

A molecular phylogeny of world Tachinidae...finally

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A summary of ...

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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.

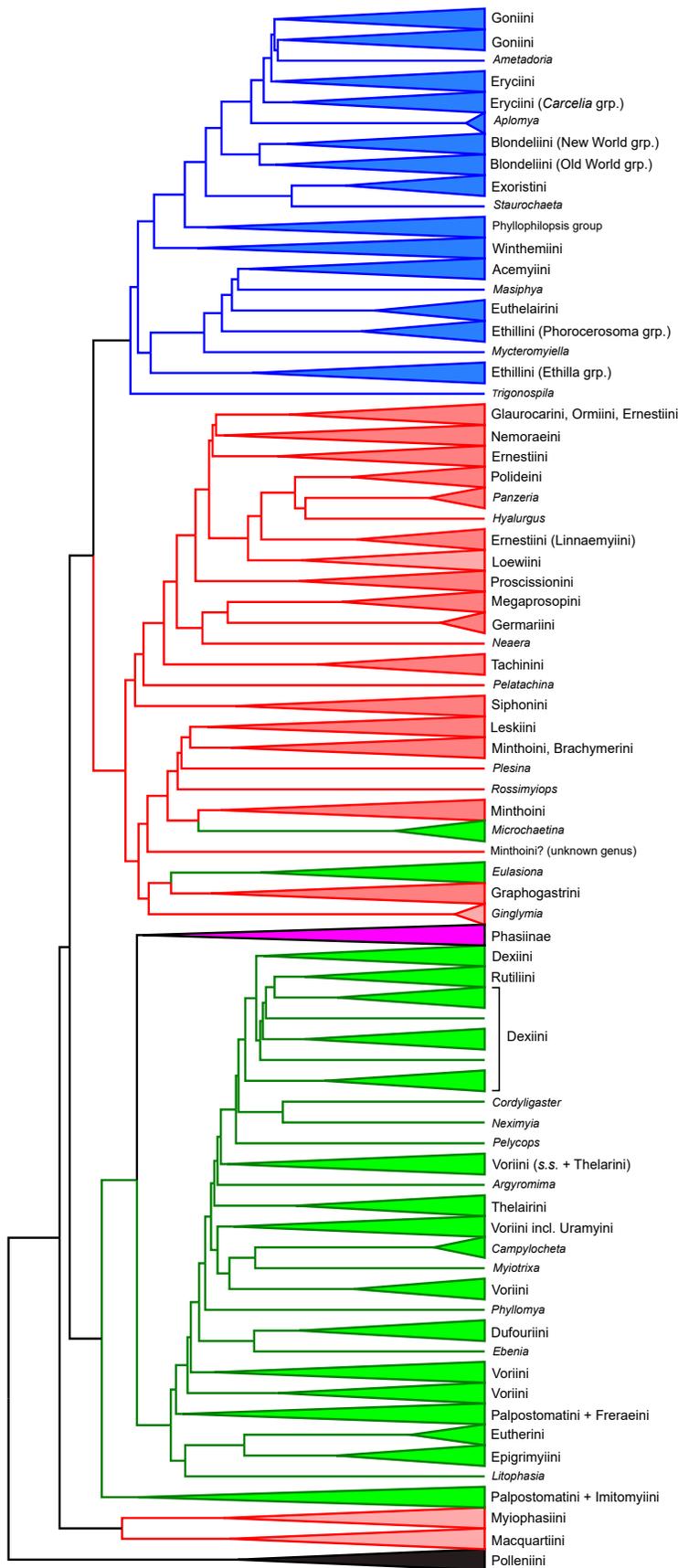


Figure 1. A summary tree of relationships recovered from our molecular phylogenetic analyses of Tachinidae. This tree is based on a Maximum Likelihood analysis using the program IQtree. Major tribes and other clades are collapsed and intervening genera indicated. Exoristinae are in blue (top), Tachininae 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 genus *Neximyia* are included. Only the hemipteran 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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