

Molecular Systematics of the Subfamily Phasiinae
(Diptera: Tachinidae)

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ABSTRACT

The subfamily Phasiinae (Diptera: Tachinidae) is composed of obligate endoparasitoid flies that attack heteropteran insects, many of which are important agricultural pests. To lay a foundation for future studies in phasiine life history and their potential for use as biological control agents, the phylogenetic relationships within Phasiinae were explored with nucleotide sequences of two genes, CAD and LGL. A total of 63 taxa for CAD and 73 taxa for LGL were included in the analyses, representing 58 genera. Maximum likelihood inference methods were employed to reconstruct phylogenetic relationships in separate analyses of each gene and in a combined dataset. Phylogenetic reconstructions generally supported recent morphological classifications based on oviposition strategies and postabdomen characters. All tribes in Phasiinae were recovered as monophyletic or could become so with minor changes to current classification schemes. Tachinidae was recovered as a monophyletic family, and the monophyly of the subfamilies Tachininae, Exoristinae, and Phasiinae was resolved with varying levels of statistical support. Dexiinae was paraphyletic. Significant results include the following proposed taxonomic revisions: 1) removing *Litophasia* from Catharosiini, 2) transferring *Euclytia*, *Eliozeta*, *Ectophasia*, and *Clytiomya* from Phasiini to Gymnosomatini, 3) including *Strongygaster* and *Rondaniooestrus* in Phasiinae, 4) placing *Rondaniooestrus* and *Opesia* in Strongygastrini, 5) creating a new tribe for *Xysta*: Xystiini, 6) placing *Hermya* at the base of Strongygastrini in its own tribe, Hermyni, rather than in Cylindromyiini, and 7) including *Litophasia*, *Euthera*, and *Epigrimyia* in Dexiinae.

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CHAPTER I

LITERATURE REVIEW

Introduction and Objectives

Tachinidae

Tachinidae is a vastly diverse dipteran family composed entirely of endoparasitoid flies (Stireman et al. 2006). Four subfamilies are included: Phasiinae, Dexiinae, Exoristinae, and Tachininae (O'Hara & Wood 2004). With over 10,000 described species worldwide, tachinids are among the largest and most morphologically diverse families of insects (Crosskey 1980) and aside from the parasitic Hymenoptera, the largest parasitoid group (Stireman 2002).

Tachinids have experienced such astounding adaptive success in part due to their varied choice in hosts. The family includes both generalist species and specialists, which collectively attack a multitude of hosts from 14 different orders of arthropods. They primarily attack insects (Arnaud 1978; O'Hara & Wood 2004) but also parasitize scorpions (Williams & Arnaud 1990), centipedes (Wood & Wheeler 1972), and spiders (Vincent 1985). By preying on phytophagous insects such as lepidopteran caterpillars and hemipteran bugs, tachinids play an important role in regulating pest populations in natural ecosystems and controlled agricultural environments (Nishida 1966; Karban & English-Loeb 1997; Coombs 2004; Stireman & Singer 2003).

The taxonomy of Tachinidae is notoriously difficult and confusing (Sabrosky & Arnaud 1965; Crosskey 1976; Tschorsnig 1985; O'Hara & Wood 2004; Stireman 2006). They appear to be a recent and actively radiating group of insects (Guimarães 1971) and this recent evolution has led to numerous “intergrades” between species that blur the lines between intraspecific variation and unique taxa (Townsend 1908). Additionally, there is

widespread convergence of character traits (homoplasy) throughout the family resulting in very few clear synapomorphies that distinguish genera, tribes, or even subfamilies. Of the four subfamilies (Phasiinae, Exoristinae, Dexiinae, and Tachininae), the only defined monophyletic group is Dexiinae, whose genera are classified together based on unique male terminalia characters (Tschorsnig 1985; Wood 1987). The other subfamilies are defined based on the presence of a collection of multiple character traits and/or life history traits that are difficult to identify and contain many exceptions. Due to the high level of morphological homoplasy, molecular systematics has the potential to provide a much needed, more concisely defined taxonomy that has eluded morphologists for decades.

Phasiinae

Phasiinae are the smallest subfamily of the Tachinidae, but due to constant taxonomic rearrangement, there is uncertainty about specific numbers of species and genera. It is estimated that there are approximately ninety genera in nine-eleven tribes worldwide.

Taxonomy

Phasiinae are taxonomically separated from other tachinid subfamilies by their parasitism of heteropteran hosts (Coquillett 1897); oviparity (oviposition of unembryonated macrotypic eggs) (O'Hara 1985); and an elongated hypandrium in the male postabdomen (Tschorsnig 1985; Richter 1992). However, none of these traits is a true synapomorphy as *Epigrimyia*, *Beskia*, *Euthera*, and *Strongygaster* also attack Heteroptera but are classified in Dexiinae or Tachininae; many Exoristinae are oviparous

as well; and *Litophasia* (Phasiinae: Catharosiini) does not have an elongated hypandrium. As a result, there remains uncertainty about the monophyly of the subfamily.

Basal relationships are poorly defined in Tachinidae as a whole and within the Phasiinae specifically (Stireman et al. 2006). Part of the difficulty lies in contradicting traits of Phasiinae. The two oviparous lineages within Tachinidae (Phasiinae and some Exoristinae) have historically been considered evolutionarily basal (Verbeke 1962; Stireman et al. 2006) due to their “primitive” egg type. However, both Herting (1983) and Tschorsnig (1985) thought that Phasiinae contained the most derived terminalia characters and should be considered a more recent clade. The phasiine choice of hosts also indicates a recent divergence as the ancestral host of Tachinidae is thought to be more similar to a lepidopteran caterpillar than a heteropteran bug (Stireman et al 2006). Phasiines are difficult to place taxonomically due to these competing traits. They have primitive eggs and oviposition strategies, but highly derived external morphology and host use. This means phasiines are either a recent divergence and have maintained basal oviposition strategies throughout their evolution, or a basal group and a heteropteran may have been the original tachinid host.

However, an ancestral heteropteran host is contrary to the current hypothesis that tachinids evolved from a sarcophagid-like ancestor (O’Hara & Wood 2004). Because most tachinid larvae are relatively tolerant of toxins, an ancestor that thrived in carrion (as many sarcophagids still do) is plausible (Gauld et al. 1992). This unique ability may have preadapted phasiines to exploit larvae of chemically defended insects like stink bugs and their relatives (Stireman et al. 2006). Exploiting heteropterans as new hosts may have been an early host-shift that was facilitated by the phasiines’ tolerance for noxious

compounds. Since many heteropterans are chemically defended, phasiines were able to multiply rapidly in the relatively enemy-free space (Jeffries & Lawton 1984; Aldrich et al. 2006). A thorough phylogenetic analysis of the subfamily will provide evidence for which historical path is more likely. This information can be used across the family to infer basal relationships and trace the evolution of host use and oviposition strategies.

Identification

Although it is the least speciose tachinid subfamily, Phasiinae also contains the most morphologically diverse species. Many display cryptic coloration patterns or mimic the bright colors that usually indicate toxicity on other insects (aposematism). As a result, several genera look remarkably similar to various hymenopteran species. For example, the abdomen of *Cylindromyia mirabilis* from the southwestern USA mimics an ichneumonid wasp (Townsend 1908), and most species in the tribes Cylindromyiini, Gymnosomatini, and Trichopodini have bright red, orange, or black and yellow abdomens that mimic the warning colors of predatory wasps and bees (Waldbauer et al. 1977).

Phasiines can be superficially distinguished from other tachinids by their vivid coloration and sparingly bristled abdomen. There are several morphological traits scattered throughout the subfamily that are unique among tachinids. For example, in the Leucostomatini, females have a horizontal pair of toothed forceps at the tip of the abdomen, a structure thought to assist in mating behavior (Reinhard 1956; Cantrell 1988). Also, in the mostly Neotropical tribe Trichopodini, several genera have uniquely enlarged oar-shaped setae on their hind tibia, giving them the common name “feather-legged flies” (Townsend 1908).

Life History

Phasiines identify potential hosts through the use of specialized antennal receptors that are extremely sensitive to host pheromones (Aldrich et al. 2006). Many phasiines are more adept at locating host species than even their hosts are of locating each other (Aldrich et al. 1989). Most commonly, they are attracted to sexual aggregation pheromones of the male bugs and as a result generally parasitize more males than females. Because of their distinctive ability to use pheromone cues as kairomones, phasiines hold great promise as biological control agents.

Immediately after a suitable host is found, gravid females deposit a planoconvex egg on or within their target host. While some phasiines lay their eggs on the external surface of the host, others have developed a piercing ovipositor from modified sternites and are capable of injecting an egg directly into the host. Such a modification reduces the chance of losing the egg/larva via the host rubbing it off or consuming it. If laid externally, eggs hatch almost immediately after deposition and the larvae burrow through the ventral side of the egg and directly through the host's integument into the hemocoel.

Once inside the host's body cavity, the larvae feed on fluids without killing the host. Larvae may induce changes in the corpora allata of their host and thereby reduce their host's reproductive activity and success (Clausen 1940; Panov et al. 1972; Beckage 1985; Higaki 2003). Larvae often overwinter as parasitoids and emerge from their hosts the following spring when the hosts emerge from diapause. Phasiines are not capable of discerning a parasitized host from one that has not been parasitized and will sometimes oviposit on a previously parasitized host. Such superparasitism results in intra-host competition for space and resources. Usually, only one larva will mature to adulthood. If

it is a large host, however, several larvae may emerge to pupate, but the adults are usually stunted.

Many phasiine host species are important agricultural pests and have shared a close co-evolution with their parasitoid enemy that has affected their relationship with their own host plants. Because of this close historical relationship, a predictive and well-supported taxonomy will provide fertile research ground for future studies in biological control, co-evolution of interspecies complexes, pheromone attractants, and tritrophic ecological interactions.

Objectives

A molecular systematic analysis of Phasiinae using the nuclear coding genes *rudimentary* (CAD) and *lethal giant larvae* (LGL) was conducted to infer a well-supported phylogeny that can be used to achieve the following objectives:

1. Determine whether or not Phasiinae is monophyletic
2. Assess the monophyly/validity of tribes in Phasiinae
3. Resolve basal relationships within Phasiinae
4. Determine the sister group of Phasiinae
5. Infer the taxonomic affinities of the following ambiguous taxa: *Strongygaster*, *Rondaniooestrus*, *Euthera*, *Epigrimyia*, and *Litophasia*

Importance of Phasiinae

Economic Impacts

Endoparasitoid flies in the subfamily Phasiinae attack members of Heteroptera and play an important role in the agricultural economy. Phasiines reduce host populations by decreasing the reproductive potential of their host during growth and development and then killing most individuals upon emergence. Many of their hosts are prominent agricultural pests and include the destructive *Nezara viridula* (southern green stink bug), *Euschistus servus* (brown stink bug), and multiple *Lygus* spp. (tarnished plant bugs) (Coquillett 1897; Arnaud 1978). Few heteropterans are species-specific pests, so numerous crops are affected by numerous pest species. These pests cause significant damage by reducing the yield and quality of crops like corn, soybean, alfalfa, and cotton; orchards that produce apples, peaches, and pears; and vegetable fields that produce squash, pumpkins, and strawberries (Jones 1988; Schaefer & Panizzi 2000; Corrêa-Ferreira et al. 2002; McPherson & McPherson 2010).

It is impossible to accurately calculate the monetary loss caused by every heteropteran pest across every crop, but the cost is undoubtedly enormous. For example, annual crop losses from stink bugs and plant bugs on soybean yield alone reached \$27.2 million in Georgia in 1993 (McPherson & McPherson 2010), and *Oebalus* (rice bug) caused \$13 million in rice damage in Texas in 2000 (McPherson & McPherson 2010). Thorough and detailed analyses of the economic losses from heteropteran pests are given in *Heteroptera of Economic Importance* (Schaefer & Panizzi 2000) and *Stink Bugs of Economic Importance in America North of Mexico* (McPherson & McPherson 2010).

Most of these pests are known hosts of at least one, and in many cases several, phasiine species. As such, there is an untapped wealth of biological control research that could be integrated into pest management practices.

Along with the recurring problems from native pests, growers in the coming years also face emerging threats from invasive species like *Halyomorpha halys* (brown marmorated stink bug) and *Megacopta cribraria* (kudzu bug). Both species are nuisance pests as they can overwinter in large aggregations in residential homes, but *M. cribraria* has also become a destructive pest in soybean fields, while *H. halys* has the potential to wreak havoc on fruit and vegetable production in the US. Both invasive species have already been exploited by native phasiine parasitoids. *Phasia robertsonii* has been reared from *M. cribraria* (Ruberson et al. 2013) and both *Euclytia flava* and *Trichopoda pennipes* have been reared from *H. halys* (Aldrich et al. 2006; Tillman et al. 2010).

Because of their extreme sensitivity to host pheromones, phasiines are excellent candidates for native control of invasive pests. Many heteropteran pheromones are chemically similar and at times just different isomers of the same compound. This similarity can lead to a cross-species attraction and new host associations by phasiines when a new, slightly different pheromone is introduced. Use of native species for biological control has many potential benefits. Evaluation of a foreign species for release on native soil is expensive and time-consuming. There is also a danger that the non-native species will switch hosts and begin attacking native species. These hazards are avoided by the use of a parasitoid species that is already present and a natural part of the ecosystem.

Despite their potential, however, some phasiines have had mixed success when released in biological control programs. The most widely used phasiines for such purposes are members of the genus *Trichopoda*. The Argentine parasitoid *Trichopoda giacomellii* has been established as an annual parasitoid of *Nezara viridula* (southern green stink bug) in Australia (Coombs & Sands 1999; Coombs 2003) and *T. pennipes* and *T. pilipes* have suppressed populations of the same pest in Hawaii (Nishida 1966; Debach 1962; Howarth 1991; Johnson et al. 2005). However, *T. pennipes* has had only mixed success in controlling populations of *Anasa tristis* (squash bug) when introduced into the northwestern U.S. (Sabrosky 1955; Clausen 1956; Dietrick & van den Bosch 1957; Picket et al. 1996).

The inconsistent success of *Trichopoda* biocontrol programs may be a result of a cryptic species complex composed of pheromone strains which are not best suited to control the pest of interest. In this instance, each cryptic species is distinguished from all others by host preference/pheromone attraction (Aldrich et al. 1987). For example, a single morphological species of *T. pennipes* may have certain populations that are sensitive to the pheromones of *N. viridula*, and other populations that are only attracted to the pheromones of *A. tristis*. This confusion has led to uncertainty about which species or host race a biocontrol program is actually releasing and has resulted in ineffective biological control of target pests. *Euclytia flava* also displays pheromone strain potential, and it may be common throughout the subfamily (Aldrich & Zhang 2002). Discovering and typing potential pheromone strains will enhance the selection of the most appropriate biocontrol agent and result in more effective pest control while minimizing detrimental effects on the environment and human society.

The foundation of a successful biological control program is the accurate identification of natural enemies (Gareipy et al. 2007). Without precise identifications, the program may fail. Precise taxonomy and updated/or accurate molecular identification techniques are vital information that must be obtained before a potential natural enemy is released to control a pest (Bigler et al. 2005). Despite their potential to control heteropteran crop pests, phasiines are under-studied taxonomically and simple identification tools are absent. This research attempts to provide a stable classification system as well as several molecular markers that may be used for simple and rapid species identification.

Ecological Impacts

Phasiines fulfill two critical roles in their environment: pollinator and secondary consumer. In part due to their difficult morphology and confusing classification system, few studies have focused on the specific role of phasiines in an ecosystem. However, their functions and benefits are easily inferred from the limited information about phasiines that is available combined with numerous studies on similar pollinators and parasitoids.

The significance of pollination ecology to flowering plants is well studied (Faegri et al. 1966; Kevan et al. 1990; Klein et al. 2007), with Levin (1970) suggesting that pollinators are as vital to the health of plant populations as physical resources such as light and moisture. In fact, up to two-thirds of flowering plant species rely on insects for reproduction (Axelrod 1960; Tepedino 1980). As pollinators, phasiines contribute to the continued health of ecosystems by ensuring that flowering plants continue to reproduce. Adult phasiines require a continuous source of sugar reserves to maintain enough energy

for flight. Most of them obtain the nutrients they need from pollen and nectar and thus form a symbiotic relationship with numerous plant species; the phasiines receive energy and the plants are pollinated. Several studies have documented the importance of phasiines in meadow and forest communities, specifically in the pollination of *Metrodorea* spp. (Rutaceae) by *Cylindromyia* (Pombal & Morellato 2000); of *Polygonum* (knotweeds, Polygonaceae) by *Ectophasia* (Momose & Inoue 1993); and *Asclepias* (milkweeds, Apocynaceae) by *Gymnoclytia* and *Trichopoda* (Nihei & Schwarz 2011). Additionally, because their hosts are also feeding on plants, phasiines become a prominent member of their habitat as they assist in plant reproduction and reduce the population of plant-damaging insects.

An estimated 25% of all insect species are parasitoids (Godfray 1994) and because insects themselves make up approximately 80% of all currently discovered species, parasitoids may comprise up to 20% of all animal life (Smith et al. 2007). The sheer number of parasitoid species attests to their integral role in habitat health. Phasiine parasitoids are no exception and interact with their environment as secondary consumers. Almost all phasiine hosts are phytophagous insects, leading to a tritrophic interaction among parasitoid, host, and host plant that is ecologically important. The significance of this three-fold interaction is just beginning to be explored (Hawkins & Sheehan 1994; Gentry & Dyer 2002; Lill et al. 2002). By their parasitism of heteropteran hosts, phasiines regulate the population of primary consumers and thereby directly influence plant and ecosystem health. This three-tier system of tachinid ecology is essential for the health of many ecosystems and was used by the well-known population ecologist M.P.

Hassell to develop many of his influential ideas about insect community structure (Hassell 1968, 2000; Stireman et al. 2006).

Although specific impacts of phasiines have yet to be fully explored, it is well known that parasitoids in general can have an enormous effect on their host populations and directly influence the evolution of their hosts and their ecosystem. For example, tachinid parasitoids of lepidopteran larvae account for at least half the caterpillar deaths due to parasitism (Janzen 1981, 1988; Sheehan 1994; Stireman & Singer 2003). Such intense predation exerts selection pressure on vulnerable populations and causes behavioral changes in order to minimize parasitism (Ebert & Hamilton 1996; Hart 1994). Some of these host modifications include the evolution of cryptic coloration or defensive compounds, nocturnal feeding strategies, or the initiation of defensive maneuvers when a host is attacked. Additionally, tachinids can cause phytophagous insects to change their host plant preferences from plants that contain the highest nutritional value to plants that reduce their chances of parasitism (O'Hara 2008). This trade-off in evolutionary value between nutrition and potential mortality for tachinid host species results in a change in plant community structure and species composition.

Taxonomic History of Phasiinae and Selected Genera

Phasiinae

Most modern tachinid experts agree on a four-subfamily classificatory system for the Tachinidae (Herting 1984; Wood 1987; Herting & Dely-Draskovits 1993; Tschorsnig & Richter 1998; O'Hara & Wood 2004; Tachi & Shima 2010). However, relationships within and among the subfamilies are poorly understood and are under constant rearrangement. A basal position is poorly supported for any subfamily and multiple scenarios have been proposed. Phasiinae was proposed as the basal lineage due to their egg morphology by Richter (1992), who also placed (Tachininae + Dexiinae) as the most derived group. This arrangement was similar to the proposed (Phasiinae + Exoristinae) and (Tachininae + Dexiinae) of Herting (1966, 1983). However, Dexiinae has also been proposed as the sister group to Phasiinae by Shima (1989) who placed them as potentially basal to (Exoristinae + Tachininae) (O'Hara & Wood 2004). Due to the small number of subfamilies, a molecular phylogeny that defines relationships among even a single subfamily like Phasiinae can contribute much to a broader picture of tachinid evolution and history.

Over the past century, phasiine tribes have been constantly rearranged based on new morphological characters and generic revisions. For this reason, there is not a consensus among experts about how many tribes there are in Phasiinae or which tribes should be included and which should be removed. Each tribe falls into one of three categories when all classifications are consulted: strictly Phasiinae, Phasiinae or Tachininae, and Phasiinae or Dexiinae. Six traditional tribes are universally accepted as

phasiines: Phasiini, Gymnosomatini, Trichopodini, Cylindromyiini, Leucostomatini, and Catharosiini. Two additional tribes are sometimes split from these: Cinochiriini from Leucostomatini, and Hermyini from Cylindromyiini. Three tribes occupy an ambiguous area between Phasiinae and Tachininae: Strongygastrini, Rondaniooestrini, and Parerigonini. Additionally, three more tribes are split by experts between Phasiinae and Dexiinae: Eutheriini, Epigrimyiini, and Imitomyiini. There are also two older phasiine tribes that have yet to be either confirmed as legitimate taxa or removed from Phasiinae in a modern analysis of the tribe: Tarassini and Euscopolioterygini. At either extreme, the number of tribes in Phasiinae ranges from six to sixteen (Crosskey 1973, 1976; Herting 1984; Tschorsnig 1985; Wood 1987; Herting & Dely-Draskovits 1993; Tschorsnig & Richter 1998; Ziegler 1998; Richter 2004; O'Hara et al. 2009). A molecular phylogenetic analysis that includes genera from many of these mobile taxa has the potential to significantly clarify the confusion of phasiine classification. All six of the core phasiine tribes and twelve of the sixteen possible phasiine tribes are included in this analysis.

Many genera in Phasiinae have confusing taxonomic histories when primary sources are examined. Several genera are in desperate need of modern revision (i.e. *Strongygaster*, *Trichopoda*). Early dipterists did not have the same quality of identification tools and resources as we do today and there were significant language and geographic barriers between specialists living on different continents. Many descriptions were incorrect and sometimes specimens belonging to multiple genera were described as a single genus. For example, the early 20th-century dipterist C.H. Townsend was a prolific “splitter” who named and described most of the 20+ genera in Trichopodini. Many of these genera are monotypic and would certainly be synonymized in a modern

revision of the tribe. But for now, Trichopodini remains the largest tribe in Phasiinae by number of genera. Rather than a detailed examination of all the taxonomic travelling our modern phasiine species have done, short summaries of selected genera will be provided that have been derived from reviews and classifications by experts in the field.

Strongygaster

Strongygaster was first named and described by Macquart (1834) based on *Tachina globula* Meigen (1824). Townsend (1908) later described three different genera: *Hyalomyodes*, *Clistomorpha*, and *Strongygaster*, which were later revised by Curran (1927) and Brooks (1942), but the three genera were collapsed into *Strongylogaster* by Wood (1987).

