

Mr. Nik Wiman, Department of Entomology, Washington State University, Tree Fruit Research and Extension Center, 1100 N. Western Ave, Wenatchee, Washington 98801, USA [Tel: 509-663-8181, ext. 277; E-mail: nwiman@wsu.edu]

Dr. Isaac Winkler, Postdoctoral Research Associate, Cornell College, Mt Vernon, Iowa 52314, USA [E-mail: isw971@gmail.com]

Dr. Helena K. Wirta, Spatial Foodweb Ecology Group, Department of Agricultural Sciences, University of Helsinki, FI-00014, Helsinki, FINLAND [E-mail: helena.wirta@helsinki.fi]

Dr. D. Monty Wood, (retired from) Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, CANADA

- Dr. Norman E. Woodley, 8920 S Bryerly Ct., Hereford, Arizona 85615, USA [Telephone: 240-750-7629; E-mail: normwoodley@gmail.com]
- Mr. Nigel Wyatt, Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UNITED KINGDOM [Tel: 0207 942 5197; E-mail: npw@nhm.ac.uk]
- Dr. Erick Yabar L., P.O. Box 115, Cusco, PERU [E-mail: e_yabar@yahoo.com]
- Mr. Theo Zeegers, Eikenlaan 24, NL 3768 EV Soest, THE NETHERLANDS [Tel: + 35 5885858; E-mail: th.zeegers@xs4all.nl]
- Dr. Zhang Chuntian, Liaoning Key Laboratory of Evolution and Biodiversity, Shenyang Normal University, 253 North Huanghe Street, Shenyang 110034, P.R. CHINA [Tel: 86 (24) 86578950; Fax: 86 (24) 86579052; E-mail: chuntianzhang@aliyun.com]
- Dr. Joachim Ziegler, (retired from) Museum für Naturkunde, Leibniz-Institute for Research on Evolution and Biodiversity, Invalidenstrasse 43, 10115 Berlin, GERMANY [E-mail: joachim.ziegler@mfn-berlin.de]
- Mr. Manuel A. Zumbado, Unidad de Atrópodos, Instituto Nacional de Biodiversidad (INBio), 22-3100, Santo Domingo, Heredia, COSTA RICA [Tel: 506-507-8222; Fax: 506-507-8274; E-mail: mzumbado@inbio.ac.cr]