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Overview of Tachinid parasitoids classification (Tachinidae, Diptera)

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ABSTRACT

The track of the higher classification of the Tachinidae (Diptera) is showed in the last few decades. Particularly, when the classification of the family was improved and focused on the investigations that employed molecular data in the analyses. This paper deals on study of the family in phylogenetic and taxonomic directions. Whereas, some taxa in the past was a problem where to place in a satisfied and accurate position within the family. When employment with molecular data, it was appropriate resolution to explore the relationships of the parasitoid family, and many questionable higher taxa were resolved. Nevertheless, certain taxa need to be studied in more depth aided by new approaches, because the molecular studies on Tachinidae until now are insufficient.

Key words : Molecular, parasitoid, phylogenetic, Tachinidae

INTRODUCTION

The Tachinidae are the second largest family within Diptera after Tipulidae, with nearly 10000 described species all over the world (Pape *et al.*, 2011; Zhang, 2011; O'Hara, 2013a, O'Hara, 2013b; Scholl and Wiens, 2016), and many unknown and so diverse (Inclán, and Stireman, 2011). All tachinids are endoparasitoits of almost 15 orders of Arthropods (Smith *et al.*, 1955; Arnaud, 1978; Smith *et al.,* 2006; Smith *et al.,* 2007; Richter, 2008a; Richter, 2008b; Richter, 2010; Stireman *et al.*, 2006; von Ellenreider *et al.*, 2015). The most species parasitize on larval instars of Lepidoptera (Barbosa and Caldas, 2004), Coleoptera (Stireman and Singer, 2003) and Symphyta (Hymenoptera) or adult beetles (Purrington *et al.,* 1990; Reeves and O'Hara, 2004), as well as Hemiptera (Arnaud, 1978; Sutherland and Baharally, 2002; Aldrich, 2006, Aldrich, 2007; Stireman *et al.*, 2006; Cerretti, 2010; Golec *et al.,* 2013; Cerretti *et al.*, 2014). All these hosts are pests on important plants, so tachinids play important roles in biological control (Babendreier *et al.*, 2005). Tachinid members are an important constituent of insect societies in the entomological ecosystem. As parasitoids, Hymenopteran parasites are the most diverse and important immediately followed by Tachinidae. For instance, estimated parasitism frequencies by tachinids averaging 10% or more in the comprehensive rearing programs of lepidopteran larvae (Stireman and Singer, 2003; Stireman *et al.*, 2009, Stireman *et al.*, 2017). In addition, tachinids have been displayed with effective role in regulating particular host populations and controlling outbreaks of insect pests (Brodmann *et al.,* 1997; Hernandez *et al.,* 2009). More currently, the possibility employment of tachinids for biological control remains to be assessed in diverse systems, including bromeliad weevils (Wood and Cave, 2006), palm weevils (Nihei and Pavarini, 2011), the prickly pear cactus moth (Pemberton and Cordo, 2001), and sugarcane borers (Vargas *et al.,* 2015). Instead of using the chemicals that may be employed with biological agents to complement each other (Zargar *et al.,* 2017).

The previous taxonomic analyses suggested monophyly of some groups (Tschornig, 1985; Wood, 1987; O'Hara, 2013a) divided Polideini into nine tribes in two subfamilies. Morphological and molecular analyses was used to clarify relationships of

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the large clades of Tachinidae (Stireman, 2002; Tachi and Shima, 2002, Tachi and Shima, 2008, Tachi and Shima, 2010; Cerretti and Tschorsnig, 2010; Cerretti *et al.*, 2012, Davis, 2012; Zhao, *et al.,* 2013; Winkler *et al.*, 2015; Pohjoismäki, *et al.,* 2016; Blaschke *et al.*, 2018), and only one study has used molecular data to examine inclusive phylogenetic relationships of taxa that constituent the family (Stirman *et al.*, 2019). Our review goals were (i) Survey of some molecular phylogeny studies of Tachinidae that may play a good role in the future works to understand the evolutionary relationships among Tachinidae and can use this knowledge to improve tachinid classification and (ii) Show off the placement of Tachinidae within its superfamily (Oestroidea) and the taxa within the subfamilies (Dexiinae, Exoristinae, Phasiinae, and Tachininae).