Morphologically, *Strongygaster* appears to be a phasiine and consequently was placed with other “classic” phasiines in Gymnosomatidae (Townsend 1936) and in Phasiinae by modern taxonomists (Guimarães 1971; Herting 1984; Tschorsnig 1985; Richter 1993). However, *Strongygaster* is set apart from other phasiines due to its wide range of hosts, which includes Orthoptera (Kevan & Koshnaw 1988), Coleoptera (Arnaud 1978), Hymenoptera (Eggleton & Belshaw 1992; Feener 2000), Lepidoptera (Lange 1950), Dermaptera (Sabrosky & Braun 1970; Firlej 2005), and Diptera (Ferrar 1977). They also possess a uterus (ovoviviparity) indicating a placement outside Phasiinae (Wood 1987). Due to this trait and because phasiines are grouped together largely based on their obligate parasitism of heteropteran hosts, O’Hara & Wood transferred *Strongygaster* to Tachininae in 2004. This placement is now generally accepted (Stireman et al. 2006; Cerretti et al. 2009; Inclan & Stireman 2011).

There is some confusion among experts as to whether or not *Strongygaster* actually parasitizes Heteroptera. The most recent treatments of the genus have specifically noted the lack of heteropteran hosts (Wood 1987). Tschorsnig & Richter 1998; O'Hara & Wood 2004; Gammelmo & Sagvolden 2007; Davis 2012), and many earlier studies only mention multiple beetle hosts without directly commenting on Heteroptera (Thompson 1954; Arnaud 1978; Smith & Kok 1983). Other references cite hemipteran hosts, but fail to provide a suitable reference (Purington et al. 1990; Katsoyannos & Aliniaze 1998; Nalepa & Kidd 2002; Reeves & O'Hara 2004; Kenis et al. 2008).

However, when *Strongygaster*'s former synonym *Hyalomyodes* is taken into account, several references for heteropteran hosts emerge. Parasitism of *Megalotomus parvus* (Alydidae) by *Hyalomyodes* is described by Santos & Panizzi (1997) and *Hyalomyodes* has also been recorded as emergent from *Euschistus heros* (Pentatomidae) (Panizzi & Oliveira 1999). These papers were published in South America where *Hyalomyodes* is not currently synonymized with *Strongygaster* in the most recent catalogue of that region (Guimarães 1971). Additionally, in the course of this research, *Strongygaster triangulifera* was reared from a harlequin bug (Pentatomidae: *Murgantia histrionica*) in eastern Tennessee. This rearing establishes a new host association and conclusive evidence that *Strongygaster* does indeed parasitize Heteroptera.

Rondaniooestrus

Rondaniooestrus Villeneuve is a unique monotypic genus containing the only known tachinid parasite of honey bees. First named and described in 1916 from South Africa, *Rondaniooestrus* was placed near *Rondania* in the Rhinophorinae group of

Girschner. Its biology and immature forms were described by Skaife in 1921, but a taxonomic position was not assigned.

No specific systematic position was given until Mesnil (1939) placed it in the Dufouriini of Dexiinae. However, he later agreed with Verbeke's (1962) analysis of the genus and placed it near Strongygastrini in the Phasiinae (Mesnil 1966). Dupuis, on the other hand, disagreed and excluded both Strongygastrini and Rondaniooestrini from his monograph of Phasiinae (1963) (O'Hara 2013). Additionally, Crosskey (1984) placed *Rondaniooestrus* in Tachininae in its own tribe Rondaniooestrini due to its superficial morphological similarity to *Strongygaster* and the shared host (Hymenoptera).

Litophasia

Litophasia Girschner, 1887 is known only from a few specimens in two species, one from Europe and one from South Africa. *Litophasia*'s placement in Tachinidae has been debated. Two of the synapomorphies used to discern the monophyly of Tachinidae are the presence of meral bristles and an enlarged postscutellum (Wood 1987). *Litophasia* has neither of these characters (Crosskey 1984; Wood 1987; Tschorsnig & Richter 1998), and was initially thought to belong in the Rhinophoridae.

Dear and Herting (1980) considered *Litophasia* a phasiine in the tribe Catharosiini and used characters of the female postabdomen to support the placement. *Litophasia* females possess a piercing ovipositor, which is commonly found in Phasiinae but never in the Rhinophoridae. However, no hosts are known from either Europe or South Africa that would more securely place *Litophasia* in Phasiinae. Consequently, *Litophasia* was placed in Dexiinae and aligned with the Eutheriini and Epigrimyiini on the basis of male terminalia characters by Tschorsnig (1985).

Euthera

An excellent modern review and revision of *Euthera* Loew, 1866 was published by O'Hara (2012). The systematic portion of his research is summarized here. *Euthera* has been placed in its own tribe Eutherini (Crosskey 1973, 1976), sometimes as a sister taxon to the rare European genus *Redtenbacheria* (Herting 1984; Herting & Dely-Draskovits 1993; Ziegler 1998; Richter 2004; O'Hara et al. 2009). As with the other genera examined, there is uncertainty about the subfamilial placement of *Euthera* with various experts placing it in either Phasiinae or Dexiinae.

Egg morphology and host association (Pentatomidae) indicate placement in Phasiinae and this classification has been followed by many authors (Crosskey 1976; Cantrell 1983; Cantrell & Crosskey 1989; Herting & Dely-Draskovits 1993; Ziegler 1998; Richter 2004). However, some authors have chosen to align *Euthera* with the Dexiinae based on the ovolarviparity of the females and terminalia characters of the male (Tschorsnig 1985; O'Hara & Wood 2004; Shima 2006; O'Hara et al. 2009; Cerretti 2010; Wood & Zumbado 2010). Therefore, *Euthera* may represent a basal dexiine (Shima 1989) or an aberrant phasiine (O'Hara 2012).

Epigrimyia

Epigrimyia Townsend, 1891 is in a similar taxonomic position as *Euthera*: some experts place the genus in Phasiinae, others in Dexiinae. Townsend initially described the genus and placed *Epigrimyia* in his subfamily Pyrrhosiinae (= Phasiinae) in 1891 and gave it its own tribe in 1908. He then reassigned *Epigrimyia* from Epigrimyini to Cylindromyiini (Phasiinae) in 1912.

Despite its historical placement in Phasiinae (Guimarães 1971; Herting 1983), *Epigrimyia* was transferred to Dexiinae by Tschorsnig (1985) in his examination of male postabdomen characters. *Epigrimyia* shares a suite of terminalia traits with dexiines, and does not have an elongated hypandrium as do most phasiines. To further confuse classification, *Epigrimyia* shares host associations with both Dexiinae (i.e., Coleoptera [Townsend 1891]) and Phasiinae (i.e., Heteroptera [Biehler & McPherson 1982]). The new taxonomic position of *Epigrimyia* in Dexiinae was followed by Wood & O'Hara (2004), but its placement is still far from certain.

CHAPTER II
MOLECULAR SYSTEMATICS OF PHASIINAE

Materials and Methods

Specimen Sampling and Preservation

Phasiinae was sampled to provide representative specimens of as many tribes as possible, as well as characteristic genera of other subfamilies and outgroup taxa. A total of 75 specimens representing 58 genera and 70 species were included in the molecular data sets (Table 1). Most phasiine tribes were included except the Tarassini and the Euscopolioterygini, two extremely rare South American tribes containing a total of three genera. Tachininae was represented by three genera in three tribes, Exoristinae by five genera in five tribes, and Dexiinae by ten genera in nine tribes. Nine genera representing the following outgroup families were included: Muscidae (1), Oestridae (2), Sarcophagidae (2), Calliphoridae (3), and Rhinophoridae (1).

Adult phasiines feed on nectar, are strongly attracted to heteropteran pheromones, and are found in open fields of flowers. Collecting was mostly performed with an aerial net by specifically targeting desired specimens. Sweeping and flight-intercept trapping were also utilized to capture the smaller, inconspicuous species. Heteropteran pheromone attractants (AgBio, Westminster, CO) were employed to attract additional species. All specimens were frozen or placed in 95% ethanol until DNA sample preparation. If frozen, the specimens were thawed, pinned, and the three right legs were removed and placed in 95% ethanol. Morphology was therefore preserved for later species identification while still extracting viable DNA. For very small specimens it was sometimes necessary to use the whole body to extract enough useful DNA. Purified DNA samples were stored at -20°C (Moulton & Wiegmann 2004).

Table 1. Taxa and collection site information for specimens used in the molecular analysis of Phasiinae. Sequences (CADI, CADII, LGL) used for each species included are marked with an X.

<u>Family</u>	<u>Tribe</u>	<u>Genus</u>	<u>Species</u>	<u>Country, State: Co</u>	<u>CADI</u>	<u>CADII</u>	<u>LGL</u>
<u>OUTGROUP</u>							
Muscidae		<i>Musca</i>	<i>domestica</i>	USA, TN: Knox			X
Oestridae		<i>Cephenemyia</i>	sp.	USA, NM: Grant	X	X	
Sarcophagidae		<i>Macronychia</i>	sp.	USA, OH: Greene	X	X	X
Calliphoridae		<i>Mesembrinella</i>	sp.	Ecuador	X	X	
Oestridae		<i>Cuterebra</i>	<i>austeni</i>	USA, AZ: Pima	X	X	X
Calliphoridae		<i>Pollenia</i>	sp.	USA, TN: Knox	X	X	X
Rhinophoridae		<i>Melanophora</i>	<i>roralis</i>	USA, OH: Greene			X
Calliphoridae		<i>Lucilia</i>	<i>sericata</i>	USA, OH: Greene			X
Calliphoridae		<i>Opsodexia</i>	sp.	USA, OH: Scioto	X	X	X
<u>INGROUP</u>							
<u>Subfamily</u>	<u>Tribe</u>	<u>Genus</u>	<u>Species</u>	<u>Country, State: Co</u>	<u>CADI</u>	<u>CADII</u>	<u>LGL</u>
Tachininae	Siphonini	<i>Siphona</i>	<i>cristata</i>	USA, NM: Grant	X	X	X
	Tachinini	<i>Epalpus</i>	<i>signifer</i>	USA, TN: Knox	X	X	X
	Ernestiini	<i>Panzeria</i>	<i>ampellus</i>	USA, OH: Greene	X	X	X
	Rondaniooestrini	<i>Rondaniooestrus</i>	<i>apivorus</i>	South Africa	X	X	X
	Strongygastriini	<i>Strongygaster</i>	sp.	USA, TN: Knox			X
	Strongygastriini	<i>Strongygaster</i>	<i>triangulifera</i>	USA, OH: Greene	X	X	X
	Acemyini	<i>Ceracia</i>	<i>dentata</i>	USA, OH: Greene	X	X	X
Exoristinae	Winthemini	<i>Winthemia</i>	<i>deilephilae</i>	USA, AZ: Cochise	X	X	X
	Exoristini	<i>Tachinomyia</i>	<i>acosta</i>	USA, OH: Greene	X	X	X
	Blondeliini	<i>Blondelia</i>	<i>polita</i>	USA, NM: Tarrant	X	X	X
	Goniini	<i>Hyphantrophaga</i>	<i>hyphantriacae</i>	USA, AZ: Graham	X	X	X
	Eryciini	<i>Lespesia</i>	<i>datanarum</i>	USA, OH: Hocking	X	X	X
Dexiinae	Campylochetini	<i>Campylochaeta</i>	<i>semiothisae</i>	CAN, Ontario	X	X	X
	Epigrimyiini	<i>Epigrimyia</i>	sp.	USA, OH: Greene	X	X	X
	Eutherini	<i>Euthera</i>	<i>setifacies</i>	USA, NM: Grant	X	X	X
	Palpostomatini	<i>Eutrixia</i>	<i>exilis</i>	USA, OH: Hocking	X	X	X
	Dufouriini	<i>Oestrophia</i>	sp.	USA, AZ: Maricopa	X	X	X
	Uramyini	<i>Uramya</i>	<i>pristis</i>	USA, OH: Greene	X	X	X
	Rutiliini	<i>Rutilia</i>	<i>regalis</i>	AUS, Queensland	X	X	X
	Dexiini	<i>Billaea</i>	sp.	USA,GA: Rabun	X	X	X
	Dexiini	<i>Ptilodexia</i>	<i>harpasa</i>	USA, OH: Hocking	X	X	X
	Sophiini	<i>Cordyligaster</i>	sp.	USA, TN: Sequatchie	X	X	X
	Thelairiini	<i>Thelaira</i>	<i>americana</i>	USA, OH: Greene	X	X	X
	Voriini	<i>Voria</i>	<i>ruralis</i>	USA, WV: Hampshire	X	X	X
Phasiinae	Cylindromyiini	<i>Hemyda</i>	<i>aurata</i>	USA, TN: Knox	X	X	X
		<i>Phania</i>	<i>funesta</i>	Italy	X	X	X
		<i>Besseria</i>	sp.	South Africa	X	X	X
		<i>Besseria</i>	<i>atra</i>	CAN, Ontario	X	X	X
		<i>Prolophosia</i>	<i>petiolata</i>	Israel	X	X	X

Table 1. (Continued)

<u>Subfamily</u>	<u>Tribe</u>	<u>Genus</u>	<u>Species</u>	<u>Country, State: Co</u>	<u>CADI</u>	<u>CADII</u>	<u>LGL</u>
<u>INGROUP</u>							
Phasiinae	Cylindromyiini	<i>Cylindromyia</i>	sp.	South Africa	x	x	x
		<i>Cylindromyia</i>	sp.	South Africa	x	x	x
		<i>Cylindromyia</i>	sp.	USA, AZ: Coconino			x
		<i>Cylindromyia</i>	<i>mirabilis</i>	USA, NM: Torrance	x	x	x
		<i>Cylindromyia</i>	sp.	USA, TN: Knox	x	x	x
	Hermiyini	<i>Hermya</i>	sp.	Burundi	x	x	x
	Catharosiini	<i>Catharosia</i>	<i>pygmaea</i>	USA, TN: Knox	x	x	x
		<i>Litophasia</i>	sp.	South Africa	x	x	x
	Leucostomatini	<i>Weberia</i>	<i>digramma</i>	Israel	x	x	x
		<i>Labigastera</i>	<i>nitidula</i>	Italy	x	x	x
		<i>Clairvillia</i>	<i>biguttata</i>	Israel,	x	x	x
		<i>Leucostoma</i>	sp.	USA, AZ: Coconino	x	x	x
	Phasiini	<i>Leucostoma</i>	sp.	USA, TN: Knox	x	x	x
		<i>Xysta</i>	<i>holosericea</i>	Israel	x	x	x
		<i>Opesia</i>	<i>grandis</i>	Italy	x	x	x
		<i>Elomya</i>	<i>lateralis</i>	Israel	x	x	x
		<i>Phasia</i>	sp.	South Africa	x	x	x
		<i>Phasia</i>	<i>splendida</i>	USA, TN: Knox	x	x	x
		<i>Phasia</i>	sp.	USA, AZ: Coconino			x
		<i>Clytiomya</i>	<i>dupuisi</i>	Italy	x	x	x
		<i>Ectophasia</i>	<i>oblonga</i>	Israel	x	x	x
		<i>Euclytia</i>	<i>flava</i>	USA, CA: Ventura	x	x	x
		<i>Eliozeta</i>	<i>helluo</i>	Italy	x	x	x
	Gymnosomatini	<i>Gymnosoma</i>	<i>fuliginosa</i>	USA, TN: Knox	x	x	x
		<i>Gymnosoma</i>	sp.	USA, AZ: Coconino	x	x	x
	Trichopodini	<i>Gymnoclytia</i>	<i>immaculata</i>	USA, TN: Knox	x	x	x
		<i>Xanthomelanodes</i>	<i>arcuata</i>	USA, TN: Knox	x	x	x
		<i>Xanthomelanodes</i>	<i>flavipes</i>	USA, AZ: Coconino	x	x	x
		<i>Aucalona</i>	sp.	Costa Rica	x	x	x
		<i>Trichopoda</i>	<i>pennipes</i> 1	USA, TN: Knox	x	x	x
		<i>Trichopoda</i>	<i>pennipes</i> 2	USA, TN: Knox			x
		<i>Trichopoda</i>	<i>pennipes</i> 3	USA, TN: Knox			x
		<i>Trichopoda</i>	<i>pennipes</i> 4	USA, TN: Knox			x
		<i>Trichopoda</i>	<i>lanipes</i>	USA, VA: Floyd	x	x	x
		<i>Trichopoda</i>	<i>lanipes</i>	USA, TN: Knox	x	x	x
		<i>Trichopoda</i>	<i>plumipes</i>	USA, SC	x	x	x
		<i>Trichopoda</i>	<i>plumipes</i>	USA, FL: Liberty			x

Extraction and Sequencing

DNA was extracted from single specimens preserved in 95% ethanol. The extraction was performed according to the manufacturer's protocol using a Fermentas™ genomic DNA extraction kit with a few modifications. Gene amplification was performed using MasterCycler (Eppendorf North America, Westbury, NY) thermal cyclers. PCR reactions were carried out using Hotstart Ex Taq (TakaraMirus, Shiga, Japan) per the manufacturer's suggested protocol with 1-1.5 µL of template DNA and 2 µL of 6 pmol of forward and reverse primer in a 50-µL reaction. Custom primers for CAD and LGL were designed by J. K. Moulton (Table 2). Thermal cycling parameters were as follows: 30 s denaturation at 94°C; 5 cycles of 94°C for 30 s, 56°C for 15 s and 72°C for 1.5 min; 5 cycles of 94°C for 30 s, 51°C for 15 s and 72°C for 1.5 min; 30 cycles of 94°C for 30 s, 46°C for 15 s and 72°C for 1.5 min, and a final extension for 5 min at 72°C.

The subsequent PCR products were electrophoresed through a 1% agarose gel at 115V for 25 min, excised from the gel, purified with QiaQuick Gel Extraction kits and eluted in 35 µL of elution buffer (10 mM Tris, pH 8.5). Purified PCR products served as templates for sequencing reactions using the same primers used in PCR reactions at 50% concentration. Both strands of each product were then cycle-sequenced using Big Dye Terminator Cycle Sequencing kits (Applied Biosystems, Carlsbad, California). Sequencing reactions were cleaned using Centri-sep purification columns (Princeton Separations, Adelphia, New Jersey) and sent to the Molecular Biology Resource Facility at the University of Tennessee.

Table 2. Custom primers for CAD and LGL used in molecular analysis of Phasiinae with sequence direction indicated (Forward [F] / Reverse [R])

Gene	Primer Name	F/R	Sequence (5' → 3') ¹	Length
<u>CADI</u>	CAD_54F	F	GTNGTNTTYCARACNNGNATGGT	23-mer
	CAD_54FM	F	GTNGTNTTYCARCCNNGGYATGGT	23-mer
	CAD_53F	F	GGNGARGTNGTNTTYCARAC	20-mer
	CAD_57F	F	TCNATGACNGAYCGYTCRTAYAG	23-mer
	CAD_405R	R	GCNGTRTGYTCNGGRTGRAAYTG	23-mer
	T'podine_CAD_P1R	R	TTCVAGRTCTTCSGGACCAGC	21-mer
	Melanoph_CAD_P1R	R	CCAATGGCAAAGTCTCAGTG	20-mer
<u>CADII</u>	CAD_320F	F	TTYGGNATYTGYYTGGGYCAYCA	23-mer
	tCAD_P2F	F	AAYTTNCCRTGYATYCAYCAYGG	23-mer
	THAX_CAD_P2F	F	GGACGTTGCTTTATGACATCTC	22-mer
	GLEX_CAD_P2F	F	TGTTTCATGACTTCWCAAAAYC	22-mer
	CAD_Mesemb_P2F	F	GGCACTGGGCGTTGTTATA	19-mer
	Oestroph_CAD_P2F	F	GTATACATCTTGATACAAAG	20-mer
	Epigrimy_CAD_P2F	F	TTACAAATGCCAATGACGGT	20-mer
	Billaea_CAD_P2F	F	CCTTGTAATACATCACGGA	19-mer
	CAD_680R	R	GCRTCYCKNACMACYTCRTAYTC	23-mer
	tCAD_P2R	R	GGRTCYAARTTYTCCATRTTRCA	22-mer
<u>LGL</u>	LGL_38F	F	CARCAYGGNTTYCCNCAYAARCC	23-mer
	LGL_Tach_P2F	F	AARGCNGGNGARGARCARGA	20-mer
	LGL_36F	F	ACNGCNCARCAYGGYTTYCC	19-mer
	LGL_Tach_P2F2	F	GGHCAYGGNCARAGYGT	17-mer
	LGL_Intron_Fwd_CU	F	GCNTAYGGYGAYCAYAAAYTG	20-mer
	LGL_472R	R	CACNCCNGTRCARTCCCARAA	21-mer
	LGL_617R	R	ARYTGRTCRTGNCCYTTCCA	20-mer
	LGL_Tach_P1R	R	CGRTTWATRYTYTRCA	16-mer
	LGL_Tach_P2R	R	GGYAWRTCRTCYTGRTTYTCRTG	23-mer
	LGL_466R	R	AAYTTNACNGARCCRTCCTC	23-mer

¹ W=A/T; Y=C/T; R=A/G; M=A/C; K=G/T; H=A/T/C; B=C/G/T; N=A/T/C/G.

Alignment and Phylogenetics

Sequences from opposing strands were reconciled and verified for accuracy using Sequencher 4.2.2 (Gene Codes Corp., Ann Arbor, Michigan). Exon-intron boundaries were identified in Sequencher. The single introns of CAD and LGL were each removed manually for all sequences using the GT-AG rule while maintaining a continuous open reading frame (Rogers & Wall 1980). All sequences will be deposited in GenBank and their accession numbers will be made available at a later date.

Initial alignment of nucleotides and amino acids was performed using OPAL (Wheeler & Kececioglu 2007) in Mesquite 2.74 (Madison & Madison 2010). Codon positions in the final nucleotide matrix were designated using MacCLADE 4.08 (Madison & Madison 2005). Maximum likelihood (ML) was performed using RAxML 7.0.3 (Stamatakis 2006; Stamatakis et al. 2008). Data were partitioned into codons and analyzed using the evolutionary model GTRGAMMAI with 1,000 rapid bootstrap replicates.

Phylogenetic analysis using ML was conducted through the version of RaxML available within the CIPRES portal (Miller et al. 2010). Node robustness was measured by conducting 1000 bootstrap replicates (= bootstrap scores or BS) and by concordance of tree topologies resulting from analyses of CAD, LGL and a concatenated data set of CAD + LGL.

Results

Sequence Data

CAD

Sixty-three taxa were included in the phylogenetic analysis of CAD. Sequence lengths ranged from 1410 bp to 1623 bp with an average length of 1608 bp.

