

In Memoriam: Agnieszka Draber-Mońko

THE TACHINID TIMES

ISSUE 32

A tachinid phylogeny
... finally

... and a checklist!

Brain control by *Leskia*

Billaea takes on huge
oak-boring beetles

News from the Essig Museum

FEBRUARY 2019

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DISTRIBUTION

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 2020 issue of *The Tachinid Times* to the editor by the end of January 2020.

FRONT COVER A hoodoo in a rarely-visited badland area between the Bisti Wilderness and Chaco Culture NHP, New Mexico (USA).

Photo: J.E. O'Hara, 9 September 2018

TABLE OF CONTENTS Located in the Coyote Buttes on the Arizona-Utah border (USA), the Wave is famous for its mesmerizing swirls of multi-hued Navajo sandstone.

Photo: J.E. O'Hara, 15 May 2018

BELOW Monument Valley in southern Utah (USA) as viewed from the north on Hwy. 163 near mile maker 13 (a.k.a. Forrest Gump Point).

Photo: J.E. O'Hara, 8 May 2018





Figure 1. Panoramic view of a mature cork oak dehesa in the summer season. Dehesa La Vieja, Cornalvo Natural Park, Extremadura, Spain, July 2008. (Photo: Luis M. Torres-Vila / SSV.)

Billaea adelpha (Loew) (Diptera: Tachinidae) as a larval parasitoid of large oak-living cerambycids in Southwestern Spain

by Luis M. Torres-Vila¹ and Hans-Peter Tschorsnig²

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Introduction

Oak forests are widespread in the Mediterranean Basin, occupying more than two million hectares in Southwestern Iberia alone. Most lowland oak forests in this area have experienced a huge man-made transformation during past centuries, so their primeval climax stage has almost completely disappeared. At present, oak forests occur as a savannah-like open woodland (the so-called *dehesa* in Spain and *montado* in Portugal) which sustain a well-defined traditional agro-silvo-pastoral use shaping landscape multiplicity. Lowland dehesas are typically populated by sclerophyllous and evergreen oak (*Quercus*) species, mostly holm oak (*Q. ilex* L.) and cork oak (*Q. suber* L.), over an often limited or absent woody understory and a grassland formed by annual and perennial species for pasture (Fig. 1). In higher or cooler areas, open woodlands may also be populated by marcescent/deciduous oaks, mainly pyrenean oak (*Q. pyrenaica* Willd.) but also gall oak (*Q. faginea* Lam.), though these species occur more typically in denser upland and hillside forests. Dehesa woodlands constitute the most important forest ecosystem in SW Iberia with outstanding socio-economic, ecological and biodiversity values (Montero *et al.* 1998, Moreno & Pulido 2009, Bugalho *et al.* 2011, Torres-Vila *et al.* 2017a), which hosts the highest levels of biological diversity in Europe (Cowling *et al.* 1996, Ramírez-Hernández *et al.* 2014, Vodka *et al.* 2009), so the dehesa ecosystem is considered a biodiversity hotspot (Medail & Quezel 1999, Myers *et al.* 2000) protected under the EU Habitats Directive (CEC 1992).

Three large xylophagous cerambycids are usually associated with these oak species, two Cerambycinae, namely *Cerambyx welensii* (Küster) (*Cw*) and *Cerambyx cerdo* L. (*Cc*), and one Prioninae, *Prinobius myardi* Mulsant (*Pm*) (López-Pantoja *et al.* 2008, 2011, Torres-Vila *et al.* 2017a,b). The life cycles of *Cw*, *Cc* and *Pm* typically occur in old, decayed and/or diseased oak trees, so that these longhorn beetles are included among the highly diverse assemblage of saproxylic (wood dwelling) insects. This functional group is important in wood degradation and

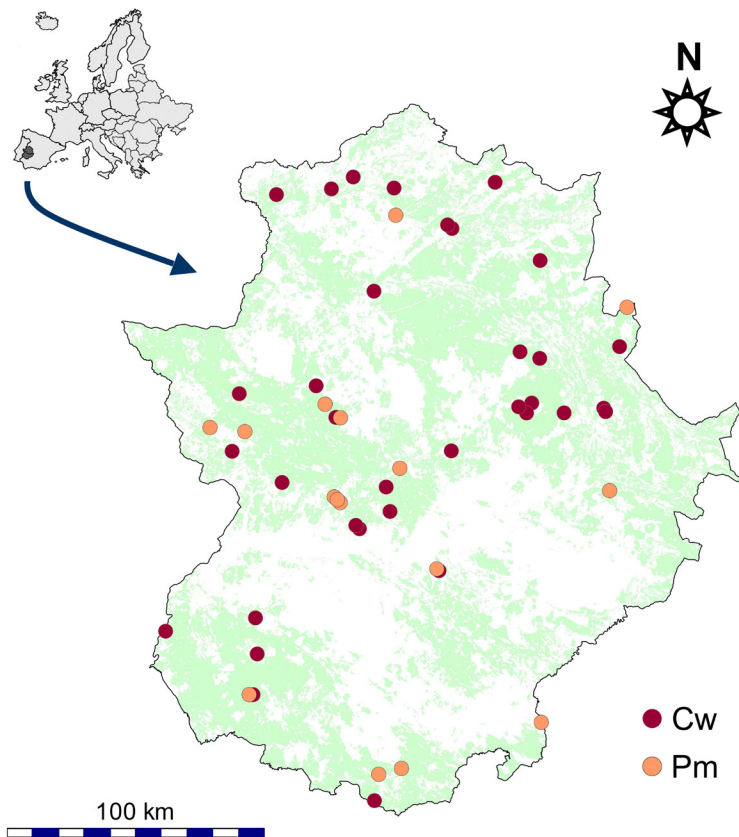


Figure 2. Records of *Billaea adelpha* parasitizing cerambycid larvae of either *Cerambyx welensii* (Cw) or *Prinobius myardi* (Pm) compiled during our 6-year study (2011–2016) in Extremadura (SW Spain). The forest cover layer (holm oak, cork oak, pyrenean oak and gall oak species pooled) is superimposed in green color. (Artwork: F. Javier Mendiola / Luis M. Torres-Vila.)

hollow formation in old trees, which will be later used as shelters by a large array of species, greatly contributing to the biodiversity in oak forests (Speight 1989, Grove 2002, Buse *et al.* 2008). However, as *Cw* and *Cc* are primary saproxylic beetles that need living wood for larval development, they also colonize young/healthy trees and can become harmful or pest species. The pest and legal status of the target cerambycids differs markedly depending on the geographical and forest context. *Cw* is an emerging pest involved in oak decline in Iberia (López-Pantoja *et al.* 2008, Torres-Vila *et al.* 2012, 2016); *Cc* is a protected species in Europe (CEC 1992, IUCN 2010) although also reported as a harmful or pest species in several circum-Mediterranean and Black Sea countries (Torres-Vila 2017); and *Pm* is a secondary/minor pest (López-Pantoja *et al.* 2011). The three longhorn species exhibit a typical western Palaearctic distribution with respective ranges widely overlapping in southern Europe. In SW Iberia, they are widespread, share a similar ecological niche, and often coexist in sympatry. Wood quality and host tree species are major factors shaping larval resource partitioning (Torres-Vila *et al.* 2017a).

In the described scenario, and despite its potential importance, very few data are reported in the literature about the natural enemies (particularly larval parasitoids) of these large cerambycids. In the last years our research group has studied the distribution, ecology and behavior of *Cw*, *Cc* and *Pm* in the region of Extremadura (SW Spain) in order to set up an integrated management strategy in dehesa woodlands. From a recent study on the larval ecology of these cerambycids (Torres-Vila *et al.* 2017a) we had the opportunity to collect and rear a large number of larvae and to obtain their parasitoids. Here we report on the field and laboratory results obtained, from which it is deduced that the tachinid *Billaea adelpha* (Loew) is by far the main larval parasitoid in the study area. We also provide some interesting data about the ecology and behavior of this fly species.

Study area

Our study area was the whole region of Extremadura (SW Spain), which extends over 41,634 km² (Fig. 2). The climate is typically Mediterranean with dry and hot summers (up to 40°C). Samples of cerambycid larvae were taken during six consecutive years (2011–2016) in the above mentioned oak species. Geographical coordinates were taken for each sampled tree. Sampling effort was standardized as far as possible to adequately cover geographical, altitudinal and host oak ranges.

Cerambycid species

Cw, *Cc* and *Pm* adults are large (about 25–60 mm), blackish-brown in color and show sexual dimorphism, with antennae longer in males (Fig. 3). The three species are univoltine, flying from late May to late August, with flight peaks occurring from late June to early July (*Cw* and *Cc*) or a little later (*Pm*). Adult daily activity occurs typically at dusk and early evening. *Cw* and *Cc* adults feed mainly on tree sap and exudates while *Pm* adults do not feed at all. Mated females lay eggs into bark crevices, pruning cuts and cork stripping wounds. Larvae are xylophagous mainly on oak species (see above). After hatching, neonate larvae bore subcortically and then tunnel increasingly wider and longer galleries into sapwood and heartwood (Figs. 5, 7). Larval development usually lasts 2–4 years and pupation occurs in early (*Pm*) or late summer (*Cw* and *Cc*) within a pupal cell constructed ad hoc by the larvae inside the sapwood. The pupal stage lasts about one month, but while *Pm* adults leave the tree to reproduce in the same summer, emerged *Cw* and *Cc* adults overwinter in a pre-reproductive stage until late spring in the following year. Colonized trees can be easily identified by the presence of adult exit holes and larval frass (Fig. 4). Larval galleries may cause huge physiological, mechanical and structural damage to oaks, and even tree death in the worst instances (Duffy 1953, Bense 1995, Vives 2000, López-Pantoja *et al.* 2011, Torres-Vila *et al.* 2016, 2017a,b).

Larval sampling

Candidate oaks were selected based on the presence of adult exit holes in the bark and larval galleries in pruning cuts or debarked wounds, very often with larval frass (Fig. 4). Some samples were also taken from firewood piles/woodsheds when the log source was known (about 15% of samples). Selected trees/branches were cut with a chainsaw (Fig. 6) and the resulting bolts carefully dissected looking for cerambycid larvae, using metal wedges



Figure 3. Adults of the three species of large oak-living cerambycids: *Cerambyx welensii* (top), *Cerambyx cerdo* (middle) and *Prinobius myardi* (bottom), (males of each species on the left). (Photos: Emilio Echevarría. Plate: Luis M. Torres-Vila.)



Figures 4–9. Cerambycid host larvae, damage and field sampling. **4.** Abundant larval frass in an old cork oak. **5.** Large *Prinobius myardi* larvae surprised inside their galleries. **6.** Newly fallen branch with cerambycid galleries cut into bolts with a chainsaw. **7.** Cut section of a holm oak bolt showing larval damage in the inner heartwood. **8.** *Prinobius myardi* larvae in a newly-opened holm oak bolt. **9.** Laboratory rearing of field-collected cerambycid larvae. (Photos: Luis M. Torres-Vila / SSV.)

and a sledgehammer (Figs. 5–8). All larvae in each sampled bolt were collected, individually arranged in aerated plastic containers, referenced and taken to the laboratory in portable coolers. Larvae were scored according to their body length as small (<20 mm), medium (20–40 mm) or large (>40 mm). Larvae of *Cerambyx* and *Prinobius* were easily differentiated as the first possess a ferruginous-pigmented band on the pronotum frontal margin and rounded mandible tips while in the second the frontal band is missing and mandibles are pointed. Field-collected larvae were individually reared at room temperature (22–28°C and 50–70% relative humidity) in aerated 140 ml plastic containers on an agar-based artificial diet (Fig. 9) (Morales-Rodríguez *et al.* 2015). Rearing containers were regularly inspected and emergence of parasitoids noted. Tachinid larvae were maintained in the laboratory until adulthood (Fig. 13) and then identified to species (by the second author).

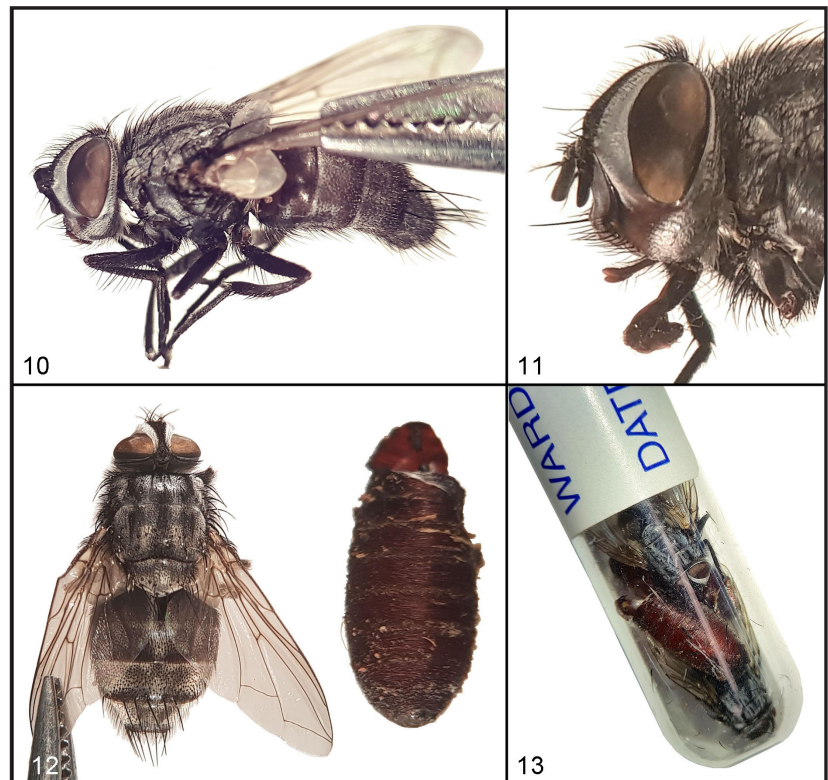
Data analysis

Mean parasitism rate (i.e., mean of parasitism percentages in larval samples, including 0% values) was used to assess the effects of host species (*Cw* vs. *Pm*), larval size (small, medium or large) and oak species (holm, cork or pyrenean oak) on parasitism pressure. The number of *Cc* larvae collected was very low (see Torres-Vila *et al.* 2017a about this fact), so this species was not considered in this study. The effect of host size on the number of parasitoids emerged per parasitized larva was also examined. Data were analyzed through Kruskal-Wallis tests (Mann-Whitney U test for two-sample contrasts) using SYSTAT software.

Vouchers and DNA barcoding

Voucher specimens of the reared tachinids (all *Billaea adelpha*) were deposited in the entomological collection of the senior author's institution. The specimens are preserved dry in 35 labeled vials (references 01T to 35T), each vial containing all individuals (adults and puparia) obtained from a single parasitized beetle larva.

Five *Billaea adelpha* adults among those obtained in this study were DNA barcoded (COI gene fragment) and sequences will be publicly available online through GenBank database.



Figures 10–13. *Billaea adelpha* individuals (all males) obtained in the laboratory from field-collected cerambycid larvae. **10.** Adult lateral view. **11.** Adult head lateral view. **12.** Newly-emerged fly and puparium remains. **13.** Tube with the set of parasitoids emerged from a single host larva. (Photos: Rafael López / Luis M. Torres-Vila / SSV.)

Results

More than 400 oak trees were inspected and 500 bolts from 348 trees (181 holm oaks, 113 cork oaks and 54 pyrenean oaks) were finally dissected. A summary of the number of larval samples recovered and larvae number (collected and parasitized) arranged by host cerambycid and oak species is shown in Table 1. The tachinid fly *Billaea adelpha* (Loew) (Figs. 10–12) was the only larval parasitoid detected in both *Cw* and *Pm*, being widespread throughout the entire region (Fig. 2) and over a broad altitudinal range (162–1315 m). However, parasitism rates by *B. adelpha* were rather low in both *Cw* and *Pm* (Table 1). Parasitism pressure was almost twice in *Cw* than in *Pm* (Table 1) although such difference was not significant (Mann-Whitney test, $U_1 = 24782.5$, $P = 0.95$).

Oak species in which host larvae lived did not affect parasitism rate in both *Cw* (Kruskal-Wallis test, $U_2 = 2.92$, $P = 0.23$) and *Pm* ($U_1 = 2079.0$, $P = 0.30$). Hence, oak species were pooled in subsequent analyses. Note that degrees of freedom in these tests differ between cerambycid species as *Pm* larvae were never found in pyrenean oak (Table 1).

Table 1. Mean parasitism rates by *Billaea adelpha* on *Cerambyx welensii* (*Cw*) and *Prinobius myardi* (*Pm*) larvae recorded in Extremadura (SW Spain) during our 6-year study (2011–2016).

Host cerambycid	Oak species	Larval samples ¹	Larve number		Parasitism rate (%)	
			Collected	Parasitized	mean ± SE	range
<i>Cw</i>	holm oak	105	417	17	5.03 ± 1.78	0-100
<i>Cw</i>	cork oak	138	747	12	2.44 ± 1.09	0-100
<i>Cw</i>	pyrenean oak ²	89	273	17	4.33 ± 1.48	0-100
Total <i>Cw</i>		332	1437	46	3.77 ± 0.82	0-100
<i>Pm</i>	holm oak	115	969	21	2.23 ± 0.71	0-50
<i>Pm</i>	cork oak	34	174	3	0.90 ± 0.75	0-25
<i>Pm</i>	pyrenean oak	0	0	–	–	–
Total <i>Pm</i>		149	1143	24	1.93 ± 0.57	0-50
Total <i>Cw</i> + <i>Pm</i>		481	2580	70	–	–

¹ number of dissected bolts with at least one cerambycid larva for each host species / oak species combination.

² one parasitized *Cw* larva from gall oak. Note that *Pm* larvae were never found in pyrenean oak.

SE: standard error of the mean.

Host larval size and the origin of the wood (trees vs. firewood) in which cerambycid larvae were collected had a noticeable effect on the parasitism exerted by *B. adelpha* (Fig. 14). Parasitism rate depended on larval size at collection time, with overall higher values in large than in small larvae and intermediate values in medium-sized larvae (see total panel in Fig. 14), both in *Cw* ($U_2 = 5.84$, $P = 0.05$) and in *Pm* ($U_2 = 5.26$, $P = 0.07$) although in the last species significance was close to the limit. Host larval size did not affect the number of flies that emerged from a single parasitized larva (large vs. medium plus small larvae pooled), in both *Cw* ($U_1 = 118.0$, $P = 0.55$) and *Pm* ($U_1 = 21.0$, $P = 0.70$). The number of parasitoids per larva did not differ either between cerambycid species ($U_1 = 311.5$, $P = 0.99$) with values of 3.08 ± 0.51 , 1–13 (mean ± SE, range) in *Cw*, and 2.94 ± 0.84 , 1–14 in *Pm*.

Regarding the effect of wood origin, the most striking outcome was observed in large larvae (Fig. 14). Thus, parasitism rate in large *Pm* larvae was significantly higher in firewood than in trees ($U_1 = 1096.0, P < 0.05$), the trend in large *Cw* larvae being similar although not significant ($U_1 = 3198.0, P = 0.12$).

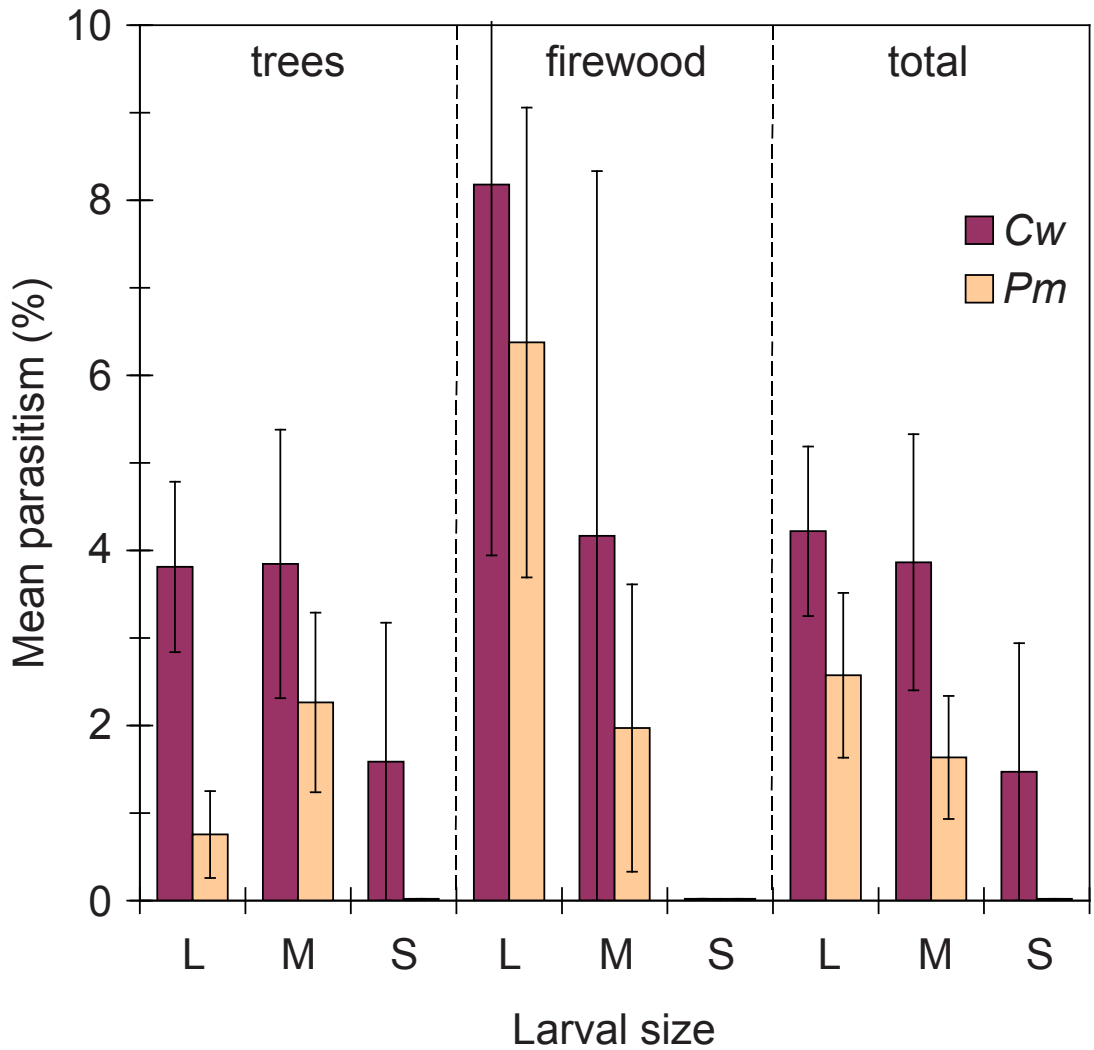


Figure 14. Effects of wood origin (trees vs. firewood) and larval size of *Cerambyx welensii* (*Cw*) and *Prinobius myardi* (*Pm*) on mean parasitism rate by *Billaea adelpha*. Data recorded in Extremadura (SW Spain) during our 6-year study (2011–2016). Host larvae were scored according to their body length at collection time as small (S: <20 mm), medium (M: 20–40 mm) or large (L: >40 mm). Vertical lines are the standard error of the mean. See text for a detailed statistical analysis.

The dextine *Billaea* Robineau-Desvoidy is a large genus of worldwide distribution (O'Hara 2013) that includes seven known species in the Iberian Peninsula (Tschorsnig & Báez 2002). Our target species, *B. adelpha*, has a mainly western Palaearctic distribution and towards the east it reaches Azerbaijan (Herting 1984). *Billaea adelpha* occurs in practically all of Europe (Tschorsnig *et al.* 2004) including Iberia (Tschorsnig 1992, Almeida *et al.* 2017). However, this tachinid fly prefers dry and warm areas so it is rare in North and Central Europe and more common in Southern Europe (Tschorsnig & Herting 1994). Its occurrence in Extremadura (both in Cáceres and Badajoz provinces) had already been previously reported from field-captured adults on umbels of Apiaceae plants and in the shade of large stones (Tschorsnig 1992), as well as from laboratory-obtained adults emerged from field-collected parasitized larvae (Tschorsnig 2017). Like other *Billaea* species (Allison *et al.* 2000, Tschorsnig 2017), *B. adelpha* exhibits a clear parasitic specialization on coleopteran larvae, mainly cerambycids (including several subfamilies such as Cerambycinae, Lamiinae and Prioninae), having been also cited from a buprestid and a scarabaeid (Tschorsnig 2017). Although the distribution of *B. adelpha* is relatively well known, information on its biology, ecology and especially host range remains scarce and fragmentary (as in most tachinids) (Cerretti & Tschorsnig 2010, Dindo 2011); this despite the fact that tachinid flies are a main group of parasitoids of insect pests in agriculture and forestry. The data provided in this paper attempt to reverse a little this undesirable situation.