Overview of the Taxonomic Position of Tachinidae

The characteristic of Tachinidae as endoparasitism of insects, developed labrum of the mouthparts in the 1st larval instars, and swollen subscutellum in adult, supported tachinid group as monophyletic (Wood, 1985; Pape, 1992; Wood, 1987; O'Hara, 2020). However, taxonomic position within a family have been little various among many authors who dealt with family (O'Hara *et al.*, 2009; O'Hara, 2013a; O'Hara and Cerretti, 2016). Herting (1984) studied and began some stability with morphological and molecular analyses recently with proposed schemes in para- and polyphyletic groups (Cerretti *et al.*, 2015; Blaschke *et al.*, 2018). The four subfamilies in 1984 classified in common by Herting for the Palaearctic Region. Blaschke *et al.* in 2018 transferred Epigrimyiini and Eutherini to the Dexiinae (formerly in Phasiinae) and revealed the tribe Imitomyiini. The taxonomic position of the tribes in Tachinidae are various over time and it still did not reach agreement on it globally (O'Hara, 2013b). Despite several tribes with high homogeneity and more characteristics (Exoristini, Siphonini, Cylindromyiini), remaining, of debatable tribes as monophyletic, include vastly diverse forms (e.g., Blondeliini, Eryciini, Voriini) that may overlap in appearance with other groups. There are progresses in understanding of constituents and relationships of some taxa (Wood, 1985; Shima, 1996; O'Hara, 2002). Famous studies by Herting (1957) and Ziegler (1998) on female, male genitalia, larvae, puparia and eggs, respectively were informative. However, recent molecular analyses have the great ability to resolve complex debatable and problematic taxa within Tachinidae (Stirman *et al.*, 2019).

Stireman (2002) investigated Nearctic Exoristinae relationships using molecular data (28S rDNA and EF-1?) erecting the tribes Blondeliini, Exoristini and Winthemiini. This study supported Tachinidae and Exoristinae as monophyletic groups; however, Tachininae and Phasiinae were para-phyletic or polyphyletic. After that, Tachi and Shima (2010) analyzed Palaearctic Exoristinae employing 18S, 16S, white, and 28S, therefore, resolved the most tribes, where included Goniini. However, in these analyses, remaining subfamilies (Tachininae, Dexiinae and Phasiinae) poorly represented. Cerretti *et al.* (2014) used the morphological data as a first inclusive study to analyze the family including nearly 500 species. These phylogenetic studies established relationships among the most clades, supposed monophyly of some groups and presented several new relationships included: (i) A non-monophyletic Tachininae with one grade (Myiophasiini + Palpostomatini) as sister to the remaining of Tachinidae, (ii) Dexiinae + Phasiinae as sister to Exoristinae + (most) Tachininae, (iii) Phasiinae arising from within Dexiinae and (iv) Exoristinae arising from within Tachininae.

Relationships within the Exoristinae and Tachininae were poorly resolved and highly sensitive to model assumptions. Using different genes (18s, 28s, COI, EF?, TPI, CAD, LGL, MCS, MAC), Winkler *et al.* (2015) clarified the relationships of the subfamilies, greatly asserting the hypotheses Cerretti *et al.* (2014) and placed the Polleniinae (Calliphoridae) as a sister to Tachinidae (Cerretti *et al.*, 2017). Despite, this study used only 22 genera/tribes, inferred relationships within tribes for them. Blaschke *et al.* (2018) carried out a deep analysis of Phasiinae employing molecular genes (CAD, LGL, MCS, MAC) and included 128 taxa/80 genera. This is strong molecular phylogenetic analysis of tachinidae**,** robustly founding the structure of the subfamily and its tribes and hypothesizing Dexiinae and Phasiinae as sister groups.

Stireman *et al.* (2019), proposed the

most robust molecular phylogeny of tachinid group to date. The exemplars included 504 terminal taxa/359 genera/54 tribes. The most groups were covered, exceptionally, Anacamptomyini, Iceliini, Protohystriciini and Trichodurini. They got molecular genes (CAD, 28S, MCS and MAC). As in former investigations (Winkler *et al.*, 2015; Cerretti *et al.* 2017; Stireman, *et al.,* 2019), they agreed strongly with Cerretti *et al.* (2014) that the calliphorid Polleniinae as a sister 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.

Subfamily Phylogenetic Taxonomy

The analyses supported the subfamily relationships showing in former morphological (Cerretti *et al.*, 2014) and molecular (Winkler *et al.*, 2015; Blaschke *et al.*, 2018; Stirman *et al.* 2019) reconstructions, that gathered Dexiinae with Phasiinae and Tachininae with Exoristinae as groups. Macquartiini and Myiophasiini that is greatly supported as sister to the remaining Tachinidae and the morphologically strange tribes Palpostomatini and Imitomyiini that is strongly considered as sister to Dexiinae + Phasiinae. Excluding, these two small clades, the four subfamilial monophyly is strongly supported, independently, unlikely, in the morphological analysis (Cerretti *et al.*, 2014).