LGL

Seventy-three taxa were included in the phylogenetic analysis of LGL. Sequence lengths ranged from 948 bp to 1116 bp with an average length of 1108 bp.

Maximum Likelihood Phylogeny

The ML trees generated for CAD and LGL were similar in general topology but differed in their resolution of outgroup taxa and non-phasiines. Both trees produced nearly identical clades throughout the Phasiinae and placed questionable taxa in the same taxonomic positions. The combined analysis of CAD + LGL further corroborated the results from the individual gene topologies; well-resolved clades had even clearer resolution, and the poorly supported nodes were still unresolved. Specific tree topologies from each analysis (CAD, LGL, and CAD + LGL) are discussed below.

CAD

The inferred phylogeny generated from CAD produced a monophyletic Tachinidae and recovered a monophyletic Tachininae, Exoristinae, and Phasiinae (Figure 1). Tribal relationships in the Phasiinae were recovered with strong support and all currently recognized tribes were recovered as monophyletic except the Phasiini and Catharosiini.

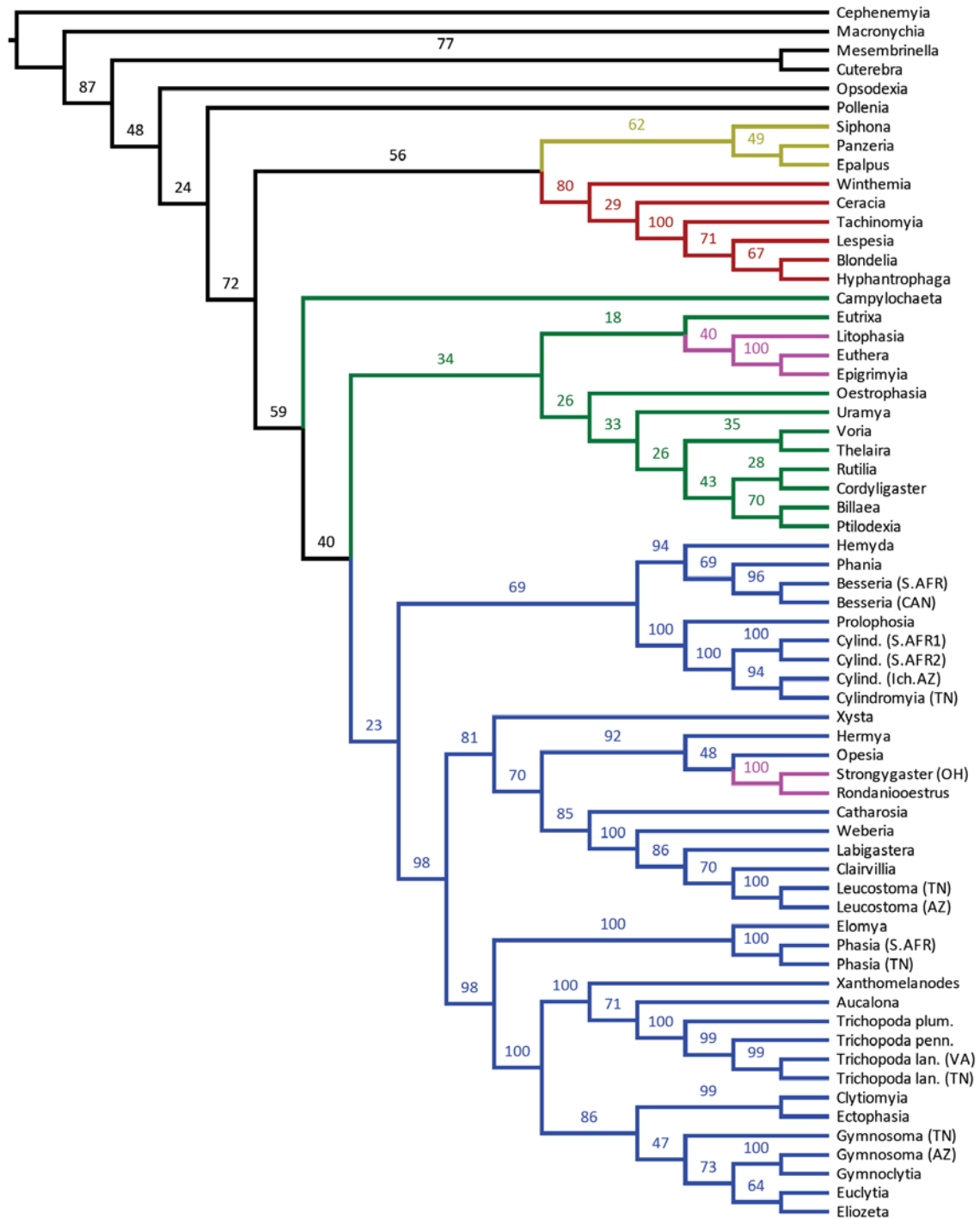


Figure 1. Inferred Maximum Likelihood phylogeny of Tachinidae emphasizing the subfamily Phasiinae using the nuclear coding gene CAD with subfamilies identified for reference. **Blue:** Phasiinae, **Green:** Dexiinae, **Red:** Exoristinae, **Yellow:** Tachininae, **Black:** Outgroup taxa, **Pink:** Uncertain subfamily placement

The monophyly of Tachinidae was supported (BS = 72), but the sister group to Tachinidae remained unresolved. *Pollenia*, a calliphorid parasitoid of earthworms, was placed as sister taxon to the Tachinidae, however, bootstrap support was low (BS = 24).

Tachininae and Exoristinae

Of the six tachinines included, only three belong strictly in Tachininae (*Siphona*, *Panzeria*, and *Epalpus*). These formed a monophyletic clade with moderate support (BS = 62). The other three nominal tachinines (*Strongygaster*, *Rondaniooestrus*, and *Ceracia*) have uncertain subfamily placement in current classification schemes, with *Strongygaster* and *Rondaniooestrus* sometimes placed in Phasiinae, and *Ceracia* in Exoristinae.

Ceracia was placed in a monophyletic Exoristinae (BS = 80). CAD created a ladderized exoristine clade that placed *Winthemia* as the basal exoristine (BS = 80) followed by *Ceracia* (BS = 29) and the rest of the exoristines *Tachinomyia*, *Lespesia*, *Blondelia*, and *Hyphantrophaga* (BS = 100).

Dexiinae

One phasiine (*Litophasia*) was placed in an otherwise mostly monophyletic Dexiinae and forms a clade with two other taxa of questionable taxonomic placement, *Euthera* and *Epigrimyia* (BS = 40). The strictly dexiine *Eutrixia* was included as a basal taxon in this clade (BS = 18). *Campylochaeta* was recovered outside Dexiinae as the basal taxon of Dexiinae + Phasiinae. This placement made Dexiinae paraphyletic. The monophyly of Dexiinae minus *Campylochaeta* is very poorly supported (BS = 34). Additionally, none of the nodes throughout the clade have strong support except *Euthera* + *Epigrimyia* (BS = 100).

Phasiinae

Tribal relationships in the Phasiinae were strongly supported, with all tribes recovered. The Trichopodini were recovered with extremely high support (BS = 100), and allied with the Gymnosomatini (BS = 86). This clade formed the sister group to the Phasiini (BS = 100). The Gymnosomatini definitively included the genera *Clytiomya*, *Ectophasia*, *Euclytia*, and *Eliozeta*, which are taxonomically considered to belong to Phasiini by most authors. This three-tribe clade of (Trichopodini + Gymnosomatini) + Phasiini was strongly supported as monophyletic (BS = 98).

Within the Gymnosomatini, two *Gymnosoma* specimens were included; one from Tennessee and one from Arizona. Unexpectedly, these two individuals did not group together. The Arizona specimen was recovered with *Gymnoclytia* and formed a clade of Gymnosomatini *sensu stricto*. The other *Gymnosoma* was imbedded deep in the clade as a basal taxon to (*Gymnosoma* (AZ) + *Gymnoclytia*) + (*Euclytia* + *Eliozeta*).

The Leucostomatini were recovered as a monophyletic group (BS = 100) and together with *Catharosia* (Catharosiini) were placed as the sister clade to a strongly supported, but unexpected group composed of *Strongygaster*, *Rondaniooestrus*, *Opesia*, and *Hermya* (BS = 92). *Xysta* was placed as the basal phasiine in the Leucostomatini + Strongygastrini clade and this clade then formed a sister group with the Phasiini + (Gymnosomatini + Trichopodini) clade. In total, this clade comprised eight phasiine tribes and was recovered as monophyletic (BS = 98).

The Cyldromyiini were recovered basal to the other phasiine tribes and were composed of two distinct subtribal groups. *Hemyda*, *Phania*, and *Besseria* formed one clade (BS = 94) while *Cylindromyia* spp., and *Prolophosia* formed the other (BS = 100).

Collectively, the Cyldromyiini were recovered with reasonable support (BS = 69).

While tribal groups were recovered almost perfectly, the monophyly of Phasiinae was poorly supported (BS = 23).

LGL

The molecular analysis of LGL recovered all phasiine tribes in expected locations except Catharosiini and allowed placement of difficult taxa in their appropriate subfamilies (Figure 2). However, bootstrap scores were lower than CAD at higher levels of the phylogeny and neither Dexiinae nor Tachininae was recovered as monophyletic. *Catharosia* was not recovered within the Phasiinae, but rather was placed by itself as the most basal tachinid.

The inferred phylogeny recovered the Tachinidae as a strongly supported monophyletic group (BS = 91). The two calliphorids included, *Lucilia* and *Opsodexia*, were placed together (BS = 86) as the sister group to Tachinidae.

Tachininae and Exoristinae

LGL was unable to recover the Tachininae as a monophyletic unit. *Panzeria* and *Epalpus* were placed together (BS = 67), but *Siphona* and *Ceracia* were placed in an adjacent clade as basal exoristines. However, support for this location was low (BS = 19).

Exoristinae was recovered as a monophyletic group (BS = 97), but unlike the topology from CAD, *Ceracia* was not included in the Exoristinae with strong support (BS = 59). The composition of the exoristine clade was similar to CAD with *Winthemia* as the basal exoristine (BS = 97) followed by *Tachinomyia*, *Blondelia*, *Lespesia*, and *Hyphantrophaga* (BS = 100).

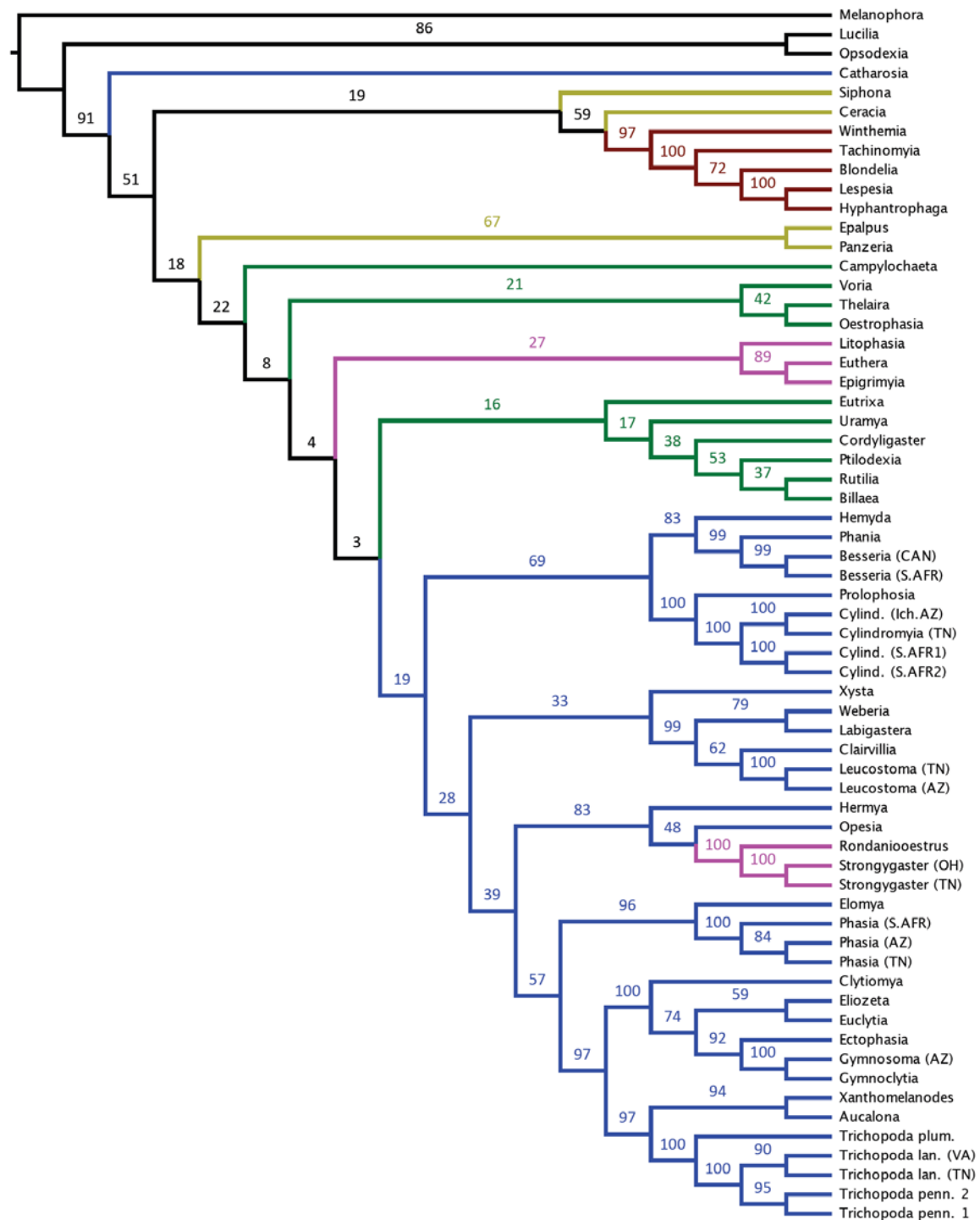


Figure 2. Inferred Maximum Likelihood phylogeny of Tachinidae emphasizing the subfamily Phasiinae using the nuclear coding gene LGL with subfamilies identified for reference. Blue: Phasiinae, Green: Dexiinae, Red: Exoristinae, Yellow: Tachininae, Black: Outgroup taxa, Pink: Uncertain subfamily placement

Dexiinae

Dexiinae was recovered as a paraphyletic clade with very little support for relationships. In the middle of the ladderred dexiines, the difficult taxa *Litophasia*, *Euthera*, and *Epigrimyia* formed their own clade. This placement agrees with the analysis of CAD and implies that these taxa belong in the Dexiinae. *Euthera* and *Epigrimyia* were recovered as sister taxa with strong support (BS = 89).

The rest of the dexiines were ladderred into three groups with *Camplyochaeta* occupying the lone basal position. *Voria*, *Thelaira*, and *Oestrophasia* were recovered together, albeit with little support (BS = 21). The rest of Dexiinae were recovered as one clade, also with low support (BS = 16).

Phasiinae

Phasiine tribes were strongly supported and were positioned similarly to the orientation of tribes from CAD. The Trichopodini were recovered with extremely high support (BS = 97), with two subtribal groups recovered: *Trichopoda* spp. and *Xanthomelanodes* + *Aucalona*. As with CAD, the Trichopodini were allied with the Gymnosomatini (BS = 100) with high support (BS = 97). This clade then formed the sister group to the Phasiini (BS = 96). The inferred phylogeny from LGL agreed with the one produced from CAD and placed the genera *Clytiomya*, *Ectophasia*, *Euclytia*, and *Eliazeta* in Gymnosomatini rather than Phasiini.

LGL supported the placement of Strongygastrini + Rondaniooestrini in the Phasiinae (BS = 100) and mirrored CAD by including *Opesia* and *Hermya* in the same clade as those tribes (BS = 83). However, unlike CAD, which positioned this clade as sister to the Leucostomatini, LGL placed this clade as basal to the Phasiini +

(Trichopodini + Gymnosomatini) with the Leucostomatini + *Xysta* clade basal to the whole group.

The Leucostomatini were recovered as a monophyletic group (BS = 99) with two subtribal groups: *Weberia* + *Labigastera* (BS = 79) and *Clairvillia* + *Leucostoma* (BS = 62). LGL diverged from CAD in the placement of *Xysta*. CAD positioned *Xysta* as the basal taxon to the Leucostomatini clade + Strongygastrini clade. In LGL, *Xysta* is basal to the Leucostomatini alone and this clade then forms a basal group to the clade containing Strongygastrini. However, there was little statistical support for this arrangement (BS = 33).

As with CAD, the *Cylindromyiini* were recovered basal to the other phasiine tribes and were composed of two distinct subtribal groups. *Hemyda*, *Phania*, and *Besseria* spp. formed one clade (BS = 83) while *Cylindromyia* spp. and *Prolophosia* formed the other (BS = 100). Collectively, the *Cylindromyiini* were recovered with reasonable support (BS = 69), but were not included with the rest of Phasiinae with confidence (BS = 19).

Because of *Catharosia*'s aberrant placement as the basal tachinid, there was little support for a monophyletic Phasiinae even without *Catharosia* included as a phasiine (BS = 19).

CAD + LGL

The ML phylogeny generated for the concatenated data set of CAD + LGL included 75 taxa. The overall topology favored the CAD dataset and was very similar to that phylogeny. Bootstrap scores for each clade were generally enhanced throughout the tree, increasing statistical support for taxonomic positions. The inferred phylogeny

generated from CAD + LGL produced a monophyletic Tachinidae and recovered a monophyletic Tachininae, Exoristinae, and Phasiinae (Figure 3). Tribal relationships in the Phasiinae were recovered with strong support and all currently recognized tribes were recovered as monophyletic except the Phasiini and Catharosiini.

The monophyly of Tachinidae was supported (BS = 73). The common house fly, *Musca domestica*, was used to root the tree. Nine outgroup taxa were included, although several were only represented by CAD or LGL rather than both sequences. The three calliphorid taxa *Pollenia*, *Lucilia*, and *Opsodexia*, along with the rhinophorid *Melanophora*, formed the moderately supported sister group to the Tachinidae (BS = 49).

Tachininae and Exoristinae

The tachinines (*Siphona*, *Panzeria*, and *Epalpus*) formed a monophyletic clade with moderate support (BS = 59). *Ceracia* was placed in a monophyletic Exoristinae (BS = 94) with higher support than in CAD alone. A ladder exoristine clade was produced with *Ceracia* at its base (BS = 94), followed by *Winthemia* (BS = 66) and the rest of the exoristines *Tachinomyia*, *Blondelia*, *Lespesia*, and *Hyphantrophaga* (BS = 100).

Dexiinae

As in the CAD analysis, *Litophasia* was placed in an otherwise mostly monophyletic Dexiinae and formed a clade with *Euthera* and *Epigrimyia* (BS = 47). This clade was attached to the Dexiinae (minus *Campylochaeta*) with little support (BS = 29). *Campylochaeta* was recovered outside Dexiinae as the basal taxon of Dexiinae +

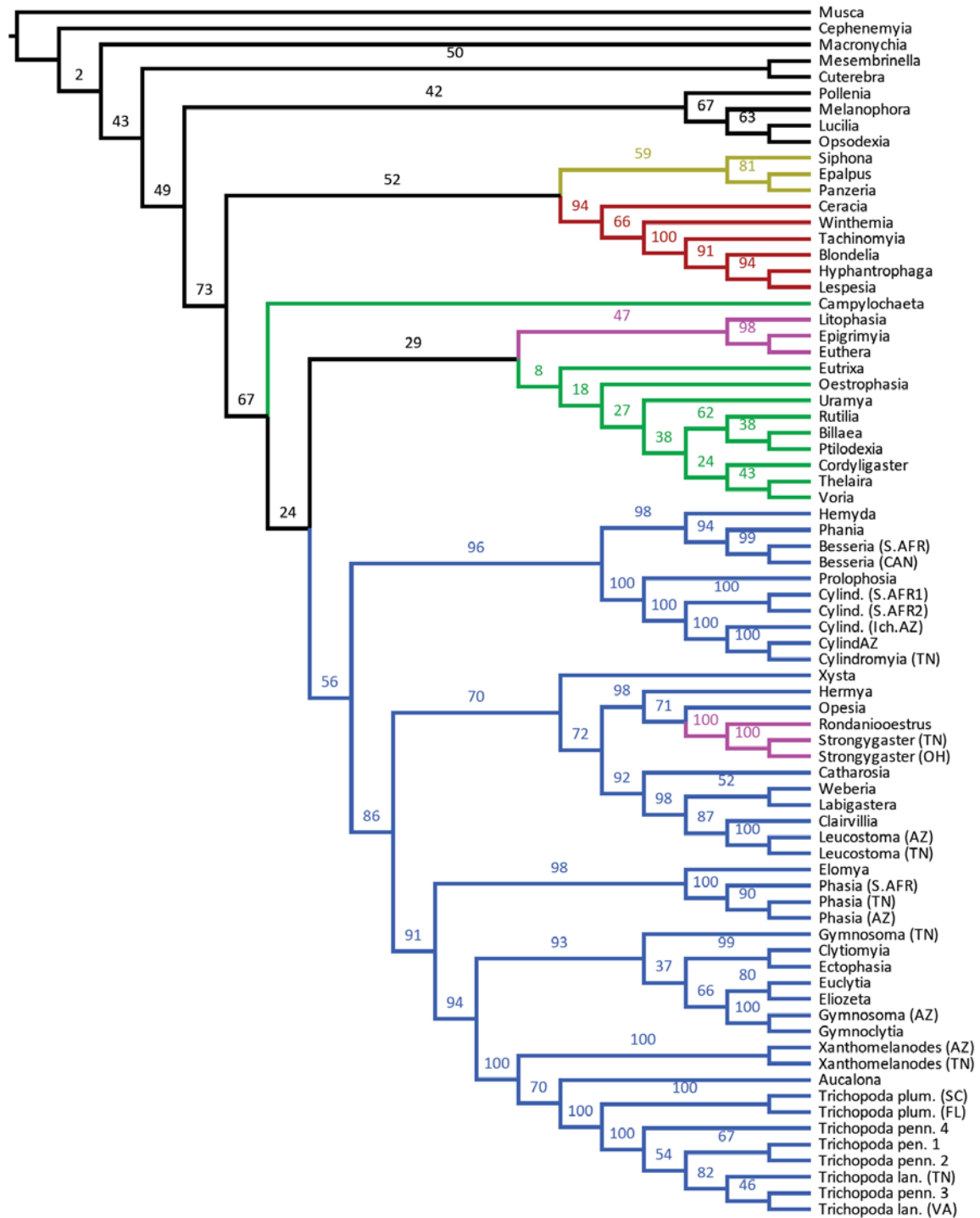


Figure 3. Inferred Maximum Likelihood phylogeny of Tachinidae emphasizing the subfamily Phasiinae using the concatenated data set of CAD + LGL with subfamilies identified for reference. Blue: Phasiinae, Green: Dexiinae, Red: Exoristinae, Yellow: Tachininae, Black: Outgroup taxa, Pink: Uncertain subfamily placement

Phasiinae. This placement made Dexiinae paraphyletic. All dexiine branches remained unresolved. The best supported group contained (*Billaea* + *Ptilodexia*) + *Rutilia* (BS = 62).

