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Phylogenetic Reconstruction of Exoristinae Using Molecular Data: a Bayesian re-analysis

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Phylogenetic reconstruction of Exoristinae using molecular data: a Bayesian re-analysis (by J.O. Stireman III)

A few years ago I published the results of a phylogenetic analysis of New World Exoristinae based on molecular data from two genes, 28S rDNA and Elongation Factor 1-alpha (Stireman 2002). In that study I employed parsimony, neighbor joining, and maximum likelihood inference methods to generate phylogenetic reconstructions, and explored a variety of weighting schemes and combinations of the sequence data (i.e. each gene separately and both together). The results of these analyses generally supported recent taxonomic hypotheses (e.g., Herting 1984; Wood 1987; O’Hara and Wood 2004). For example, Tachinidae and Exoristinae were reconstructed as monophyletic in most analyses, as were the Exoristini, Winthemini, and Blondeliini. However, there were also some ambiguous and unexpected results. First, representative taxa of Tachininae and Phasiinae (used as outgroups) failed to support monophyly for either of these subfamilies. Also, species of the genera *Masiphya* (Masiphyni), *Ceracia* (Tachininae), and *Phyllophilopsis* (Blondeliini) tended to form a clade that varied widely in position between reconstructions. Perhaps most interesting, all reconstructions indicated a paraphyletic or polyphyletic Goniini. Finally, and most disturbing, was the fact that my representative of *Drino* (*D. incompta*) was often reconstructed near the base of Exoristinae joining taxa from other subfamilies (at least in analyses of EF1 alpha) even though all morphological considerations would place this taxon with other “Eryciini”.

Due to limitations in the software available to me at the time I was engaged in this study, I was limited to parsimony analyses when using the combined data (both genes). This is because I was unable to partition the data and assign different models of evolution to each gene in a single search (which was necessary, given that one gene codes for a protein and the other for a functional RNA product). Recent developments in phylogenetic analysis techniques, particularly the use of Bayesian inference methods, allow partitioning of the data, assigning different models of substitution to these partitions, and faster searching of tree likelihood surfaces. Here I briefly present a Bayesian reanalysis of the data from my 2002 paper

using the program MrBayes 3 (Ronquist and Helsenbeck 2003).

Methods

Please see Stireman (2002) for collecting, sequencing, and alignment methods. A total of 57 taxa were included in the analysis (40 tachinid genera) and 1997 total characters were used (899 Eflalpha and 1098 28S). Difficult to align

“gappy” regions of 28S were subsequently excluded. The Bayesian search was run for 100,000 generations (sampled every 100) with four chains (3 heated) and a burn-in of 50,000 generations. Separate models of nucleotide substitution were estimated for each of four partitions corresponding to the 28S gene, and each codon position of the Eflalpha gene, with initial uniform priors (details of