Phasiinae

Subfamily Phasiinae is the smallest one of Tachinidae yet still include over 600 known species belonging to 100 genera (O'Hara and Wood, 2004a; O'Hara and Wood, 2004b; Richter, 2004; O'Hara *et al.*, 2009; Evenhuis, 2013; O'Hara and Cerretti, 2016). However, some of the most morphological variations within Tachinidae can be found in this subfamily. Some phasiines are recognizably tachinids, being garbed in traditional black and grey with large bristles on their abdomen. Others are uniquely beautiful mimics of wasps and bees, with reduced setation and contrasting banding patterns or bright colouration. Among the more notable wasp mimics are *Penthosia satanica* (Bigot), *Formicophania elegans* Townsend and *Cylindromyia mirabilis* (Townsend) (O'Hara, 2012b). The hosts of Phasiinae are almost exclusively adults of true bugs (Hemiptera, suborder Heteroptera) and are unusual among tachinid hosts in being highly mobile and protected by a hardened cuticle (in contrast to caterpillars and other larval Holometabola) (McPherson and McPherson, 2000; Coombs, 2002; Coombs, 2004; Cerretti and Tschorsnig, 2010; Nihei and Pavarini, 2011; Nihei, 2016; Tschorsnig, 2017).

The first molecular phylogenetic treatment with subfamily Phasiinae was done in 2018 by Blaschke *et al.* (2018), and molecular sequences was abundantly included in Stireman *et al.* (2019) examinations (CAD, MAC, and MCS). Phylogenetic relationships among taxa within Phasiinae recovered are greatly identical. The both established robust monophyly of Phasiinae, although the branch linking Cylindromyiini to the remaining Phasiinae is short and this tribe may join the Dexiinae. Blaschke *et al.* (2018) resolved Strongygastrini and Parerigonini within Phasiinae and corresponded in study of Stireman *et al.* (2019). Tribe Phasiini has rearrangements as following: Gymnosomatini became include Cistogaster Latreille, *Clytiomya* Rondani, *Ectophasia* Townsend, *Eliozeta* Rondani and *Euclytia* Townsend; *Opesia* Robineau-Desvoidy transferred to Strongygastrini; and *Xysta* Meigen to Xystini (Blaschke *et al.*, 2018; Stireman *et al.* 2019). Also, in Parerigonini, Blaschke *et al.*'s analysis treated with it as related to Parerigonini (*Parerigone* Brauer, *Zambesomima* Walker), Cylindromyiini (*Australotachina* Curran, *Pygidimyia* Crosskey, *Neobrachelia* Townsend) or Zitini as a new tribe (*Zita* Curran, *Leverella* Baranov). *Penthosia* van der Wulp was transferred to Hermyini (formerly Cylindromyiini). Stireman *et al.* (2019) analysis different from that of Blaschke *et al.* (2018) in phasiine relationships by: (i) *Zita* and cf. *Leverella (*Zitini) are not monophyletic (*Leverella* was monophyletic in Blaschke *et al.,* (2018), (ii) Leucostomatini and Catharosiini constructed as a grade, (iii) *Xysta* and Zitini + Parerigonini are sisters, and (iv) *Imitomyia* linkes the Palpostomatini in characteristic group more than Dexiinae and Phasiinae. It can be regarded the good synapomorphy of the Phasiinae is that the basiphallus fused with distiphallus (Shima, 2015a; Shima, 2015b; Shima, 2015c; Shima, 2015d; Blaschke *et al.*, 2018). Stireman *et al.* (2019) added few taxa of phasiinae that didn't present in Blaschke *et al.* (2018) analysis, including Chinese ambiguous genus belongs to Parerigonini, an Australian *Australotachina species*, and Chilean *Phaeodema*, which joins *Neobrachelia* to form sister group to the remaining Phasiinae.

Dexiinae

Dexiinae is the third tachinid-subfamily in the world species number based on shared derived features of the male terminalia. In particular, male dexiines possess a hinged connection between the basiphallus and distiphallus of the phallus (or aedeagus) that is not found in other tachinids. Dexiines species considered as parasitoids on Lepidoptera, Coleoptera (larva and adult), Hymenoptera (Symphyta) and beside Phasiinae some dexiine's members parasitoid on Heteroptera (Smith *et al.,* 2006; Smith *et al.,* 2007; Smilanich *et al.,* 2009; Wood and Zumbado, 2010).