Phasiinae

Tribal relationships in the Phasiinae were strongly supported, with all tribes recovered (Fig. 4). The Trichopodini were recovered with extremely high support (BS = 100), and allied with the Gymnosomatini (BS = 93). This clade then formed the sister group to the Phasiini (BS = 98). The Gymnosomatini again included the genera *Clytiomya*, *Ectophasia*, *Euclytia*, and *Eliazeta*. This three-tribe clade of (Trichopodini + Gymnosomatini) + Phasiini was strongly supported as monophyletic (BS = 91).

The Leucostomatini were recovered as a monophyletic group (BS = 98) and together with *Catharosia* (Catharosiini) were placed as the sister clade to a strongly supported, but unusual group composed of *Strongygaster*, *Rondaniooestrus*, *Opesia*, and *Hermia* (BS = 98). *Xysta* was placed as the basal phasiine in the Leucostomatini + Strongygastrini clade and this clade then formed a sister group with the Phasiini + (Gymnosomatini + Trichopodini) clade. In total, this clade comprised eight phasiine tribes and was recovered as monophyletic (BS = 86).

The Cylindromyiini were recovered basal to the other phasiine tribes and were composed of two distinct subtribal groups as in the single gene analyses. Collectively, the Cylindromyiini were recovered with much stronger support in the combined analysis than in either CAD or LGL by themselves (BS = 96). While tribal groups were recovered almost perfectly, the monophyly of Phasiinae was only moderately supported (BS = 56).

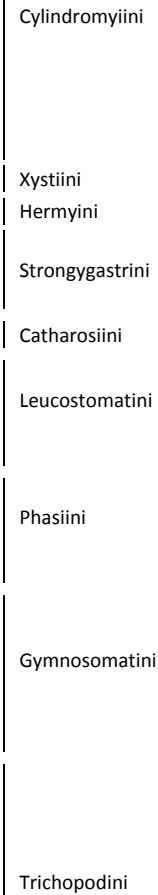


Figure 4. Inferred Maximum Likelihood phylogeny of Phasiinae emphasizing tribal relationships using the concatenated data set of CAD + LGL. Tribes are identified for reference.

Discussion

Outgroup Taxa

Outgroup taxa were included from numerous families and many of the genera have uncertain taxonomic placement. The calliphorid and rhinophorid genera grouped together with moderate support, but did not fall into their respective families. There was little support for the relationships generated for the other outgroup taxa. However, their inclusion was necessary to show the monophyly of Tachinidae, which was adequately recovered (BS = 73 in CAD + LGL).

Exoristinae and Tachininae

The five genera of Exoristinae were recovered as a monophyletic subfamily, supporting the earlier works of Stireman (2002) and Tachi & Shima (2010). Included in the Exoristinae is the mobile taxon *Ceracia*, which has been placed in Tachininae by some authors (Tschorsnig 1985). *Ceracia* belongs to the tribe Acemyiini and was included with the monophyletic Exoristinae with strong support (BS = 94 in CAD + LGL). This placement agrees with the original designation of the genus in Exoristinae (Davis 2012) and provides additional evidence that *Ceracia* is an exoristine.

Tachininae was recovered as a monophyletic group as well, although with only moderate support (BS = 59 in CAD + LGL). A total of six tachinines were included, but three of these genera (*Strongygaster*, *Rondaniooestrus*, and *Ceracia*) were definitively placed in other subfamilies by the molecular evidence.

Dexiinae

Dexiinae is the only tachinid subfamily with synapomorphic character traits. Unfortunately, this morphological certainty did not translate well into molecular evidence for the group. Dexiinae were not recovered as a monophyletic group; *Campylochaeta* fell outside the Dexiinae + Phasiinae as a basal taxon. Also, no node was supported above 62% in the entire clade in the combined analysis, and most branches had less than 39% support. Additional taxon sampling may be necessary to recover Dexiinae as a monophyletic subfamily.

When compared to the highly supported tribal relationships in the Phasiinae, the dexiine tribes seem to be poorly resolved simply due to under-representation. If Dexiinae can be sampled as extensively as Phasiinae was sampled, tribes and subfamily structure may emerge as clearly as they did with Phasiinae. Because of their obviously interwoven taxonomy and close relationship with Phasiinae, Dexiinae requires such an analysis to clarify relationships within and between both subfamilies.

Trichopodini

Three genera from Trichopodini were included in the molecular analysis: *Aucalona*, *Xanthomelanodes*, and *Trichopoda*. Because *Trichopoda* contains the most prominent phasiine biological control agents and there seem to be pheromone biotypes within the genus, several different species and individuals were included. The tribe was strongly supported in the ML tree, with BS scores of 100 in all three analyses. *Xanthomelanodes* was the basal taxon, followed by *Aucalona* and the *Trichopoda* species. The two subgenera of *Trichopoda* were recovered and *T. lanipes* was recovered as the most derived species group. Interestingly, one *T. pennipes* specimen aligned with

the *T. lanipes* species rather than *T. pennipes* (CAD + LGL = 82). This result, combined with personal examination of numerous individuals of both species, indicates a potential interbreeding population between *T. pennipes* and *T. lanipes*; they may not be different species.

Gymnosomatini

Some experts have suggested that the Trichopodini and the Gymnosomatini should be considered one tribe (Tschorsnig 1985). The phylogeny does indicate a close sister group relationship between the tribes, but they form two distinct clades and individual tribes should be maintained. However, there were some unexpected results in regard to the specific genera that were included in Gymnosomatini. According to the current classification, only two genera of Gymnosomatini were included in this analysis; *Gymnosoma* and *Gymnoclytia*. The molecular evidence relocated four additional genera from the Phasiini to the Gymnosomatini: *Clytiomya*, *Ectophasia*, *Euclytia*, and *Eliozeta*. The high support for the monophyly of Gymnosomatini recovered in all analyses indicates that a tribal rearrangement of these genera is warranted.

Several authors have noticed morphological discrepancies within the Phasiini between these genera and other Phasiini, but no official taxonomic change has been made. In his analysis of male postabdomen characters, Tschorsnig (1985) included *Ectophasia* and *Eliozeta* in his treatment of Gymnosomatini due to several synapomorphic characters that united them as a monophyletic group. His proposed classification is supported by this molecular analysis, which indicates that male postabdomen characters are phylogenetically informative.

Phasiini

The molecular phylogenies demonstrate that the genus-rich tribe Phasiini has historically been a dumping group for a large variety of genera without evidence of direct evolutionary history. As mentioned above, the topologies indicate a removal of four genera from the Phasiini to the Gymnosomatini. Additionally, *Opesia* and *Xysta* are recovered outside the Phasiini and will be discussed later. The abandonment of Phasiini by these six genera leaves only *Phasia* and *Elomya* in the Phasiini. The tribe is recovered conclusively as the monophyletic sister taxon to the Trichopodini + Gymnosomatini clade.

Leucostomatini and Catharosia

The four genera included from the Leucostomatini were recovered as a well-supported monophyletic group. Basal to the Leucostomatini in the combined analysis was *Catharosia*, indicating a close relationship between the tribes. Both tribes are among the few phasiine groups whose females possess a piercing ovipositor, and their placement together is evolutionarily credible.

Litophasia is currently placed in Catharosiini and was one of the taxonomically ambiguous genera this analysis was intended to clarify. While the placement of *Litophasia* inside or outside of the Phasiinae is still uncertain, the topology clearly places it outside Catharosiini. *Litophasia* will be discussed below along with *Euthera* and *Epigrimyia*.

Strongygastrini

Taxonomically, the Strongygastrini and Rondaniooestrini have been placed by various authors in both Phasiinae and Tachininae. Their similar morphology indicates a

sister-group relationship between the two genera and this analysis confirms the proposed close relationship between *Strongygaster* and *Rondaniooestrus* (BS = 100). In a visual comparison of the genes, these two genera differed by <10% which is little enough to warrant a possible merging of the genera into *Strongygaster* alone (Smith et al. 2006). At the very least, *Rondaniooestrus* should be removed from its monotypic tribe and placed in Strongygastrini. Additionally, the subfamily placement of these two seemingly intermediate taxa is resolved.

Strongygaster and *Rondaniooestrus* fall within the Phasiinae as the furthest nodes of the sister clade to Leucostomatini + *Catharosia*. Their phylogenetic placement, combined with the earlier affirmation of heteropteran parasitism in *Strongygaster*, definitively places these two genera in Phasiinae. This placement implies several unique evolutionary developments. *Strongygaster* would be the only phasiine that practices ovolarviparity, a convergent trait shared with most other non-phasiine tachinids. It would also be the only phasiine with multiple extra-heteropteran hosts of different orders. Perhaps this more derived characteristic of the female postabdomen allowed *Strongygaster* to exploit the host defenses of such an incredible diversity of insect prey.

Opesia, currently in Phasiini, is the closest phasiine relative of the Strongygastrini, and should perhaps be included in the latter tribe (BS = 71 in CAD + LGL). Little is known of the biology of *Opesia* although it has a long and varied taxonomic history, carrying both the name *Strongygaster* and *Xysta* at different times (O'Hara & Wood 2004). It has a similar morphology to *Strongygaster*, which is itself distinguished from the similar *Phasia* by only a few characters (Wood 1987). The similar morphology of Strongygastrini and Phasiini has confused the taxonomic history of these

tribes, but this analysis indicates that molecular evidence can be used to differentiate the two distinct groups.

Hermya

Some authors have chosen to place *Hermya* within Cyldromyiini, while others assign the genus its own tribe. In this investigation, *Hermya* is unrelated to any of the cylindromyines, but rather allies with the Strongygastrini as its sister taxon. This position is supported by Herting's 1957 study of female postabdomen characters. He suggested that the uniquely flattened morphology of *Strongygaster*'s eighth sternite may have been derived from the spoon-shaped sternite of *Hermya*. The monophyletic clade that includes *Hermya*, *Opesia*, and the Strongygastrini is highly supported (BS = 98 in CAD + LGL), and if further evidence for this grouping is discovered it could perhaps become a tribe of its own.

Xysta

The Strongygastrini clade forms a sister group to the Leucostomatini + *Catharosia* clade. *Xysta* is placed at the base of the combined clade. While it is currently in Phasiini, *Xysta* has unique female terminalia morphology unlike any other tachinid. The genera in Phasiini possess piercing ovipositors that allow direct insertion of eggs into their hosts. However, *Xysta* has a specialized corkscrew ovipositor that sets it apart from other phasiines (Herting 1957). Herting also postulated *Xysta* being a potentially basal phasiine due to the characteristic morphology of its postgenital plate which it shares with other non-phasiine taxa.

The *Xysta* + ((Strongygastrini + *Hermya*) + (Leucostomatini + *Catharosia*)) clade forms a sister group to the Phasiini + (Trichopodini + Gymnosomatini) and this group

forms a monophyletic group of phasiines with high support (BS = 86 in CAD + LGL). This core group of phasiines is recovered consistently and with high support and may be a convenient group around which to draw a subfamily line.

Cylindromyiini

A monophyletic *Cylindromyiini* is strongly supported (BS = 96 in CAD + LGL). Two subtribal groups are formed that correspond with Tschorsnig's examination of the tribe in 1985. According to the male terminalia, *Hemyda*, *Besseria*, and *Phania* are closely related, and *Prolophosia* and *Cylindromyia* also share a common morphology. This designation is duplicated in the present molecular phylogeny with strong support and further supports the effectiveness of male terminalia characters to delineate taxonomic groups.

Phasiinae

While *Cylindromyiini* is certainly a distinct group, this analysis fails to definitively place it within the *Phasiinae*. *Cylindromyiini* was recovered as the sister group to a well-supported clade comprised of several traditional phasiine genera/tribes, forming a monophyletic though weakly supported *Phasiinae*. The combined analysis of CAD + LGL yielded only a BS of 56% for this grouping. A potential solution would be to split the subfamily along these statistical lines and create a monophyletic *Phasiinae* and a new monophyletic subfamily *Cylindromyiinae*.

However, *Cylindromyiini* shares many traits with *Dexiinae* and several dexiines have historically been placed in *Cylindromyiini* (notably *Epigrimyia* and *Beskia*). Before *Cylindromyiini* can be elevated to subfamily status, the status of *Dexiinae* and its relationship to *Phasiinae* needs to be solidified. This analysis only poorly supports

dexiine groups, and is not an adequate foundation for a subfamily rearrangement. The inclusion of more data, either molecular or morphological, will help strengthen recovered relationships between Dexiinae and the aforementioned basal divergence within Phasiinae, i.e., Cylindromyiini plus the remaining taxa.

Litophasia, Epigrimyia, and Euthera

Litophasia, *Epigrimyia*, and *Euthera* hold the distinction of appearing in the taxonomy as both phasiines and dexiines. Both *Epigrimyia* and *Euthera* parasitize Heteroptera and *Litophasia* is currently in Catharosiini. However, morphological evidence places them all in the Dexiinae (Tschorsnig 1985). While the molecular evidence also suggests a placement in Dexiinae, their taxonomic position remains uncertain due to the low statistical support of the group.

Curiously, these taxonomically ambiguous genera group together in the molecular analysis and form their own monophyletic group just outside the Dexiinae. While there is evidence that the placement of *Euthera* and *Epigrimyia* as sister taxa is legitimate (CAD + LGL = 98), inclusion of *Litophasia* in the group as well as the position of the entire clade is highly suspect. There is very little statistical support for the group, and therefore, no certain taxonomy can be inferred from the data.

Most dexiines are beetle parasitoids and this clade contains all genera that attack both beetles and true bugs. This indicates that they may share an evolutionary history based on a single new host association in a *Euthera/Epigrimyia* ancestor. However, further analyses may recover a monophyletic Dexiinae and maintain the phylogenetic position of this unique clade outside and basal to the Dexiinae. Such a tree could be interpreted as supporting a paraphyletic Phasiinae (including Phasiinae *sensu stricto*,

Cylindromyiini, and *Litophasia* + (*Euthera* + *Epigrimyia*). The monophyletic Dexiinae would then be nested within the Phasiinae and would have arisen due to a host shift from true bugs to beetles.

Summary

A molecular systematic analysis of Phasiinae using the nuclear coding genes *rudimentary* (CAD) and *lethal giant larvae* (LGL) was conducted to infer a well-supported phylogeny. The objectives are listed and results are discussed below.

Determine whether or not Phasiinae is monophyletic.

The currently recognized classification of Phasiinae was not recovered as monophyletic. However, the results indicated a removal of *Litophasia* and *Euthera* from Phasiinae to join *Epigrimyia* in Dexiinae is warranted. With these taxa removed, Phasiinae does appear to be monophyletic. Although the statistical support for Phasiinae monophyly is disappointingly low (CAD + LGL = 56), there was strong support for the monophyly of a clade consisting of the majority of phasiine tribes (Trichopodini, Gymnosomatini, Phasiini, Leucostomatini, Catharosiini, Strongygastrini, Hermyini, and Xystiini) (CAD + LGL = 86). Also, support for the monophyly of the sister group to this large clade, the Cylindromyiini, was highly significant (CAD + LGL BS = 96).

Assess the monophyly/validity of tribes in Phasiinae

CAD and LGL were shown to be excellent delineators of phasiine tribal relationships with the exception of LGL and *Catharosia*. The analysis mirrored current classification with high support in most tribes. This corroboration between morphology and molecular datasets lends credibility to the taxonomic rearrangements suggested by the molecular evidence. Such revisions include the following:

- 1) Removing *Litophasia* from Catharosiini
- 2) Transferring *Euclytia*, *Eliazeta*, *Ectophasia*, and *Clytiomya* from Phasiini to Gymnosomatini
- 3) Including *Strongygaster* and *Rondaniooestrus* in Phasiinae
- 4) Placing *Rondaniooestrus* and *Opesia* in Strongygastrini
- 5) Creating a new tribe for *Xysta*: Xystiini
- 6) Placing *Hermya* at the base of Strongygastrini in its own tribe Hermiyini rather than in Cyldromyiini

These revisions would create nine monophyletic tribes in Phasiinae that are each strongly supported by molecular evidence (BS at least 71).

Resolve basal relationships within Phasiinae.

LGL placed *Catharosia* as the basal taxon of the entire family, a result that is probably anomalous (e.g., long branch attraction) as both CAD and the combined analysis placed it in the middle of Phasiinae. Cyldromyiini is consistently recovered as a potential basal clade of Phasiinae and sister to a clade comprised of most other phasiine tribes. Cyldromyiini shares more symplesiomorphies with Dexiinae than do other phasiine taxa, so a taxonomy that indicates a close relationship between these two groups is supported morphologically.

An analysis of oviposition strategies overlaid on this phylogeny provides some interesting insights into the evolution of the phasiines piercing ovipositor. The tribes that are known to possess a piercing ovipositor are basal (Cyldromyiini, *Xysta*, *Catharosia* Leucostomatini, and Phasiini); while the most derived tribes (Trichopodini and Gymnosomatini) do not have such a specialized ovipositor. The only exception to that

rule is *Hermya* and the Strongygastrini. These taxa lack a piercing ovipositor and are nested within those tribes that do.

The only other tachinids to possess such specialized ovipositors are scattered throughout the Dexiinae and the Exoristinae. Whether piercing ovipositors were a basal trait or independently evolved in separate lineages, it is clear that there is widespread convergence of oviposition strategies throughout the Tachinidae.

Determine the sister group of Phasiinae

Each individual data set as well as the concatenated dataset agree that Dexiinae is the sister group to Phasiinae. While the specific demarcation between these two subfamilies is still unclear, morphological and now molecular evidence agree that these two groups have shared a close evolutionary history. This inferred relationship has ramifications on which life history traits can be used to construct classifications within the Tachinidae. Exoristinae has been proposed as the sister group to Phasiinae based on similar egg morphology and oviposition strategy. If Dexiinae is the sister group rather than Exoristinae, those traits will lose some credibility as indicators of evolutionary history. Dexiinae and Phasiinae share several common hosts through *Euthera*, *Epigrimyia*, and *Beskia*. Because of this relationship, weighting host use affinity during classification may result in a more accurate taxonomy.

Infer the taxonomic affinities of the following ambiguous taxa: Strongygaster, Rondaniooestrus, Euthera, Epigrimyia, and Litophasia

Strongygaster and *Rondaniooestrus* can be included confidently in Phasiinae, being placed deep within the group with strong support (CAD + LGL = 98). *Litophasia* does not belong in Catharosiini and should instead be tentatively placed in Dexiinae

along with *Euthera* and *Epigrimyia*. The consequences of these placements are twofold. First, placing *Euthera* and *Epigrimyia* in Dexiinae destroys the monophyly of the subfamily based on host use as they both attack true bugs but would no longer be in Phasiinae. Similarly, parasitizing heteropterans is no longer a synapomorphic character trait for the Phasiinae, as *Rondaniooestrus* only attacks honeybees instead of true bugs. Classification changes suggested by this analysis are summarized in Fig. 5 and Table 3.

Future Direction

This phylogeny lays the foundation for future tribal revisions and highlights the need for a modern analysis of the tribes and genera in this important parasitoid subfamily. CAD and LGL have shown to be phylogenetically informative and useful indicators of tachinid relationships. These genes were also able to recover phasiine tribes with high levels of statistical support and illuminate the proper classification scheme for several confusing taxonomic problems. However, both genes failed to recover Dexiinae with any confidence or relationships within it.

The phylogenetic uncertainty of the Dexiinae may be stabilized by additional genomic and taxon sampling. Inadequate tribal representation could have contributed to the mediocre phylogeny as a result of localized long branch attraction. This problem is easily addressed by the inclusion of more taxa, certainly at least one additional genus per tribe. Specific inclusion of *Beskia* (Epigrimyini) and *Redtenbacheria* (Eutheriini) will provide evidence for or against the close relationship of *Litophasia*, *Euthera*, and *Epigrimyia* and their placement in the Dexiinae. Including several equally or even more informative genes could also aid in recovery of more robust nodes within Dexiinae.