Our results show that *B. adelpha* is widespread in SW Spain across a broad spatial and altitudinal range. Hence, *B. adelpha* is able to complete its life cycle in an ample array of habitats, from the warmer and drier lowland woodlands inhabited by evergreen sclerophyllous oaks to the wetter and colder mountains populated by deciduous oaks where it usually snows in winter. This fly species was the only larval parasitoid detected on *Cw* and *Pm* larvae despite intense field sampling, which suggests that the pressure exerted by this group of natural enemies on large oak-living cerambycids is rather low. Kenis & Hilszczanski (2007) already noted in their review the lack of published information on the natural enemies of *Cw* (as *C. velutinus* Brullé) and they compiled the few available data about *Cc*. In fact, the present study constitutes the second record (*Cw*) and the first formal report (*Pm*) about the parasitism of *B. adelpha* on large oak-living cerambycid species, two host-parasitoid associations recently compiled by Tschorsnig (2017).

Mean parasitism rates by *B. adelpha* were rather modest in both *Cw* and *Pm* irrespective of oak species, but values ranged widely from one stand to another reaching levels of even 100% in *Cw* (Table 1). Such a parasitism pressure is similar to that displayed by *B. monohammi* (Townsend) on either *Monochamus scutellatus* (Say) (0.6–7.5%) (Soper & Olson 1963) or *Monochamus carolinensis* (Olivier) (<5%) (Reagel *et al.* 2012), but appreciably lower than the 9.3–18.9% of *B. irrorata* (Meigen) on *Saperda populnea* (L.) (Tsankov & Georgiev 1991), the 27.9% of *B. triangulifera* (Zetterstedt) on *Saperda scalaris* (L.) (Campadelli & Gardenghi 1991), or the >28% of an undescribed *Billaea* species on *Acanthocinus princeps* (Walker in Lord) (Allison *et al.* 2000). The higher parasitism detected in large rather than in small larvae suggests that parasitization by *B. adelpha* in early host stages should be rare. A similar fact occurs in the congeneric species *B. irrorata*, which usually emerges from full-grown host larvae (Smith *et al.* 2004).

Neither cerambycid species or host size had a significant effect on the number of parasitoids that emerged from a single host larva, which averaged about 3 flies per larva, even if in large larvae it was not infrequent to obtain more than 10 parasitoids. In our case, the number of parasitoids per larva was similar to that reported in *B. triangulifera* parasitizing *S. scalaris* (Campadelli & Gardenghi 1991), but quite a bit lower than in *Rasiliverpa agrianomei* (Mesnil) parasitizing *Agrianome fairmairei* (Montrouzier) (whose large larvae are the so-called

“ver de bancoule”), as in this parasitoid-host association an average of 15 parasitoids per host larva occurs in a range of 2–59 (Cochereau 1970). It is interesting to note here that in our study, parasitoids often emerged from their host some days after the field collection date, which suggests that the high stress suffered by host larvae when extracted from the wood could somehow accelerate the emergence pattern of *B. adelpha*. Such a temporal asynchrony is not trivial since, if parasitoids in the wild emerge from a host larva before it has completed their future exit gallery, then the adult flies will inevitably die cloistered inside the tree.

The effect of wood origin on *B. adelpha* parasitism rate (especially on large *Cw* larvae) was an unexpected finding. The three cerambycid species studied require living trees and do not oviposit in firewood under natural conditions. However, larvae already present in the wood before being cut can continue their development and successfully complete their life cycle, sometimes at the cost of a reduced final adult size (Torres-Vila *et al.* 2018). Higher *B. adelpha* parasitism rates in firewood than in trees could occur if cerambycid larvae are less protected in the firewood. The oviposition strategy of *B. adelpha* females has not been observed or described but is very likely practically the same as it is for the closely related species *Billaea pectinata* (Meigen), as studied by Tölg (1910) and summarized by Herting (1960). *Billaea pectinata* lays thin membranous eggs from which neonate larvae immediately hatch and begin actively searching for host beetle larvae in their immediate surroundings (decayed wood). Tölg (1910) found that the tachinid larvae must find a host in one day, otherwise it will die. Experimental survival was nevertheless observed up to four days after ovi(larvi)position, but parasitization of host larvae was no longer possible. Indirect ovi(larvi)position has also been reported in the congeneric species *B. triangulifera* (Campadelli & Gardenghi 1991).

Indirect oviposition requires that newly-hatched tachinid larvae (planidia) must locate suitable host larvae on their own, either by waiting for them to pass by or by actively searching for them. This behavioral process is mediated by semiochemical compounds (Dindo & Nakamura 2018). Indirect oviposition likely evolved as an adaptive response whereby tachinid females may reach (otherwise inaccessible) endophytic host larvae living concealed within their host plants in galleries often protected by frass plugs – a case well exemplified by our wood-boring cerambycid species. In this so cryptic scenario, our results suggest that parasitization success by *B. adelpha* is substantially improved in firewood piles, possibly because female flies can penetrate through the large holes in the cut sections of the logs, accessing more easily the host galleries and laying their eggs (larvae) closer to host larvae.

We have found that *B. adelpha* is widespread in SW Spain, and conclude that despite rather low parasitism rates in oak-living cerambycids, the large variability among larval samples suggests that this tachinid could exert a significant parasitic pressure in some instances.

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A molecular phylogeny of world Tachinidae...finally

by John O. Stireman III

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A summary of ...

Stireman, J.O. III, Cerretti, P., O'Hara, J.E., Blaschke, J.D. & Moulton, J.K. (2019)

Molecular phylogeny and evolution of world Tachinidae (Diptera).

Molecular Phylogenetics and Evolution (preprint, 19 pp.)*

<https://doi.org/10.1016/j.ympev.2018.12.002>

We have finally published the first comprehensive molecular phylogeny of Tachinidae! This project began more than seven years ago as a collaborative venture between an international team of tachinid researchers including myself, Jim O'Hara, Pierfilippo Cerretti, and Kevin Moulton. The project involved numerous other researchers and students who provided specimens from around the world, helped generate sequence data, aided with identifications, and provided taxonomic advice (see acknowledgements in the paper). Most notably, Jeremy Blaschke (PhD student of Moulton, and ultimately a coauthor on the phylogeny paper) led our molecular phylogenetic analysis of the subfamily Phasiinae (Blaschke *et al.* 2018) and Isaac Winkler (Post-doc of Stireman) led efforts to produce a framework phylogeny of the family (Winkler *et al.* 2015) that served as the foundation for an expanded analysis.

The final data set included 504 terminal taxa, consisting of 359 tachinid genera across 54 tribes. All major lineages were included, although a few small tribes are missing including, among others, Anacamptomyini (I was disappointed we did not acquire any of these), Iceliini, Trichodurini, and Protohystriciini. We obtained sequence data from four genes (28S, CAD, MCS, and MAC) resulting in an alignment of nearly 8000 base pairs. However, not all taxa were sequenced for all genes. For traditional Sanger sequencing, this is a pretty huge data set, which explains in part why it took us so long to put it together.

We will leave more detailed examination and analysis of our results for the paper, which we are happy to distribute. However, we thought that we might provide a summary of some of the major results here (Figure 1). For clarity (and to limit redundancy) we have not indicated support values for nodes in our summary figure. Support was high for most clades, however the short lengths of some of the internal branches are indicative of uncertainty in relationships.

Sister group

As in our previous analyses (Winkler *et al.* 2015, Cerretti *et al.* 2017), we found strong support for the calliphorid subfamily Polleniinae as sister group to Tachinidae. Despite a lack of obvious morphological connections between these clades, the consistency of this result across different loci and analyses suggests that the relationship is robust, and we hope to find confirming evidence from other sources. Relationships among other oestroid outgroups (e.g., Sarcophagidae, Rhinophoridae, Ulurumyiidae and various Calliphoridae lineages) largely mirror those found in our previous analyses (e.g., Cerretti *et al.* 2017), but some of these relationships were not strongly supported.

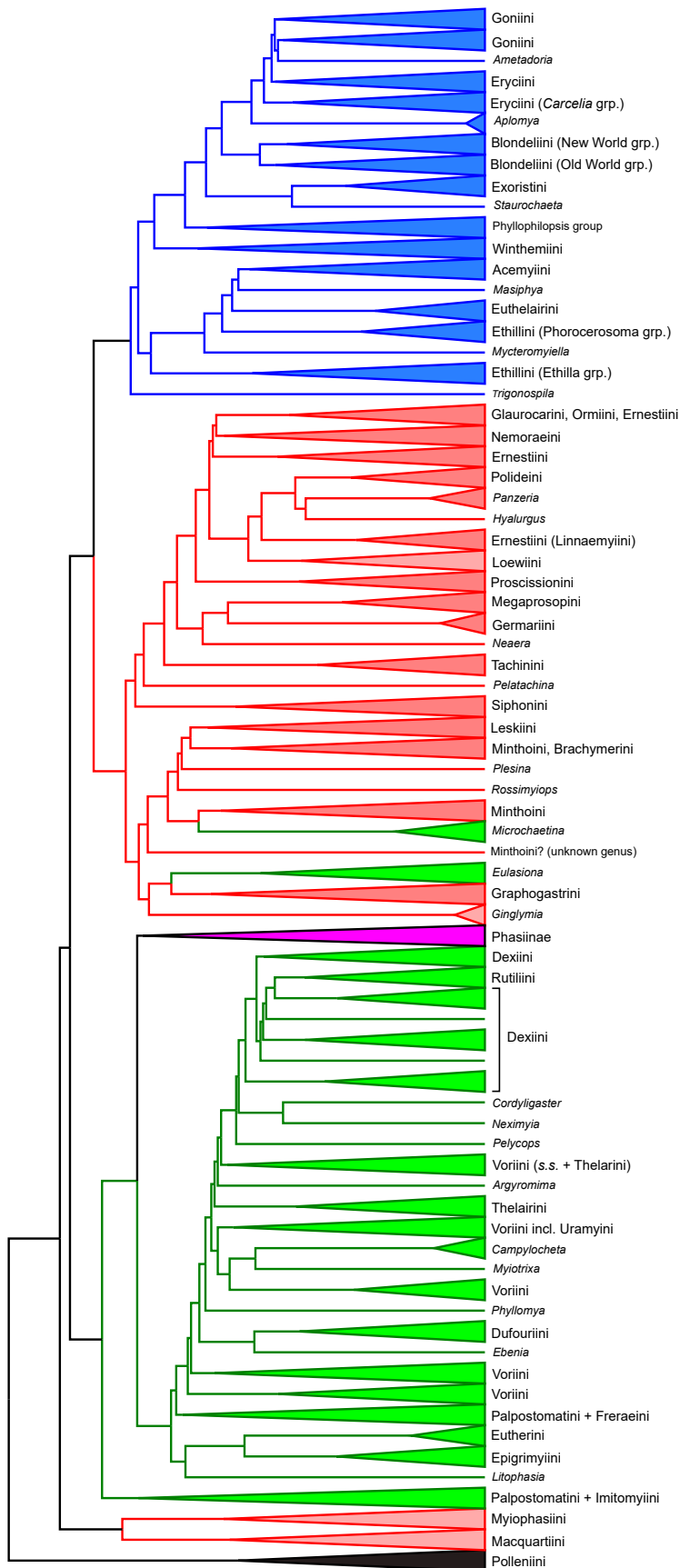


Figure 1. A summary tree of relationships recovered from our molecular phylogenetic analyses of Tachinidae. This tree is based on a Maximum Likelihood analysis using the program IQtree. Major tribes and other clades are collapsed and intervening genera indicated. Exoristinae are in blue (top), Tachininae in red/pink, Phasiinae (condensed into a single clade) in purple, Dexiinae in green, and sister group in black.

Subfamilies

Each of the four tachinid subfamilies was generally reconstructed as monophyletic, with Phasiinae + Dexiinae and Exoristinae + Tachininae forming sister clades with strong support. Exceptions included a basal Macquartiini + Myiophasiini (Tachininae) clade, sister to all other Tachinidae, and a group of Palpostomatini + Imitomyiini (Dexiinae) sister to Dexiinae + Phasiinae. In addition, two genera of Dexiinae are found within the Tachininae, *Microchaetina* and *Eulasiona*. Sequences from multiple specimens confirm these unexpected placements.

We did not include a detailed examination of the subfamily Phasiinae in our study because this group was previously examined in depth by Blaschke *et al.* (2018), and our results (based on much of the same data) were largely consistent with that previous analysis in terms of the composition and relationships. One notable difference is that we found strong support for *Imitomyia* belonging to a clade outside either Phasiinae and Dexiinae as mentioned above. For brevity, we have collapsed the phasiines into a single clade (Figure 1) and we urge readers to see Blaschke *et al.* (2018) for an in-depth treatment of the group.

Dexiinae

Relationships among the Dexiinae proved to be much more confused than we expected. Most major tribes of Dexiinae are para- or even polyphyletic in our analyses and many of the relationships between various lineages are not well-resolved. Palpostomatini and Dufouriini are split into two lineages each (the latter not shown in Fig. 1). Voriini *s.l.* (including Uramyini, Thelairini, Campylocheta, etc.) form a broad grade of lineages connected by a somewhat uncertain backbone of short branches. The Dexiini are well supported as a monophyletic group, but only if Sophiini, Rutiliini, and the odd Australian parasitizing tribes Eutherini and Epigrimyini are well resolved as monophyletic groups. These sister tribes are joined by the enigmatic genus *Litophasia* as found by Blaschke *et al.* (2018).

Tachininae

The subfamily Tachininae has widely been considered a bit of a “junk group” where taxa that do not clearly belong elsewhere are often placed, although they do share the trait of ovariparity. There are no clear synapomorphies for the subfamily and it contains a diverse array of taxa, from tiny siphonines and graphogastrines (e.g., *Phytomytera*) to monstrous, spine-covered tachinines, and just about everything in-between. Therefore, it is a little surprising that the subfamily hangs together as well as it does in our analyses, minus the beetle-attacking Macquartiini and Myiophasiini, which do not seem to fit anywhere very well morphologically.



Figure 2. *Microtropesa* sp., a strikingly beautiful member of the Tachinini from Australia. This genus was included in our molecular analysis. (Photo by Matt Duncan.)

Our analysis divides the Tachininae into two major clades. One clade (the “*Mintho*-Leskiini group”) includes the leskiines, minthoines, graphogastrines and some refugee Dexiinae (see above), and the other (the “Tachinini group”, Fig. 2) contains the Siphonini, all the large-bodied tachinine tribes (Tachinini, Ernestiini, Polideini, Nemoraeni), and a sprinkling of other small tribes (e.g., Germariini, Neaerini, Ormiini). The first group is somewhat confusing. The Leskiini form a well-supported clade, but the minthoines are a grade of lineages, and the graphogastrines form a surprising clade with *Eulasiona* (Voriini) and *Ginglymyia* (Leskiini). The Tachinini group is bit better behaved in terms of tribe monophyly, except for the Ernestiini and Loewiini, which are dispersed into several clades. Most other tribes are strongly supported monophyletic clades (e.g., Tachinini, Siphonini, Polideini), but relationships between some tribes are not consistently resolved, such as those between the Ernestiini (in part), Nemoraeni, and “Glaurocarini-Ormiini-Ernestiini” assemblage (see also Inclán *et al.* 2018).

Exoristinae

As expected, the exoristines formed a well-supported monophyletic group, and there were relatively few surprises among the reconstructed relationships of clades. Perhaps the most striking results were: 1) the position of *Trigonospila* (Blondeliini) as sister to all other exoristines, 2) another clade of blondeliines, the *Phyllophilopsis* group, as sister to Exoristiini + Blondeliini + Eryciini + Goniini, and 3) *Aplomya* as sister group to Eryciini + Goniini. In most other respects our findings confirm previous phylogenetic studies of the subfamily (e.g., Stireman 2002;

Tachi and Shima 2010). However, we were just shy of a monophyletic Goniini (microtype egg group) because of a wayward *Ametadoria*.

In addition to reconstructing phylogenetic relationships within the Tachinidae, we also examined the evolution of egg type (ovipary, ovarvipary, and ovarviparous microtype eggs) and host associations (at the level of host order). I will save discussion of these results for the paper itself; suffice it to say that our results were not entirely consistent with those of Cerretti *et al.* (2014) based on their morphological phylogenetic analysis.

With the increased reliance on more efficient and powerful high-throughput genomic approaches, we believe it will not be long before many of the hypotheses generated in our study can be tested more rigorously and perhaps some of the more difficult areas can be better resolved. To be sure, if the cost efficiency and ease of these approaches had been realized a little sooner we probably would have adopted such a genomic approach. (We actually did generate eight tachinid transcriptomes as part of this project that will hopefully be combined with other such data to help solidify major relationships in the future.) Still, it may be that the radiation of some lineages such as the Voriini *s.l.* and major tribes of Tachininae were so rapid that no amount of genetic or morphological data will ever be able to convincingly resolve them. We hope that our present analysis will provide a framework for, and help to spur future studies of, the evolutionary relationships of this diverse and fascinating clade of parasitoid flies. For our own part, we plan to use these phylogenetic results to examine the rapid evolutionary radiation of tachinids and to help reassess current classification in the near future.

* Note – due to some errors and miscommunication with the editors and publisher, and their policy of making uncorrected proofs available online (which we are opposed to), several uncorrected versions of our paper may be circulating. We would be happy to send anyone a final, corrected version of the paper upon request.

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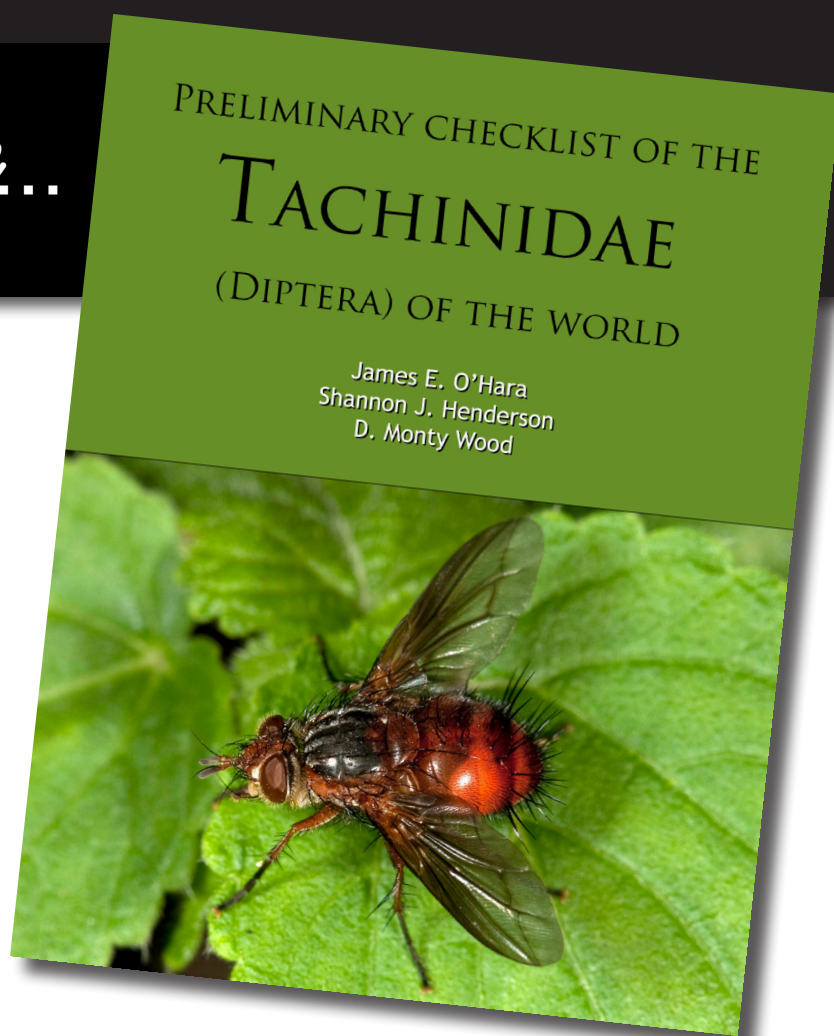
Introducing the...

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Cover photo by S.A. Marshall

[As narrated by senior author]



Link to the homepage of the *Preliminary Checklist of the Tachinidae of the World*:
<http://www.nadsdiptera.org/Tach/WorldTachs/Checklist/Worldchecklist.html>

Historical background

A long time ago before entomology became my passion and profession, I was an undergraduate student at Carleton University in Ottawa looking for a summer job to pay my tuition in September. I was a biology student with an interest in insects and was taking what courses I could on them but had no clear idea where this might lead. Then one fateful day in the spring of 1977 I was told by a lab instructor that the Canadian National Collection of Insects (CNC) was looking for a summer student to assist with the preparation of a manual on flies. I was interviewed (the sole candidate), hired on the spot, and started work in the Diptera Unit the first week of May. My job was to attach name labels to mylar plates of flies drawn by Ralph Idema for volumes 1 and 2 of the upcoming *Manual of Nearctic Diptera* (McAlpine *et al.* 1981, 1987). This brought me into close proximity with all the coordinators of the *Manual* (see Cumming *et al.* 2011 for more on them) and my thoughts of becoming an insect systematist began to take shape. Before my first summer was over (I returned for a second), Monty Wood had offered me a part-time job throughout the school year to assist him with his research on Tachinidae.

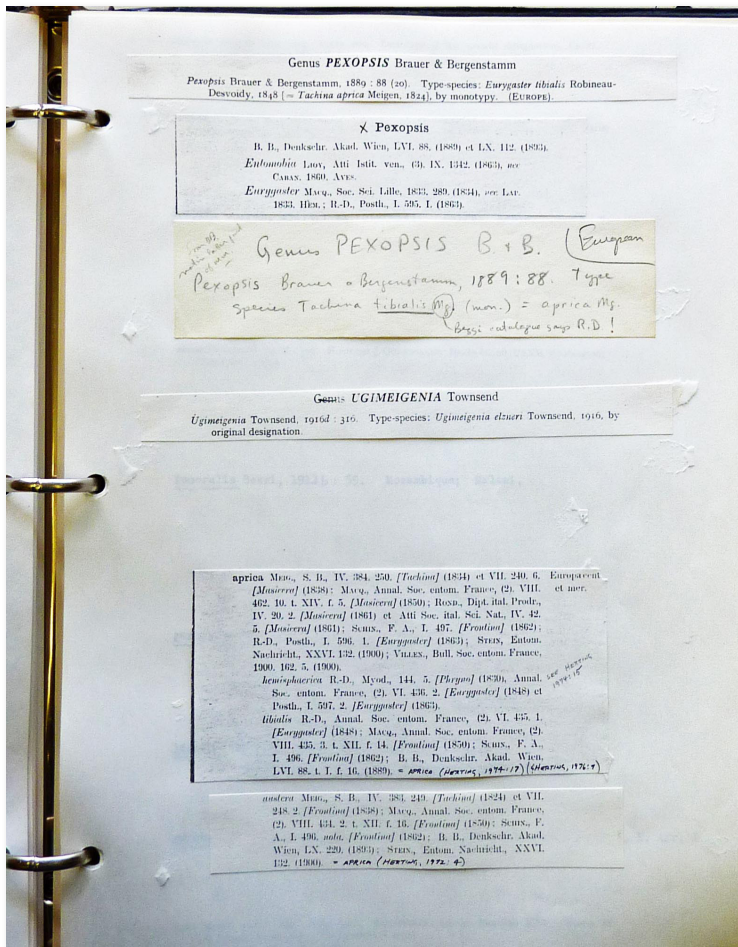


Figure 1. Monty's early cataloguing efforts consisted of binders with information about names photocopied from various catalogues and glued on pages. This binder dates from 1978.

paper in binders. Art Borkent continued with this task after I left but the time was not right for this plan to progress at a steady pace. Computers and databases were in the future and the demands of the *Manual of Nearctic Diptera* (MND), a huge revision of the Blondelliini (Wood 1985), and a phylogenetic study of the Nematocera (Wood & Borkent 1989) intervened for the next decade or so. Progress was made mostly in the form of notes in existing catalogues and in the memory banks of Monty's mind, constantly moving forward as types were examined in the world's collections, as specimens were acquired from hither and yon, and as character systems were deciphered to yield their secrets.