Subfamily Dexiinae are robust monophyletic group apart from the assemblage of Palpostomatini (*Palpostoma*, *Eutrixopsis*) and Imitomyiini (*Imitomyia*) that placed with Dexiinae + Phasiinae as sisters. The clade of *Euthera* + Epigrimyiini + *Litophasia* is a sister to the remaining of Dexiinae that was established by Blaschke *et al.* (2018) and Stireman *et al.* (2019). Voriini and Dexiini are defined sisters that appeared with complex phylogenetic relationships. The following mixture of (remaining) Palpostomatini, Dufouriini, Freraeini, and Telothyriini comprised some clades. The voriine lineages (included previous tribes Campylochetini, Uramyini, and Thelairini) and Myiotrixini, finally leading to Dexiini + Voriini s.s, Stireman *et al.* (2019) results partly supported by the wide vision of Voriini adopted by Herting (1960), Mesnil (1966), and O'Hara and Cerretti (2016), but even in this taxonomic arrangement the group remains paraphyletic with respect to Dexiini. Stireman *et al.* (2019) gave some well supported relationships within the "voriine grade" are worth highlighting. First, the Voriini s.s. are strongly supported as a clade in close association with several genera of the former Thelairini. The former Uramyini are also well-supported as a voriine clade with close relationships to the genera *Micronychiops*, *Trafoia*, and *Muscopteryx.* Stireman *et al.* (2019) proposed that the majority of Dufouriini represented in the tree form a well-supported clade, nested among voriines that are more traditional.

This restricted Dufouriini clade corresponds to those taxa with changed pregonites as recognized by O'Hara and Wood (2004a). Finally, *Phyllomya*, placed in the subtribe Phyllomyina by Mesnil (1966), and was reconstructed as a lone lineage, without apparent close association with any other included taxon by Stireman *et al.* (2019). But in Stireman *et al.* (2019) all of their analyses, across data sets and inference methods, consistently reconstructed *Myiotrixa* within Dexiinae, although its exact position within the voriine grade varies. *Myiotrixa* possesses a hinged phallus characteristic of Dexiinae (although apparently lacking an epiphallus), further supporting its placement among the dexiines. Dexiini are a clade, with consideration of including Rutiliini. As reconstructed by Stireman *et al.* (2019), there are three generic groups (lineages) in the tribe Dexinii: a *Dinera* group, *Rutilia* group, and their sister, *Dexia* group. The *Dinera* group consisted of several lineages, *Oligooestrus* and the voriine genus *Trochilodes* early branching New World groups. The *Rutilia* group consisted of Rutiliini nested within a larger clade of primarily Australian Dexiini, with the exception of the widespread Old World Genus *Prosena*. *Cordyligaster* (Sophiini) and *Neximyia* placed as strange sister to Dexiini. Possession of a dexiine-like phallus supports Stireman *et al.* (2019) in their reconstruction of *Neximyia* within the Dexiinae.

Tachininae

The Tachininae is the second largest subfamily, with vast heterogeneity subfamily, containing a plenty of different tribes. Its hosts are variable between insects and centipede, which parasites on 7 insect orders (Lipedoptera, Hymenoptera, Coleoptera, Orthoptera, Dermaptera, Diptera and Embiotera) and Lithobiomorpha. Therefore, it can be employed in controlling these arthropods (Gariepy *et al.,* 2007).

Macquartiini and Myiophasiini, Tachininae are robust clades and subfamily interrelationships well resolved in the analyses of Stireman *et al.* (2019). Stireman *et al.* (2019) recovered two genera *Microchaetina* and *Eulasionanewly,* newly included in the Tachininae (previously Dexiini then Voriini). The first, as the *Mintho*-leskiine assemblage, composed of the tribes Graphogastrini, Minthoini, Leskiini and Brachymerini, in addition to the genera *Eulasiona* and *Microchaetina*. The second major lineage of Tachininae, the Tachinini group, contains a diverse assemblage of tribes including Siphonini, Pelatachinini, Tachinini, Neaerini, Germariini, Megaprosopini, Proscissionini, Loewiini, Ernestiini, Polideini, Nemoraeini, Ormiini, Germariochaetini and Glaurocarini [in part]. The most of these tribes were recovered as monophyletic. Ernestiini and Loewiini were divided into two or three lineages. The tribe Tachinini can recognized by its large bodies, many spines, and its relationships proposed the explosive radiation. The sister to this well-defined clade varies, either consisting of a large ernestiine-polideine complex or a Megaprosopini-Germariini clade. *Pelatachina*, *Germaria* and *Neaera* occupy isolated branches supporting the classification of each as a small unique tribe, however the last two tribes consistently formed a clade with the dexiine-like Megaprosopini across analyses. The tribe Loewiini was divided among three clades: *Loewia* and *Eloceria, Hyalurgus*, sister to *Panzeria*, *Triarthria* near *Ormia.* Whole these taxa were temporarily placed within Loewiini (O'Hara and Wood, 2004a), and distributed in two tribes as supported by Herting (1984). *Linnaemya,* Ernestiini groups, a *Panzeria* lineage and some in Glaurocarini included in Ernestiini. This polyphyly has also been suspected on morphological grounds. The motley collection of taxa grading into Glaurocarini, comprising some Ernestiini (e.g., *Chlorotachina*), *Triarthria*, *Ormia*, and the Glaurocarini (including an undescribed genus), were very strongly supported. Interestingly, as in previous analyses (Inclán *et al.*, 2017), Stireman *et al.* (2019) did not find evidence for a close association between the nocturnal/crepuscular Orthoptera-attacking tribes Glaurocarini and Ormiini, although they both belong to the same larger clade. The tribe Proscissionini was supported as a clade. Some of relationships that still little doubtful, including the accurate place of Germariini + Neaerini, among genera of Ernestiini. In addition, some intergeneric relationships within well-supported tribes, such as Polideini and Leskiini, are not accurate Stireman *et al.* (2019).