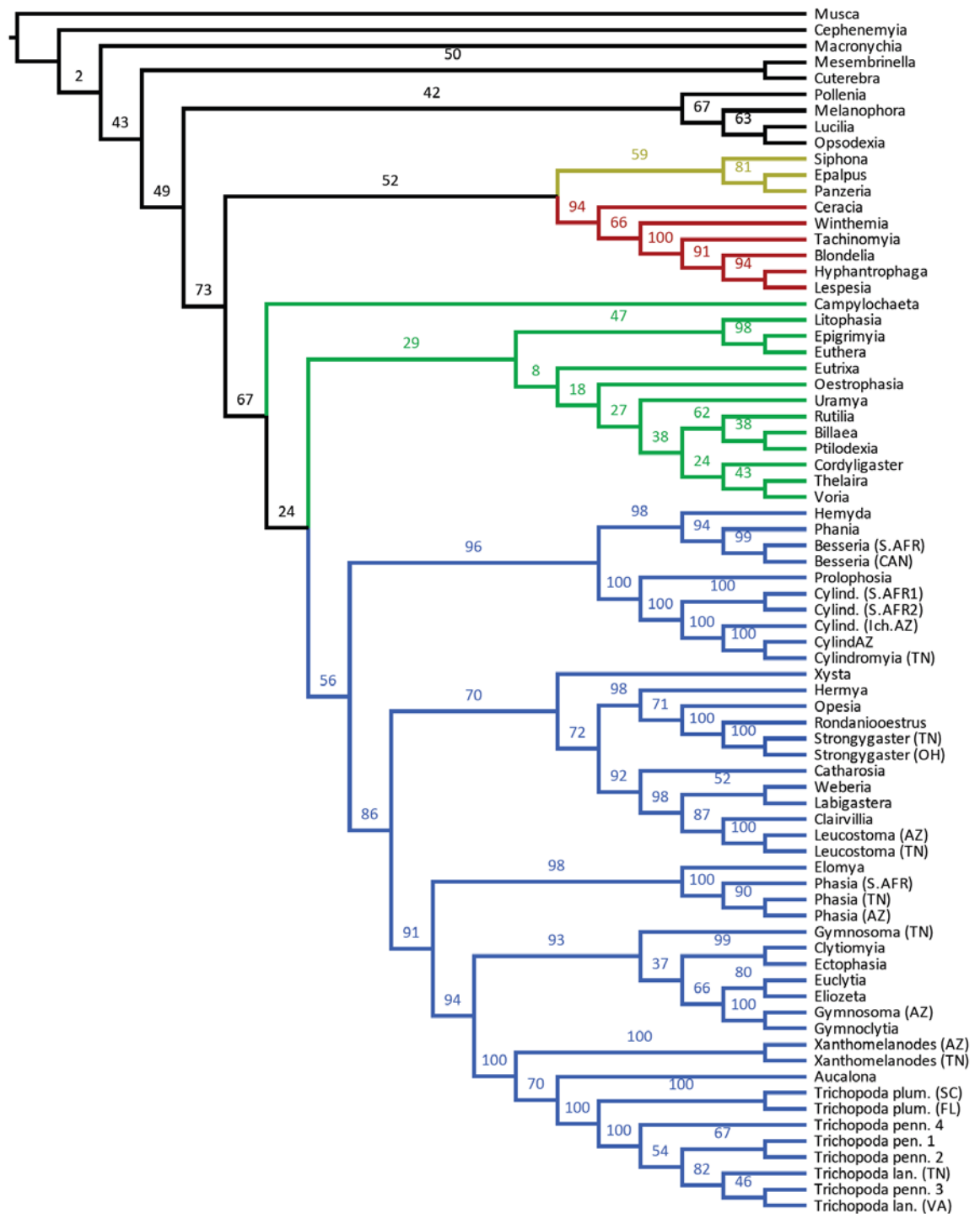


Figure 5. Proposed classification of Tachinidae based on the inferred Maximum Likelihood phylogeny of CAD + LGL with proposed subfamilies identified for reference. Blue: Phasiinae, Green: Dexiinae, Red: Exoristinae, Yellow: Tachininae, Black: Outgroup taxa

Table 3. Proposed classification changes to Tachinidae inferred from molecular phylogenies of CAD and LGL: Highlighted boxes denote change

<i>Current Classification</i>			<i>Revised Classification</i>		
Subfamily	Tribe	Genus	Subfamily	Tribe	Genus
Phasiinae	Catharosiini	<i>Catharosia</i>	Phasiinae	Catharosiini	<i>Catharosia</i>
		<i>Litophasia</i> (S.Afr.)			
	Cylindromyiini	<i>Besseria</i>		Cylindromyiini	<i>Besseria</i>
		<i>Besseria</i> (S.Afr)			<i>Besseria</i> (S.Afr)
		<i>Cylindromyia</i>			<i>Cylindromyia</i>
		<i>Cylind.</i> (Ich.)			<i>Cylind.</i> (Ich.)
		<i>Cylind.</i> (S.Afr)			<i>Cylind.</i> (S.Afr)
		<i>Cylind.</i> (S.Afr)			<i>Cylind.</i> (S.Afr)
		<i>Hemyda</i>			<i>Hemyda</i>
		<i>Phania</i>			<i>Phania</i>
		<i>Prolophosia</i>			<i>Prolophosia</i>
	Eutheriini	<i>Euthera</i>		Gymnosomatini	<i>Clytiomya</i>
					<i>Ectophasia</i>
	Gymnosomatini	<i>Gymnoclytia</i>			<i>Eliozeta</i>
		<i>Gymnosoma</i>			<i>Euclytia</i>
	Hermiini	<i>Hermia</i>			<i>Gymnoclytia</i>
	Leucostomatini	<i>Clairvillia</i>			<i>Gymnosoma</i>
		<i>Labigastera</i>		Hermiini	<i>Hermia</i>
		<i>Leucostoma</i> (TN)			
		<i>Leucostoma</i> (AZ)		Leucostomatini	<i>Clairvillia</i>
		<i>Weberia</i>			<i>Labigastera</i>
	Phasiini	<i>Clytiomya</i>			<i>Leucostoma</i> (TN)
		<i>Ectophasia</i>			<i>Leucostoma</i> (AZ)
		<i>Eliozeta</i>		Phasiini	<i>Weberia</i>
		<i>Elomya</i>			<i>Elomya</i>
		<i>Euclytia</i>			<i>Phasia</i>
		<i>Opesia</i>			<i>Phasia</i> (S.Afr)
		<i>Phasia</i>		Strongygastrini	<i>Opesia</i>
		<i>Phasia</i> (S.Afr)			<i>Rondaniooestrus</i>
		<i>Xysta</i>			<i>Strongygaster</i>
	Trichopodini	<i>Aucalona</i>		Trichopodini	<i>Aucalona</i>
		<i>Trichopoda</i>			<i>Trichopoda</i>
		<i>Trichopoda</i>			<i>Trichopoda</i>
		<i>Trichopoda</i>			<i>Trichopoda</i>
		<i>Trichopoda</i>			<i>Trichopoda</i>
		<i>Trichopoda</i>			<i>Xanthomelanodes</i>

Table 3. (Continued)

<i>Current Classification</i>			<i>Revised Classification</i>		
Subfamily	Tribe	Genus	Subfamily	Tribe	Genus
Phasiinae	Trichopodini	<i>Xanthomelanodes</i>	Phasiinae	Xystiini	<i>Xysta</i>
Dexiinae	Campylochetini	<i>Campylochaeta</i>	Dexiinae	Campylochetini	<i>Campylochaeta</i>
	Dexiini	<i>Ptilodexia</i>		Dexiini	<i>Ptilodexia</i>
		<i>Billaea</i>			<i>Billaea</i>
	Dufouriini	<i>Oestrophia</i>		Dufouriini	<i>Oestrophia</i>
	Epigrimyiini	<i>Epigrimyia</i>		Epigrimyiini	<i>Epigrimyia</i>
	Palpostomatini	<i>Eutrixia</i>		Eutheriini	<i>Euthera</i>
	Rutilliini	<i>Rutilia</i>		Litophasiini	<i>Litophasia</i>
	Sophiini	<i>Cordylogaster</i>		Palpostomatini	<i>Eutrixia</i>
	Thelariini	<i>Thelaira</i>		Rutilliini	<i>Rutilia</i>
	Uramyini	<i>Uramya</i>		Sophiini	<i>Cordylogaster</i>
	Voriini	<i>Voria</i>		Thelariini	<i>Thelaira</i>
Exoristinae	Blondeliini	<i>Blondelia</i>		Uramyini	<i>Uramya</i>
	Eryciini	<i>Lespesia</i>		Voriini	<i>Voria</i>
	Exoristiini	<i>Tachinomyia</i>	Exoristinae	Acemyiini	<i>Ceracia</i>
	Goniini	<i>Hyphantrophaga</i>	Exoristinae	Blondeliini	<i>Blondelia</i>
	Winthemiini	<i>Winthemia</i>		Eryciini	<i>Lespesia</i>
Tachininae	Acemyiini	<i>Ceracia</i>		Exoristiini	<i>Tachinomyia</i>
	Ernestiini	<i>Panzeria</i>		Goniini	<i>Hyphantrophaga</i>
	Rondaniooestrini	<i>Rondaniooestrus</i>		Winthemiini	<i>Winthemia</i>
	Siphonini	<i>Siphona</i>	Tachininae	Ernestiini	<i>Panzeria</i>
	Strongygastrini	<i>Strongygaster</i>		Siphonini	<i>Siphona</i>
	Tachini	<i>Epalpus</i>		Tachini	<i>Epalpus</i>
Calliphoridae		<i>Opsodexia</i>	Calliphoridae		<i>Opsodexia</i>
		<i>Mesembrinella</i>			<i>Mesembrinella</i>
		<i>Pollenia</i>			<i>Pollenia</i>
Oestridae		<i>Cuterebra</i>	Oestridae		<i>Cuterebra</i>
		<i>Cephenomyia</i>			<i>Cephenomyia</i>
Rhinophoridae		<i>Melanophora</i>	Rhinophoridae		<i>Melanophora</i>
Sarcophagidae		<i>Macronychia</i>	Sarcophagidae		<i>Macronychia</i>

Catharosia is a unique genus that presents a long-branch attraction problem. *Litophasia* was included in an attempt to shorten that branch, but failed to do so. Other genera obviously positioned within Catharosiini should be included in future analyses to help determine the true taxonomic position of *Catharosia*. Phylogenies generated from CAD and LGL indicate that several taxonomic revisions throughout Phasiinae are warranted. Phasiini especially is in need of revision as many of its genera appear to belong to other tribes. An examination of tribal names and structure would modernize the subfamily and better reflect the molecular evidence.

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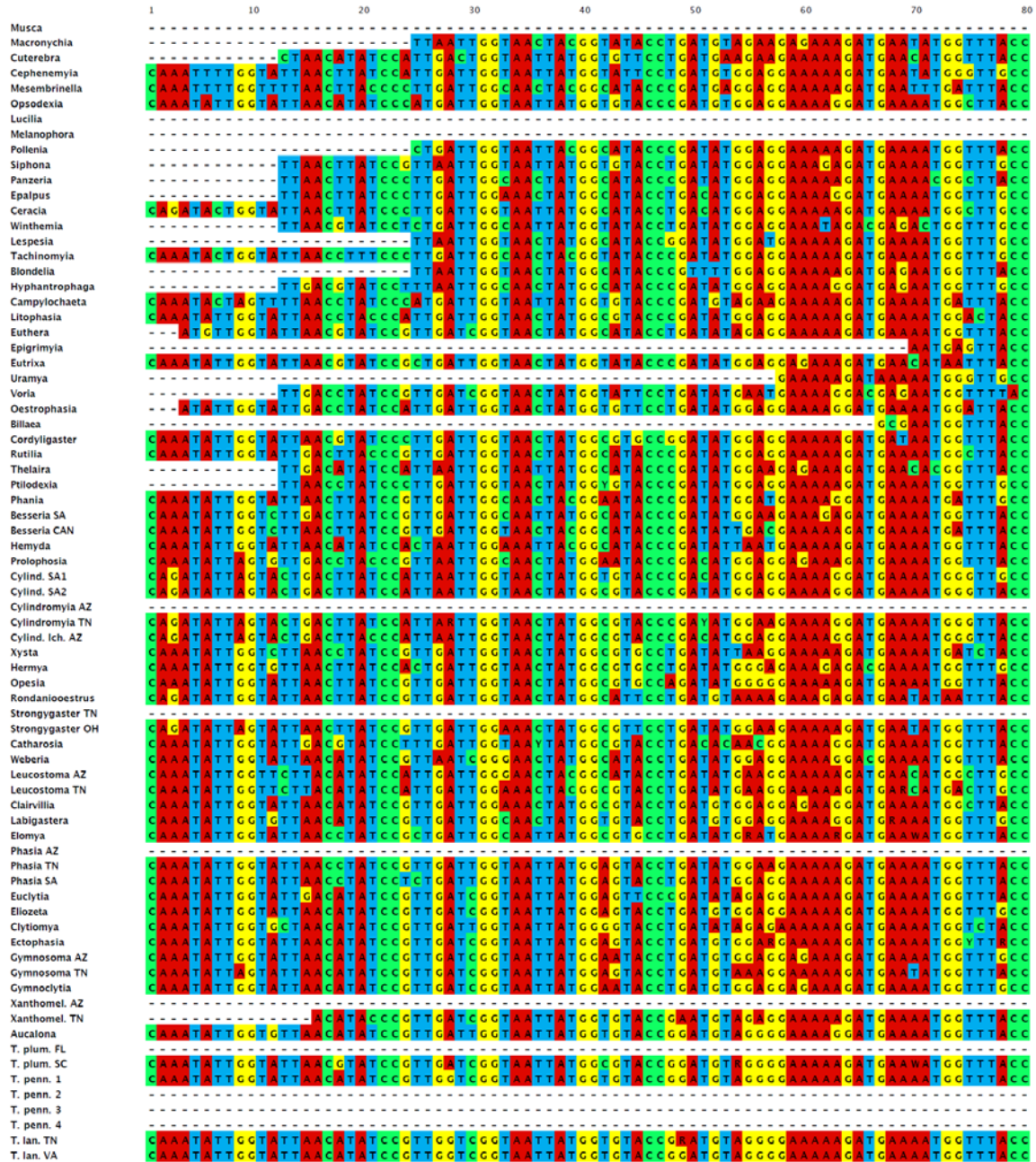
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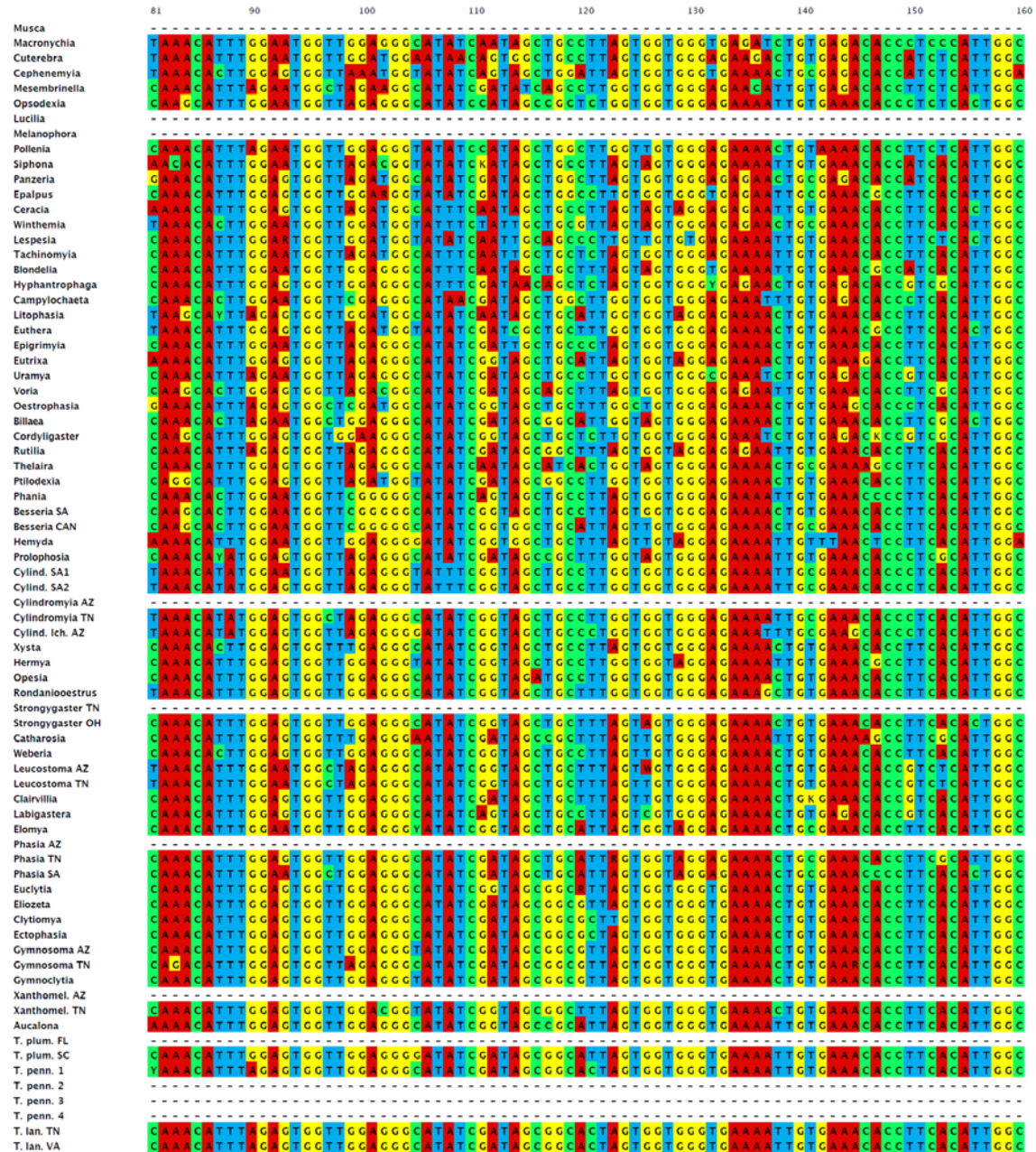
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APPENDIX

Appendix 1. Concatenated Dataset of CAD + LGL Sequences



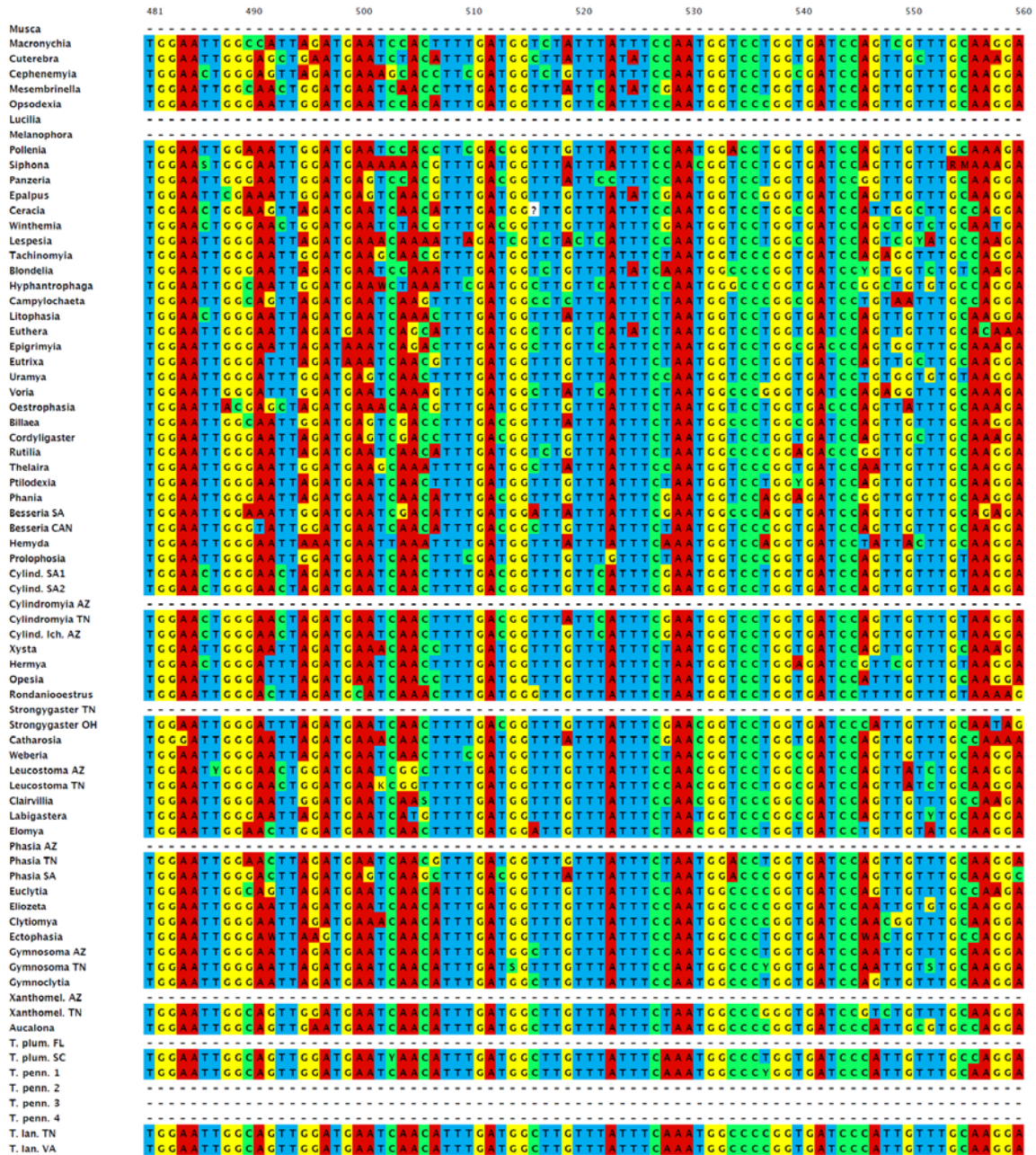


81

82

	321	330	340	350	360	370	380	390	400
Musca									
Macronychia									
Cuterebra									
Capniemyia									
Mesembrinella									
Opsodexia									
Lucilia									
Melanophora									
Pollenia									
Siphona									
Panzeria									
Epalpus									
Ceracia									
Winthemia									
Lespesia									
Tachinomyia									
Blondelia									
Hyphantrophaga									
Campylochaeta									
Litophasia									
Euthera									
Epigrimyia									
Eutrixia									
Uramya									
Voria									
Oestrophia									
Billaea									
Cordyligaster									
Ruttila									
Thelaira									
Ptilodexia									
Phania									
Besseria SA									
Besseria CAN									
Hemyda									
Prolophosia									
Cylind. SA1									
Cylind. SA2									
Cylindromyia AZ									
Cylindromyia TN									
Cylind. Ich. AZ									
Xysta									
Hermya									
Opesia									
Rondaniooestrus									
Strongygaster TN									
Strongygaster OH									
Catharosia									
Weberia									
Leucostoma AZ									
Leucostoma TN									
Clairvillia									
Labigastera									
Elomya									
Phasia AZ									
Phasia TN									
Phasia SA									
Euclytia									
Eliozeta									
Glytiomya									
Ectophasia									
Gymnosoma AZ									
Gymnosoma TN									
Gymnoclytia									
Xanthomel. AZ									
Xanthomel. TN									
Aucalona									
T. plum. FL									
T. plum. SC									
T. penn. 1									
T. penn. 2									
T. penn. 3									
T. penn. 4									
T. lan. TN									
T. lan. VA									