I had just one school year left after my first stint as a summer student in the Diptera Unit in 1977. By early 1978 I had to make a decision about what to do after graduation in the spring (with a B.Sc.), and after (hopefully) a second summer in the Diptera Unit. My interest in insect systematics had continued to grow but the influence of Dr. Henry Howden at Carleton University had me thinking about beetles and not flies as a career choice. Everyone recommended the esteemed Dr. George Ball at the University of Alberta in frigid Edmonton as the supervisor to strive for. I wrote him in January 1978 enquiring about the possibility of becoming a Master's student under his direction and suggested working on carabid beetles, his speciality. He promptly wrote back with an encouraging letter and asked me to submit a formal proposal to the Department of Entomology. By the time that proposal was submitted in late March my allegiance to beetles had waned and I outlined instead a taxonomic revision of *Siphona*

I was soon smitten by Tachinidae but was also too naive to be afraid of them – Monty, after all, seemed to know most of them by heart and had a visual memory of where they were in the massive collection. Monty had a plan to reclassify the world Tachinidae and with that in mind he had me photocopy pages from the various regional catalogues and glue names together on pages as the first step towards reordering the family (Fig. 1). His own thoughts on classification were in close agreement with the work of the Europeans (principally Louis Mesnil and Benno Herting) but the earlier rearrangement of Nearctic tachinids by Sabrosky & Arnaud (1965) had only moved slightly in that direction and the Neotropical tachinids, as catalogued by Guimarães (1971), were still mired in the legacy of the notorious “splitter”, C.H.T. Townsend. I did not understand much of this at the time but the allure of systematics was definitely taking a hold on me and I could see how solving taxonomic puzzles was more than just working on bugs. Besides, travelling to remote places in search of exotic treasures (new species) held a certain appeal to me.

So that was the start of the world Tachinidae project. Strips of paper with names arranged on sheets of

Meigen, the Tachinidae having won out as a result of Monty's enthusiasm for the family. I was accepted and off I went to Edmonton in late August 1978. While there I completed a Master's (1981) on *Siphona* and a Ph.D. (1987) on the Siphonini.

Things were happening back in Ottawa while I was pursuing my graduate studies out west. Monty was busy with research and publications but was also itching to spend a greater amount of time in the field. As the 1980s were coming to a close he had been to the North five or six times (Fig. 2) and had been excited to discover tachinid faunal connections between the northeastern part of the Palaearctic Region and northwestern North America (see Lafontaine & Wood 1988). Monty had had an interest in Neotropical tachinids since his university days and was beginning to get more involved with this fauna. This region not only has the largest tachinid fauna in terms of described species (3032 according to O'Hara, Henderson

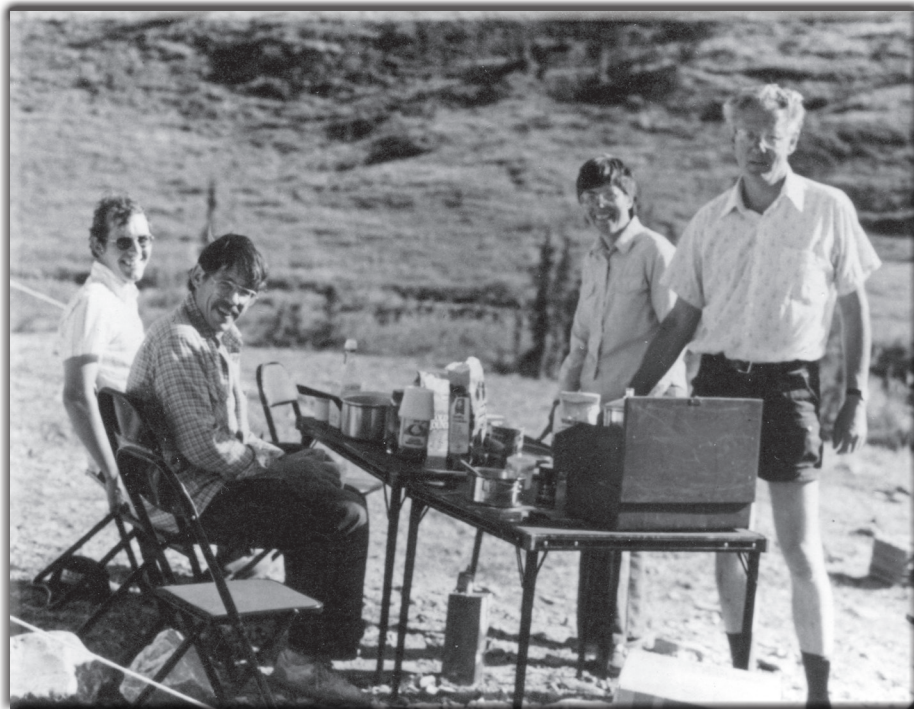


Figure 2. Expedition to the Firth River, Yukon Territory (Canada), 1984. Left to right: Don Lafontaine, Milt Campbell, and Grace and Monty Wood.

& Wood 2019) but a staggering number of undescribed species also exist in collections and presumably many more species await discovery in nature. Monty had plans to extensively collect in the most diverse areas he could reach in order to broaden his knowledge of the fauna. He also wanted more visits to the world's collections to match up the types and names of Macquart, Wiedemann, van der Wulp and others who had described Neotropical species, and more frequent trips to the USNM [National Museum of Natural History] in Washington to study their 900 or so Townsend types. However, this master plan did not sit well with Monty's management. He was expected to concentrate on taxonomic problems of more direct relevance to Canada instead of reordering the whole family. For a time Monty took trips to the Neotropics at his own expense but in 1986, after 22 years with Agriculture & Agri-Food Canada and the CNC, he chose early retirement in order to pursue his own research path. He has continued his association with the CNC as an Honorary Research Associate from that day forth. It did not take long for Monty to adapt to his new-found freedom. He renewed his efforts to better understand Neotropical tachinids and began wintering in Costa Rica as a way to better learn its little-known fauna while also escaping Ottawa winters.

I completed my Ph.D. studies in 1987 and in 1989 moved back to Ottawa to accept a research position in the same Diptera Unit where I had worked as a summer student in 1977 and 1978. One of my first tasks was to reorganize the Tachinidae collection, then comprising perhaps 20 cabinets (now about 50). The collection was essentially arranged according to the classification of Sabrosky & Arnaud (1965) and this was hindering my ability to become familiar with it. Monty had made extensive changes to North American genera in his *Blondeliini* conspectus and MND Tachinidae chapter (Wood 1985, 1987). This was not a problem for Monty because he had memorized where the

genera were physically located and could think of a genus in one classification and find it in the collection under another. Monty consented to a rearrangement of the collection with some trepidation and afterwards was initially lost when using it even though it and his classification now matched.

As time went on I realized that a new catalogue to the Tachinidae of America north of Mexico was needed. Our collection was organized to match the generic changes published since Sabrosky & Arnaud (1965) but I wanted to look up information about names without a lot of searching, bearing in mind that the Internet was still in its infancy. I proposed to Monty a joint project that eventually resulted in the publication of our *Catalogue of the Tachinidae (Diptera) of America North of Mexico* (O'Hara & Wood 2004).

Our early catalogues

Our North American catalogue was my first exposure to a relational taxonomic database. As we explained in our introduction (O'Hara & Wood 2004: 2):

“We used the software program *Platypus*® Version 1.1 (CSIRO, Australia) to input catalogue data and programmed a custom output from the underlying Microsoft Access® 97 database to obtain the desired format. Final changes and the index were made in Corel WordPerfect® 8.”

Platypus was a nice, intuitive program with easy navigation and pop-up screens for information entry (Fig. 3). It unfortunately died an early death before it could be refined and broadly marketed. In fact, we were using it before the planned output options were developed and when it was abruptly discontinued (for budgetary reasons, if I remember correctly) we had to find a clever co-worker (Jennifer Read) who could program an output for us.

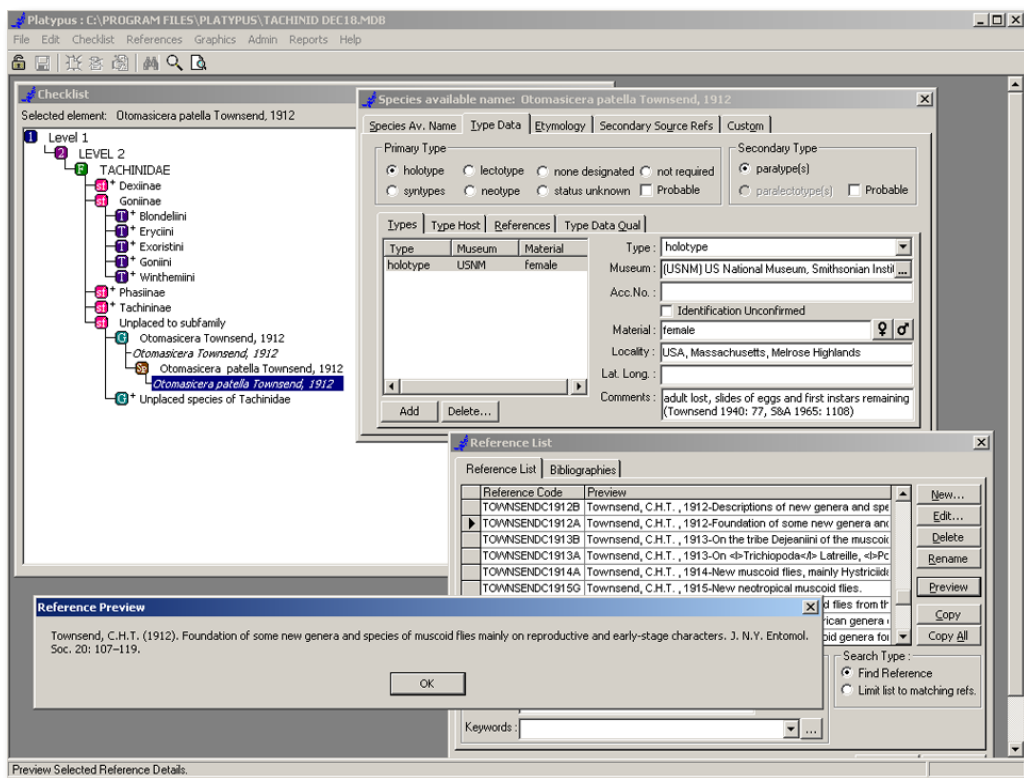


Figure 3. Screenshot of *Platypus*® (CSIRO, Australia), a relational database for managing taxonomic, geographic, and bibliographic information.

It was Monty, not me, who was planning to continue down the cataloguing path towards a world catalogue after our North American one was finished. He was still examining little-known tachinid taxa and accumulating notes about them. Technology had progressed significantly since his early efforts at cataloguing in the 1970s. He asked his friend and colleague, Manuel Zumbado (then with Instituto Nacional de Biodiversidad, Costa Rica), to build him a simple FileMaker® Pro database in which he could record names, type information, notes, and their original and present (or planned) placements. Monty, with the help of his wife Grace, went through most of the existing catalogues to enter information from them along with notes he had written about the types he had examined.

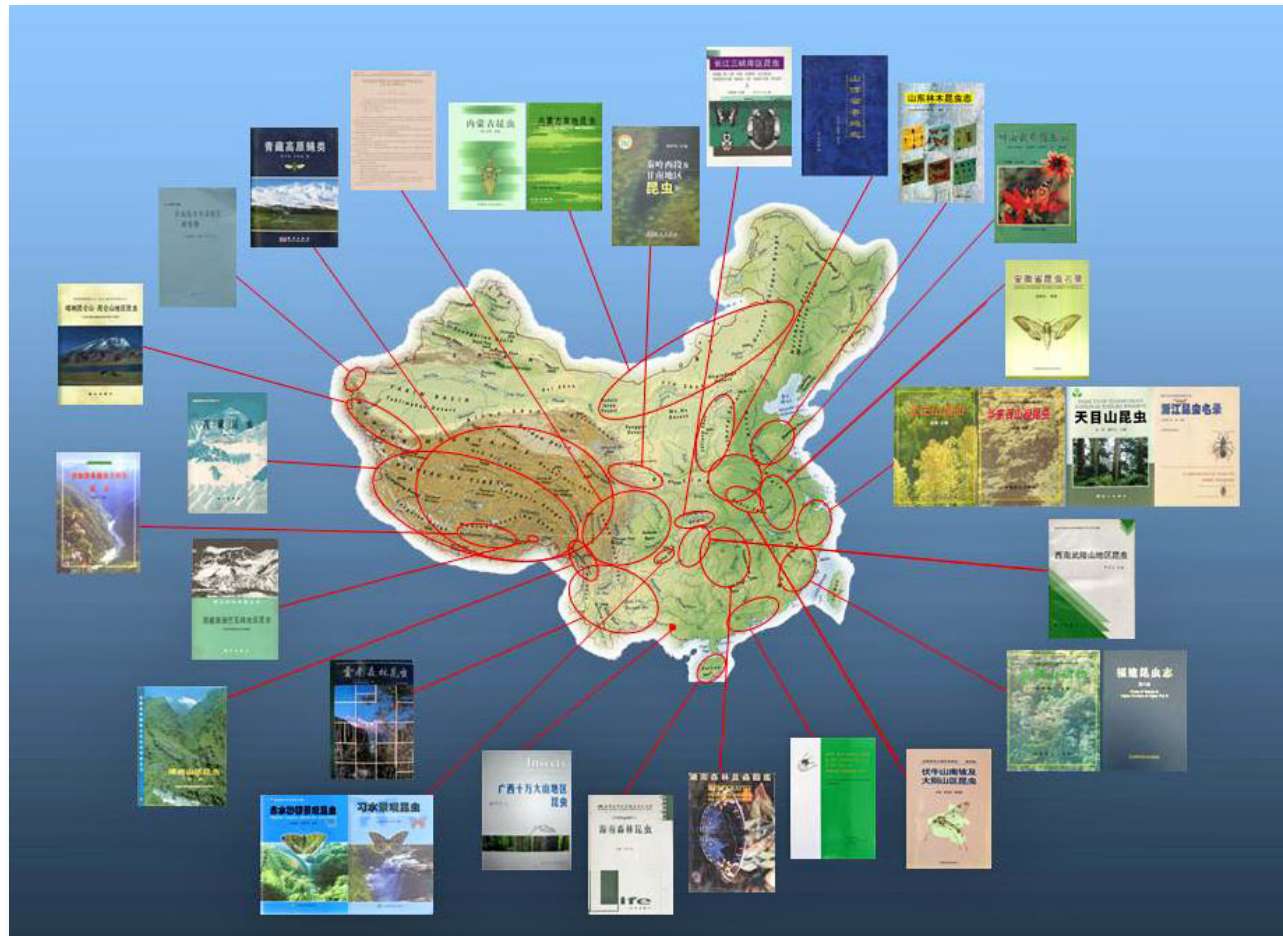


Figure 4. Map of China with book covers of 31 of the 40 faunal surveys published between the 1980s and 2008 that recorded tachinids within their areas of coverage (outlined in red ovals). (From O’Hara, Shima & Zhang 2008.)

While Monty was proceeding with his cataloguing efforts, I found myself being drawn more and more into the world of names. This was self-serving at first because I wanted to keep up with what was going on in the world of Tachinidae and organizing literature and keeping track of names was part of this. I soon realized that with my website and newsletter I could make some of the information I was gathering for myself available to a broader audience. I developed that idea into the *World Genera of the Tachinidae (Diptera) and Their Regional Occurrence* and posted the first version of this PDF document on our website in 2005. This resource has since progressed through to the current (tenth) version and is now coauthored with my technician Shannon Henderson (O’Hara & Henderson 2018).

I soon took on a new cataloguing project on the tachinids of China with my colleagues Hiroshi Shima (Kyushu University, Japan; since retired but still active) and Chuntian Zhang (Shenyang Normal University, China). China was, and continues

to be, of interest to my employer because it is potentially the source of both invasive insect species and their biological control agents. I was dutifully trying to keep up with the literature on Chinese tachinids but was falling behind. The Chinese were surveying insects all over the country (Fig. 4) and describing new species at a feverish rate. An authoritative review of Chinese tachinids had been published in *Flies of China* by the renowned Chinese tachinid expert Chien-ming Chao in 1998 (Chao *et al.* 1998) (see biography by Zhang & Hao 2008) but this resource was quickly becoming outdated. The number of known tachinid species in China jumped from 754 in 1998 (Chao *et al.* 1998) to almost 1100 ten years later (O’Hara 2008). Chao had kindly kept me supplied with his own papers over the years and Monty had been collecting literature from everywhere in the years before my arrival in Ottawa so I had a good start on Chinese literature. I gathered together the research papers, bought all the books on faunal surveys (Fig. 4), and received otherwise unobtainable works from Chuntian.

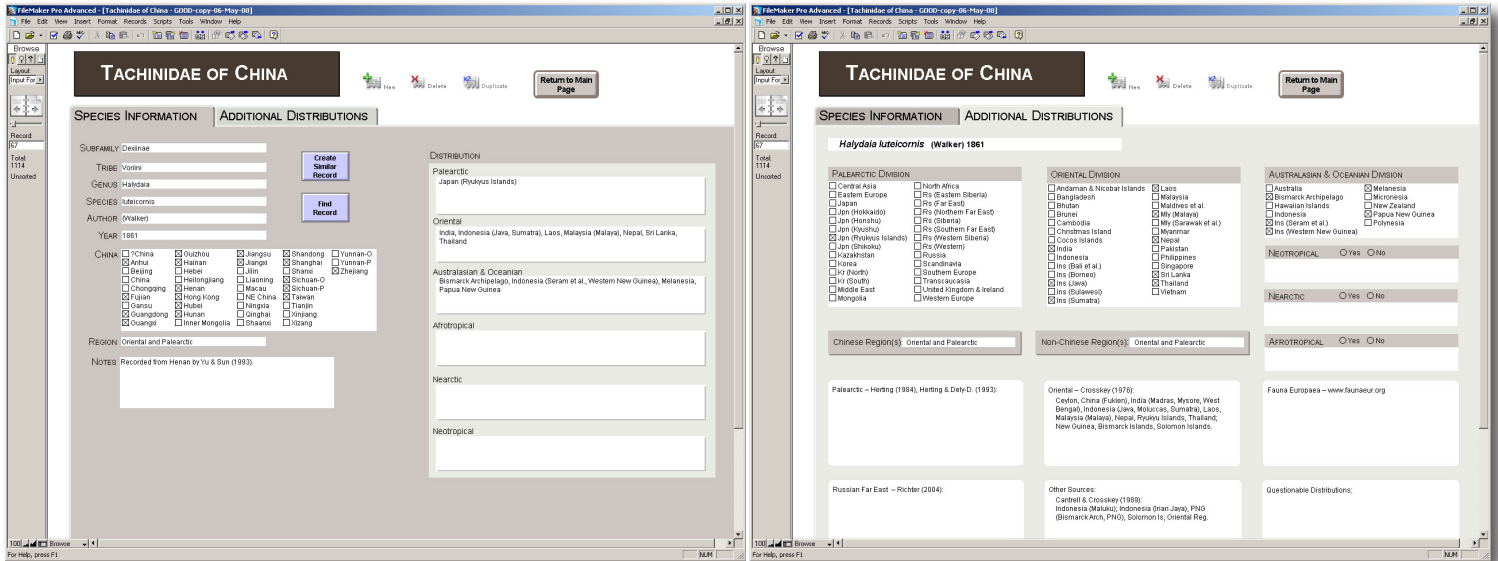


Figure 5. Distribution of *Halydaia luteicornis* (Walker) within (left) and outside (right) China as recorded in the FileMaker® Pro distributional database developed by Shannon.

The cataloguing of the Tachinidae of China was done largely in a Word document because we had no relational database to use for it. We did, however, benefit from a relatively simple distributional database that Shannon, just recently hired, developed for us using FileMaker® Pro (Fig. 5). This allowed us not only to input distributional data but to examine biogeographical aspects of the distributions as well. For example, the highest numbers of tachinid species in China, and highest numbers of endemic species (per province), were recorded from Sichuan and Yunnan (Fig. 6). We came to the following conclusions about the Tachinidae of China in a presentation given at the XXIII International Congress of Entomology in Durban, South Africa in 2008 (O’Hara, Shima & Zhang 2008):

1. 1114 species were recorded from China.
2. 404 species (36%) were recorded as endemic to China.
3. There is a gradual transition in the tachinid fauna from north to south in China, although overall there is a greater affinity with the Palearctic than the Oriental Region.
4. Chinese endemics are concentrated in the south.
5. The Hengduan Mountains biodiversity ‘hotspot’ [essentially consisting of extreme eastern Xizang, western half of Sichuan, and northwestern tip of Yunnan] is exceptionally rich in Tachinidae as evidenced by the high number of species and endemics recorded from Sichuan and Yunnan.
6. Sichuan and Yunnan together had a known fauna of 539 tachinid species, representing 48% of all species known from China. Of this number, 190 species were endemic to Sichuan + Yunnan.



Figure 6. Number of tachinid species per province in China; total number in blue and number of species endemic to China (not province) in red. (From O'Hara, Shima & Zhang 2008.)

We were also able to more broadly compare the tachinid fauna of China with that of the rest of the world and in particular the Palaearctic Region (Fig. 7). Our conclusions based on these comparisons were summarized as follows (O'Hara, Shima & Zhang 2008):

1. The most species were shared with Japan, Europe, and Russian Far East.
2. A relatively high number of species were shared with Caucasus.
3. In the Palaearctic Region, biologically rich areas shared the most species with China.
4. In the Oriental Region, relatively few species were shared with China as a whole.

The cataloguing of the Chinese Tachinidae came to a close with the publication of *Annotated Catalogue of the Tachinidae (Insecta: Diptera) of China* (O'Hara, Shima & Zhang 2009). I had hoped for us to publish a separate paper on the biogeography of Chinese Tachinidae but due to other distractions on my part this never came to pass.

I gained more experience with the subtleties of nomenclature and the desirable attributes of a taxonomic catalogue while working on the Tachinidae of China. This resulted in an expanded section at the beginning of our catalogue on such matters as name-bearing types, avoidance of assumption of holotype, lectotypifications, type localities, and geographic divisions (information basically akin to the small print you never read that comes with the instructions for small household appliances). I could already recognize some slight imperfections in the North American catalogue of O'Hara & Wood (2004) that few readers would notice but were irritating to me.

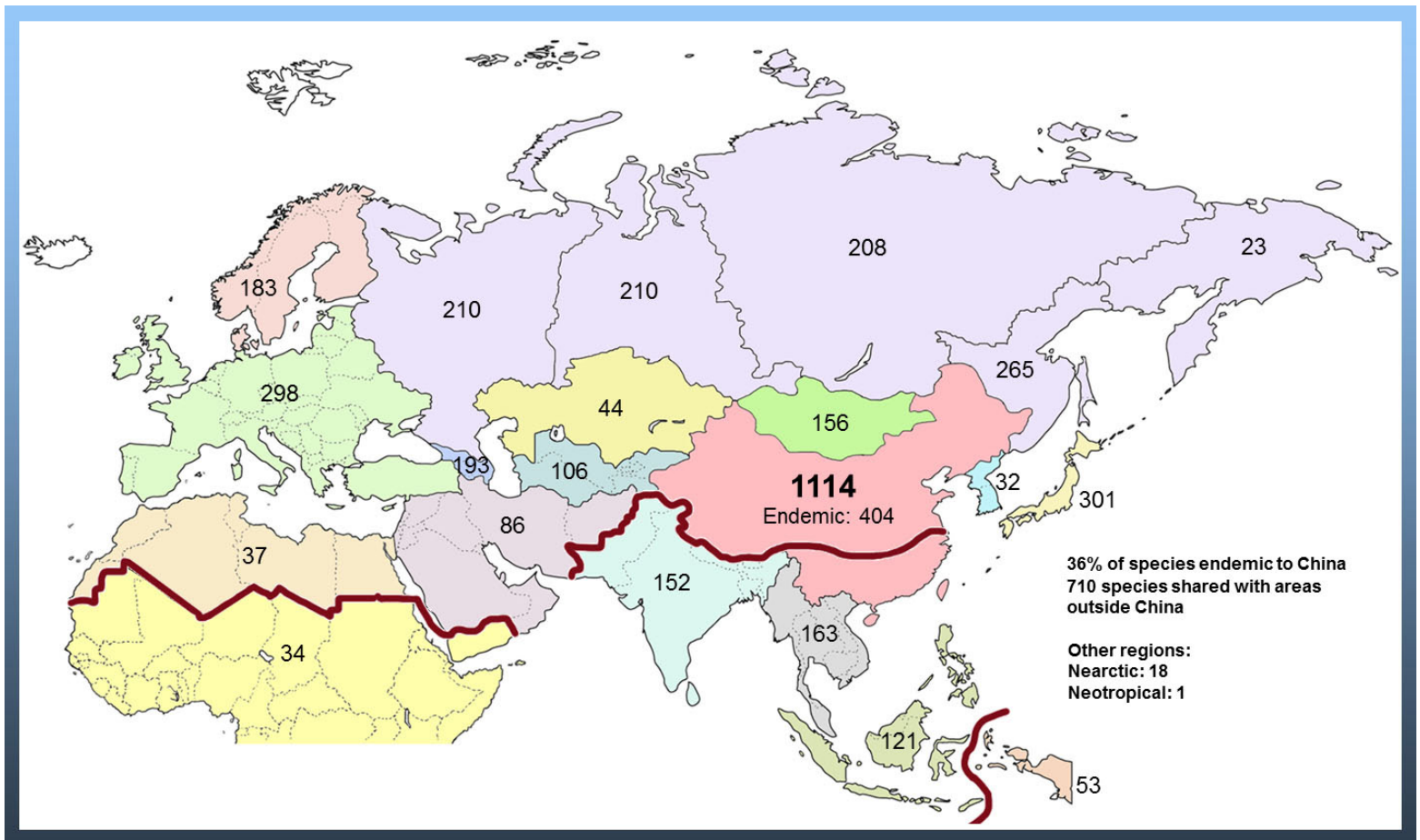


Figure 7. Number of tachinid species shared between China and other parts of the world, with an emphasis on the Palearctic Region. (From O’Hara, Shima & Zhang 2008.)