Exoristinae

The Exoristinae, dominant tachinid subfamily in the globe, contain almost one-half of all known species belonging to 601 genera (O'Hara, 2013a). It is so hard to identify the subfamily acceptably because the strange diversity in morphology and female reproductive habits. Exoristine members have wide host-range, whereas its hosts extend to eight insect orders, including, Lepidoptera, Coleoptera, Orthoptera, Hymenoptera, Dermaptera, Diptera, Dictyoptera and Phasmatodea (Stireman, 2001; Stireman, 2005) Dindo and Nakamura (2018) examined two species as within the genus Exorista as parasitoids.

According to Stireman *et al.* (2019) study of the supported subfamily Exoristinae, which basally is branching ethillini, to the winthemiini and exoristini, to the groups of blondeliini and the eryciini+goniini gather. This reconstruction corresponded with other divisions of the tribes in Exoristinae, but the position of a few genera disagree with these classification schemes. However, genus *Trigonospila* (blondeliini) is positioned as sister to remaining subfamily or included in ethillini. This position is in agreement with the results reported by Tachi and Shima (2010) and Cerretti *et al.* (2014). Other blondeliini include a *hyllophilopsis* group and *Staurocheta.* Besides that, most tribes monophyly of Exoristinae are erected. Only Ethillini excluded; relationships within Ethillini by Stireman *et al.* (2019) well predicted by Cerretti *et al.* (2012) depending on external characters, egg, and host, which primarily divided into three groups (*Ethilla*, *Mycteromyiella* and *Phorocerosoma*). The other Blondeliini are constructed as a monophyletic that is divided into two major groups: A *Meigenia* and *Blondelia* clades. Although relationships within the former clade are resolved, the latter vary in the analyses. Some authors considered Eryciini as paraphyletic group (Stireman, 2002; Tachi and Shima, 2010; Stireman *et al.*, 2019). Stireman *et al.* (2019) suggested that *Aplomya is* sister to all remaining of Eryciines (+ Goniiin), a *Carcelia* and *Erycia* groups included the most in eryciini and originated between the formers. Genus *Ametadoria* (eryciini) arose within tribe Goniini, where it joined with *Gonia* or *Pales-Frontiniella* group. Stireman *et al.* (2019) suggested Goniini as monophyletic tribe despite the failure to reconstruct as a clear group. Herting (1957) and Cerretti *et al.* (2014) satisfied that it is monophyletic based on the morphological data.

CONCLUSION

According to the studies that we surveyed on the higher taxonomic classification of Tachinidae using molecular data, it is very important to clarify the phylogenetic relationships of the clades of the family. As a result of our survey, there are robust support for that calliphorid subfamily Polleniinae are sister to Tachinidae, proposing that the parasitic habit precedes the origin of tachinids (Winkler *et al.,* 2015). Each of the subfamilies and numerous recently known tribes were recovered, except in some lineages especially within Dexiinae and Tachininae. Therefore, molecular data have to be employed in the following studies on the family clades in more depth, because some lineages still unresolved as said above, because that would probably resolve some problematic tachinid lineages that were not resolved in the previous analyses. The confusion of accurate interpretation of the tachinid evolution and unsettled classification due to the Homoplasy. Although some recent studies contributed to clarify relationships of higher clades of Tachinidae, phylogenetic support in several parts in these analyses is unsatisfying. These surveyed results can be considered as a base for future phylogenetic and evolutionary studies of this significant family.

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