84



86

87

	801	811	820	830	840	850	860	870	880							
Musca	TACCAATG	GCCAAAG	GATAGG	TCCAAATG	GAAGGT	TTTTC	CAAGC	AGAAAG	CCCTT	ACTTCT	GGTAC	AGTTTC	TCCG	GAAG		
Macronychia	TACCAATG	GCCAAAG	GATAGG	TCCAAATG	GAAGGT	TTTTC	CAAGC	AGAAAG	CCCTT	ACTTCT	GGTAC	AGTTTC	TCCG	GAAG		
Cuterebra	CACCTAAT	GCCAAATG	TAGT	TACAAAG	GGAAGG	ATAAT	TTC	TAAAG	CAAAAA	CCCTT	ATTTT	CTG	TACAA	TTTTC	ACCG	GAAG
Cephenemyia	TACCAATG	GCCAAATG	CTGT	TCCAAATG	GAAGGT	TTTTC	CAAGC	AGAAAG	CCCTT	ACTTCT	GGTAC	AGTTTC	TCCG	GAAG		
Mesembrinella	TACCAATG	GCCAAAG	TAGG	TCCAAATG	GAAGGT	TTTTC	CAAGC	AGAAAG	CCCTT	ATTTCT	GGTAC	AGTTTC	TCCG	GAAG		
Opsodexia	TACCAATG	GCCAAAG	TAGG	TCCAAATG	GAAGGT	TTTTC	CAAGC	AGAAAG	CCCTT	ATTTCT	GGTAC	AGTTTC	TCCG	GAAG		
Lucilia																
Melanophora																
Pollenia	TACCAATG	GCCAAAG	TAAAG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Siphona	TACCAATG	GCCAAATG	GACAAAT	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Panzeria	TACCAATG	GCCAAAG	GACAAAT	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Epalpus	CACCAATG	GCCAAAG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Ceracia	CACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Winthemia	TACCAATG	GCCAAAG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Lespesia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Tachinomyia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Blondelia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Hyphantrophaga	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Campylochaeta	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Litophasia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Euthera	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Epigrimyia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Eutrika	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Uramya	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Voria	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Oestrophasia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Billaea	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Cordyligaster	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Rutilla	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Thelaira	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Ptilodexia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Phania	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Besseria SA	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Besseria CAN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Hemyda	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Protophobia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Cylind. SA1	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Cylind. SA2	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Cylindromyia AZ																
Cylindromyia TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Cylind. Ich. AZ	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Xysta	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Hermya	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Opesia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Rondaniooestrus	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Strongygaster TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Strongygaster OH	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Catharosia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Weberia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Leucostoma AZ	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Leucostoma TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Clairvillia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Labigastera	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Elomya	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Phasia AZ	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Phasia TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Phasia SA	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Euclytia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Eliozeta	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Clytiomya	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Ectophasia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Gymnosoma AZ	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Gymnosoma TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Gymnoclytia	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Xanthomel. AZ																
Xanthomel. TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
Aucalona	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
T. plum. FL	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
T. plum. SC	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
T. penn. 1	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
T. penn. 2																
T. penn. 3																
T. penn. 4																
T. lan. TN	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	
T. lan. VA	TACCAATG	GCCAAATG	GACAGG	TCAAAT	GGAAGT	TTAAT	CCAGAAAC	GAAAG	CCCTT	ATTTT	CTG	TACAA	TTTTC	TCCG	GAAG	

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	1121	1130	1140	1150	1160	1170	1180	1190	1200																																					
Musca	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	G	C
Macronychia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cuterebra	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	T	
Cephenemyia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Mesembrinella	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	T	
Opsodexia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Lucilia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Melanophora	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Pollenia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Siphona	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Panzeria	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Epalpus	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	T	
Ceracia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Winthemia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Lespesia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Tachinomys	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Blondelia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Hyphantrophaga	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Campylochaeta	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Litophasia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Euthera	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Epigrimyia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Eutrixia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Uramya	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Voria	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Oestrophasia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Billaea	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cordyligaster	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Rutilla	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Thelaira	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Ptilodexia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Phania	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Besseria SA	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Besseria CAN	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Hemyda	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Prolophosia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cylind. SA1	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cylind. SA2	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cylindromyia AZ	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cylindromyia TN	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Cylind. Ich. AZ	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Xysta	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Hermya	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Opesia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Rondanilloestrus	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Strongygaster TN	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Strongygaster OH	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Catharosia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Weberia	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Leucostoma AZ	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Leucostoma TN	C	A	T	T	A	A	G	C	C	A	T	G	A	A	A	G	A	A	A	A	T	T	C	C	A	A	T	T	G	C	T	A	C	A	A	A	C	T	T	C	A	A	G	G	C	
Clairvillia	C	A	T	T	A	A	G	C																																						

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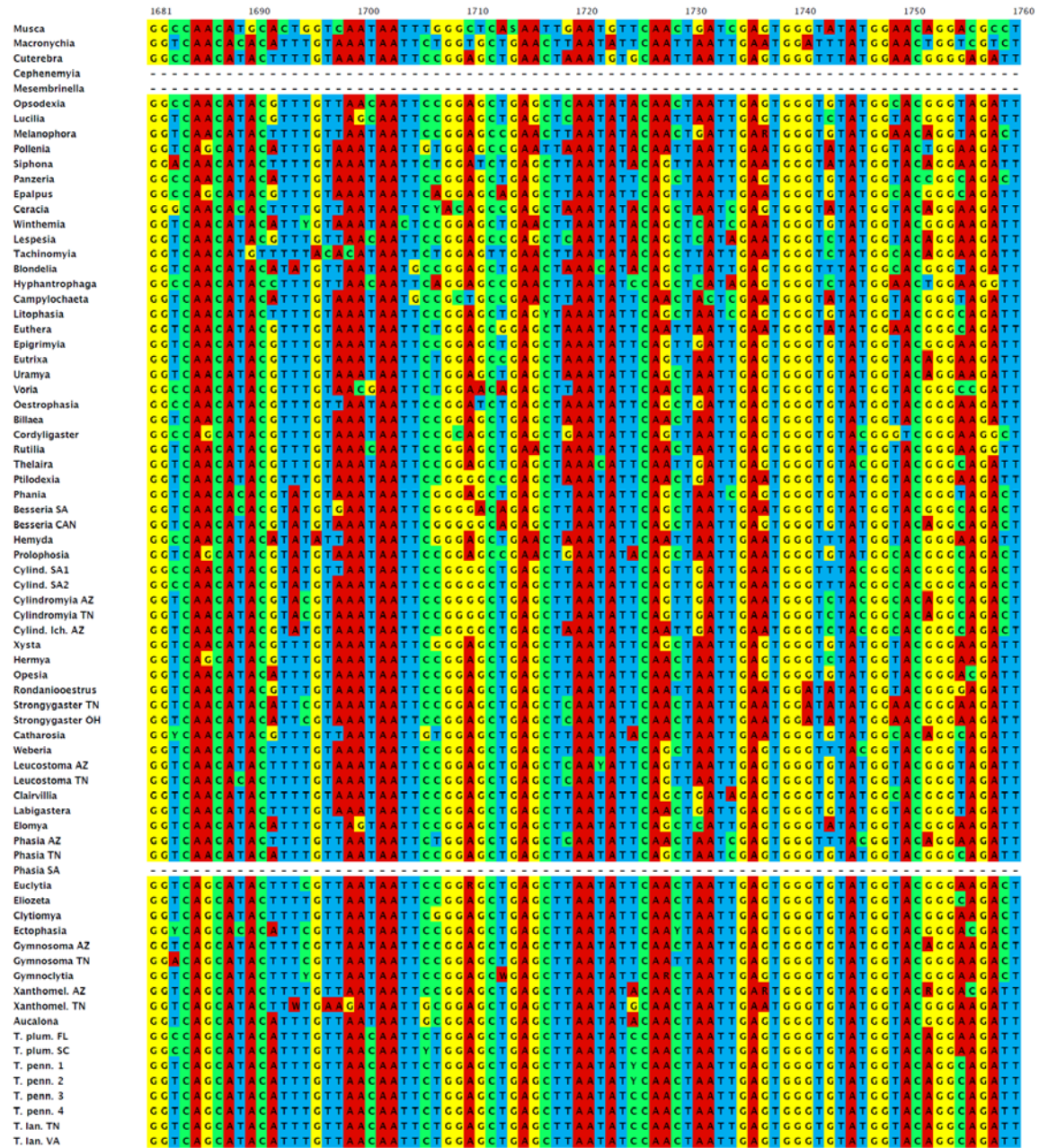
95

	1361	1370	1380	1390	1400	1410	1420	1430	1440
Musca	T T A A G A T T T T G G G T A C A C C C T C A A A T C T T T A T T G A G C T G A A G T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Macronychia	T T A A G A T T T T G G G T A C A C C C T C A A A T C T T T A T T G A G C T G A A G T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Cuterebra	T T A A G A T T T T G G G T A C A C C C T C A A A T C T T T A T T G A G C T G A A G T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Cephenemyia	T T A A G A T T T T G G G T A C A C C C T C A A A T C T T T A T T G A G C T G A A G T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Mesembrinella	T T A A A A T T T T G G G C A C T C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Opsodexia	T C A A G A T T T T G G G Y A G T C C C T C A A A T C C T T A T T G A G C T G G G T C G C A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Lucilia									
Meianophora									
Pollenia	T C A A G A T T T T G G G T A C T C C C A T T A A G T C A A T C A T G A G C T G A A G A T C G C A A A A T G T T T G C T G A A C G T T A A A T G A A A T T								
Siphona	T T A A A A T T T T G G G T A C C C C C A T C A A A T C C A T T A T G A G C T G A A G A T C G T A A A A T T T T G C T G C C G T T A A A T G A A A T T								
Panzeria	T C A A G A T T T T G G G T A C T C C C A T C A A A T C C A T T A T G A G C T G A A G A T C G C A A A A T T T T G C T G C C G T T A A A T G A A A T T								
Epalpus	T T A A G A T T T T A G G C A C T C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G C A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Ceracia	T T A A A A T T T T A G G T A C C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C T G A A C G T T A A A T G A A A T T								
Winthemia	T A A G G A T T T T G G G T A C C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G G A T C G C A A A T T T T G C G G A A C G T T A A A T G A A A T T								
Lespesia	T C A A A T T T T G G G T A C T C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C C G A A C G T T A A A T G A A A T T								
Tachinomyia	T T A A A A T T T T G G G T A C T C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C C G A A C G T T A A A T G A A A T T								
Blondelia	T T A A A A T T T T G G G T A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C C G A A C G T T A A A T G A A A T T								
Hyphantrophaga	T A A G A A T T T T G G G C A C T C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G C A A A A T T T T G C C G A A C G G T A A A T G A A A T T								
Campylochaeta	T C A A A A T A C T G G G T A C C C C A T T A A A A T C C A T T A T T A A A T G A A A C C G A A G A T C G T A A A A T T T T G C A G A A C G G T A A A T G A A A T T								
Litophasia	T T A A G A T A T T A G G T A C C C C A T T A A A T C C A T T A T G A G A C C G A A G A T C G T A A A A T T T T G C A G A A C G G T A A A T G A A A T T								
Euthera	T G A A G A T A T T A G G T A C C C C A T T A A A T C C A T T A T G A G A C A G G A T C G A A A A A T T T T G C A G A A C C G T A A A T G A A A T T								
Epigrimya	T G A A G A T T T T A G G T A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G A A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Eutrixia	T C A A A A T A T T A G G T A C C C C A T T A A A A T C A T A A T G A A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Uramya	T C G G G A T A T T A G G T A C T C C C A T C A A A T C C A T T A T T A A A T G A A C T G A A G A T C G T A A A A T T T T G C A G A C G G T A A A T G A A A T T								
Voria	T C A G R A T A C T G G G A A C C A A T C A A A T C C A T T A T G A G A C C G A A G A C G G Y A A A A T T T T G C A G A C G G T A A A T G A A A T T								
Oestrophasia	T T A A A A T A T T A G G C T C C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A C G G T A A A T G A A A T T								
Billaea	T C A A A A T A C T A G G T A C C C C A T T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G G T A A A T G A A A T T								
Cordyligaster	T C A A A A T A C T G G G T A C C C C A T T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G G T A A A T G A A A T T								
Rutilla	T T A A G A T T T T G G G T A G C C C A T C A A A T C C A T T A T T A A T G A G A C T G A A G A C G T A A A T T T T T G C T G A A C G T T A A A T G A A A T T								
Thelaira	T C C G T A T T T G G G T A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G A A A A T T T T T C C A G A A C G T T A A A T G A A A T T								
Ptilodexia	T C A A A A T A C T A G G T A C C C A T T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Phania	T G A A G A T A T T A G G T A C T C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Besseria SA	T G A G G A T T T T A G G T A C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Besseria CAN	T G A G G A T T T T A G G T A C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Hemyda	T T A A G A T T T T G G G T A C C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Protophobia	T C A A A A T A T T A G G C A C Y C C C A T C A A G T C C A T T A T G A G A C C G A A G A T C G T A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Cylind. SA1	T C A A A A T A T T G G G C A C G A T C A A G T C C T T T A T G A G A C T G A A G A T C G T A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Cylind. SA2	T C A A A A T T T T G G G C A C T C C T A T C A A G T C C T T T A T G A G A C C G A A G A T C G T A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Cylindromyia AZ									
Cylindromyia TN	T C A A A A T A T T G G G C A C T C C T A T C A A G T C C T T T A T G A G A C T G A A G A T C G T A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Cylind. Ich. AZ	T C A A A A T A T T G G G C A C T C C T A T C A A G T C C T T T A T G A G A C T G A A G A T C G T A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Xysta	T T A A A A T T T T A G G C A C C C C A T C A A A T C C A T T A T G A G A C T G A A G A T C G C A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Hermya	T T A A A A T T T T A G G C A C C C C A T C A A A T C C A T T A T G A G A C C G A A G A T C G T A A A A T T T T G C C G A A C G T T A A A T G A A A T T								
Opesia	T T A A A A T T T T A G G T A C C C C A T C A A A T C C A T T A T G A G A C C G A A G A T C G T A A A A T T T T G C A G A C C G T T A A A T G A A A T T								
Rondaniooestrus	T T A A A A T T T T A G G T A C C C C A T C A A A T C C G T T A T G A A A C T G G A T C G C A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Strongygaster TN									
Strongygaster OH	T T A A A A T T T T G G G T A C T C C T T C A A T T T A T G A G C T G G G C G T A A A A T T T T G C G A A C G T T A A A T G A A A T T								
Catharosia	T C A A G A T T T T G G G T A C C C C A T T A A A T C A A T T A T G A A C T G A A G A T C G C A A A T T T T G C A A A C G T T A A A T G A A A T T								
Weberia	T C A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C G A A A C G T T A A A T G A A A T T								
Leucostoma AZ	T C A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G C A A A A T T T T G C G G A A C G T T A A A T G A A A T T								
Leucostoma TN	T C A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G C A A A A T T T T G C G G A A C G T T A A A T G A A A T T								
Clairvillia	T T A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G Y A A A A T T T T G C G A A A C G T T A A A T G A A A T T								
Labigastera	T T A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C G A A A C G T T A A A T G A A A T T								
Elomya	T T A A G A T T T T A G G A C C C C A T T A A A T C C A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C G A A A C G T T A A A T G A A A T T								
Phasia AZ									
Phasia TN	T C A A G A T T T T A G G T A C C C C A T C A A A T C C A T T A T G A G A C T G G G A T C G T A A A A T T T T T C T G A A C G T T A A A T G A A A T T								
Phasia SA	T T A A G A T T T T A G G T A C C C C A T C A A A T C A A T T A T G A G A C T G G G A T C G T A A A A T T T T T G C A G A A C G T T A A A T G A A A T T								
Euclytia	T C A A G A T T T T A G G C A C C C C A T T A A A T C A A T T A T G A G A C T G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Eliozeta	T T A A G A T T T T A G G C A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Clytiomya	T T A A G A T T T T A G G C A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Ectophasia	T T A A G A T T T T A G G C A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G C A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
Gymnosoma AZ	T T A A G A T T T T A G G C A C C C C A T T A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Gymnosoma TN	T T A A G A T T T T A G G C A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C C A A A C G T T A A A T G A A A T T								
Gymnoclytia	T T A A G A T T T T A G G C A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Xanthomel. AZ									
Xanthomel. TN	T T A A G A T T T T A G G T A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G A A A A A T T T T G C A A A C G T T A A A T G A A A T T								
Aucalona	T C A A G A T T T T G G G T A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A C C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
T. plum. FL									
T. plum. SC	T C A A G A T T T T G G G T A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
T. penn. 1	T C A A G A T T T T G G G Y A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A G A A C G T T A A A T G A A A T T								
T. penn. 2									
T. penn. 3									
T. penn. 4									
T. lan. TN	T C A A G A T T T T G G G T A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								
T. lan. VA	T C A A G A T T T T G G G T A C C C C A T C A A A T C A A T T A T G A G A C A G A A G A T C G T A A A A T T T T G C A A A C G T T A A A T G A A A T T								