It was during the cataloguing of Chinese Tachinidae that I began to entertain thoughts of a grander plan to catalogue the Tachinidae of the world. I did not particularly want to go down this path for several reasons: 1) it would be a long-term project that would likely curtail significant revisionary work for many years; 2) it would require careful up-front planning and a sophisticated relational database; and 3) Monty was already working towards this goal. (I suppose I could add a fourth reason, unfounded optimism, because later in my announcement of the project I wrote “An optimistic guess might put the length of this project at five years, but it could take seven or eight”, O’Hara 2008: 7.)

I must have let my mind wander in unguarded moments towards thoughts of a world catalogue. Would it not be useful to have all the world’s tachinid names and distributions in one place in a single classification scheme? We already had nearly all the literature. Shannon had shown an aptitude for database development. Monty’s database was more taxonomically than nomenclaturally oriented and did not include distributions. A few discussions and e-mails later and a plan was born. It was initially conceived to be an international collaboration involving myself, Monty Wood, Vera Richter, Hiroshi Shima, and Shannon Henderson [Shannon Mahony at the time] (O’Hara 2008). The team has since dwindled to just the three of us in Ottawa for the simple reason that most of the work is literature-based and primarily concerns names, dates, types, distributions, and the interpretation of various nomenclatural quandaries. The other aspect of the work—revising the classification to adapt to the community’s and our (mostly Monty’s) perceptions of tachinid relationships—is, at the database level, merely a matter of changing names and species groupings.

The plan for a world Tachinidae catalogue centred around finding or creating a relational database that would suit our needs. This was back in 2007. Computer technology was well advanced by then and I suspected there was a taxonomic database out there that we could use and would have a longer life expectancy than *Platypus*. Most taxonomic databases were strong on specimen data and weak on nomenclatural data (e.g., *Mandala*, <https://www.gbif.org/tool/81360/mandala>). The list of possibilities was quickly narrowed down to none; we would have to create our own.

By this time I knew exactly what I wanted a cataloguing database to do. I did not know if it was possible, but my criteria were well established. We would be dealing with not just the 1500 valid names of genera and 8500 valid names of species of Tachinidae (O'Hara & Henderson 2018) but all the non-valid names as well, roughly doubling the total number of names. There were then all the other types of names to work into the mix: justified and unjustified emendations, names suppressed by the *Code* (ICZN 1999), available names of unrecognized species (*nomina dubia*), unavailable names (e.g., misspellings, manuscript names), *nomina oblita* and *nomina protecta*; to name all but the most obscure. All the various sorts of name-bearing types would need to be accommodated with standards applied for lectotypifications (see lengthy discussion in O'Hara, Shima & Zhang 2009: 10–11). For distributions, the world would have to be subdivided geographically in a sensible manner and synchronized with some major divisions already in use in regional catalogues (e.g., the divisions of Russia and the former Soviet Union as used in the Palaearctic catalogue of Herting & Dely-Draskovits 1993: 7–8). The boundary between the Nearctic and Neotropical regions would be arbitrarily set at the border between Mexico and the United States because the distributions of Mexican Tachinidae are too poorly known to adopt a boundary inside Mexico as advocated by Griffiths (1980). A boundary between the Palaearctic and Oriental regions in China would have to be set based on our experience with Chinese Tachinidae because there was no agreement on the boundary in the literature (indeed, the “boundary” is in reality a transition zone but something more definite was needed for cataloguing purposes). Place names (for type localities and geographic divisions) would have to follow as much as possible a standard reference to avoid arbitrary and even multiple spellings.

Catalogue of World Tachinidae database

Shannon felt that FileMaker Pro would provide a suitable platform for the sort of database I was thinking of. She went off to Toronto for advanced training while I thought about the user screens we might want and how they might be linked together to mirror a taxonomic hierarchy and lead off to screens on types and distributions at the most appropriate point. Perhaps the most fundamental decisions were to keep all literature in EndNote (where we had it already) and all taxonomic and nomenclatural information in FileMaker, and to separate names into the primary categories of subfamily, tribe, valid genus, available genus, valid species, and available species and to have these major options available on the homepage (Fig. 8).

We discussed how all the information listed in the last paragraph of the previous section might be incorporated into the database. I was only interested in how all these linkages would appear to the user, for instance how to get from an available species name to type data, or where emendations would be entered. The programming side was up to Shannon. I knew that the programming of the database would take months and likely involve the solving of complex problems beyond Shannon's formal training. No one at our Centre had advanced expertise in FileMaker

and Shannon would eventually solve the more perplexing obstacles by seeking the assistance of geek-level FileMaker Pro online forums.

Magically (or so it seemed to me) the database began to take shape. As the need for the distributional component approached I sat down with atlases and taxonomic catalogues for a couple of weeks and divided up the world, using *The Times Comprehensive Atlas of the World* (Times Books 2007). We also started lists of “standards” pertaining to how strings of information might be ordered to always appear in the same way. For example, here are three examples of data associated with two valid (uppercase bold italics) and one invalid (uppercase italics) generic names:

PROSOPEA Rondani, 1861d: 36 (as subgenus of *Frontina* Meigen, 1838, as “*Prosopèa*”). Type species: *Frontina (Prosopea) instabilis* Rondani, 1861 (as “*P. Instabilis* Mihi”) (= *Frontina nigricans* Egger, 1861), by original designation.

BRACHYMERIA Brauer & Bergenstamm, 1889: 116 [also 1890: 48]. Type species: *Pachystylum letochai* Mik, 1874 (as “*Letochae* Mik”, an improper correction from Mik’s original spelling of “*Letochai*”, an epithet based on the surname *Letocha* [see Article 32.5.2.1 of ICZN 1999]), by monotypy.

SCHAUMIA Robineau-Desvoidy, 1863b: 43. Type species: *Tachina inclusa* Hartig, 1838, by fixation of O’Hara *et al.* (2009: 46) under Article 70.3.2 of ICZN (1999), misidentified as *Tachina bimaculata* Hartig, 1838 in the fixation by monotypy of Robineau-Desvoidy (1863b, as “*Tachina bi-maculata*”).

The database was completed about ten years ago and except for minor tweaks is still the same now as it was then. Fig. 8 shows the homepage and Fig. 9 has a walk-through of the main screens of data associated with the species *Compsilura concinnata* (Meigen), a well-known tachinid of Old World origin that was introduced into the Nearctic Region for biological control purposes.

To see data on *C. concinnata* in the database (Fig. 9), the user can start on the *Compsilura* valid genus screen (upper left) or the *C. concinnata* valid species screen (middle left). If starting on the former, then the user has the option of accessing screens on the three available generic names (one of which is also the valid name and the others are synonyms) or selecting a species from the full list of valid species names. Selecting “*concinnata*” opens the valid species screen for this species. Here, summaries are visible of the full output for the species and also (separately) its distribution. A list of the 25 available names associated with the valid name (one name also being the valid name and the others are synonyms) is included to the right of the valid name data. A click on “*Tachina concinnata*” opens the

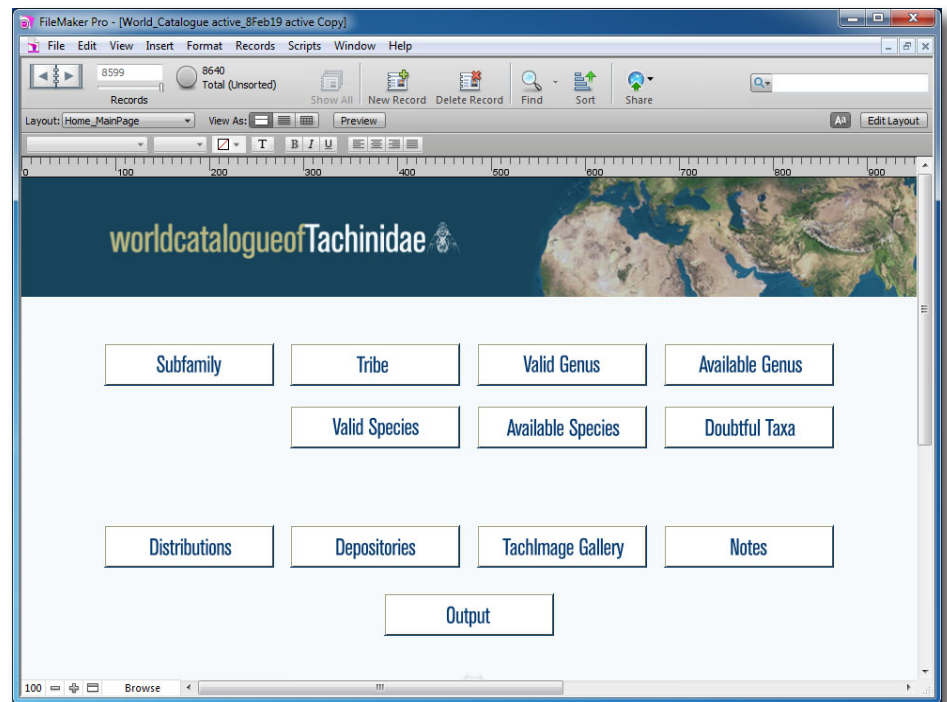


Figure 8. Home page for *Catalogue of World Tachinidae* database.

Figure 9. [Caption for figure on previous page.] Shown here are the main entry screens for *Compsilura concinnata* (Meigen) in the *Catalogue of World Tachinidae* database. In the upper left is the valid genus screen for *Compsilura* Bouché (the available genus screen is not shown). A click on “*concinnata*” in the species list opens the screen in the middle left, the valid species screen for *C. concinnata* (Meigen). A click on “*Tachina concinnata*” opens the screen in the upper right (right side of screen cropped), the available species screen for *Tachina concinnata* Meigen. A click on “Revise Type Information” opens the screen in the middle right, one of the Type Information screens (the one for Primary Type; there are other screens for Type Depository and Type Locality). Back on the valid species screen in the middle left, a click on “Distribution” opens the screen in the lower left, the main Distribution screen. This screen is the portal to additional distribution screens for each region. A click on “Palaeartic” opens the screen in the lower right (right side of screen cropped), the one for Europe (other tabs to the right of “Europe” open screens for other parts of the Palaeartic). A click on “Map” opens a reference map showing the divisions of the western Palaeartic.

available name screen (top right) and provides details about the name, author, date, page, and other names that might be associated with it (e.g., misidentifications, unjustified emendations, incorrect spellings). Clicking on “Revise Type Information” (right middle) opens the first screen of data associated with the name-bearing type. Other screens deal with “Type Depository” and “Type Locality”. All the type data is summarized in the preview window at the bottom of the screen. Distributions are associated only with valid species names, so back on the *C. concinnata* valid species screen (middle left) a click on “Distribution” opens the main screen for this species’ distribution (lower left). Each region is accessed separately to reach additional input screens. A complete summary of the distribution is given on the right side of the main screen. Clicking on “Palaeartic” opens the first screen associated with that region (lower right). The first screen is the one for Europe and countries with records for *C. concinnata* can be checked off here before toggling to screens with the other parts of the Palaeartic Region. Clicking “Map” opens a screen (middle right) showing a reference map to the major divisions of the western Palaeartic.

We have been populating the database with information about names, types, distributions and so forth for about ten years. Summer students helped initially but now most of the data entry is by Shannon and some by me and this gives us more control over the accuracy and consistency of the information going into the database. Virtually all the data from the catalogues on America north of Mexico (O’Hara & Wood 2004), China (O’Hara, Shima & Zhang 2009) and the Afrotropical Region (O’Hara & Cerretti 2016) has been entered, information has been entered but not completely verified for the Oriental Region (Crosskey 1976) and for Australasian and Oceanian Regions (Cantrell & Crosskey 1989), more work is needed (especially on name-bearing types) for the Neotropical Region (Guimarães 1971), and for the Palaeartic Region (Herting & Dely-Draskovits 1993) there is an especially large amount of work to do particularly on synonyms at the species level and name-bearing types.

Each year in January, Shannon performs a search for literature on Tachinidae using all the resources available to us through the library services of Agriculture and Agri-Food Canada. We also receive literature from colleagues, for which we are most grateful. All the new literature is compiled and listed each year in *The Tachinid Times*. The new literature is checked for new taxa, taxonomic changes, nomenclatural acts and distributions, and this information is entered into our database to keep it current. A spin-off from this activity is the irregular publication of *World Genera of the Tachinidae (Diptera) and Their Regional Occurrence* (O’Hara & Henderson 2018).

Checklist of World Tachinidae

Outputs from the *Catalogue of World Tachinidae* database can be programmed as desired. Shannon has created a few but our most popular is a full catalogue along the lines of O’Hara, Shima & Zhang (2009) and O’Hara & Cerretti (2016). Data for special purposes, such as numbers of genera or species by region, is exported into Excel for easy handling.

Exporting to text files is not as user friendly as exporting to Excel; in fact, there is no provision for an output to Microsoft Word. The best that can be achieved is a decent output to a PDF that then needs massaging in Word. We have reached a point where we have confidence that our data on the valid names of genera, and on the valid names and distributions of species, of Tachinidae is ready for circulation. We realize that in a project of this magnitude we surely have made mistakes and have overlooked relevant sources but we hope these are few. To mitigate this problem we have decided to call our checklist “preliminary” and to publish it electronically on our *Tachinidae Resources* website rather than in a peer-reviewed journal. This way we can correct and update it on an irregular basis in the same fashion as our world genera document.

The layout of the checklist is simple. It is a listing of species arranged by genus, tribe and subfamily. Each species is identified by a name (in bold italics), author and date (with these last two in parentheses if the species is no longer in its original genus). Following this is the distribution. Distributions are cited in an order and manner described in a lengthy section at the beginning of the checklist under Materials and Methods. Maps to regions and in some cases subregions are provided for easy reference. Cited below the distribution in the checklist is the original combination of the species name (in italics) followed by author and date. Each tribe starts on a new page and the page header throughout the checklist displays the proper subfamily and tribe. There is no index for two reasons: 1) it is time-consuming to compile, and 2) it is not as valuable as it used to be given that the text is searchable and the checklist is not meant to be printed.

The classification in the checklist is generally that in common use as determined by the authors (but let us know of inadvertent errors) but has some rearrangements here and there among Neotropical Tachinidae for the more obvious misplacements in the past. The bulk of the taxonomic changes we anticipate making in the future will be based on years of study by Monty Wood and will appear in the Chilean and New World catalogues (see below).

Where are all the species?

Six years ago I published an article entitled, *Where in the world are all the tachinid genera?* (O’Hara 2013). Genera were dealt with again by O’Hara & Henderson (2018) so here I will only briefly comment on the distribution of species of Tachinidae.

The number of described species of Tachinidae is constantly changing as new species are described and the names of others are being moved into synonymy. In our database we are also in the process of moving *nomina dubia* out of our lists of valid species. These are names of unrecognized species; usually names for which the name-bearing type is lost or has not been examined and matched to a species. These names are technically valid but

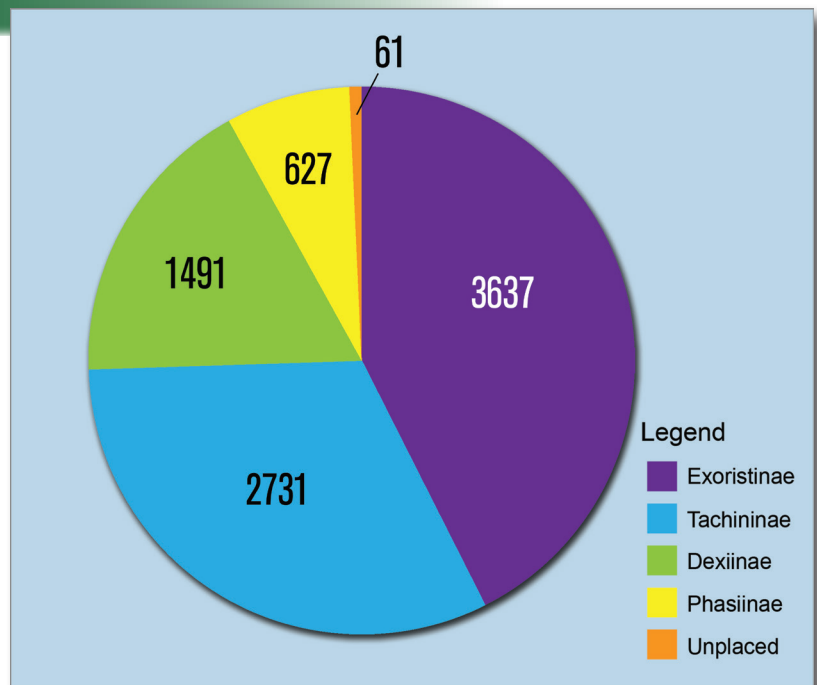


Figure 10. Number of species of Tachinidae per subfamily. Total = 8547.

because they are unrecognized we like to group them at the end of a genus in our catalogues and we do not count them among the valid species of a genus. According to these criteria the number of tachinid species listed in our checklist (version 1.0) is 8547. The number of species per subfamily is shown in Fig. 10. From largest to smallest the subfamilies are Exoristinae, Tachininae, Dexiinae and Phasiinae. Interestingly, the greatest morphological diversity is in the Phasiinae and Tachininae, and the subfamily with the most tribes is Tachininae with 24. Some rearrangements may be necessary within the family as a result of the recent molecular phylogeny of Stireman *et al.* (2019), most significantly regarding the tachinine tribes Macquartiini + Myiophasiini that were reconstructed as a basal clade sister to the rest of the Tachinidae.

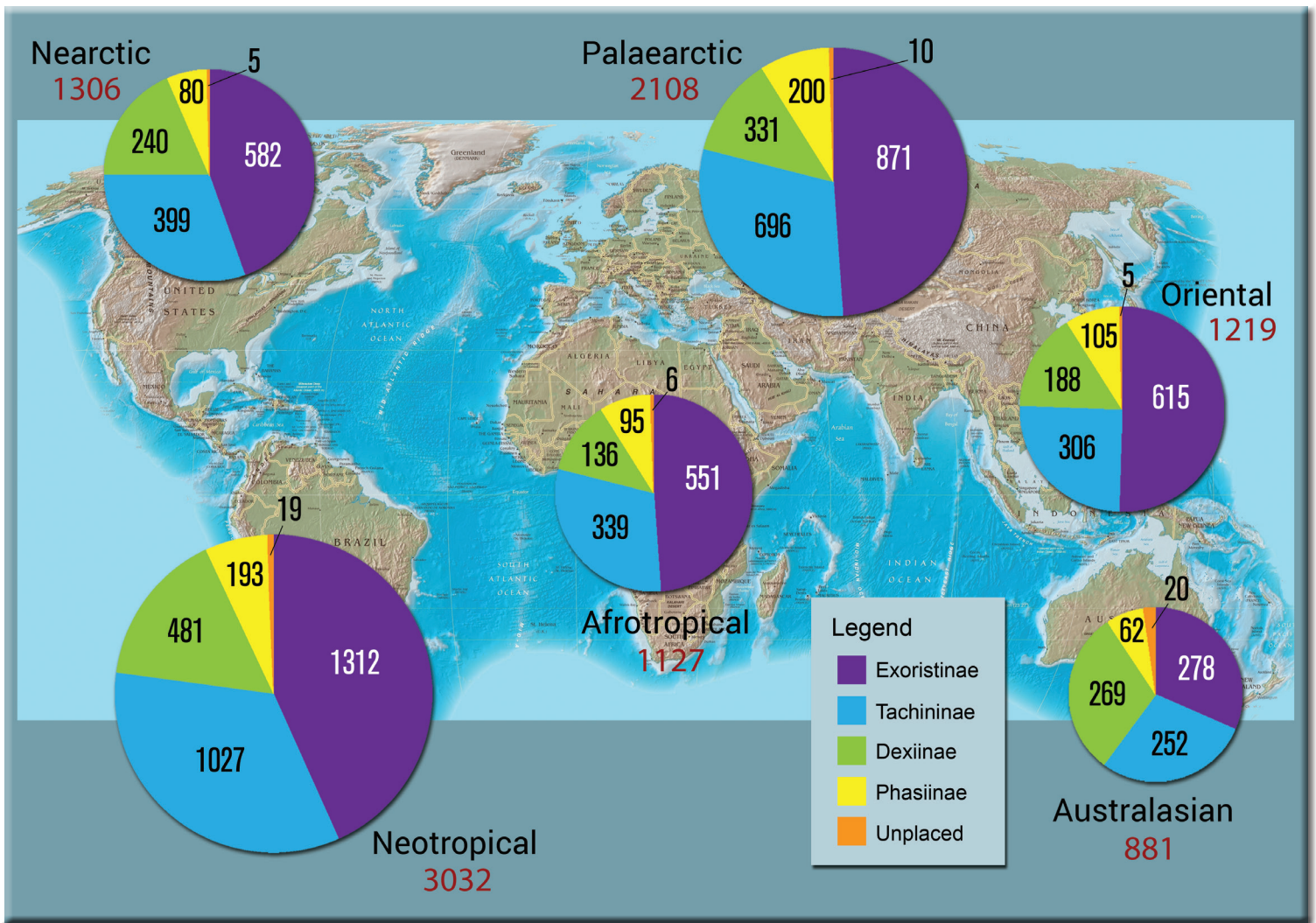


Figure 11. The number of described species of Tachinidae by biogeographic region and subfamily is shown in proportionally-sized pie charts. The total number of species per region is shown in red and the total number of species in the world is 8547.

The distribution of species by subfamily and number is shown in proportionally-sized pie charts for each biogeographic region in Fig. 11. These numbers are based on described species and the true sizes of the faunas are not accurately reflected by the pie charts. The Neotropical fauna is vastly underestimated; its true size could be twice or several times larger than the already-large known fauna. The faunas of the Nearctic and Palaeartic regions are better known and the number of undescribed species in each might be closer to 20% of the described species, although in the latter region the fauna of the western part is well known and most of the new species will be found

in the eastern part (especially in the Palaearctic portion of China). The percentage of undescribed species in the Afrotropical Region is uncertain but is likely significantly higher than for the Nearctic and Palaearctic Regions. The tachinid faunas of the Oriental and Australasian regions are much more diverse than indicated by their described species. O'Hara *et al.* (2004) estimated that Australia might have a tachinid fauna of over 3000 species and this could put the Australasian fauna in contention for second place after the Neotropical fauna when the world's tachinid fauna is better known.

The proportional sizes of tachinid subfamilies are also shown in Fig. 11. These are also a reflection of the revisionary work that has been done in each region but the relative proportions are likely more meaningful among regions than are the numbers of described species. If we accept this premise, then the Exoristinae are dominant in all regions except the Australasian where, interestingly and uniquely, the known faunas of the Exoristinae, Tachininae and Dexiinae are virtually the same size. In the other regions there is the same trend as there is in the world (Fig. 10) with the size of subfamilies decreasing in the same order: Exoristinae, Tachininae, Dexiinae and Phasiinae.

The future

Our ultimate goal is to produce a catalogue of world Tachinidae to the same level of detail as in the China and Afrotropical catalogues (O'Hara, Shima & Zhang 2009, O'Hara & Cerretti 2016). I cannot say for sure that we will reach this goal because some aspects of cataloguing the Palaearctic fauna, such as interpreting every name-bearing type and type locality for every available species in whatever language the information is given, is a slow process. We may need to reassess what we can achieve in a reasonable amount of time.

In the short term we have a detailed catalogue of the Tachinidae of Chile in a well advanced state. This is being prepared in collaboration with our colleague Christian González of the Instituto de Entomología, Universidad Ciencias de la Educación, Santiago, Chile. The next catalogue after that is expected to encompass all of the New World Tachinidae, replacing the catalogues of Guimarães (1971) and O'Hara & Wood (2004). Maybe in a future version of the world checklist we can add additional information, perhaps including bibliographic citations to the available species names and citing the few thousand relevant references in a bibliography at the end of the checklist.

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Manipulation of host behavior by *Leskia aurea* (Fallén) (Tachinidae)

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Host behavioral manipulation by parasites and parasitoids is a well-known phenomenon (Poulin 2013, Libersat *et al.* 2009). Popular examples include parasitic fungi, which force their insect host to climb and die in an open location from which the fungal spores will spread best to the environment, and horsehair worms that guide the host to jump into water before dying (e.g., McAuliffe 2016). Many parasitoid wasps are also known to induce behavioral changes in their host, which benefit the parasitoid development (Libersat & Gal 2013, Alford *et al.* 2016). The exact mechanisms of host manipulation are poorly known, but they are thought to be achieved by specific inhibition or activation of host neural signaling pathways by chemicals or proteins secreted by the parasite.