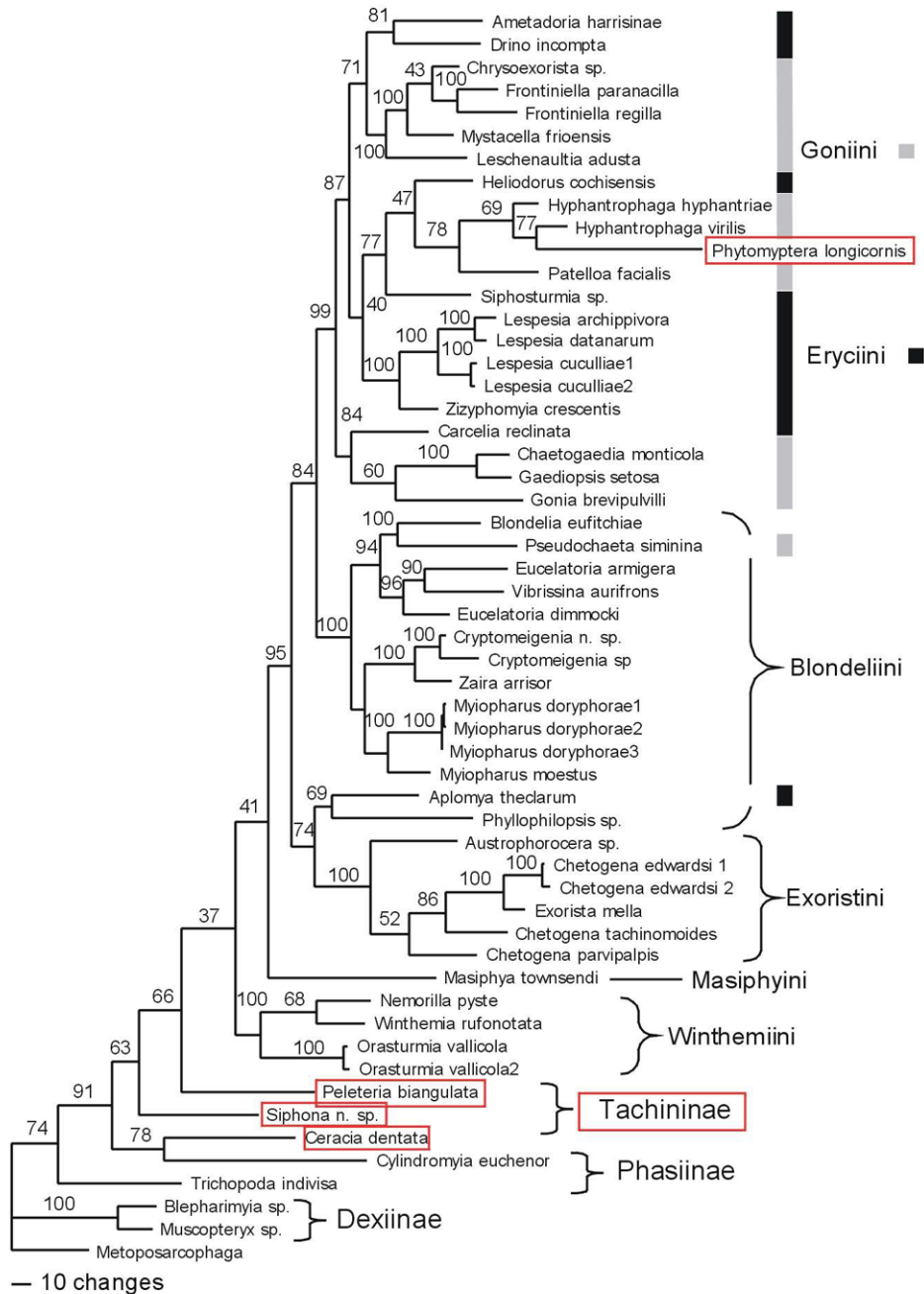


Figure 1. Majority rule consensus of trees from the posterior distribution of the Bayesian analysis of Exoristinae. Numbers above branches indicate the credibility values for each subtended clade (i.e., percentage of all 501 retained trees from the posterior distribution containing the subtended clade). Subfamily and/or tribal associations are indicated by braces, vertical bars, and in the case of Tachininae, red boxes. See text for additional information.

the resulting models and parameter estimates are available upon request).

Results

A summary of the trees from the posterior distribution is given in Figure 1 (mean marginal likelihood: -13425.40). Numbers along branches indicate the clade credibility values of particular nodes (i.e. the percentage of trees from the posterior distribution that contained that node). Goniini are indicated by the vertical gray bar to the right of the cladogram, Eryciini are indicated by the black bars, and Tachininae are indicated by red boxes. Other subfamilies and tribes are indicated by braces to the right of the reconstruction.

Discussion

The consensus tree from the Bayesian analysis generally supports previous conclusions based on alternate tree reconstruction techniques (e.g., parsimony, maximum likelihood), though it also suggests some unique relationships. One valuable aspect of the current Bayesian analysis is that it permits both the assessment of the support for clades in a reasonable amount of time (unlike bootstrapped maximum likelihood searches) and the use of detailed models of substitution partitioned across genes (and/or codon positions, as done here). Thus, nodes with relatively poor support can be easily identified.

The family Tachinidae is weakly supported in the current analysis. Although the two dexiines cluster together strongly (both in the same tribe, Voriini), Tachininae and Phasiinae are reconstructed as paraphyletic and Exoristinae has only weak support (37%). These confusing relationships among subfamilies and the weak support for basal nodes suggest that these genes are probably not appropriate for assessing deep relationships within tachinids, perhaps due to substitutional saturation (homoplasy). The occurrence of the tachinine *Phytomyptera* within the Goniini is inexplicable, perhaps a case of long-branch attraction. This placement is certainly incorrect.

Many relationships indicated in the Bayesian analyses do conform to taxonomic treatments and morphological groupings, often with strong support. Winthemiini, Exoristini, and Blondeliini (with the exception of *Phyllophilopsis*) are all supported in 100% of trees. The clade Goniini + Eryciini is supported by 99% of trees (with the exception of *Aplomya*, which may reflect truly distinct affinities). Again, however, the presence of *Pseudochaeta* in the Blondeliini is unlikely and probably a consequence of long-branch attraction (this taxon was also quite mobile in previous analyses). As in all other analyses of these data, the microtype egg possessing Goniini are not recovered as monophyletic. Interestingly, *Masiphya* occupies an intermediate position between the Winthemiini and the rest of the Exoristinae, which seems appropriate

based the distinctiveness of the Masiphysiini and their possession of unembryonated macrotype eggs. A close affinity of *Aplomya* with Exoristini in the tree is also supported by the possession of unembryonated macrotype eggs.

It is difficult to assess how much the current Bayesian analysis aids in our understanding of tachinid relationships. Many relationships inferred from morphology were recovered (tribes, subtribes, genera), suggesting that these classificatory schemes may reflect phylogenetic relationships quite well. On the other hand, a few obviously incorrect phylogenetic placements (e.g., *Phytomyptera* and *Pseudochaeta*) raise doubts about which other relationships indicated by the cladogram might be misleading. Only continued analyses with more taxa, more genetic data, and more morphological data (from a variety of life stages and morphological systems) will allow us to gain a better understanding of the evolutionary history and relationships of Tachinidae, and through this an understanding of how their oviposition strategies and host associations have evolved. The current analysis, though flawed, represents a step in that direction.

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***Sturmiopsis* specimens needed for molecular systematics study (by A. Mitchell)**

Sturmiopsis parasitica (Curran) is a widespread species throughout eastern and western Africa. It has been released in South Africa as a biocontrol agent of *Eldana saccharina* Walker, a pyralid stemborer found primarily in sugarcane but also in maize and sorghum. However, *S. parasitica* has also been recorded from Crambidae (*Chilo* spp.) and even Noctuidae (e.g. *Busseola fusca*). A molecular systematics study in progress is revealing the existence of biotypes within *S. parasitica*, with obvious implications for biocontrol. We wish to expand our study