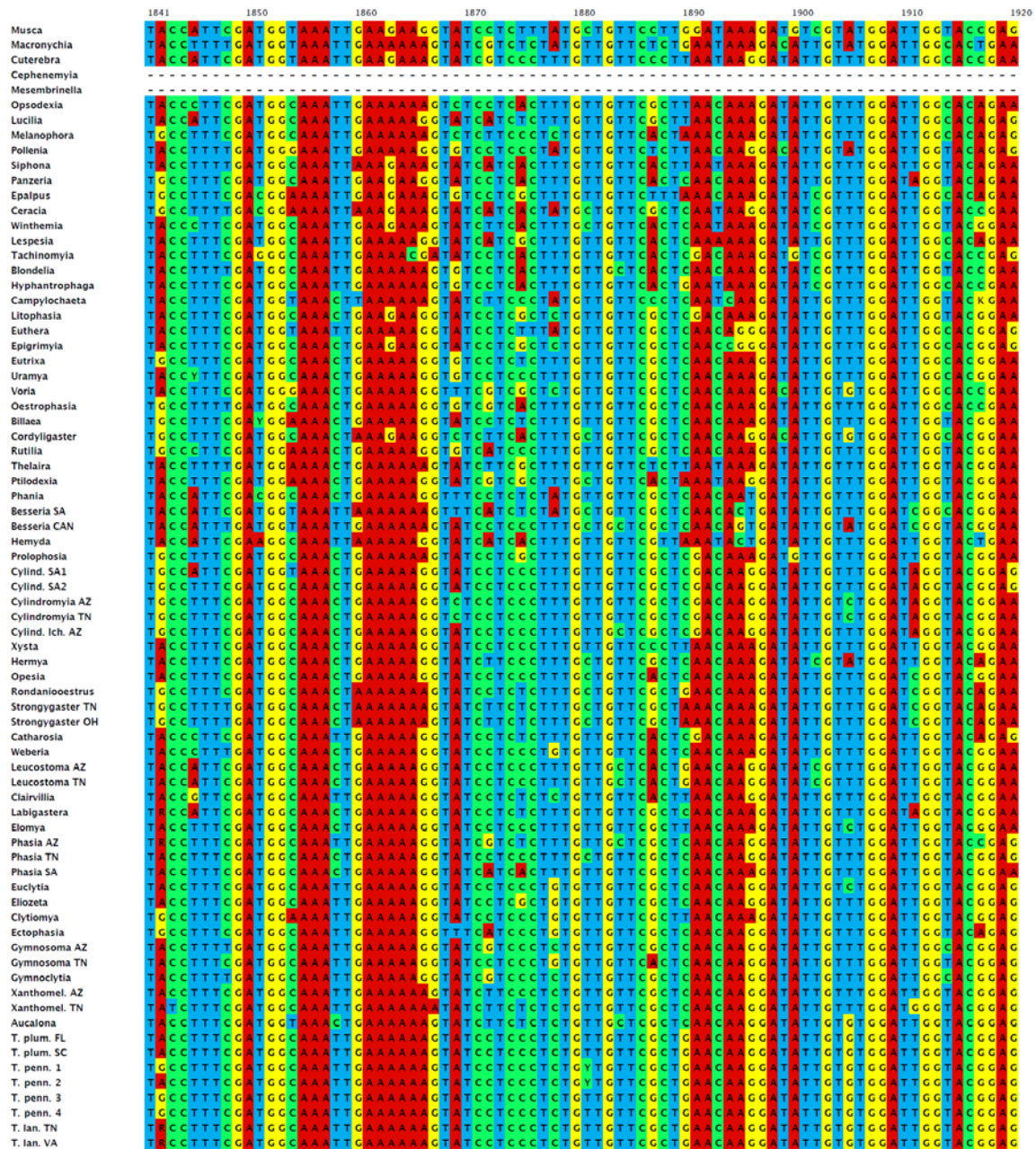
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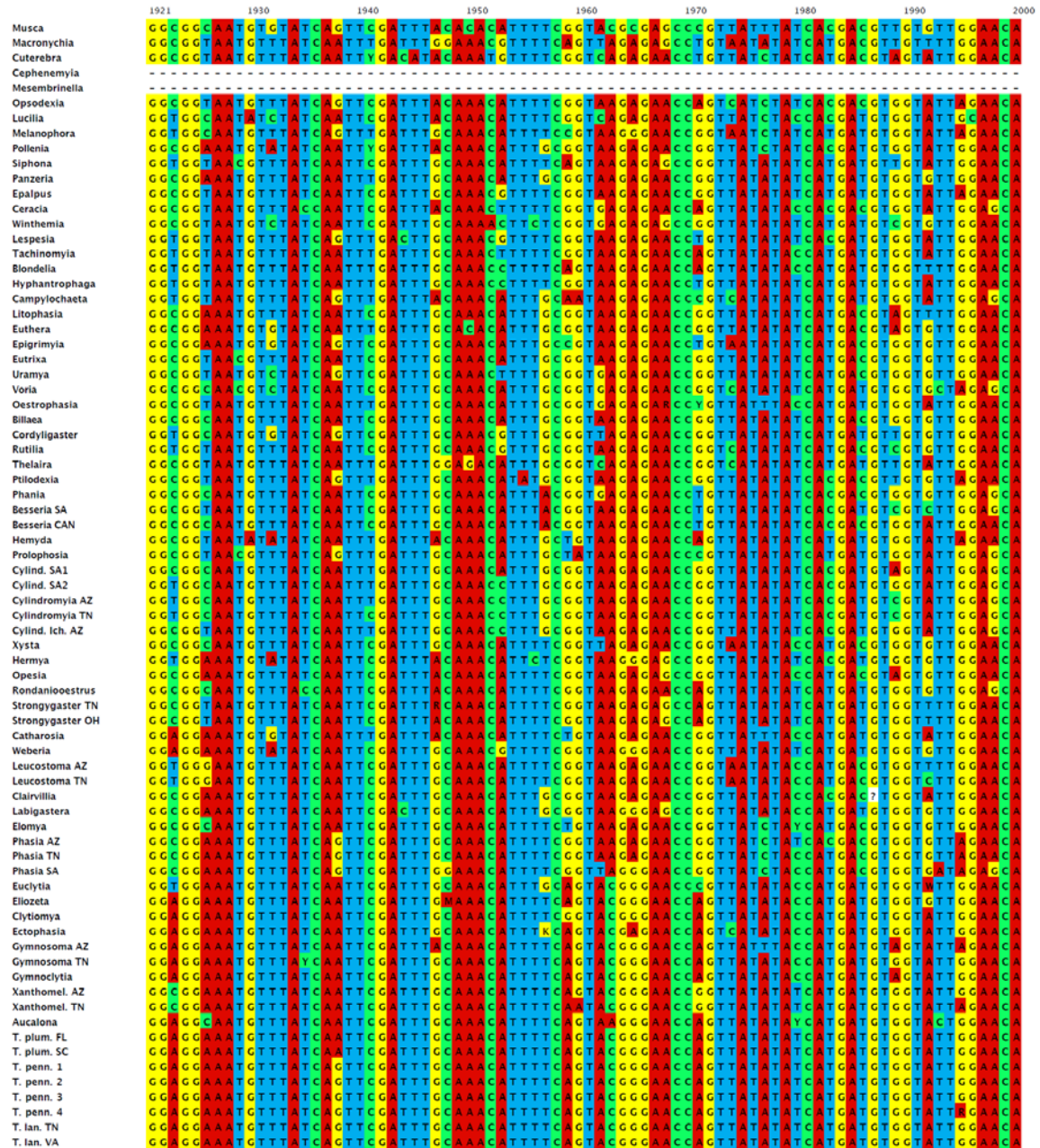
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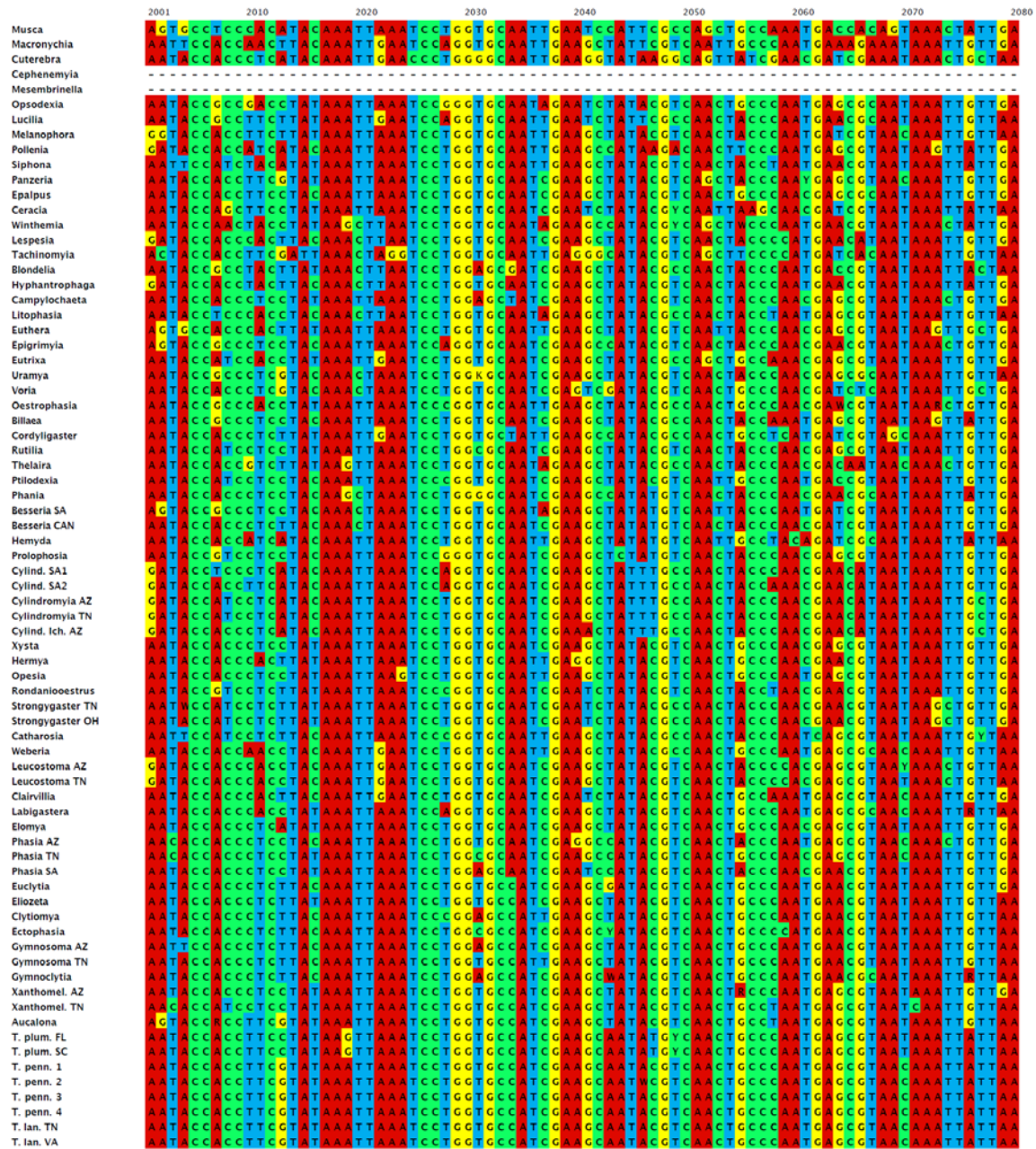
	1601	1610	1620	1630	1640	1650	1660	1670	1680
Musca	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Macronychia	GACAGGCTTTGGCT	---	---	GGAAACACGAC	GGAGCTGT	CAAACTTTTGG	CAACCAAGGT	GTAGAGTTT	AT
Cuterebra	GCCAGGCTTTGGCT	---	---	GGAAACACAC	GGAGCTGT	CAAACTTTTGG	CAACCTGG	GTG	CAATTTT
Cephenemyia	---	---	---	---	---	---	---	---	---
Mesembrinella	GCCAGGCTTTGGCT	GGCTCA	GGCA	---	---	---	---	---	---
Opsodexia	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Lucilia	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Melanophora	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Pollenia	GCCAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Siphona	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Panzeria	GGCAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Epalpus	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Ceracia	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Winthemia	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Lespesia	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Tachinomyia	AGCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Biondella	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Hyphantrophaga	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Campylochaeta	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Litophasia	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Euthera	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Epigrammia	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Eutrixia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Uramya	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Voria	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Oestrophasia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Billaia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cordyligaster	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Rutilla	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Thelaira	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Ptilodexia	GACAGGCTTTGGCT	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Phania	AGCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Besseria SA	AGCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Besseria CAN	AGCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Hemyda	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Prolophosia	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cylind. SA1	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cylind. SA2	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cylindromyia AZ	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cylindromyia TN	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Cylind. Ich. AZ	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Xysta	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Hermiya	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Opesia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Rondaniloestrus	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Strongygaster TN	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Strongygaster OH	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Catharsia	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Weberia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Leucostoma AZ	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Leucostoma TN	GCCAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Clairvillia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Labigastera	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Elomya	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Phasia AZ	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Phasia TN	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Phasia SA	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Euclytia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Eliozeta	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Clytiomya	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Ectophasia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Gymnosoma AZ	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Gymnosoma TN	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Gymnoclytia	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Xanthomel. AZ	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Xanthomel. TN	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
Aucalona	GACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. plum. FL	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. plum. SC	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. penn. 1	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. penn. 2	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. penn. 3	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. penn. 4	---	---	---	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. lan. TN	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT
T. lan. VA	AACAGGCTTTGGCT	GGCTCA	GGCA	GGTTC	CAAACTGG	GTATG	CAAACTGG	GTG	CAATTTT

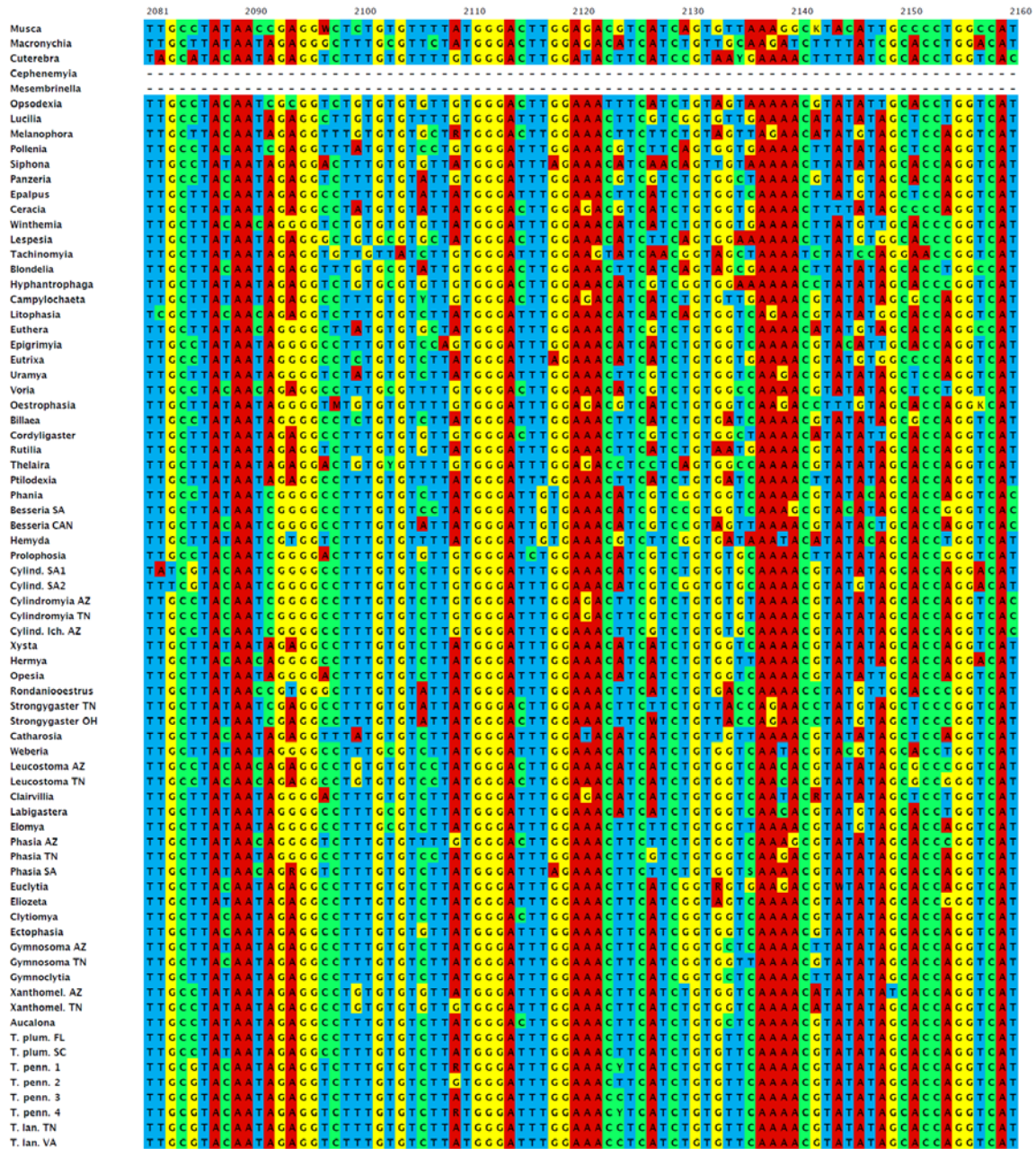


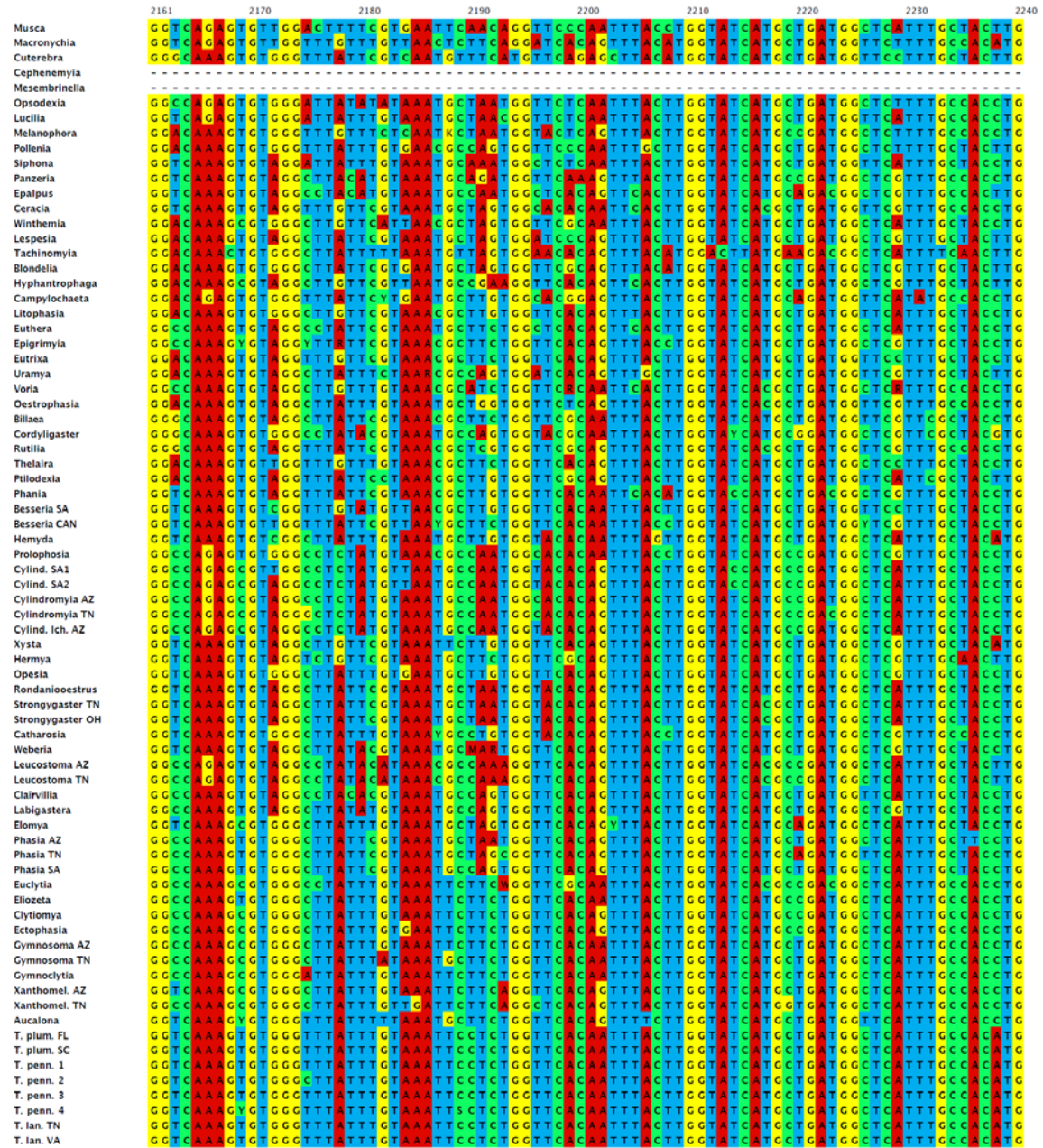
	1761	1770	1780	1790	1800	1810	1820	1830	1840
Musca	CTTGTGCTTCACTGCTGCAAAACAAATTCAGTTCTTGTGGGAACCCGCC	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Macronychia	TTTGTCTTTAACTGGGGCAATCAGTTAAATTTTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cuterebra	TTTATCTTTAACTGGGGCAATCAGTTAAATTTTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cephenemyia									
Mesembrinella									
Opsodexia	TTTGTGCTTCACTGCTGCAAAACAAATTCAGTTCTTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Lucilia	ATTATCTCTGAGGGCTGCAATCAATTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Melanophora	TTTGTGCTTCACTGCTGCAAAACAAATTCAGTTCTTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Pollenia	CTGTCACTGCTGAGGCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Siphona	TTTATCACTTCACTGAGCCAAATCAGCTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Panzeria	TTTATCACTGACTGAGGCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Epalpus	TTTGTCACTGACTGAGGCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Ceracia	CTGTCACTGACTGAGGCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Winthemia	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Lespesia	TTTGTGCTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Tachinomyia	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Blondelia	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Hyphantrophaga	TTTGTCTTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Campylochaeta	TTTATCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Litophasia	CTGTCACTGACTGAGGCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Euthera	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Epigrimyia	TTTGTGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Eutrixia	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Uramya	CTGTCTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Voria	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Oestrophasia	TTTGTCTTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Billaea	TTTGTGCTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cordyligaster	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Rutilla	TTTGTCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Thelaira	TTTATCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Ptilodexia	TTTATCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Phania	TTTATCACTTCACTGCTGCCAATCAGTTGATATTGTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Besseria SA	TTTATCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Besseria CAN	TTTATCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Hemyda	TTTATCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Prolophosia	TTTATCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cylind. SA1	TTTGTGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cylind. SA2	TTTGTGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cylindromyia AZ	TTTATGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cylindromyia TN	TTTATGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Cylind. Ich. AZ	TTTATGCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Xysta	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Hermya	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Opesia	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Rondaniooestrus	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Strongygaster TN	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Strongygaster OH	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Catharasia	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Weberia	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Leucostoma AZ	TTTGTCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Leucostoma TN	TTTGTCCCTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Clairvillia	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Labigastera	TTTGTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Elomya	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Phasia AZ	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Phasia TN	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Phasia SA	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Euclytia	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Eliozeta	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Clytiomya	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Ectophasia	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Gymnosoma AZ	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Gymnosoma TN	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Gymnoclytia	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Xanthomel. AZ	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Xanthomel. TN	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
Aucalona	TTTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. plum. FL	CTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. plum. SC	CTATCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. penn. 1	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. penn. 2	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. penn. 3	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. penn. 4	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. lan. TN	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						
T. lan. VA	CTCTCACTTCACTGCTGCCAATCAGTTAAATTTTGGGAACCCCTCT	GGT	GGTACCTTGGTGGCTATAAAAGTAT						