I would like to report here an obvious behavioral change in a lepidopteran host parasitized by a tachinid, *Leskia aurea* (Fallén) (Tachininae, Leskiini). *Leskia aurea* is widespread in Europe, although uncommon and mostly observed as single specimens. My own northernmost record is from the shore of Lake Sompio in Finnish Lapland (68.110N, 27.460E). The species parasitizes the larvae of wood boring clearwing moths (Lepidoptera: Sesiidae), apparently mainly *Synanthedon vespiformis* (L.) and *S. myopaeformis* (Borkhausen) in Central Europe (Tschorsnig 2017). In Finland, *Leskia aurea* has been reared only from *Synanthedon spheciformis* (Schiffermüller) and *S. scoliaeformis* (Borkhausen). Parasitism rates in *S. spheciformis* can reach up to 50% (Vuola & Korpla 1978), whereas *S. scoliaeformis* is attacked more rarely (Vuola & Korpla 1977).

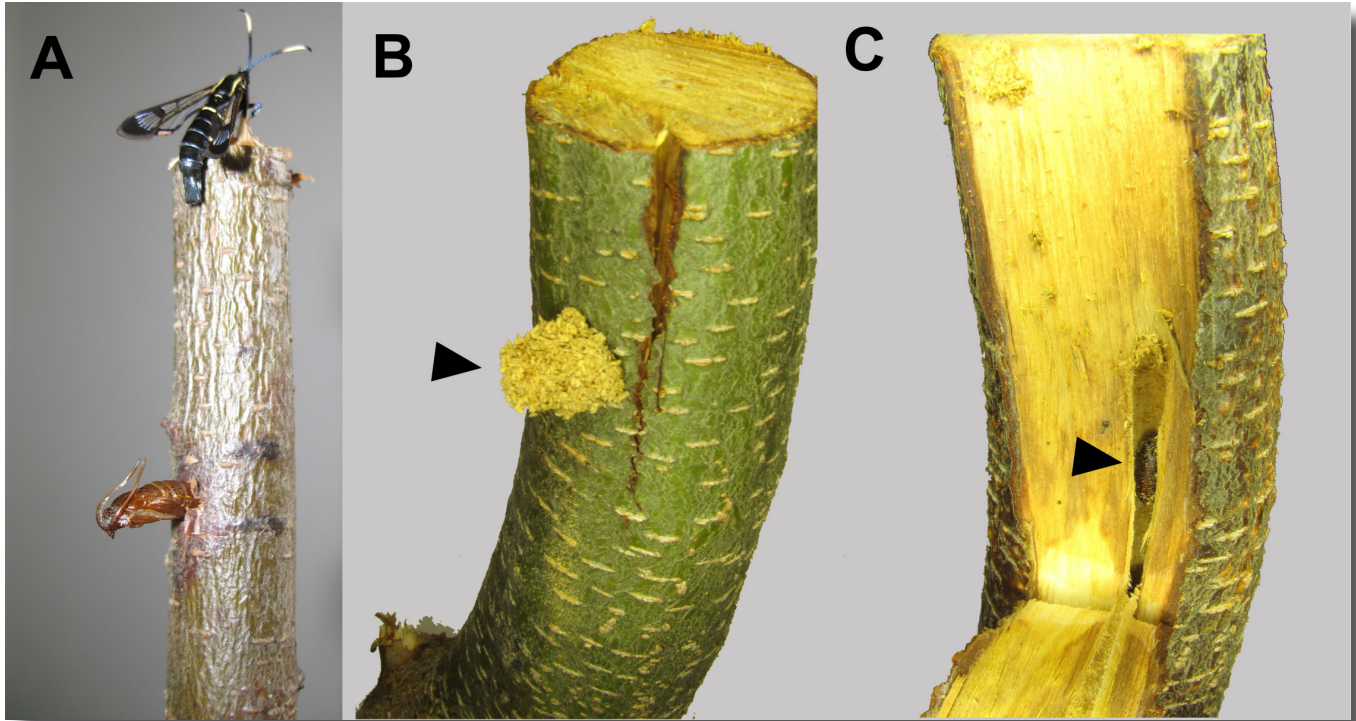


Figure 1. *Synanthedon spheciformis* clearwing and *Leskia aurea* reared from alder (*Alnus incana*) saplings. **A.** Newly emerged male *S. spheciformis* with the empty pupa halfway through the gallery exit. **B.** Larvae of *S. spheciformis* that are parasitized by *L. aurea* open the gallery exit and push out large quantities of frass mixed with silk (see arrow). **C.** The tachinid consumes the host larva completely and pupates close to the opening (see arrow). (Photos by J. Pohjoismäki.)

To the best of my knowledge, *Leskia aurea* is not only a rare example of host manipulation by tachinids in general, but also a particular example where parasitoid influence on host behavior is host specific. As the host hormones are likely to influence also the timing of the parasitoid maturation, the difference between the two hosts could be in the events preceding pupation. Notably, the main developmental difference between the two host species is that unlike *S. spheciformis*, *S. scoliaeformis* spins a cocoon. *Leskia aurea* larva could, for example, measure the host ecdysone hormone levels to decide when to kill and consume the host prior to the last molt. This activation of the parasitoid could also drive the behavioral phenotype in the host and if the host is enclosed within a cocoon, then the behavioral change cannot manifest itself. It makes intuitive sense that the behavioral phenotype in which the host larva opens the gallery exit would have an evolutionary benefit for *Leskia aurea*, by reducing the risk of the fly being trapped within the host gallery. This might also explain the higher parasitism rates in *S. spheciformis* than in *S. scoliaeformis*. These observations underscore the importance of rearing records and the basic understanding of the host biology in tachinid research.

My own records of *L. aurea* are solely from *S. spheciformis* (Figs. 1, 2). The moth larvae infest alder (*Alnus incana* (L.)) or less frequently birch (*Betula* spp.) saplings and young trees of up to 50 mm in diameter. The host plants typically grow on warm sandy soil or in otherwise barren landscapes and the main requirement seems to be that grass or other vegetation should not cover the base of the sapling. The presence of the moth larva can be detected from the extrusion of frass from the root base. Prior to pupation in late May, the full-grown larva will make an emergence tunnel, ending at 10–30 cm from the root base. The larva leaves intact bark to cover the exit, which is completely inconspicuous before the emerging moth breaks the cover, leaving the empty pupa characteristically lodged in the opening (Fig. 1A). In contrast, moth larvae parasitized by *Leskia aurea* open the exit tunnel through the bark and produce a considerable quantity of fine frass mixed with silk around the opening (Fig. 1B) (Vuola & Korpla 1978). Soon afterwards the parasitoid will kill the host and consume it completely before pupating in the host gallery a few centimeters away from the exit opening (Fig. 1C). The behavior of the parasitized larva appears to be highly typical and can be used as a diagnostic feature of *Leskia aurea* parasitism in *S. spheciformis*.

Although it seems straightforward to assume that *Leskia aurea* manipulates the larva of *S. spheciformis* to open an exit for it, the same cannot be said for parasitized larvae of the related species, *S. scoliaeformis*. *Synanthedon scoliaeformis* lives under the bark of full-grown birch trees, pupating in a cocoon under the bark. Larvae of this species parasitized by *L. aurea* spin a normal cocoon and the parasitoid pupates within this after consuming the fully grown host larva. Although I have not reared *S. scoliaeformis* myself, this behavior has been described by Vuola & Korpla (1977) and I can verify the identification of the tachinid involved. I have examined several specimens of *L. aurea* reared from *S. scoliaeformis* that are preserved with the host cocoons and empty puparia. One such series is in the collection of the Tampere Natural History Museum, Finland.



Figure 2. An adult *Leskia aurea* reared from *Synanthedon spheciformis* and recently emerged from its puparium. (Photo by J. Pohjoismäki.)

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Figure 1. Field expedition by the Entomology Department of the University of California, Berkeley, to Fort Seward, CA, in 1936. (From the Archives of the Essig Museum.)

One man's journey into the Tachinidae (Diptera)

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When I took on the task of sorting the tachinids in the Essig Museum, I knew it would be challenging. I didn't realize it would become a way of life.

The Essig Museum of Entomology on the campus of the University of California at Berkeley (UCB) has a research collection with over 5,000,000 pinned specimens. It is named in honor of Edward Oliver Essig 1884–1964, known largely for his work on aphids and other agricultural pests, but also author of general works including *Insects of Western North America* (Essig 1926). Essig was a UC professor from 1916 into the 1950s. Under his guidance, the California Insect Survey (CIS) was initiated in 1940 and became the basis for the current collection. The collection is strongest in holdings from western United States but also includes substantial material from Mexico, Central America, and the islands of the central Pacific. Field trips by staff and students to various locations, particularly within California, helped to build the collection (Fig. 1).

I had been associated with the museum off and on since the early 1960s, when I processed specimens in a work/study position. My passion for insects started early. Growing up in what was then a relatively undeveloped area of San Diego County (California), I spent a lot of time outdoors and became fascinated by butterflies, which I caught by hand (today I cannot get near them with a net). Encouraged by my family, I learned how to spread the victims and keep them in a box. But since we did not travel much, I quickly ran out of butterfly species. I inherited an insect cabinet from a distant relative and started filling it with all manner of specimens from katydids to beetles to dragonflies. It had not escaped my attention that there was an endless panoply of wasps, bees, and flies visiting the flowers of California buckwheat (*Eriogonum fasciculatum*), one of the common chaparral plants of our hillside. As my drawers started getting crowded, these insects came to dominate my collecting activities.

As a teenager, I was introduced to Charles Harbison, curator of entomology at the San Diego Natural History Museum. With endless patience, “Harby” showed me how to use a microscope and introduced me to the concept of identifying specimens with a key. I was totally engrossed trying to take obscure acalypterates through Curran’s (1934) key.

By the time I graduated high school, my cabinet contained equal portions of Diptera and Hymenoptera. I donated most of these to the San Diego museum and went off to UCB with the idea of becoming a professional entomologist. I had not thought about getting a job until a voice on the rooming-house phone asked if I was Paul Rude, did I know how to stick pins through bugs, and, if so, would I like to work in the museum? This was Jerry A. Powell, then Assistant Entomologist at the Essig Museum, now Professor Emeritus and a top specialist in Microlepidoptera. Like me, he had grown up in San Diego and had been a mentee of Charles Harbison. When I left for UCB, Harbison had called Jerry to tell him that a likely suspect was on the way.

It is a long story involving some of the notorious Berkeley hijinks of the 1960s, but I deviated from my original goal and ended up with an undergraduate degree in Communications. I spent a year in the Graduate School of Journalism and did a bit of work in radio. In 1971, I embarked on a year-long bus trip from Tijuana, Mexico, to Cochabamba, Bolivia, fulfilling an undeniable urge to see what lay beyond the Mexican hills that had been visible from my window as a child. Back in the United States, I worked a couple years in construction in Southern California and drove a taxi in San Francisco, among other jobs. But the lure of entomology drew me back to UCB, where I worked as a lab tech and field assistant for Jerry Powell and John T. Doyen, a professor and specialist in tenebrionid beetles. I was privileged to participate in many collecting trips in California and adjacent states, as well as in Baja California (Mexico).

In the mid-1970s, I filled some of the gaps in my scientific education at the local junior college, then re-applied to UCB’s Department of Entomology. I took a Masters in 1980, then worked several years at UC Davis producing integrated pest management manuals for California crops including cotton, tomatoes, and potatoes. After leaving UCD, I ended up spending most of my career as a general contractor. But when I retired at the end of 2014, I was eager to return to my original avocation. I offered my services as a volunteer to Peter Oboyski, Collections Manager



Figure 2. Peter Oboyski (left) and Paul Rude (right) examine drawers of unidentified Tachinidae in the Essig Museum of Entomology, UCB.



Figures 3–6. Four drawers of Tachinidae in the Essig Museum of Entomology, UCB. **3–4.** I started with 17 drawers like these of unsorted Tachinidae. **5.** Sorted Dexiniinae, showing some miscellaneous tribes and genera. **6.** Sorted Leskiini.

for the Essig Museum (Fig. 2). He asked which groups I was interested in, and the word “Diptera” barely escaped my lips when Pete said “follow me”. There had been no dipterist in the museum since the retirement of Frank Cole, author of *Flies of Western North America* (Cole 1969), in the 1970s. Since then, about 95 drawers of unsorted flies had accumulated: I clearly had my work cut out for me. In early 2015, I started spending two or three days a week re-acquainting myself with postorbital setae, vibrissae, and incomplete subcostas.

It took about a year and a half – with time off for a Berkeley-to-Savannah (Georgia) road trip and a couple visits to Baja – to get the flies sorted to family. Then it was time to try sorting some families to genus. I started with a few acalypterates, more or less at random, including Drosophilidae, Lauxaniidae, Sciomyzidae and Milichiidae. Having gained a bit of confidence, I ventured to look into the 17 drawers containing something like 12,000 unsorted tachinids (Figs. 3, 4). A daunting prospect indeed.

The tachinids were organized according to the *Catalog of the Diptera of America north of Mexico* (Sabrosky & Arnaud 1965). No doubt there is a rule that curation, like ontology, must recapitulate phylogeny, but with the number of tachinid tribes, this makes it tough to find anything unless you are already an expert. In order to place new specimens in the collection, or to find existing ones, I had to look up the genus in the catalog index, browse through the pages to find which tribe it was assigned to, then page forward or backward to see where that tribe was placed, after which I would try to find the appropriate drawer in the collection. All of this could easily take 15 minutes. At four flies per hour and with my retirement schedule of 20 hours a week for 30 weeks per year, that is 2,400 flies per year. I should be finished in about five years not counting time spent actually looking at specimens.

After consulting Martin Hauser, a dipterist at the California Department of Food and Agriculture in

Sacramento, I simplified things a bit. The tachs are still organized by subfamily (Fig. 5), but only the larger tribes have separate headings. “Large” can mean that the tribe has numerous genera, or that it includes one or more genera with a large number of specimens from our area. Genera of smaller tribes are filed under Miscellaneous Genera for the subfamily. For example, the Winthemiini get a heading because we have a drawer full of *Winthemia*, and the Leskiini are separated within Tachininae because we have specimens in quite a few genera (Fig. 6). On the other hand, Eutheriini, Palpostomatini, and Uramyini, which contain only one or a few genera, are filed as Misc Dexiinae. An Excel index shows where each genus is kept; a printout lives on a clipboard in the tach row.

The first pass through the tachinids took over a year. It would have taken more than a lifetime, but I concentrated first on picking out relatively recognizable taxa such as *Peleteria* and *Cylindromyia*. The objective was to make the collection more accessible, not to identify every specimen. But I gradually developed search images for other genera such as *Winthemia*, *Thelaira*, and *Leschenaultia*. I now have a pretty fair *gestalt* for 50 or 60 genera. It did not help that there are relatively few large sets of specimens; in most cases, I would have just one specimen at a time. This makes it difficult to decide on a certain character, as there is no way to check another specimen.

At first I relied only on the tachinid key in the *Manual of Nearctic Diptera* (MND) (Wood 1987). As with all large keys, it has a considerable learning curve. You have to learn how to weigh such terms as “usually”, how to extrapolate between conflicting figures, when to be suspicious of a result, and when to try both branches of a couplet. I took notes on quirks in the key, such as typos and conflicting couplets; these are summarized below in the Appendix. I would have given up soon after I began without the photos in the online *TachImage Gallery* (O’Hara & Henderson 2018). There were innumerable cases in which a quick check of the photos showed that an initial determination was far off the mark, and that I needed to start over. In other cases, it was warmly gratifying to find a portrait that looked just like my specimen! In those cases, I added a little + sign to the determination label.

I later ventured into MCAD, the *Manual of Central American Diptera* (Wood & Zumbado 2010). The MCAD key has its quirks too, but in some ways it is easier to follow. For one thing, it starts with readily visible supra-alar bristles, rather than prosternal setae that can be hard to see between the front coxae. I used it not only for Neotropical specimens, but also as a double-check for Nearctic specimens, often with good results. The big gap in coverage is Mexico, which apparently has quite a few genera or parts of genera that are not covered in either key. Let us hope that an enterprising systematist in Mexico City will one day work to fill this void.

At first, I passed over specimens from outside the United States. But as I became more confident, I started placing a few Mexican and Central American specimens too. To confirm determinations, I compared my results with identified specimens in the Essig collection, and also with specimens in the California Academy of Sciences in San Francisco and the California Department of Food and Agriculture in Sacramento.

Like all large keys, many of the couplets in both MND and MCAD refer to the same characters, so users answer the same redundant questions several times in taking a specimen through the keys. In an attempt to make the process more accessible, I have developed a searchable character matrix in Excel with the help of an online programmer (Fig. 7). The matrix is along the lines of the *MOSCHweb* key to Palaearctic Tachinidae (see Cerretti *et al.* 2012). Our much simpler system is limited for now to California genera, and is intended for less experienced users. Rather than trying to take users to a single genus, our objective is to narrow a search down to a handful of genera, each with a description and either a photo or a link to a photo source such as the *TachImage Gallery*. Users can then choose the best match. We are incorporating close-up photos of key characters. This is very much a work in progress. If you would like more information or would like to help, please contact me.

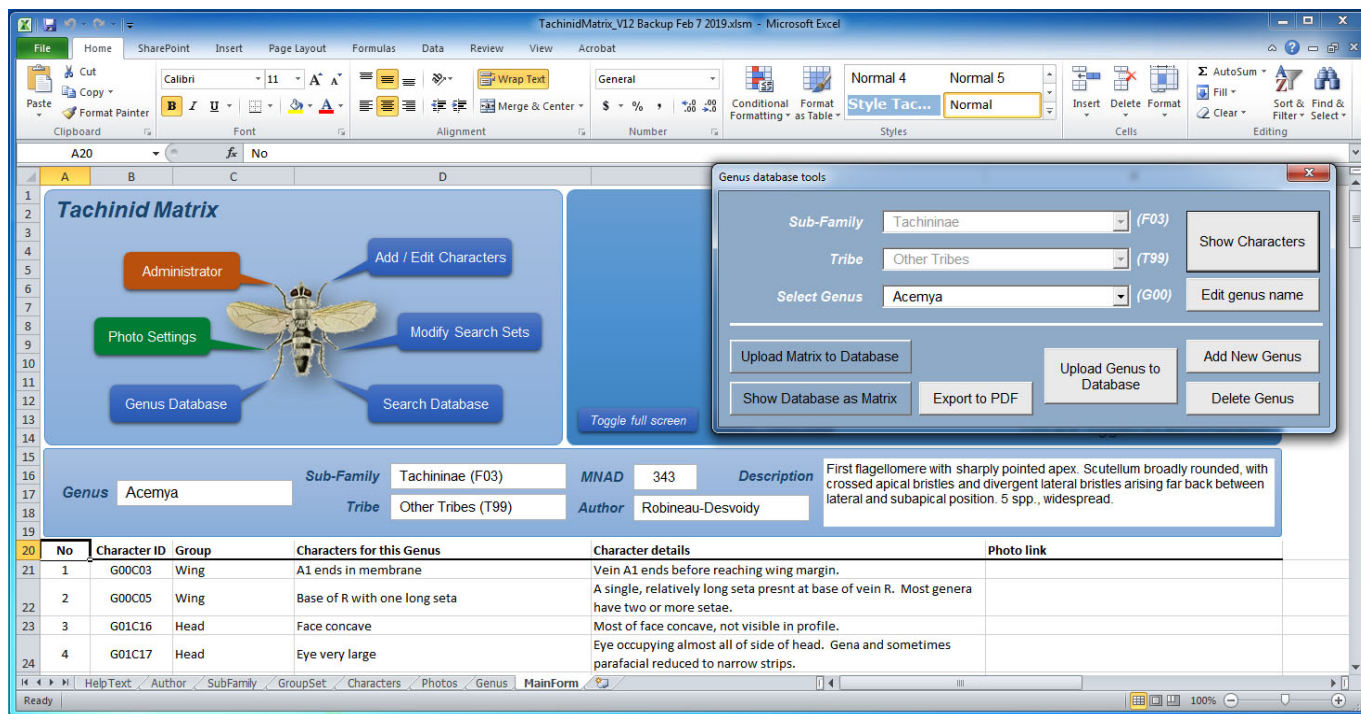


Figure 7. *Tachinid Matrix*, an Excel-based searchable character matrix developed by the author to assist with the identification of California tachinids.

By the most recent tally, the Essig collection includes 274 tachinid genera, 172 of them represented in California. There are a few genera noted in MND as not occurring in the West, including *Masiphya*, *Prooppia*, *Chaetoglossa*, and *Chaetonodexodes*. There are numerous species with reliable host records, especially from Jerry Powell’s rearings of Microlepidoptera. We still have one or two drawers of undetermined specimens from California, one from other states, two from Mexico, and two or three from other areas, mostly Costa Rica. I’ll be trying to whittle those down in coming months. In my spare time, I will also be reorganizing the collection according to the latest catalogue by O’Hara & Wood (2004).

Among the confounding features of the tachinid sort was the fleeting nature of the characters. Specimens that clearly had a bare prosternum when I first checked grew setae over the following few weeks, confounding my original determination. Others grew anipimeral bristles, lost scutellar bristles, or re-oriented their ocellar bristles. The most disturbing were those that evolved into sarcophagids while I wasn’t looking. I have searched the web for a character-stabilizing product to prevent such alterations, thus far with no results.

Continued tach exposure can produce psychological effects. A few months into the effort, I dreamed that I was sorting a tray with 115 tachs, all dark grey, all about the same size. I started picking out flies that looked similar enough to be congeneric, starting with about a dozen. The vision quickly went south: all of these turned out to be different genera. Then it got worse. The next group, this time only five specimens, all looked identical in dorsal view – same wing pattern, same pattern of pruinescence, and the same snarky expression. But no two of these were congeneric either; in fact the five specimens represented five tribes in two suborders. Then I realized that I wasn’t dreaming at all – I was wide awake at my scope in the middle of the day! With time, more pronounced symptoms developed: I woke at midnight with the feeling that my acrostical setae were shrinking and my postpronotum swelling. Fighting off the sweats, I re-read Franz Kafka’s (1915) *Metamorphosis* and took heart that it is fiction, but if the visions continue I will either seek professional help or switch to a more manageable group, perhaps Lonchopteridae or Braulidae.

In spite of the many discouraging moments, the project has rewarded me with a renewed sense of wonder at the astounding diversity of the insect world. It did not take long to become compulsive in my need to see the next bizarre tachinid face. Late at night, after hours over the scope and clearly in need of rest, I could not resist looking at “just one more”. Often, this turned out to be 20 or 30 more, but then I went to bed satisfied.

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I would not have survived this adventure without the generous support of Pete Oboyski and Martin Hauser here in California and, via the internet, Jim O’Hara of the Canadian National Collection of Insects in Ottawa, and John Stireman of Wright State University in Dayton, Ohio. Jim and John have been especially generous in identifying specimens from photos I sent them by email. Sincere thanks to all.

ACCESSORIES

For others studying tachs or other insects, I can recommend these accessories:

1. A plastic stage, assembled from inexpensive LEGO® parts available on the Internet, enables the viewing of specimens from nearly any angle without excessive handling (Fig. 8). See article by Dupont *et al.* (2015).
2. A small LED flashlight such as Streamlight’s Strion LED HL® can project an intense beam into obscure recesses where even the flexible arm of a microscope light source doesn’t quite reach, revealing setae otherwise invisible. These are also great for collecting at light, snooping under logs, etc. See <https://www.streamlight.com/en/products/detail/index/strion-led-hl>.
3. Since I work largely at home, carrying specimens back and forth, I hit upon this system for packing specimens securely into Schmidt boxes (Figs. 9, 10). For specimens in unit trays, all it takes is a strip of foam or similar material to fill any extra space between the trays and the sides of the box. Several boxes fit snugly in the insulated shopping bags sold in many grocery stores.



Figures 8–10. 8. LEGO® stage for viewing specimens at all angles. 9. Schmidt box for carrying specimens between museum and home. 10. Insulated shopping bag for carrying multiple Schmidt boxes snugly and safely.

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APPENDIX

Conflicts and typos in Wood's (1987) key to Tachinidae of America north of Mexico

Couplet 37, choice 2: "*Hind coxa bare on posteroapical margin*" → 38. This can lead to the opposite condition farther in key:

Couplet 38, choice 2: "*Apical scutellar bristles crossed ...*" → 39

Couplet 39, choice 2: "*Facial ridge bare ...*" → 48

Couplet 48, choice 2: "*Katepisternum with 2 or 3 bristles ...*" → 50

Couplet 50, choice 2: "*Vibrissa arising at level of lower facial margin ...*" → 51

Couplet 51, choice 2: "*M ending in wing margin ...*" → 52

Couplet 52, choice 2: "*Palpus pale brown or yellowish ...*" → 54

Couplet 54, choice 2: "*Anterodorsal setae of hind tibia uneven in length ...*" → 55

Couplet 55, choice 1: “*Hind with one or more setae on posteroapical margin ...*” → *Hubneria* Robineau-Desvoidy
Hence, it is not possible to identify *Hubneria* using this key.

Couplet 48, choice 1: “... *Katepisternum with four bristles arranged in a trapezoidal pattern (as in Fig. 177).*” I am not clear what “trapezoidal” has to do with it. The pattern I see in most specimens and in Fig. 177 is closer to a triangle. In any case, the choice is primarily between 4 bristles and either 2 or 3. The term is not needed for the rare exception noted in Choice 2.

Couplet 54, choice 1: “... *Abdominal tergites 2 and 3 each lacking median discal bristles*”

Choice 2: “... *Abdominal tergites 2 and 3 each with scattered median discal bristles*”

I have to wonder if these are typos. Is it actually tergites 3 and 4?

Couplet 61, choice 1: “*M ending in R_{4+5} some distance from wing margin ...*” → leads to *Erynnia* in couplet 65. But *E. condecens* as shown in *TachImage* has M and R meeting right at the margin.

Choice 2: “*M ending in wing margin separately from R_{4+5} ...*” → 67, but this leads to the opposite condition:

Couplet 67, choice 2: “*Anterodorsal bristles on hind tibia irregular ...*” → 70

Couplet 70, choice 1: “*Parafacial with setae ...*” → 71

Couplet 71, choice 1: “*Facial ridge with row of stout erect bristles ...*” → 72

Couplet 72, Choice 1: “*M ending in R_{4+5} before reaching wing margin ...*” → *Cloacina* Reinhard

Couplet 84, choice 1: “*Postpronotum with middle basal bristle displaced anteriorly, forming a triangle with outer and inner basal bristle ...*” → 85

Choice 2: “*Postpronotum with middle basal bristle more or less in line...*” → 86

Couplet 85, choice 2 leads to *Allophorocera* Hendel but specimens in the Essig collection determined by Monty

Wood as *Allophorocera arator* (Aldrich) have the postpronotal bristles in a nearly straight line, not in a triangle.

Couplet 96, choice 2: “...*if three pairs [of scutellar bristles] present, then the lateral bristles are shorter than the apical bristles ...*” → 100, 101, 102, 105, 106, 116, 118, 119, 123, 132, 135, 136, 138 → 147

Couplet 147, choice 2: “*Lateral scutellar bristle absent.*” I find this misleading. If “*lateral bristles absent*” is a possibility, then it should be mentioned in couplet 96. The reference to Fig. 184 is also misleading, as the figure shows *Eucelatoria* with laterals present but apicals absent; i.e., the laterals are infinitely longer than the apicals. I find couplet 147 especially confusing. There are species with three sets of scutellar bristles in which the apicals are apparently absent. Another interpretation might be that the apicals are strong but the subapicals are absent, but certainly the apicals are not crossed. At least some *Cryptomeigenia* follow this pattern.

Couplet 109, choice 2 → *Chetogena*. This does not work for *C. parvipalpus*, which lacks eye hair. The species then ends up in couplet 113, *Gueriniopsis*. Apparently *C. parvipalpus* is the only species with this feature. I checked the dozen or so species in the Essig Museum and the Cal. Academy; all except *C. parvipalpus* have the eye haired. Judging by what I see in collections, *C. parvipalpus* is by far the most common *Chetogena* in the western U.S. I suggest a revision along these lines:

Couplet 109, choice 2: should be “*Chetogena*, in part.”

Insert new couplet 112A after 112:

Couplet 112A, choice 1: Lower facial margin protruding; wing creased after bend of M, appearing as a stub or continuation of M → *Chetogena* in part.

Couplet 112A, choice 2: Facial margin not protruding (? not sure if this is accurate for *Gueriniopsis*); wing not creased → 113.

Couplet 114, choice 1: “*Frontal bristles descending to level of middle of facial ridge*” → *Exorista*.

To my eye, both Fig. 36 and the photo of *E. mella* in *TachImage* show the frontals extending only to the upper third of the ridge. It would be more accurate to say the frontals extend to the halfway point of the third flagellomere.

Couplet 116, choice 2: “*Apical scutellar bristles much shorter than sublateral or lateral scutellar bristles.*” The “sublateral” must be a typo for “subapical.”

Also, as in Couplet 96, the choice should probably be “Lateral scutellar bristles **either absent** or much shorter than the apical bristles.”

Couplet 118, choice 1: “*Subapical scutellar bristles divergent.*”

Choice 2: “*Subapical scutellar bristles convergent.*”

I have seen quite a few that are parallel.

Couplet 120, choice 2: “*Eye apparently bare, with hairs sparse and inconspicuous, if present ...*”

Wording is confusing. I would say “Eye bare or nearly bare. If hairs are present, they are sparse and inconspicuous.”

Couplet 126, choice 2 → *Eulasiona*

To get here you need to choose “*Eye covered with conspicuous dense hairs*” at couplet 123, choice 1, but *E. genalis* in *TachImage* has the eye bare. Same for a specimen in front of me.

Couplet 132, choice 1: “Subvibrissal ridge with a row of four or more well-developed bristles; this ridge longer than row of supravibrissal setae on facial ridge.”

Choice 2: “Subvibrissal ridge with at most three large bristles arranged in a row shorter than the row of setae above vibrissa.”

But a row with only 3 bristles can be longer than the row above the vibrissa. A row with four strong setae can be shorter.

Couplet 156, choice 2: “Postpronotum with at least three bristles, arranged in a triangle ...” → 159, 160, 162 → 163, but this leads to the opposite condition:

Couplet 163, Choice 2: “Postpronotum usually with three bristles, but if with four, then the three basal bristles arranged in a straight line ...”

Couplet 166, choice 1: “Scutum with three pairs of presutural acrostichal bristles ...”

Choice 2: “Scutum with only two pairs of presutural acrostichal bristles ...”

Any chance this is a typo? Should presutural be postsutural? Cf. couplet 336.

Couplet 218, choice 2: “... Last section of CuA_1 between half as long and twice as long ... as preceding section” → 119, 222, 223, 224 → *Kirbya* Robineau-Desvoidy

But *Kirbya aldrichi*, as shown in *TachImage*, is not even close.

Couplet 262, choice 1: “Bristles on lower part of parafacial reclinate ... extending ventrally nearly to lower margin of parafacial (Fig. 104) ...” → *Dichocera* Williston

But Fig. 204 seems to show them extending only about 2/3 of the way down. *Dichocera dichoceroides* in *TachImage* looks similar.

Couplet 279, choice 1: “ M ending in R_{4+5} well before wing margin ...” → 280, 281, 282, 283 → 284.

Couplet 279, choice 2: “... (Fig. 214)” → *Oestrophasia* Brauer & Bergenstamm

But in Fig. 214 and the *TachImage* photo for *O. clausa* the veins meet at the wing margin.

Couplet 288, choice 1 → *Vanderwulpia* Townsend

This works only for *V. sequens* Townsend, in which the prosternum is bare. The other species, *V. atrophopodoides* Townsend, has two pairs of strong setae on the prosternum.

Couplet 291, choice 2: “*Ocellar bristles procinate or absent ...*” → 292, 293, 294, 299, 303, 304 → 305, but this has a conflicting description:

Couplet 305, choice 1: “*Ocellar setae of female, and of both sexes of arctica (Sack), latero-clinate*” → *Trafoia* Brauer & Bergenstamm

Couplet 301, choice 1: “*Frontal bristles extending ventrally, nearly to lower margin of parafacial (Fig. 104) ...*” → *Dichocera* Williston

But Fig. 104 shows frontals reaching only the lower margin of the eye.

Couplet 314, choice 2: “*M with a distinct angular bend ...*” → 315, 316, → 317, but with no angular bend in M:

Couplet 317, choice 1: “*M not reaching wing margin, ending about where bend should be.*”

Couplet 317, choice 1: “*M not reaching wing margin, ending about where bend should be ...*” → 318

Couplet 318, choices 1 and 2 → *Bezzimyia* Townsend and *Besseria* Robineau-Desvoidy.

But the photo for *Besseria brevipennis* in *TachImage* clearly shows a normal bend in M.

Couplet 336, choice 1: “*Scutum with only one pair of presutural acrostical bristles, the posteriormost, which is situated anterior to scutellum.*”

Must be a typo, since setae next to scutellum would be postsutural. Cf. couplet 166.

Effect of short-term suboptimal temperature storage to assist large-scale production of *Exorista larvarum* (L.) (Diptera: Tachinidae)

by Maurizio Benelli

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The thesis summary given below is based on my recently defended Ph.D. thesis entitled, “Effect of short-term suboptimal temperature storage to assist large-scale production of two dipterans: *Exorista larvarum* (L.) and *Bactrocera tryoni* (Froggatt)”. This project was jointly administered by Alma Mater Studiorum Università di Bologna (Italy) and Macquarie University (Sydney, Australia), with supervisors Prof. Maria Luisa Dindo (Bologna) and Prof. Phil Taylor (Sydney), and co-supervisor Dr. Fleur Ponton (Sydney).

The thesis involved research on two dipterans: *Exorista larvarum* (L.) (Tachinidae) and *Bactrocera tryoni* (Froggatt) (Tephritidae). The focus below is on the tachinid, *Exorista larvarum*.

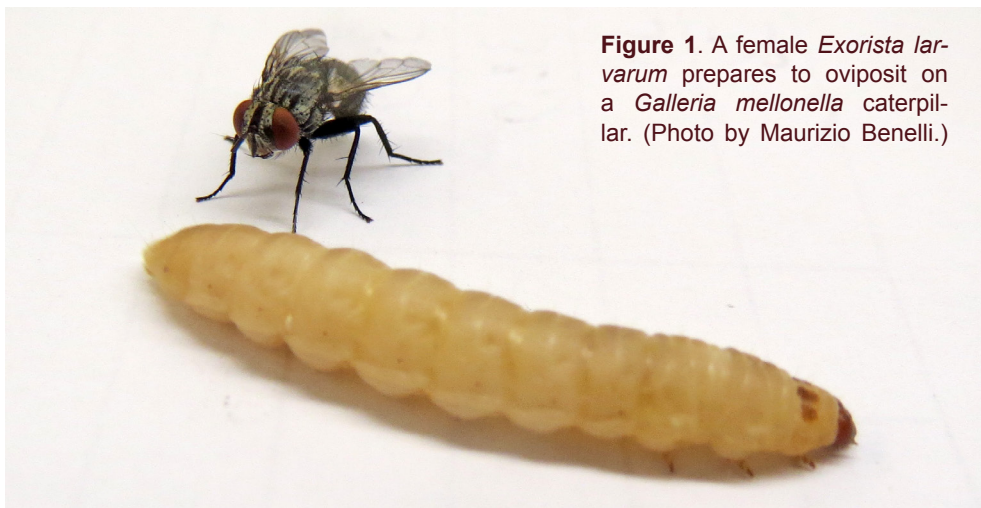


Figure 1. A female *Exorista larvarum* prepares to oviposit on a *Galleria mellonella* caterpillar. (Photo by Maurizio Benelli.)

Thesis summary

The rearing of insects has long been essential for many different purposes (research, pest management, obtainment of products such as honey, etc.) and the development of efficient rearing techniques and their refinement continue to be sought. Cold storage is a technique adopted for prolonging the developmental time of insects and thus increasing the efficiency of insect rearing. The advantages of cold storage protocols include a more flexible rearing schedule, the possibility to overcome periods of low production and, in case of beneficial insects, the synchronization of field releases with pest outbreaks in pest management programs. Native to the Palaearctic Region, *Exorista larvarum* (L.) (Diptera: Tachinidae) is a parasitoid introduced, and now established, in the United States as a biological

control agent of the gypsy moth, *Lymantria dispar* (L.). This parasitoid was chosen as a model biological control agent to develop cold storage protocols in the present Ph.D. thesis. The promising results obtained in the laboratory investigating the use of this fly for the control of several lepidopteran pest species, as well as the possibility to be easily mass reared, made *E. larvarum* a highly suitable candidate for developing a cold storage technology.

In the first study, the possibility of storing *E. larvarum* eggs at low temperatures (5°C, 10°C, 15°C and 20°C) after placement on artificial media was evaluated. Low-temperature treatments were applied in combination with the *in vitro* rearing technique, which offered the possibility to rear the parasitoid on plastic multi-well plates containing medium with no host components. This rearing method showed potential for the retrieval of eggs laid off the host that captive females oviposit on cage surfaces. Placing these eggs on artificial media is the only way to prevent their loss. By storing eggs on media at low temperatures it is possible to create a useful reserve of flies for use in colony maintenance, although some quality reductions were also observed. The best low temperature of the three tested was 15°C.

In the second study, the possibility of prolonging the pupal stage of *E. larvarum* by storing puparia at low temperatures was investigated. This study may facilitate the utilisation of tachinids in biological control programs. In fact, during mass production of tachinids in a rearing facility, fly emergence may need to be delayed before field releases with minimum impact on fly performances; for example, when the target insect pest is scarce, or it is in an unsuitable stage, or when the weather is unfavourable. The best low temperature for storing *E. larvarum* puparia was found to be 15°C.

Both studies on *E. larvarum* were performed at the Department of Agricultural and Food Sciences at the University of Bologna (Bologna, Italy). The thesis was developed in the framework of a cotutelle agreement between the University of Bologna and Macquarie University (Sydney, Australia) and explored also the effect of cold storage on the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), a tephritid fly considered the most economically damaging insect pest of Australia.

The thesis will be available online in March 2019 at the following link: <http://amsdottorato.unibo.it/8492/>.



Figures 2–5. *Exorista larvarum* development. **2.** A female *E. larvarum* ovipositing on the factitious host *Galleria mellonella* (L.) (Lepidoptera: Pyralidae). **3.** Eggs of *E. larvarum* on host. **4.** Mature third instar larva abandoning host remains. **5.** Puparium formation. (Photos by Maurizio Benelli.)

Records of the Japanese beetle and its parasitoid *Istocheta aldrichi* (Mesnil) (Diptera: Tachinidae) in Québec, Canada

by Marie-Eve Gagnon and Marjolaine Giroux

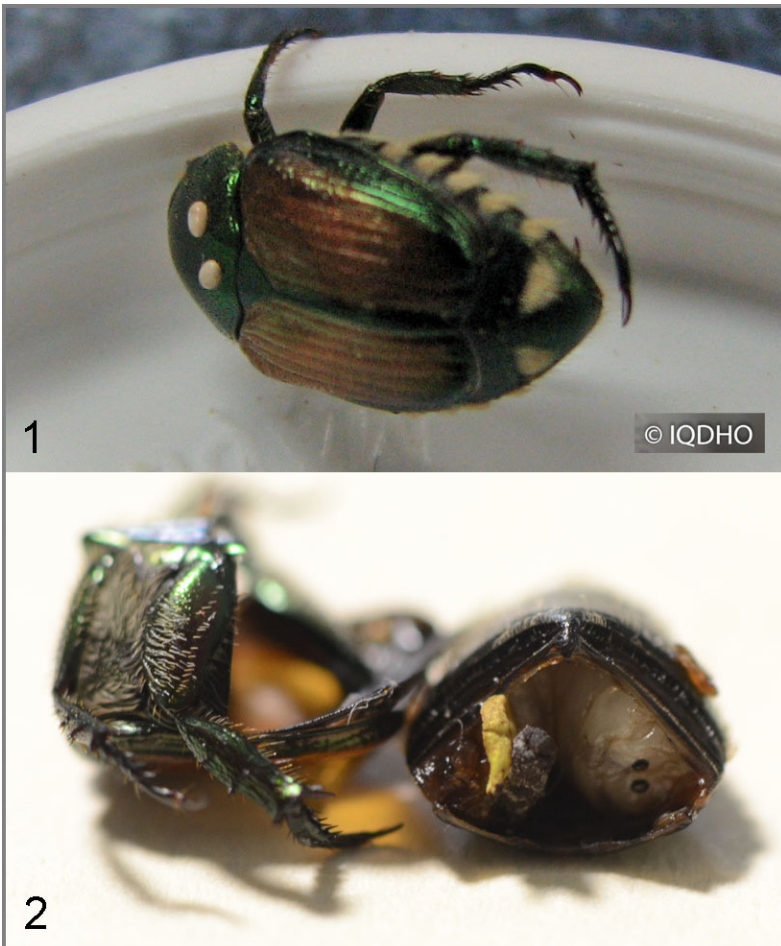
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The Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), was first discovered in North America in 1916 in New Jersey, USA (Clausen *et al.* 1927). The oldest known record in Canada is a specimen collected in 1929 from Simcoe, Ontario and housed in the Canadian National Collection of Insects in Ottawa (pers. comm., CNC

Collection Manager Owen Lonsdale). The Japanese beetle is now established throughout eastern Canada (from Ontario eastward) and has been found recently in the Vancouver area of British Columbia (CFIA 2017, 2019). Larvae of Japanese beetles feed on the roots of turf grass and other plants and adults feed on the foliage and fruit of many plants.

At the Jardin botanique de Montréal [Montréal Botanical Garden], the Japanese beetle has been a pest since 2010 (pers. comm., Stéphane Labelle). During the summer of 2017, a horticulturist at the Jardin botanique noticed small white eggs on the pronota of Japanese beetles and asked us if they could be from a parasite. This observation prompted us to investigate the source of these white eggs, and the results of this study are presented here.

Twenty adult Japanese beetles bearing white eggs on their pronota (similar to the beetle shown in Fig. 1) were collected for us at the Jardin botanique de Montréal from mid-July to the beginning of August 2017. These beetles were placed in rearing cages. After 5 or 6 days in captivity, individuals were dying. Two dead beetles were dissected and each had a fully grown fly larva in the abdomen (one shown in Fig. 2). The next day, one fly larva had formed a puparium. The remaining 18 beetles were left in the rearing container to allow the fly larvae to pupariate inside their hosts.



Figures 1–2. 1. A Japanese beetle collected in Granby (QC) in 2009 with tachinid eggs on its pronotum. (Photo courtesy of B. Mongeau, IQDHO.) 2. A dead and dissected Japanese beetle with an *I. aldrichi* larva in its abdomen. (Photo by M. Giroux, Insectarium de Montréal.)

In November 2017, the 18 remaining beetles were gently opened and we found a fly puparium in the abdomen of each one. The specimens were then placed in cold storage (4°C) for eight months. At the end of this period the specimens were returned to room temperature but no adults emerged from the puparia.

To determine the identity of the fly parasitoid, we sent half of two puparia to LifeScanner (<http://lifescanner.net/>) for DNA COI barcoding (code numbers BOLD-CK5 and BOLD-KW5; the remaining halves of the puparia are deposited in the Collection Insectarium de Montréal). LifeScanner is a DNA barcoding service for Citizen Scientists that consists of a standardized sampling kit, mobile app, and standardized laboratory workflow. Taxonomic identifications are generated through the Barcode of Life Data (BOLD) Systems ID Engine (Ratnasingham & Hebert 2007). The barcoding results identified the fly species as the tachinid *Istocheta aldrichi* (Mesnil).

Istocheta aldrichi was introduced into the United States for control of the Japanese beetle in 1920 (Potter & Held 2002). It was first reported from Canada by O'Hara (2014), who caught a single adult in Nepean (Ottawa, Ontario) in 2013. Eggs had been seen on adult Japanese beetles in Canada prior to this time but their identification as *I. aldrichi* had not been confirmed.

An Internet search by us found reports of Japanese beetles in Québec with eggs on their pronota and presumably parasitized with *I. aldrichi*. In one report, a horticulturist noted parasitized beetles in her nursery in Becancour in 2017 (<http://www.vivaces.net/ScarabeeParasitoide.html> [in French]). She also observed parasitized beetles in the Montérégie and Cantons de l'Est regions of Québec that same year. Parasitized beetles were also observed in Gatineau in 2017 (by senior author) and the Citizen Science website <https://www.inaturalist.org/> reported observations of parasitized Japanese beetles in the area of Joliette (2015) and Sherbrooke (2017). In 2018 we received a picture (Fig. 1) of a parasitized Japanese beetle caught on 21 July 2009 in Granby, Québec. Since no tachinid other than *I. aldrichi* is known to parasitize the Japanese beetle, these observations of tachinid eggs on Japanese beetles at various locations in Québec over

Table 1. Earliest records of *Popillia japonica* at locations in Québec based on a survey of entomological collections.

Locality	Year(s)	No. of specimens	Collection
Saint-Hubert	1938	1	QMOR
Farnham	1972	12	QMOR
Hull	1998	2	CMNC
Saint-Armand	1998	1	SLTC
Saint-Jean-sur-Richelieu	1999	16	SLTC
Joliette	2000	9	SLTC
Trois-Rivières	2004	1	CPTO
Laval	2007	1	CPTO
Saint-Armand	2007	4	QMOR
Mont-Saint-Hilaire	2008	2	SLTC
Saint-Armand	2008	14	IMQC
Contrecœur	2010	1	SLTC
Portneuf	2014	1	CIQ
Ste-Foy	2014	1	CIQ
Montréal	2015	41	SLTC
Rive-Sud de Québec	2015	1	CIQ
Terrebonne	2017	10	SLTC
Laval	1975–1997	17	SLTC
Frelighsburg	1994–1996	18	SLTC
Berthierville	1997–1998	31	SLTC
Longueuil	2001–2011	205	SLTC
Montréal	2001–2013	17	IMQC
Aylmer	2005–2016	26	CMNC
Contrecœur	2008–2010	10	IMQC
Capitale nationale	2015–2017	3	CIQ
Sainte-Marthe-sur-le-Lac	2016–2017	29	SLTC

Collection acronyms:

- CIQ – Collection d'insectes du Québec, Québec, QC, Canada.
- CMNC – Canadian Museum of Nature's Insect Collection, Ottawa, ON, Canada.
- CPTO – Pierre De Tonnacour collection, Ile-Perrot, QC, Canada.
- IMQC – Collection Insectarium de Montréal, Montreal, QC, Canada.
- QMOR – Collection Entomologique Ouellet-Robert, University of Montréal, Montreal, QC, Canada.
- SLTC – Stéphane Le Tirant collection, Terrebonne, QC, Canada.

the past ten years suggest that *I. aldrichi* has been in the province for some years before its presence in Canada was formally confirmed and reported by O'Hara (2014).

We started a survey of *I. aldrichi* across Québec in 2018. We plan to document the presence of this tachinid with the help of Citizen Science participants and submitted images of parasitized beetles. We are also collecting information on the Japanese beetle itself. We have already surveyed a number of collections to document their earliest records of the beetle in Québec (Table 1). The earliest specimen of a Japanese beetle in Québec that we have recorded was collected in St-Hubert by Joseph Ouellet in 1938 (1 male, QMOR).

Researchers at Agriculture and Agri-Food Canada are developing a project to survey the Japanese beetle and *Istocheta aldrichi* across Canada. We are collaborating with these researchers by surveying for this pest and its tachinid parasitoid in the province of Québec, where we will also monitor parasitism rates to evaluate the efficiency of the parasitoid. The Japanese beetle is very unpopular, but quite noticeable, and we hope to gather as much information as we can on this natural biological control agent.

Acknowledgements

We thank Maxim Larrivée (Insectarium de Montréal), Lorraine Bluteau (Jardin botanique de Montréal) for capturing the specimens, curators of the entomological collections for their help and support, and Brigitte Mongeau (Institut québécois du développement de l'horticulture ornementale [IQDHO]) for allowing us to use her picture of a parasitized beetle from Granby.

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Revisiting homonyms in the genus *Tachina* Meigen (Diptera: Tachinidae)

by James E. O'Hara

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Abstract

The rules of nomenclature regarding junior homonyms among species-group names are briefly reviewed. The status of seven species-group names in the genus *Tachina* Meigen, 1803 (Fig. 1) that were interpreted as junior homonyms and declared invalid by P.H. Arnaud Jr. in 1992 and 1994 are re-evaluated. The status of one junior primary homonym remains unchanged. Of the six other names treated as junior secondary homonyms by Arnaud, five are reinstated as valid names in the genus *Tachina*. The replacement names they had been given previously are thus invalid and fall into synonymy with the original names. The following nomenclatural changes are necessary according to the ICZN Code: *Fabriciella hispida* Tothill, 1924, **status revived** (as *Tachina* (*Nowickia*) *hispida* (Tothill)), with junior synonym *Fabriciella ampliforceps* Rowe, 1931; *Fabriciella intermedia* Reinhard, 1942, **status revived** (as *Tachina* (*Nowickia*) *intermedia* (Reinhard)), with junior synonym *Tachina californimyia* Arnaud, 1992, **new synonymy**; *Fabriciella latifrons* Tothill, 1924, **status revived** (as *Tachina* (*Rhachogaster*) *latifrons* (Tothill)), with junior synonym *Tachina oligoria* Arnaud, 1992, **new synonymy**; *Jurinia nitida* van der Wulp, 1882, **status revived** (as *Tachina* (*Rhachogaster*) *nitida* (van der Wulp)), with junior synonym *Upodemocera robinsoni* Townsend, 1915; *Fabriciella spinosa* Tothill, 1924, **status revived** (as *Tachina* (*Nowickia*) *spinosa* (Tothill)), with junior synonym *Tachina nearctica* Arnaud, 1992, **new synonymy**. Additionally, *Tachina hispida* Robineau-Desvoidy, 1830 is moved from its placement as a *nomen dubium* in Tachinidae to a *nomen dubium* in *Exorista* Meigen, 1830.



Figure 1. A male of the genus *Tachina* Meigen, *Tachina* (*Nowickia*) *latifacies* (Tothill) from North America. Images from TachImage Gallery (O'Hara & Henderson, 2018; photos by S.J. Henderson.)

Introduction

The *Manual of Nearctic Diptera* (McAlpine *et al.* 1981, 1987, 1989, hereafter the *Manual*) (Fig. 2) was the beginning of a new era in Nearctic dipterology. Dipterists were finally able to replace their worn copies of the classic *Families and Genera of North American Diptera* (Curran 1934) and at the same time pair this new manual with another recent extraordinary resource, *A Catalog of the Diptera of America North of Mexico* (Stone *et al.* 1965). Indeed, the need for a replacement of Curran's work was all the more pressing in light of the new catalogue.



Figure 2. The three volumes of the *Manual of Nearctic Diptera* (McAlpine *et al.* 1981, 1987, 1989). (Photo by J.E. O'Hara.)

The manner in which the *Manual* was planned and prepared was discussed in the introduction to the first volume and was reviewed in the later *Festschrift* honouring the coordinators of the project (Cumming *et al.* 2011, Sinclair *et al.* 2011).

Of particular significance to the subject of this article was the decision that no new taxa would be proposed in the *Manual*. Overt changes to the current classification were also frowned upon. This posed a problem for D. Monty Wood (Fig. 3), the author of the Tachinidae chapter (Wood 1987), because he was in the midst of a reclassification of Nearctic tachinids at the same time as he was preparing his chapter for the *Manual*. He wrote his key to conform to his new ideas about generic concepts and circumvented the *Manual* guidelines against new taxonomic acts by using footnotes to add species from other genera to the genera being keyed. These were *de facto* new combinations but their innocent wording escaped the ire of the other *Manual* coordinators.



Figure 3. Monty Wood in his office at the Canadian National Collection of Insects in Ottawa, ca. 1989. (Photo by J.E. O'Hara.)

The new combinations of Wood (1987) and the key itself essentially ushered in a new generic classification for North American Tachinidae. However, there were literally hundreds of new combinations and as a result some species names that were fine in their previous combinations were now homonyms. These were not identified in the *Manual* chapter and their presence was left for others to discover and sort out. The first author to take this on was Paul Arnaud of the California Academy of Sciences in San Francisco, a respected dipterist and co-author of the Tachinidae chapter in the earlier *Catalog of the Diptera of America North of Mexico* (Sabrosky & Arnaud 1965). Arnaud found what he believed to be junior homonyms in the genus *Tachina* Meigen, 1803 (Fig. 1) resulting from Wood's synonymy of *Nowickia* Wachtl, 1894 and *Metopotachina* Townsend, 1915 with *Tachina*. Six names were treated as homonyms in one paper (Arnaud 1992) and one overlooked homonym was the subject of a second paper (Arnaud 1994).

Before I discuss the papers of Arnaud (1992, 1994) and the homonyms proposed therein, I will briefly digress for a review of the meaning of “homonym” in the sense of the *International Code of Zoological Nomenclature* (ICZN 1999, hereafter the *Code*).

The *Code* requires that each species in a genus have a different name. This gets a little complicated because there are four types of species-group names:

Available name – a name that satisfies the provisions of Articles 10 to 20 in the *Code*. Generally speaking, a new species must be properly published, named, described, and represented by a name-bearing type (e.g., a holotype).

Unavailable name – a name that does not satisfy all the provisions of Articles 10 to 20 in the *Code*. This can be a manuscript name cited in a paper without a description or a name that appeared in an unpublished work (e.g., a hand-out at a congress).

Valid name – in short, an available name that is properly used for a species. *Musca domestica* Linnaeus is the valid species name for the house fly.

Invalid name – in short, an available name that is lower in priority for a species than another name (i.e., the valid name). In most species lists, these are the names listed in synonymy below a valid name.

Next we come to homonyms, which are central to the subject of this article. Here I quote the meaning of a homonym, as it pertains to species names, directly from the Glossary of the *Code* (1999: 105–106):

“In the species group: each of two or more available specific or subspecific names having the same spelling, or spellings deemed under Article 58 to be the same, and established for different nominal taxa, and either originally (primary homonymy) or subsequently (secondary homonymy) combined with the same generic name [Art. 53.3].”

Primary homonym discovered by Arnaud (1992)

Primary homonyms are generally straightforward. An author describes a species in a binomen that is exactly the same as one published previously by the same or different author. According to Article 57.2, the senior (older) name takes priority and the junior name is permanently invalid. Primary homonyms are unaffected by such taxonomic acts as moving species from one genus to another.

Paul Arnaud found one pair of primary homonyms when he investigated the status of species names in *Tachina* after the recombinations of Wood (1987). By definition, these primary homonyms existed before Wood’s key but they eluded discovery until Arnaud’s scrutiny of *Tachina* names.

***Tachina florum* Walker, 1849: 722.**

This was treated as valid by both Sabrosky & Arnaud (1965: 994) and Wood (1987: 1244). The former recognized the species as *Nowickia (Fabriciella) florum* (Walker) and the latter as *Tachina (Nowickia) florum* Walker. Arnaud (1992: 166–167) discovered that the Walker name is a junior primary homonym of *Tachina florum* Robineau-Desvoidy, 1830, a name currently in synonymy with the Palearctic species *Exorista (Adenia) rustica* (Fallén) (Herting & Dely-Draskovits 1993: 127). The name *Tachina florum* Walker is thus permanently invalid. It was replaced by the next oldest synonym and the valid name for the species became *Tachina (Nowickia) dakotensis* (Townsend, 1892) (Arnaud 1992). Later, *Tachina florum* Walker, 1849, was placed in synonymy with *Tachina (Rhachogaster) algens* Wiedemann, 1830 by O’Hara & Wood (2004: 331) but this did not affect the status of *Tachina (Nowickia) dakotensis*.

Secondary homonyms sensu Arnaud (1992, 1994)

The six species-group names treated as secondary junior synonyms by Arnaud (1992, 1994) are listed in alphabetical order by species name below and the status of each is reviewed and re-evaluated.

1. *hispida* Tothill, 1924: 265, *Fabriciella*.

COMBINATION OF SABROSKY & ARNAUD (1965: 995): *Nowickia* (*Nowickia*) *hispida* (Tothill, 1924).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina hispida* (Tothill, 1924).

HOMONYMY *SENSU* ARNAUD (1992: 166): *Tachina hispida* Tothill, 1924 *sensu* Wood (1987) was recognized as a junior secondary homonym of *Tachina hispida* Robineau-Desvoidy (1830: 189). Sabrosky & Arnaud (1965: 995) had listed one junior synonym of *hispida* Tothill, *Fabriciella ampliforceps* Rowe, 1931. Arnaud (1992: 166) replaced the invalid name *hispida* Tothill with the name of the junior synonym, with the valid name becoming *Tachina ampliforceps* (Rowe, 1931).

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina ampliforceps* (Rowe, 1931).

COMBINATION OF O'HARA & WOOD (2004: 326): *Tachina* (*Nowickia*) *ampliforceps* (Rowe, 1931).

PRESENT INTERPRETATION: *Tachina hispida* Robineau-Desvoidy, 1830 was treated by Bezzi & Stein (1907: 337) as a junior synonym of *Tachina* (*Tachina*) *larvarum* (Linnaeus, 1758). For nomenclatural reasons, *Tachina* Meigen, 1803 at the time of Bezzi & Stein (1907) was the name in use for present-day *Exorista* Meigen, 1803 (see explanation in Sabrosky 1999: 138); *Tachina* and *Exorista* are taxonomically distant genera and belong to different subfamilies.

Tachina hispida Robineau-Desvoidy was not listed in Herting (1984) and was relegated to “Doubtful taxa in Tachinidae” by Herting & Dely-Draskovits (1993: 447). This name is not so “doubtful” as it may seem. Its resemblance to *Tachina littoralis* Robineau-Desvoidy, 1830 was noted by the author himself (“Cette espèce est tout-à-fait semblable au *T. littoralis*”) and *T. littoralis* is currently treated as a junior synonym of *Exorista* (*Exorista*) *larvarum* (Linnaeus) (Herting & Dely-Draskovits 1993: 122). Bezzi & Stein (1907: 337) had also placed *littoralis* in synonymy with *larvarum* but called the genus *Tachina* (see above).

Tachina hispida Robineau-Desvoidy could be (mis)construed as a valid name of uncertain generic placement in the Tachinidae because of its listing in “Doubtful taxa in Tachinidae” (Herting & Dely-Draskovits 1993) and could technically be treated as a senior secondary homonym of *Tachina hispida* Tothill, 1924. However, this taxon clearly belongs to *Exorista* and is most likely a synonym of *Exorista larvarum* (Linnaeus) or a related species. It is not a true *Tachina* in the present sense of the genus and is not a senior homonym of *hispida* Tothill, 1924. **To avoid any ambiguity in this matter, I hereby transfer *Tachina hispida* Robineau-Desvoidy, 1830 to doubtful species status (i.e., as a *nomen dubium*) in *Exorista* Meigen, 1830.**

CURRENT STATUS: *Tachina* (*Nowickia*) *hispida* (Tothill, 1924). **Status revived.**

SYNONYMY: *Fabriciella ampliforceps* Rowe, 1931: 673–674.

DISTRIBUTION: Alaska and Northwest Territories [& Nunavut], British Columbia south to California and New Mexico, east to New York and Newfoundland (O'Hara & Wood 2004: 326).

2. *intermedia* Reinhard, 1942: 27–28, *Fabriciella*.

NEW COMBINATION OF SABROSKY & ARNAUD (1965: 993): *Metopotachina intermedia* (Reinhard, 1942).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina intermedia* (Reinhard, 1942).

HOMONYMY *SENSU* ARNAUD (1992: 167): *Tachina intermedia* (Reinhard, 1942) *sensu* Wood (1987) was recognized as a junior secondary homonym of *Tachina intermedia* Zetterstedt (1844: 1114). In the absence of a junior synonym to replace the name *intermedia* Reinhard, the new name *Tachina californimyia* Arnaud, 1992 was proposed.

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina californimyia* Arnaud, 1992.

COMBINATION OF O'HARA & WOOD (2004: 326): *Tachina* (*Nowickia*) *californimyia* Arnaud, 1992.

PRESENT INTERPRETATION: *Tachina intermedia* Zetterstedt, 1844 was treated by Bezzi & Stein (1907: 212) as a valid species name in *Ernestia* Robineau-Desvoidy, 1830 and its current combination is *Panzeria intermedia* (Zetterstedt) (Cerretti 2010: 329). It is not a senior homonym of *intermedia* Reinhard, 1942 because the two names are not (and have never been) treated together in the genus *Tachina* Meigen, 1803.

CURRENT STATUS: *Tachina (Nowickia) intermedia* (Reinhard, 1942). **Status revived.**

SYNONYMY: *Tachina californimyia* Arnaud, 1992: 167 (unnecessary *nomen novum* for *Fabriciella intermedia* Reinhard, 1942). **New synonymy.**

DISTRIBUTION: Nearctic: USA (California) (O'Hara & Wood 2004: 326).

3. *latifrons* Tothill, 1924: 260, 269, *Fabriciella*.

NEW COMBINATION OF SABROSKY & ARNAUD (1965: 995): *Nowickia (Rhachogaster) latifrons* (Tothill, 1924).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina latifrons* (Tothill, 1924).

HOMONYMY *SENSU* ARNAUD (1992: 167): *Tachina latifrons* (Tothill, 1924) *sensu* Wood (1987) was recognized as a junior secondary homonym of *Tachina latifrons* Meigen (1824: 365). In the absence of a junior synonym to replace the name *latifrons* Tothill, the new name *Tachina oligoria* Arnaud, 1992 was proposed.

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina oligoria* Arnaud, 1992.

COMBINATION OF O'HARA & WOOD (2004: 331): *Tachina (Rhachogaster) oligoria* Arnaud, 1992.

PRESENT INTERPRETATION: *Tachina latifrons* Meigen, 1824 was treated by Bezzi & Stein (1907: 392) as a valid species name in *Thryptocera* Macquart, 1834 [with genus name attributed to Brauer & Bergenstamm, 1889, in error] and is currently treated as a junior synonym of *Goniocera versicolor* (Fallén, 1820) (Andersen 1996: 49). It is not a senior homonym of *latifrons* Tothill, 1924 because the two names are not (and have never been) treated together in the genus *Tachina* Meigen, 1803.

CURRENT STATUS: *Tachina (Rhachogaster) latifrons* (Tothill, 1924). **Status revived.**

SYNONYMY: *Tachina oligoria* Arnaud, 1992: 167 (unnecessary *nomen novum* for *Fabriciella latifrons* Tothill, 1924). **New synonymy.**

DISTRIBUTION: Northwest Territories [& Nunavut] and British Columbia, south to Colorado and Kansas, east to Manitoba and Michigan (O'Hara & Wood 2004: 331).

4. *nitida* van der Wulp, 1882: 82, *Jurinia*.

NEW COMBINATION OF SABROSKY & ARNAUD (1965: 996): *Nowickia (Rhachogaster) nitida* (van der Wulp, 1882).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina nitida* (van der Wulp, 1882).

HOMONYMY *SENSU* ARNAUD (1992: 167): *Tachina nitida* (van der Wulp, 1882) *sensu* Wood (1987) was recognized as a junior secondary homonym of *Tachina nitida* Zetterstedt (1838: 646). Sabrosky & Arnaud (1965: 996) had listed one junior synonym of *nitida* van der Wulp, *Upodemocera robinsoni* Townsend, 1915. Arnaud (1992: 167) replaced the invalid name *nitida* van der Wulp with the name of the junior synonym, with the valid name becoming *Tachina robinsoni* (Townsend, 1915).

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina robinsoni* (Townsend, 1915).

COMBINATION OF O'HARA & WOOD (2004: 331): *Tachina (Rhachogaster) robinsoni* (Townsend, 1915).

PRESENT INTERPRETATION: *Tachina nitida* Zetterstedt, 1838 was treated by Bezzi & Stein (1907: 405) as a junior synonym of *Macquartia chalconota* (Meigen, 1824) and by Herting & Dely-Draskovits (1993: 314) as a junior synonym of *Macquartia tenebricosa* (Meigen, 1824). It is not a senior homonym of *nitida* van der Wulp, 1882 because the two names are not (and have never been) treated together in the genus *Tachina* Meigen, 1803.

CURRENT STATUS: *Tachina (Rhachogaster) nitida* (van der Wulp, 1882). **Status revived.**

SYNONYMY: *Upodemocera robinsoni* Townsend, 1915: 229.

DISTRIBUTION: British Columbia to California, east to Ontario and Massachusetts (O'Hara & Wood 2004: 331).

5. *pilosa* Tothill, 1924: 263, *Fabriciella*.

NEW COMBINATION OF SABROSKY & ARNAUD (1965: 995): *Nowickia* (*Nowickia*) *pilosa* (Tothill, 1924).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina pilosa* (Tothill, 1924).

HOMONYMY *SENSU* ARNAUD (1994: 208): *Tachina pilosa* (Tothill, 1924) *sensu* Wood (1987) was recognized as a junior secondary homonym of two names, *Servillia pilosa* Robineau-Desvoidy (1830: 50) and *Tachina pilosa* Walker (1853: 266). In the absence of a junior synonym to replace the name *pilosa* Tothill, the new name *Tachina garretti* Arnaud, 1994 was proposed.

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina garretti* Arnaud, 1994.

COMBINATION OF O'HARA & WOOD (2004: 327): *Tachina* (*Nowickia*) *garretti* Arnaud, 1994.

PRESENT INTERPRETATION: *Servillia pilosa* Robineau-Desvoidy, 1830 was treated by Bezzi & Stein (1907: 191) as a junior synonym of *Servillia ursina* (Meigen, 1824). It has maintained this synonymy to the present day but the valid species name was recognized as *Tachina* (*Servillia*) *ursina* Meigen by Herting & Dely-Draskovits (1993: 269) and is currently recognized as *Tachina* (*Tachina*) *ursina* Meigen (O'Hara *et al.* 2009: 180). Since *pilosa* Robineau-Desvoidy, 1830 and *pilosa* Tothill, 1924 are both currently in *Tachina*, the latter is a junior secondary homonym of the former. Arnaud (1994: 208) was justified in proposing a replacement name for *pilosa* Tothill, 1924.

Tachina pilosa Walker, 1853 is currently a valid species name in the genus *Archytas* Jaennicke, 1867, as *Archytas pilosus* (Walker). It is not a senior homonym of *pilosa* Tothill, 1924 because the two names are not (and have never been) treated together in the genus *Tachina* Meigen, 1803.

CURRENT STATUS: *Tachina* (*Nowickia*) *garretti* Arnaud, 1994.

SYNONYMY: *Fabriciella pilosa* Tothill, 1924: 263 (invalid, junior secondary homonym of *Servillia pilosa* Robineau-Desvoidy, 1830 [not also a junior secondary homonym of *Tachina pilosa* Walker, 1853 as reported by Arnaud, 1994]).

DISTRIBUTION: Alaska and Yukon, south to Oregon and New Mexico, east to New Brunswick and New Hampshire (O'Hara & Wood 2004: 327).

6. *spinosa* Tothill, 1924: 263, *Fabriciella*.

NEW COMBINATION OF SABROSKY & ARNAUD (1965: 994): *Nowickia* (*Echinomyodes*) *spinosa* (Tothill, 1924).

NEW COMBINATION OF WOOD (1987: 1244): *Tachina spinosa* (Tothill, 1924).

HOMONYMY *SENSU* ARNAUD (1992: 167): *Tachina spinosa* (Tothill, 1924) *sensu* Wood (1987) was recognized as a junior secondary homonym of *Tachina spinosa* Zetterstedt (1838: 648). In the absence of a junior synonym to replace the name *spinosa* Tothill, the new name *Tachina nearctica* Arnaud, 1992 was proposed.

COMBINATION OF O'HARA & WOOD (1998: 766–767): *Tachina nearctica* Arnaud, 1992.

COMBINATION OF O'HARA & WOOD (2004: 329): *Tachina* (*Nowickia*) *nearctica* Arnaud, 1992.

PRESENT INTERPRETATION: *Tachina spinosa* Zetterstedt, 1838 was treated by Bezzi & Stein (1907: 424) as a junior synonym of *Rhynchista prolixa* (Meigen, 1824). This synonymy is still recognized but the valid name is now *Eriothrix prolixa* (Meigen) (Herting & Dely-Draskovits 1993: 372). It is not a senior homonym of *spinosa* Tothill, 1924 because the two names are not (and have never been) treated together in the genus *Tachina* Meigen, 1803.

CURRENT STATUS: *Tachina* (*Nowickia*) *spinosa* (Tothill, 1924). **Status revived.**

SYNONYMY: *Tachina nearctica* Arnaud, 1992: 167 (unnecessary *nomen novum* for *Fabriciella spinosa* Tothill, 1924).

New synonymy.

DISTRIBUTION: British Columbia to Colorado, south to California and Arizona (O'Hara & Wood 2004: 329).

Closing Remarks

How did five of the names above get misinterpreted as junior secondary homonyms, passing through peer review and publication, and go unnoticed until now? One possible contributing factor was the timing of the two Arnaud papers: 1992 and 1994. Scientific publications were available only in hardcopy at the time. It was not as easy then as it is now to trace names through multiple, often old, sources. Reviewers may also have relied too much on the author to check that his nomenclatural actions were correct. It seems likely that the author was confused about junior homonyms and thought a species-group name proposed in the genus *Tachina* and subsequently moved elsewhere would forever be a senior homonym of another species name with the same spelling that was moved into *Tachina* later. This is not the case and two names of the same spelling must be in the same genus at the same time to be homonyms in the sense of the *Code*.

I myself fall into the category of people guilty of following the changes of Arnaud (1992, 1994) and not checking the “back story” more thoroughly. Both O’Hara & Wood (1998) and O’Hara & Wood (2004) had the opportunity to uncover the errors revealed above but instead accepted the names as proposed. Finally, after all these years, the correct valid names for these species can be used again and the proper authors are once more credited with the discovery and description of the species.

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I am thankful for the review of this article by Neal Evenhuis (Bishop Museum, Honolulu). His suggestions have led to improvements in the technical wording used herein (such as using the term “new synonymy” *sensu* Evenhuis *et al.* (2010) for objective synonyms being treated for the first time as invalid), and in the explanations about name changes.

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Figure 1. The Safari Court Hotel in the Safari Hotels and Conference Centre complex, the venue for ICD9.

9th International Congress of Dipterology Windhoek, Namibia, 25–30 November 2018

The 9th International Congress of Dipterology was held last November in Windhoek, Namibia (Fig. 1). There was a moderate turn-out of tachinid enthusiasts and some thought-provoking presentations. Of particular note was the tangible progress being made on higher-level relationships within the Tachinidae and Oestroidea. The titles and authors of tachinid-related presentations are listed below. The abstracts are given in the Abstract Volume of ICD9 that is available for download from the homepage of the *International Congresses of Dipterology* website. A few pictures of delegates are included here (Figs. 2–5).

Authors and titles are cited as given in:

Kirk-Spriggs, A.H. & Muller, B.S., eds. (2018) *Abstract volume, 9th International Congress of Dipterology*, Windhoek. xxii + 346 pp.

Oral and poster presentations

Buenaventura, E., Stireman, J.O. III, Pape, T., Cerretti, P., Thomas-Cabianca, A., Lloyd, M.W. & Dikow, T. A phylogenomic perspective of the Oestroidea (Calypttratae) using ultraconserved elements and historical museum specimens. P. 38.



Figure 2. A rendezvous of dipterists at Joe's Beerhouse in central Windhoek. Clockwise from left: John Stireman (USA), Daniel Whitmore (Germany), Pierfilippo Cerretti (Italy), Silvia Gisondi (Italy) and Arn Rytter Jensen (Denmark). (Photo by J.E. O'Hara.)

Dios, R. de V.P. & Nihei, S.S. Preliminary results of a comparative morphological study and cladistic analysis of Phasiinae (Tachinidae), based on morphological characters. P. 69.

Gisondi, S., Pape, T. & Cerretti, P. Phylogeny of Rhinophoridae and Polleniidae – toward the evolution of Oestroidea. P. 92.

Lumbers, J., Lessard, B., Rowell, D. & Yeates, D.K. Insect death metal – taxonomy and phylogeny of the Australian bristle fly genus *Rutilia* Robineau-Desvoidy (Tachinidae). P. 164.

O'Hara, J.E. The state of Nearctic Tachinidae taxonomy as revealed by a single Malaise trap, the Canadian National Collection of Insects and DNA barcoding. P. 216.

Schnitzler, F.-R. The mystery of “*Eurigaster*” *clathrata* Nowicki (Tachinidae) exposed. P. 250.

Stireman, J.O. III, Cerretti, P., O'Hara, J.E., Blaschke, J.D. & Moulton, J.K. Molecular phylogeny and evolution of world Tachinidae. P. 266.

Tachi, T., Huang, Y.-z. & Shima, H. Comparative morphology of the piercing-type ovipositor in the tribe Blondeliini (Tachinidae) and its phylogenetic implications. P. 273.

Zhang, C.-t., Wang, Q., Liu, J.-y., Yao, Z.-y., Zhao, Z., Hou, P., Liang, H.-c. & Li, X.-y. Tachinidae of the Hengduan Mountains of south-western China. P. 319.



Figure 3. Left to right: Silvia Gisondi (Italy), John Stireman (USA), Pierfilippo Cerretti (Italy) and Jim O'Hara (Canada).

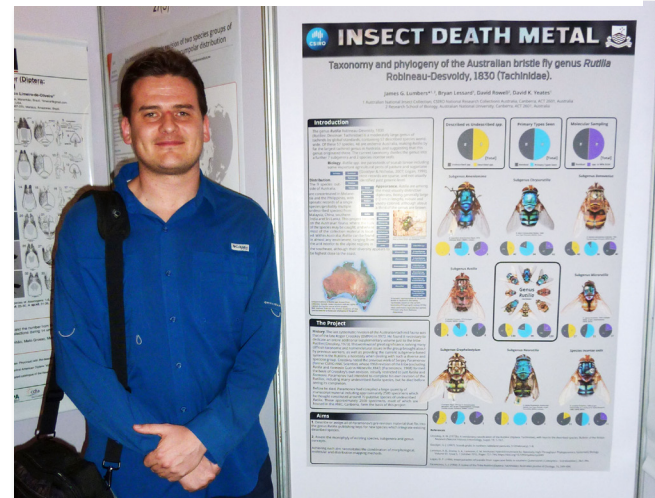


Figure 4. James Lumbers with his poster on the charismatic genus *Rutilia* R.-D. (Photo by J.E. O'Hara.)

Contributed by the editor
Jim O'Hara



Figure 5. Left to right: Socrates Letana (USA), Eliana Buenaventura (Germany), Silvia Gisondi (Italy), Pierfilippo Cerretti (Italy), John Stireman (USA), Rodrigo Dios (Brazil), Thomas Pape (Denmark), Arianna Thomas-Cabianca (Spain), Arn Rytter Jensen (Denmark), Jim O'Hara (Canada) and Rudi Schnitzler (New Zealand). (Photo courtesy of E. Buenaventura.)

STUDENT NEWS

SHIN KOMAGATA

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I am a first year doctoral student at Kyushu University in Fukuoka, Japan (Fig. 1). For my dissertation I am pursuing two separate research themes at the same time, one a taxonomic study of Japanese Phasiinae (Tachinidae) and the other an investigation into the larval behavior of tachinids inside their hosts using micro computed tomography (micro-CT) scans.

In Japan, Dr. Hiroshi Shima has been undertaking taxonomic studies of tachinid flies since the 1960s and continues this activity as a retired professor. His former student, Dr. Takuji Tachi, has taken over Dr. Shima's teaching role at Kyushu University and is himself studying the taxonomy and phylogeny of tachinid flies, while also training students in insect systematics. I am studying tachinids under the guidance of Dr. Tachi while also learning about this family of flies from Dr. Shima.

My study of the diversity of Japanese Phasiinae is based on the excellent tachinid collection of Kyushu University. There are currently 41 species of Phasiinae known from Japan (Shima 2014) and some of them are natural enemies of true bugs that are agricultural pests in the country; e.g., *Gymnosoma rotundatum* (L.) (Higaki & Adachi 2011). My work for this study is very simple: to describe new species and to create keys to identify all the Japanese species. I will also collect potential hosts from the field in an effort to expand the list of known hosts for Japanese Phasiinae, as currently documented by Shima (2006, 2015). I think that students doing this sort of traditional taxonomic and natural history research are becoming fewer in Japan (perhaps even in the world). Nonetheless, I believe that revealing local biodiversity is an important pursuit.

As I mentioned at the beginning, I am also carrying out a behavioral study of living tachinid larvae using micro-CT scans (Fig. 2). More specifically, I am investigating how the difference in the strategy of host body space use in different species of tachinids affects the parasitism style (such as host range and gregarious vs. solitary parasitism).

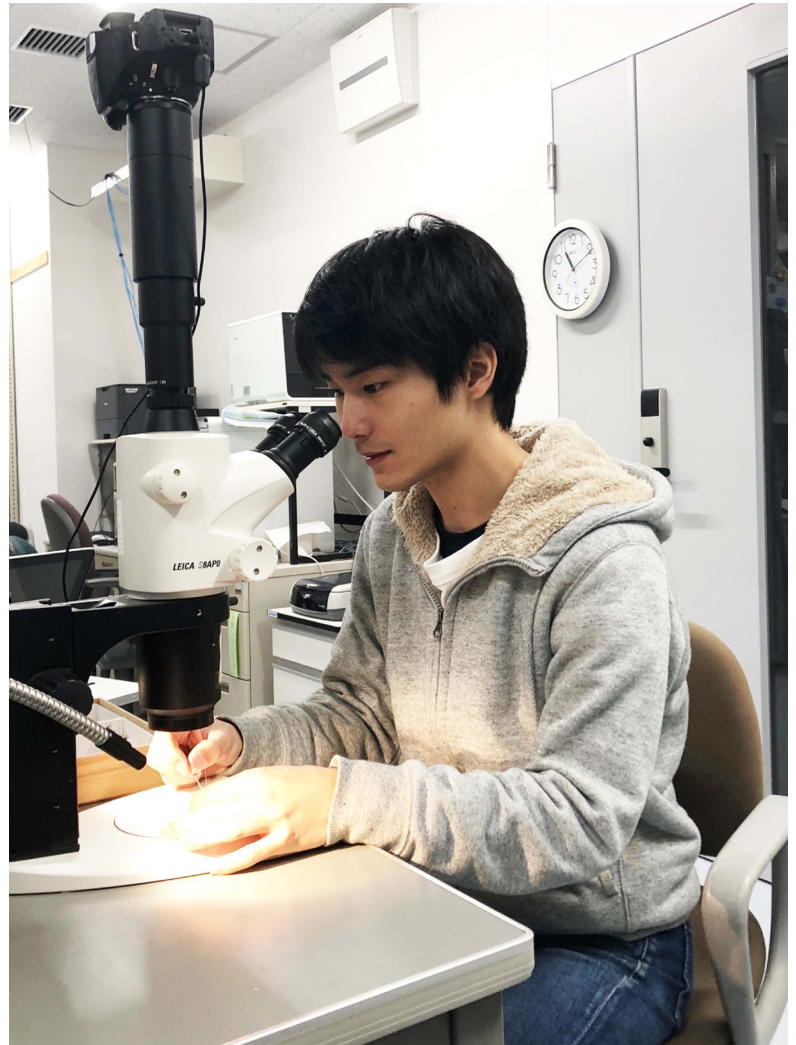


Figure 1. Shin at work in Kyushu University. (Photo by Daichi Kato.)



Figure 2. Larva of *Gymnosoma rotundatum* (L.) (red) inside the host (*Plautia stali* Scott) as visualized by micro-CT scanning. The respiratory funnel is shown in green at the hind end of the larva.

The unique life styles of tachinid flies can be seen in their larval stage and their life histories in various hosts must be attractive, interesting and diverse. However, the larval stage is hidden from our view inside the host. We have only learned a little about tachinid larval behavior in previous studies. Although observations have been few, their results have often surprised us. For example, the first instar larva of *Compsilura concinnata* (Meigen), a blondeline tachinid that parasitizes a wide range of lepidopteran caterpillars, lives between the peritrophic membrane and the midgut of the host (Ichiki & Shima 2003). The larva of *Epicampocera succincta* (Meigen) (Eryciini), a natural enemy of *Pieris rapae* (L.) caterpillars, will kill another conspecific larva when they are present in the same host (Iwao & Ohsaki 1996). It is not easy to accurately observe what is happening inside a host because after dissection the structures will be destroyed and the host and its parasitoid will be dead. In order to solve this difficult problem, I am attempting to visualize tachinid larvae inside their hosts using micro-CT scans. By using this method, we can observe the same individual many times while both the host and parasitoid are living, and we can do a “virtual dissection” at any time from various angles. Within the next two years, I hope to be able to show you the wonderful world of tachinid larvae!

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IN MEMORIAM

Agnieszka Draber-Mońko (1931–2018)

by Cezary Bystrowski

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My meetings with “Mrs. Professor” – reminiscences of a former student

Professor Agnieszka Draber-Mońko was born on December 20, 1931 in Sochaczew, Mazovia (Poland). She was the fourth of five daughters of Barbara and Kazimierz Draber. Her childhood took place during the extremely difficult period of the Second World War, the time of Poland’s occupation by Nazi Germany and Soviet Russia. As a teenager, she lost her father, who was sent to a Nazi extermination camp in 1943, and for years no one in the family knew where and how he died. After the war Agnieszka graduated from high school and studied biology, first at the University of Wrocław (for 2 years), then at the University of Warsaw. She graduated in 1956 and the subject of her M.Sc. thesis (University of Warsaw) was studies on the occurrence of flies of *Phasiinae* (Diptera) near Warsaw, with particular emphasis on the Kampinos Forest (Mońko 1957). During the entire period of her professional life, Agnieszka was associated with the Zoological Institute (later named Institute of Zoology, presently Museum and Institute of Zoology of the Polish Academy of Sciences or MaIZ PAS for short), located in a prewar building in Warsaw, at Wilcza 64 Street. It is the same building where in November 1944, just after the fall of the Warsaw Uprising, almost all pre-war collections of insects, stored in the National Nature Museum located there at that time, were burned by the occupying forces (<https://miiz.waw.pl/pl/podstawowe/574-historiamiiz>).

Details of the next stages in the professional career of Prof. Agnieszka Draber-Mońko, and a review of her scientific achievements, was presented by Dr. Waldemar Mikołajczyk in his recollections of “Jagoda”, as friends used to call her (Mikołajczyk 2018).

I met Agnieszka for the first time in the spring of 1994. I wished to learn about the systematics of tachinid flies (Diptera, Tachinidae) for the purposes of my planned doctoral dissertation. In the same year Agnieszka received the title of professor and, I think, thanks to the closing of a certain stage of her professional career, she had a bit more time to meet and conduct a kind of mentoring in the field of systematics of these parasitic flies. My visits with Agnieszka at that time were frequent and they started basically in the same way. First, I called her and made an appointment, then I went to the MaIZ PAS located in the center of Warsaw and reached the reception desk located on the ground floor, where a phone call to Agnieszka was usually made to announce my arrival. At the end of the corridor on the second floor, behind a row of insect cabinets filled with the achievements of several generations of naturalists, there were bright wooden doors and behind them, to the right, another brown door directly to her room. Just a knock, knock... and a high “please come in” on the other side, and I was with “Mrs. Professor”, that’s how I called her then.

The first things that attracted my attention upon entering Agnieszka’s room were the books, countless publications, and manuscripts arranged on tables and her desk. Agnieszka’s room was truly a naturalist’s workshop... On the left side, high shelves stretched along two walls, on which one could find the world literature on calyptrate flies.

The volumes of the *Catalogue of Palaearctic Diptera* and numerous other books stood there, evenly arranged. One could see there also the green, 13-volume series on the *Insects of Mongolia*, the red covers of the *Manual of Nearctic Diptera*, and dozens of other books, geographical atlases, and even thick binders with the works of various dipterists whose names I did not recognize at the time. Reprints were received on a frequent basis in response to postcard requests (Fig. 1).



Agnieszka Draber-Mońko (1931–2018)

In the center of the room, parallel to the standing bookshelves, there was a small, dark-brown desk. On its left side was the place where Agnieszka usually worked. On the opposite side of the desk, next to the window, there was a light-coloured wooden secretary with numerous small drawers in which was stored information about the flies of Poland. Already by then, in the mid-90s when computers were beginning to be widely used, this catalogue seemed to be an element of a departing era but we used it many times with much success during our meetings. To the right of the wooden secretary was a “food corner”, with a sink and water faucet and a fairly narrow rectangular table standing near it. Water was boiled on this table and we worked there too, peering down the black, old stereo microscope of a well-known German company that stood there. We used it often to see the morphological details of

the dipteran we were determining. On this table “science was also whirling” in the form of a large number of boxes with carefully arranged flies, microscopic preparations, and small glass vials with alcohol in larger jars that the Professor had used in her work. Just above the table, on the wall, there was a cupboard full of similar treasures, and there were also kitchen accessories stored in it: cups, spoons, plates, sugar and various types of tea, which Agnieszka served to guests visiting her laboratory. Along the western wall there was a small table with a computer, and further, to the left of the entrance door, stood another bookcase tightly filled with binders and books. Above the computer hung a round clock, noiselessly measuring the time of our meetings. This was the kingdom of Agnieszka, which she carefully and consistently built for many years, almost until the last weeks of her work. I repeatedly observed how she complemented the potential of this space by adding newly published works of colleagues and other dipterists, complementing her binders, and somehow managing this small space very effectively. It was extraordinary for me to see that she could perfectly control such a large collection of books and various publications.

To my astonishment, as it happened many times when determining various specimens of flies, Agnieszka aptly pointed out the binder with the necessary literature and then found the paper she was looking for; some keys to the determination, drawings or other necessary information. I was really fascinated by this and I suppose that I could not match her in this ability, because she had an excellent visual memory and, what is even more important, everything was perfectly arranged in her mind, and this is a feature of outstanding people. It happened quite often that after analyzing the minute details of some interesting fly that we were determining, she would say “wait, wait, I have seen this somewhere”, focused her attention and often hit the heart of the problem. That is how we worked. What took her minutes, would take me hours. The first fly that I determined under Agnieszka’s supervision was the characteristic *Eriothrix rufomaculatus*

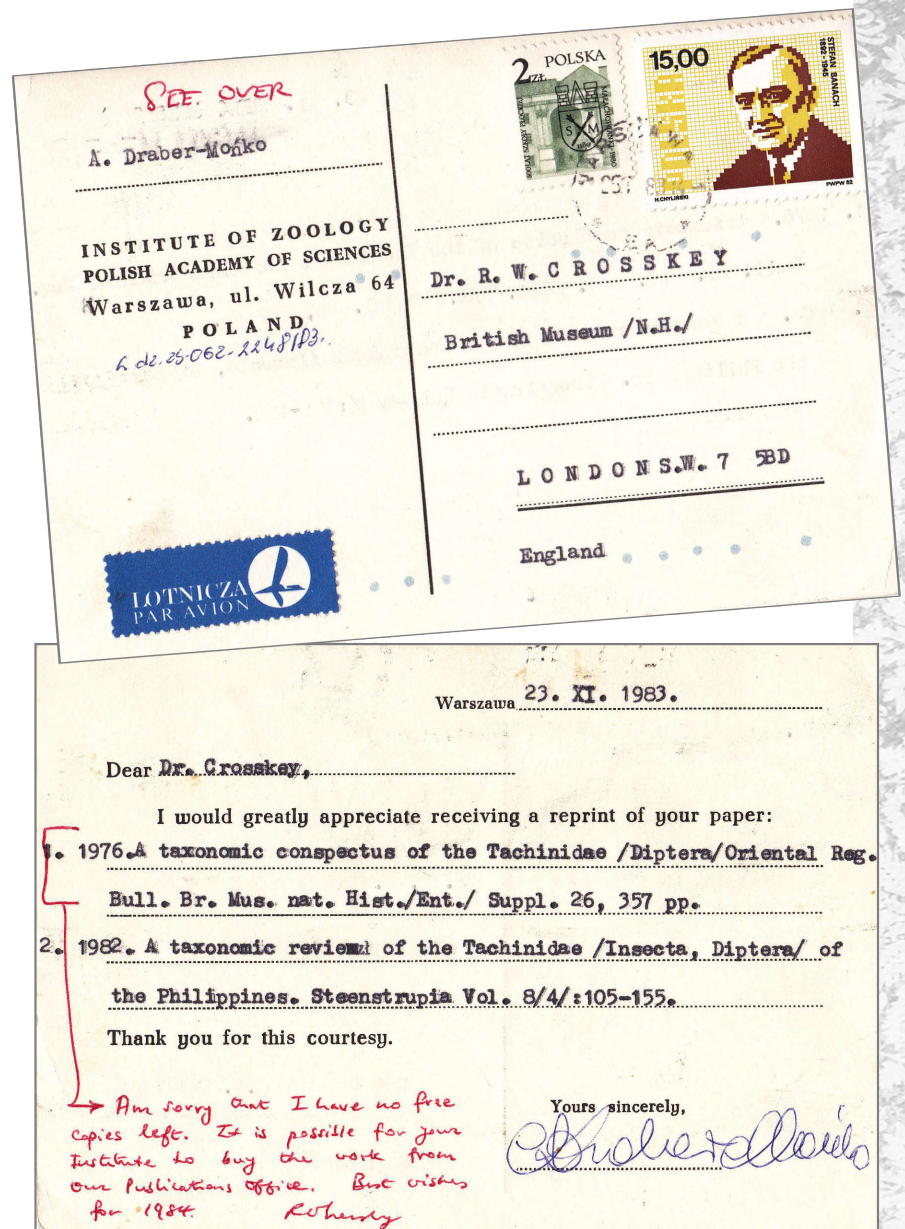


Figure 1. Postcard dated 1983 to Roger Crosskey at the British Museum of Natural History (London) requesting tachinid literature.

(De Geer), from the collection of Dr. hab. Jan Karczewski. I cannot say that it went with flying colours, but I think I finally passed the test because in time dozens of other flies followed and I got better under her careful supervision.

Our meetings also had their rituals. After sharing the latest news and solving the systematic problems that had initiated my visit, we often took a break and sat down for a meal. This took place at a small square table positioned as an extension to her desk, above which a lamp stood with a long metal shoulder and a blue lampshade. It was amazing that often during our arranged meetings, Agnieszka prepared culinary surprises; e.g., fish stews or vegetable salads, brought from home in small plastic containers and accompanied by bread and some fruits... We drank tea and feasted – you cannot call it anything else. I always tried to reciprocate the hospitality of my professor with my own culinary “surprises”, but most of the time they were only sweets or grapes. I never dared to present my own culinary experiments... During the meal there was always a theme to our conversation. I usually listened and Agnieszka told stories about people and various events related to work at the Institute, or about her field trips. She talked about hunting for flies in exotic Mongolia or mentioned her research in Poland: expeditions to the xerothermic Nida Basin, or the massif of Pieniny, or the unusual chirats (rare geological formations made up of characteristic rock piles cemented together) in the Świętokrzyskie Mountains. Although we were divided by the “space” of almost two generations, Agnieszka was open and friendly to me, sometimes joking, but most of all we were connected by stories about flies, interesting places, and fantastic species of Diptera that must be found in Poland. After listening to such stories, I drove enthusiastically to the Białowieża Forest, to the Bieszczady Mountains, or to the Świętokrzyskie Mountains in search of my dreams. Sometimes I caught some of those flies and, of course, I bragged to my professor. She accepted it with joy and clearly enjoyed my successes. One such mission was to catch a specific tachinid fly from the Białowieża Primeval Forest, of which only two specimens were present in the MaIZ PAS collection. These two individuals are badly damaged and despite many attempts are still undetermined. All that is known is that they belong to the tribe Blondelinii and were caught in the Forest in Moericke (yellow) pan traps. After that day when I learned this information and was given the “order” to find the species, I spent months in the Białowieża forest but the puzzle is still unsolved...

Among the most frequently discussed topics, we can mention stories about cooperation with Dr. hab. Jan Karczewski and his innovative, at the time, scientific concepts and research in the Jędrzejów Forest district (southern Poland). An insect cabinet with almost all the material collected by him has always been in the corridor outside the door leading to Agnieszka’s room, as I remember. We used it often, whenever there was a need to see a specific specimen or observe an important feature.

Another topic that Agnieszka sometimes mentioned was the sad story of Dr. Jan Witold Pawłowicz, who on the eve of World War II was studying the fauna in the Tatra Mountains (the only Polish mountains of alpine character) and tragically died September 1939 on the front line in the first month of the war. It was an unfortunate circumstance that in 1938 Pawłowicz was in Berlin at the VII International Congress of Entomology and gave a lecture there, and the summary of the proceedings that was published in March 1939 is in fact the only published trace of his Tatra Mountains research (Pawłowicz 1939), the rest of the material being lost during the war and occupation time.

I was not only inspired by the memories of Mrs. Professor but was also entertained by anecdotes from her life. I remember the story about an airport, which I heard several times. This happened in Ulaanbaatar, the capital of Mongolia, when the country was known as the Mongolian People’s Republic, “a friendly country from the socialist area”. As Agnieszka was passing through Customs to return to Poland, she and other passengers were searched for smuggled goods. Her personal belongings were thoroughly inspected and some items were dismantled into parts. This procedure eventually destroyed Agnieszka’s lipstick, where the agent probably hoped to find illegally exported diamonds. Of course, diamonds were not present...

The great passion of Agnieszka was the breeding of flies. She made a lot of such breeding experiments while writing her monograph on the Calliphoridae for the Polish Fauna series (Draber-Mońko 2004). I think that this monumental work is one of the most important results of her scientific work. This study took over four years and it was not an easy-to-prepare publication. Agnieszka summarized the achievements of really many authors, including the keys, descriptions of all known developmental stages, and illustrated it with more than a thousand drawings. The volume containing this publication exceeded 650 pages. She mentioned to me several times, thinking about the calliphorid larvae she had reared on liver, that “it did not smell like violets, but it was definitely worth doing”.

During one of our conversations, I also learned that the first flies that Agnieszka determined were hover flies (Syrphidae), but at the Institute she could not work on this family because it was already being studied by someone else. She also admitted that she liked butterflies. However, despite early fascinations with other insects, throughout her professional life she worked with calyptrate flies, as one of four scientists working at the MaIZ PAS. She worked there with the long-term head Prof. Przemysław Trojan, Prof. Regina Bańkowska, and Dr. Waldemar Mikołajczyk.

After a longer break in our contacts at the beginning of the present decade, I met Agnieszka at the funeral of Prof. Trojan and we agreed on a date for my next visit to the MaIZ PAS. It was 2015. Agnieszka was at that moment, I noticed, a bit pensive. When we met, I learned that she had buried her only child, daughter Grażyna (1958–2014), and that she had been struggling with a serious, incurable disease for several years. She asked me for discretion, but I knew very well that the situation was really very serious. She told me about the difficult treatment, its prospects and various problems, but also about the publications she had written and about her plans for the near future. She still had a lot to do... That day she gave me her collecting net she had used for years to catch flies, and red leather covers for glass insect containers. I accepted the gifts with some concern, not knowing what would happen in the near future. Although Agnieszka devoted a lot of time to treatment, she primarily worked. I sometimes felt bad that I was taking so much of her time. I knew that she had been working for several years, with her characteristic determination, on the Tachinidae of North Korea. Although the country is currently inaccessible, Agnieszka was systematically reviewing each subfamily based on material in the MaIZ PAS collected by staff members during six expeditions to North Korea between 1959 and 1990 (Draber-Mońko 2009, 2012, 2013, 2015, 2017).

During our unforgettable time spent together I vividly remember one visit in the winter of 2016 when we were sitting together trying to identify a tachinid I had caught in Georgia. After passing the Palaearctic key of Tschorsnig & Richter (1998) back and forth several times, we determined that it was a member of a genus we had not seen before. It seemed almost certain that the identification had been correctly carried out, despite some problems we had with couplet 332 of the key. Just to be sure, Agnieszka quickly found in her resources the original work describing the species *Ziminia masiceraeformis* (Portschinsky). She proceeded to read the original description in Latin while checking the characteristics of the species. Moments like these were really the quintessence of our meetings, and I will remember them to the end. I admired her knowledge, persistence, versatility and logical progression in which she proceeded when identifying difficult specimens. Our love for the systematics of flies was something that absolutely joined us!

The last time I met Agnieszka was on April 10, 2018, when I visited her room for the proverbial 15 minutes, for some publication and a fly larva that I had to photograph. Agnieszka, however, worked relentlessly on a summary of the achievements of Dr. hab. Karczewski. As it turned out later, it was to be her last scientific mission. It was, in fact, somehow overdue work that she still wanted to complete. It was her desire to summarize in English the work of her colleague, to make his achievements known to a broader circle of readers. Our 15 minutes stretched into more than four hours as we talked about everything, and in fact it was largely Agnieszka's monologue. She talked about herself, about her life and work. Only then did I learn about her father's death in the death camp during the

Second World War. She never did find out where exactly he was buried and I felt that even after all these years it was emotionally difficult for her. She talked about her education in the post-war period.

Also during this last meeting Agnieszka admitted to me that she had been cleaning up and organizing her room for some time, this room where she had been working for so many years, and was handing out sets of her publications that still remained. I was personally deeply stirred by the simplicity of the last things. We said goodbye banally in front of the building in which she lived, where I had driven her around 9:00 p.m. I wished her strength to continue her work and to finish the publication about Dr. hab. Karczewski. Agnieszka asked me, somehow more urgently than usual, to send greetings to my wife Monika and daughters Maria and Lena. It was raining, and I was afraid to think that maybe we were seeing each other for the last time, and I was deluding myself that maybe we would get some new chances...

Professor Agnieszka Draber-Mońko died on May 28, 2018 in Warsaw, after finishing her paper on the achievements and research of Dr. hab. Jan Karczewski that she had been working on when I last saw her. She was buried on June 7, 2018, at plot U IV4-14-6 in the North Cemetery in Warsaw, in Wólka Węglowa, where her family and friends said goodbye to her for the last time.

Acknowledgements

I want to express special thanks to Karina Kwapiszewska, Dominika Ziółkowska and Waldemar Mikołajczyk for providing important information and for discussions about the text. I am also grateful to Grzegorz Dubiel for his critical reading of the Polish manuscript. My special thanks to Robert Żóralski for translating the text into English.

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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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