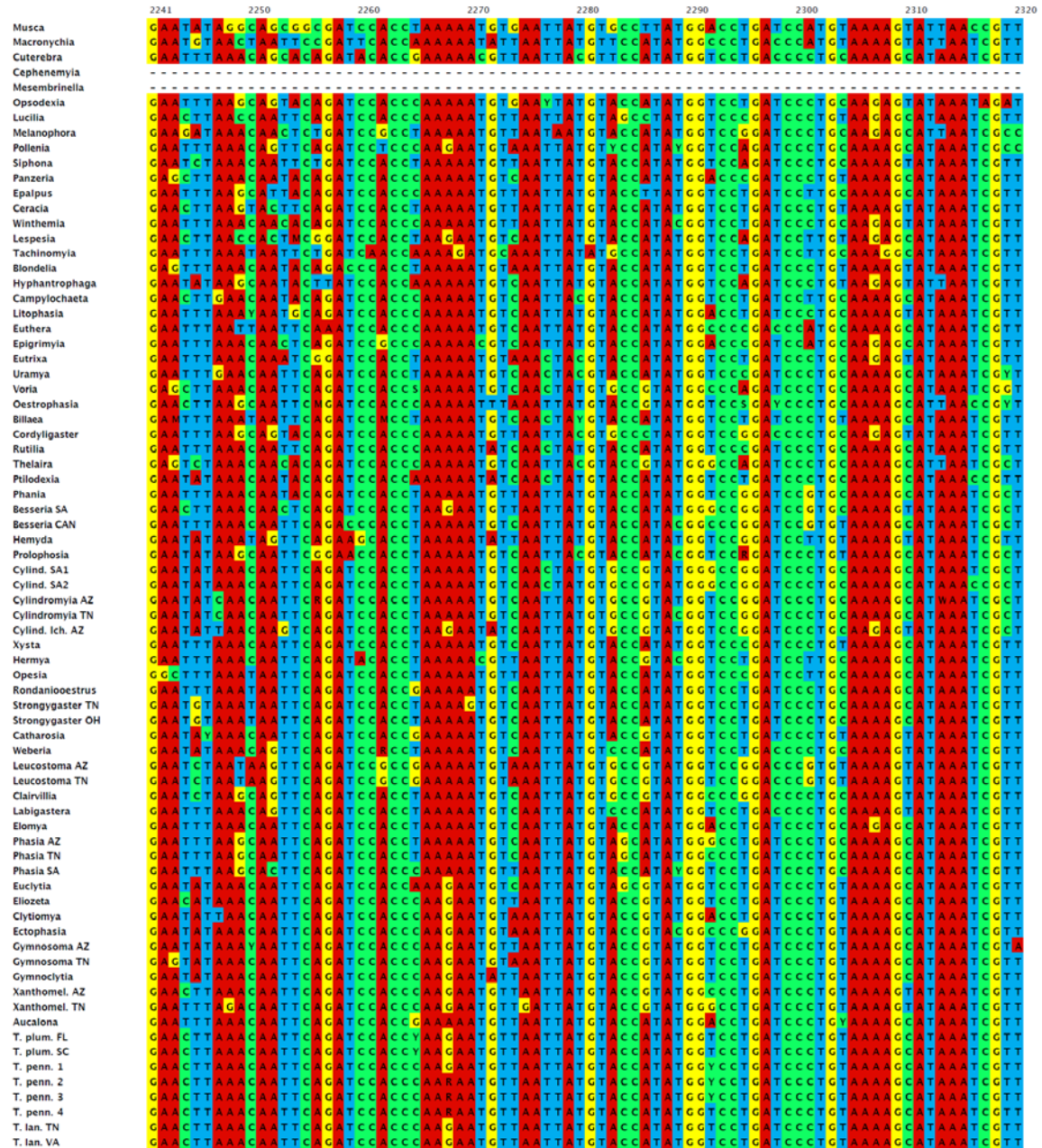


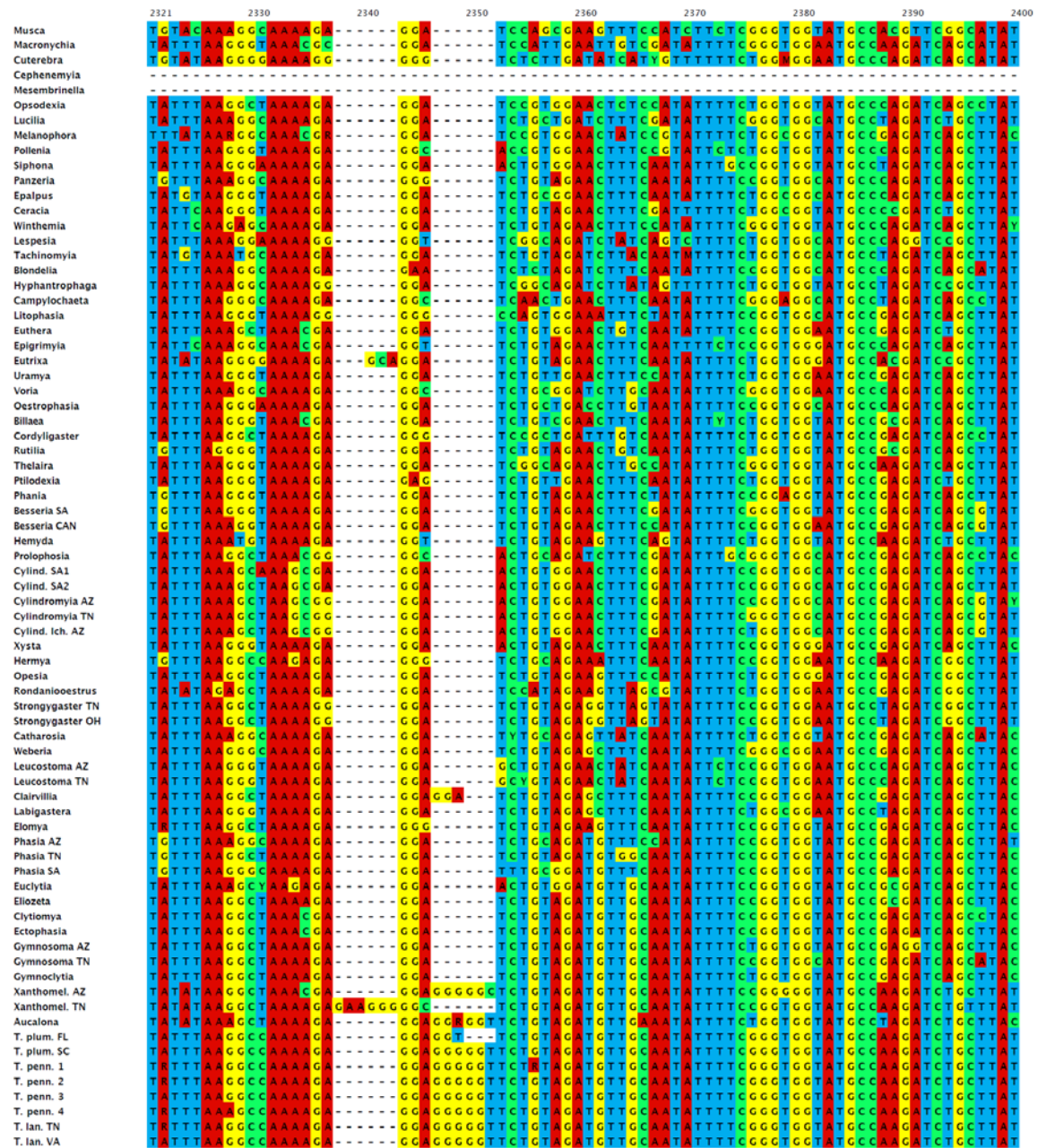


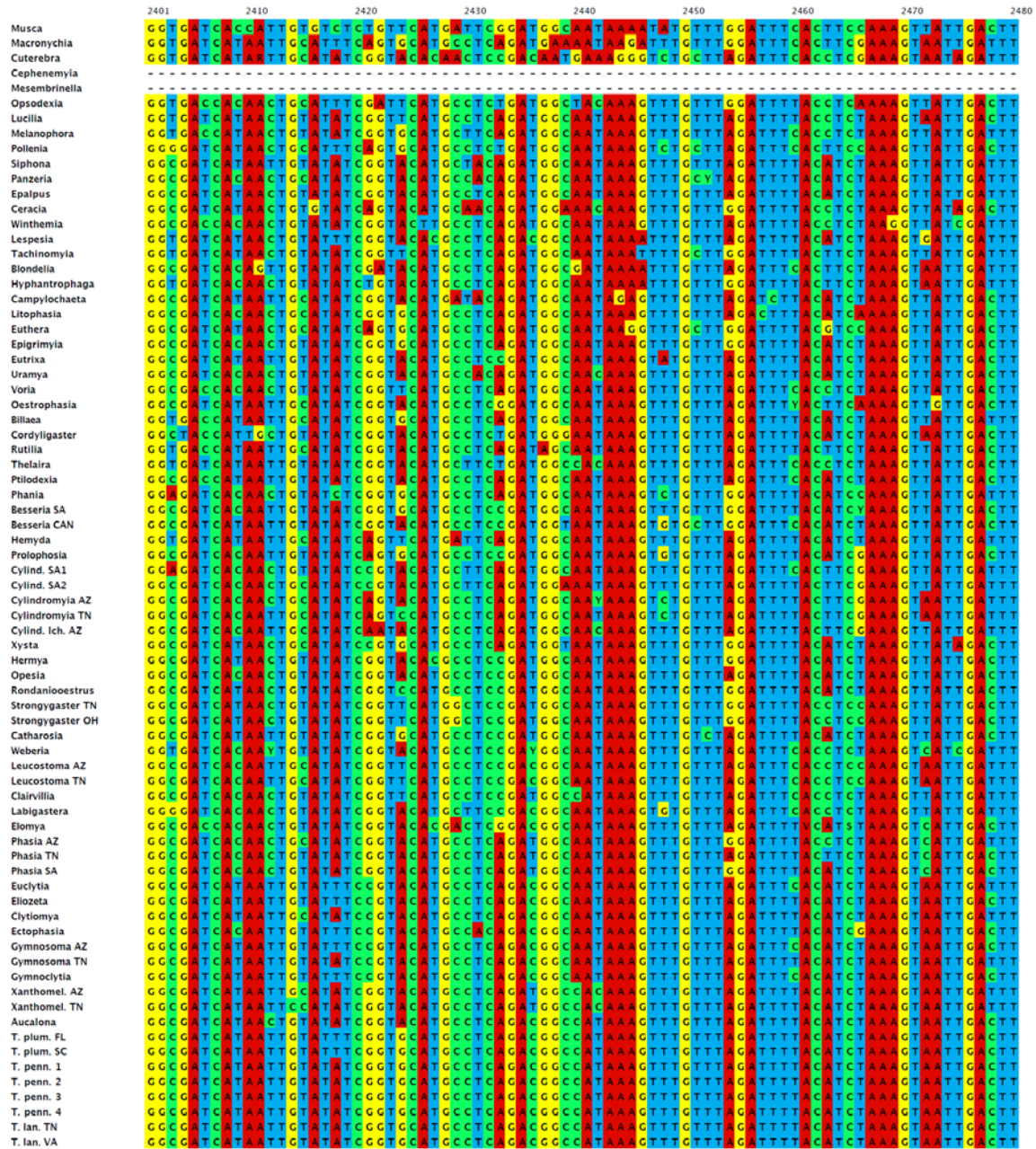


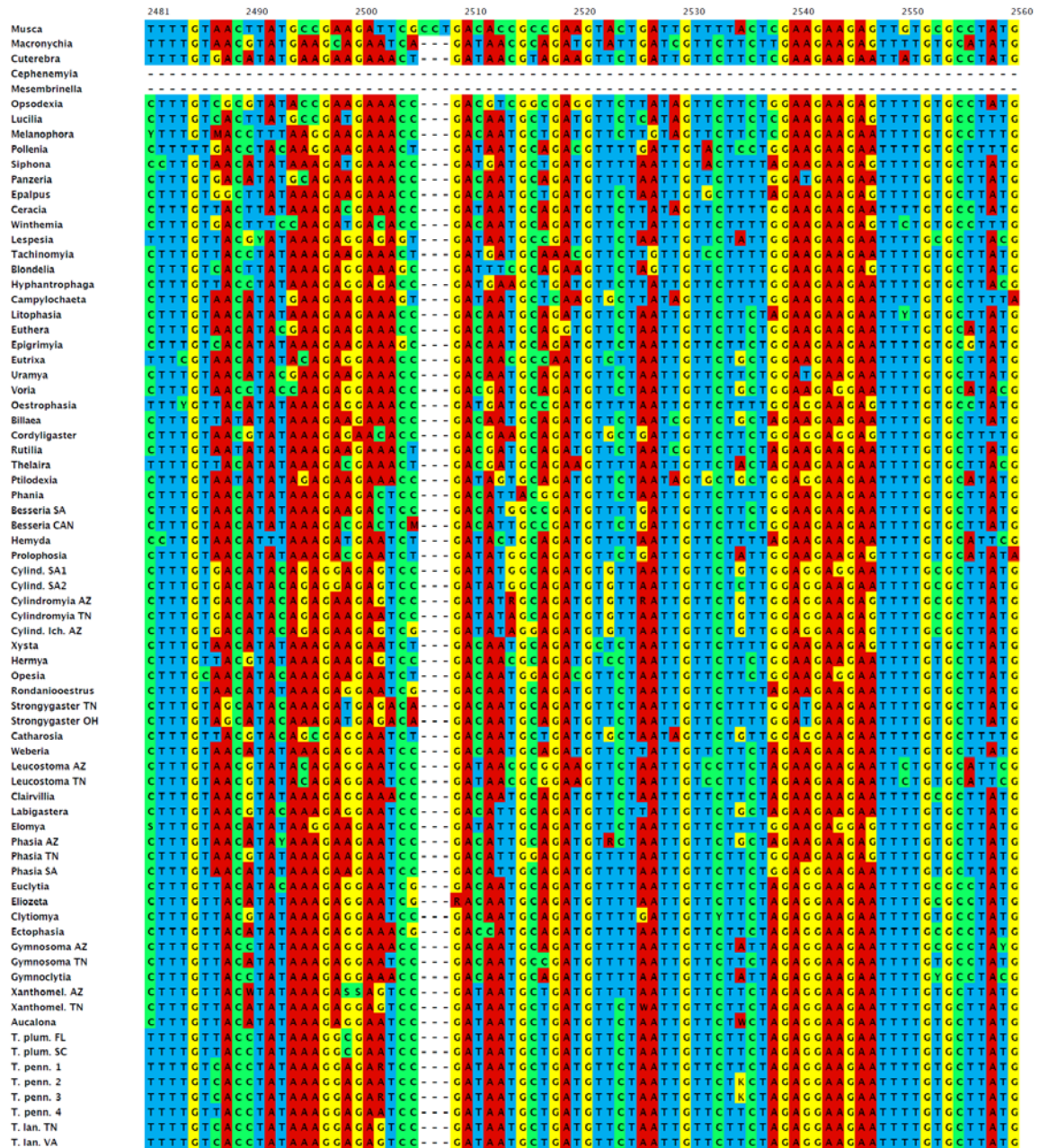


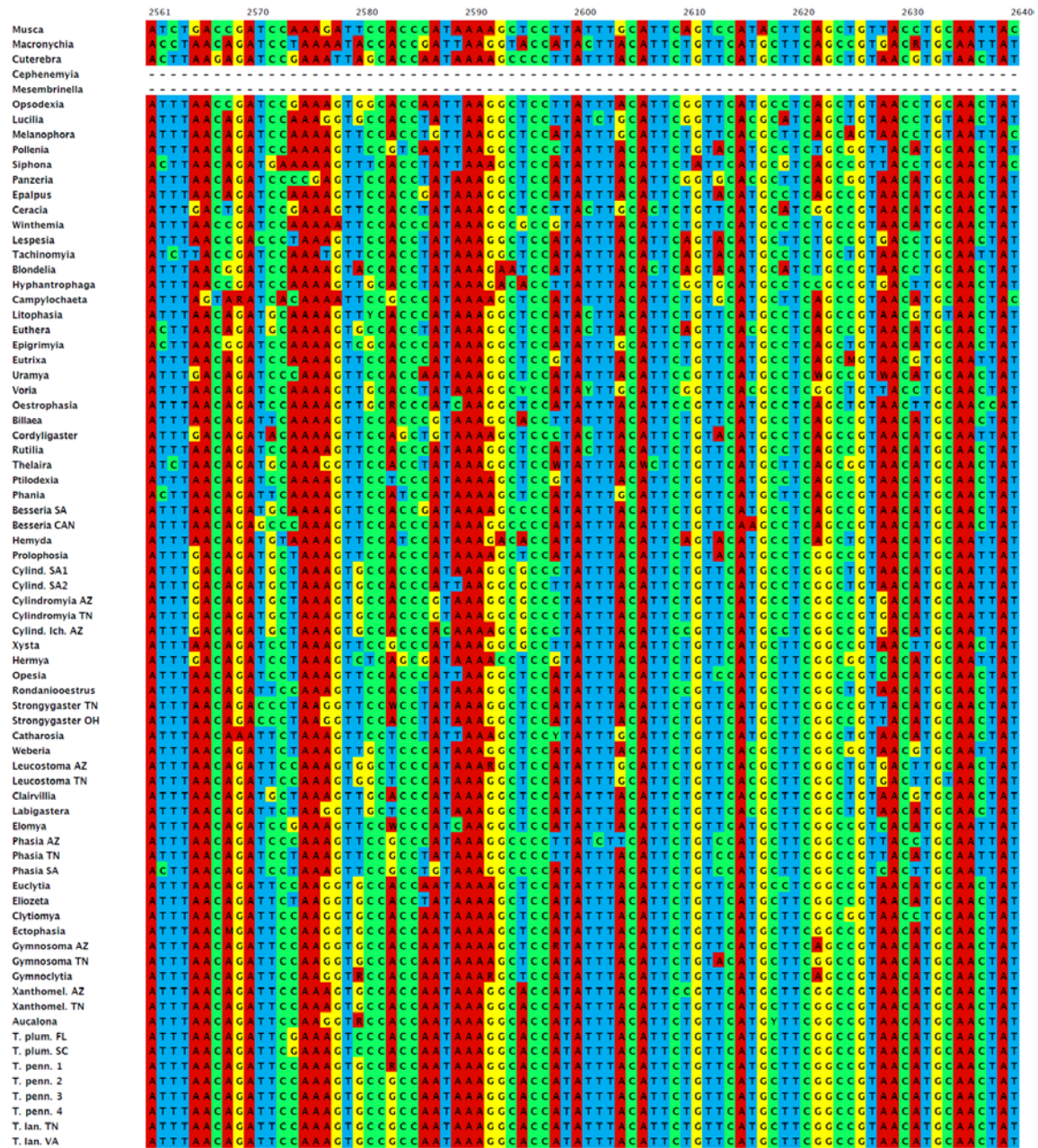


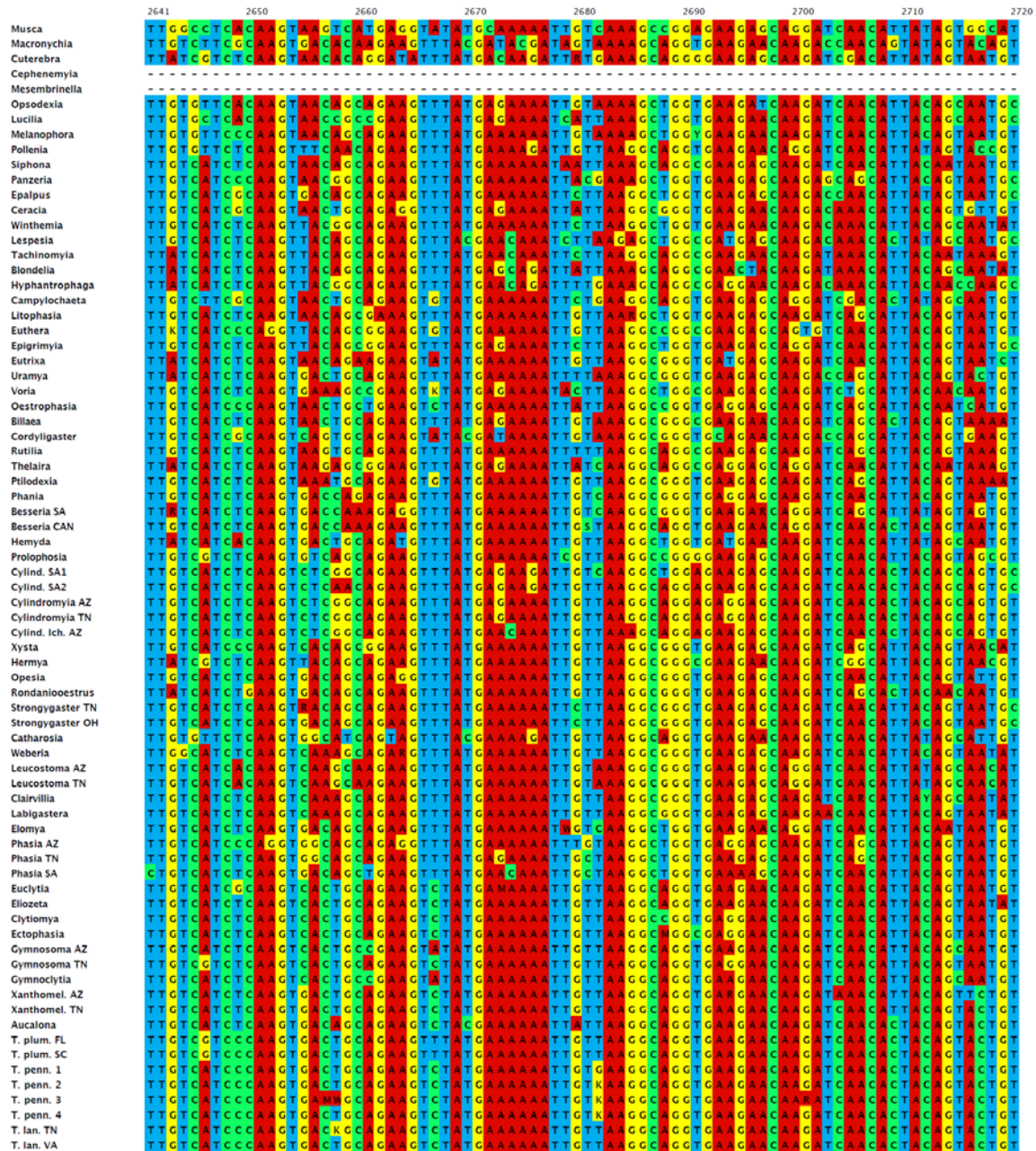












	2721	2730	2740	2750	2757																																	
Musca	T	G	A	T	G	G	C	C	T	A	T	A	A	G	G	G	A	G	G	C	A	T	T	G	G	C	A	G	A	C								
Macronychia	T	G	A	G	T	G	G	C	C	A	A	T	T	A	G	A	G	G	A	G	A	G	A	T	T	G	C	C	A	G	A	T						
Cuterebra	C	G	A	A	T	G	G	C	C	T	A	T	A	A	A	T	G	G	C	G	G	T	G	T	A	T	T	G	C	C	A	A	T					
Cephenemyia																																						
Mesembrinella																																						
Opsodexia	T	G	A	G	T	G	G	C	C	T	A	T	T	A	A	C	G	G	G	A	G	C	A	T	T	G	C	C	A	G	A	T						
Lucilia	T	G	A	G	T	G	G	C	C	A	A	T	T	A	A	T	G	G	T	A	C	A	T	T	G	C	C	C	A	G	A	A	T					
Melanophora	T	G	A	A	T	G	G	C	C	T	G	T	C	A	A	T	G	G	T	A	C	A	C	T	G	Y	C	T	G	A	A	G	A	G				
Pollenia	G	G	A	C	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	G	T	T	G	C	C	G	T	C	A	G	T			
Siphona	T	G	A	A	T	G	G	C	C	T	A	T	T	A	A	C	G	G	A	G	G	T	A	T	T	A	C	C	C	A	T	A	A	C				
Panzeria	C	G	A	G	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	T	T	T	G	C	C	A	G	A	A	T			
Epalpus	C	G	A	G	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	T	T	T	A	C	C	C	A	A	C				
Ceracia	T	G	A	G	T	G	G	C	C	T	A	T	T	A	A	T	G	G	T	G	G	C	A	T	T	T	T	A	C	C	C	A	T	G	A	A		
Winthemia	T	G	A	A	T	G	G	C	C	C	A	T	T	A	A	C	G	G	A	G	G	C	A	T	T	A	C	C	A	G	A	T	T	G	T			
Lespesia	A	G	A	A	T	G	G	C	C	T	A	T	A	A	A	T	G	G	C	G	G	C	T	G	T	T	T	A	C	C	G	A	T	G	A	C		
Tachinomyia	G	G	A	A	T	G	G	C	C	T	A	T	A	A	A	T	G	G	A	G	G	C	A	T	T	T	T	A	C	C	A	G	A	C	A	G	T	
Blondelia	T	G	A	A	T	G	G	C	C	A	A	T	A	A	A	T	G	G	T	G	G	C	A	G	T	T	A	C	C	C	A	T	A	G	C			
Hyphantrophaga	T	G	A	A	T	G	G	C	C	T	A	T	A	A	C	T	G	G	C	G	C	A	C	G	C	T	G	C	C	T	G	A	C	A	G	T		
Campylochaeta	T	G	A	A	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	A	A	C	A	T	G	A	A		
Litophasia	C	G	A	C	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	T	C	A	T	T	A	C	C	C	A	T	G	A	C		
Euthera	G	G	A	T	T	G	G	C	C	T	A	T	A	A	G	T	G	G	A	G	G	C	A	C	A	T	T	G	C	C	C	A	A	C	A	C		
Epigrimyia	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	G	C	G	A	T	A	A	C		
Eutrixia	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Uramya	G	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	T	A	T	T	T	T	A	C	C	C	A	G	A	A	C		
Voria	Y	G	A	A	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	C	C	T	G	C	C	A	G	A	G	C			
Oestrophasia	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	T	G	G	A	C	A	T	T	G	C	C	C	A	T	G	A	T			
Billaea	C	G	A	T	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Cordyligaster	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	G	T	A	T	T	G	G	C	C	A	T	G	G	T		
Rutilia	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	T	A	T	T	T	T	A	C	C	C	A	T	A	T	G		
Thelaira	C	G	A	T	T	G	G	C	C	A	A	T	T	A	A	T	G	G	G	G	G	T	A	C	A	T	T	A	C	C	C	A	G	A	A	T		
Ptilodexia	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	C	T	G	G	C	G	G	T	G	A	A	T	T	G	C	C	A	T	A	A	C		
Phania	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	C	G	G	G	G	G	T	A	T	A	C	T	G	C	C	G	A	T	G	A	A		
Besseria SA	G	A	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	G	T	T	A	C	C	C	A	G	A	A	C		
Besseria CAN	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	T	G	G	C	A	T	G	T	T	A	C	C	C	A	T	G	A	A		
Hemyda	A	G	A	T	T	G	G	C	C	A	A	T	T	A	A	T	G	G	T	G	G	C	A	T	A	T	T	A	C	C	G	A	T	G	A	T		
Prolophosia	T	G	A	A	T	G	G	C	C	C	A	T	T	A	A	C	T	G	G	A	G	G	C	A	C	T	T	T	A	C	C	C	G	A	C	C		
Cylind. SA1	T	G	A	G	T	G	G	C	C	C	A	T	T	A	A	T	G	C	G	G	A	G	G	C	A	C	A	T	T	A	C	C	G	A	C	A	G	T
Cylind. SA2	T	G	A	G	T	G	G	C	C	C	A	T	T	A	A	T	G	G	C	G	G	C	A	C	A	T	T	A	C	C	G	A	C	A	G	C		
Cylindromyia AZ	T	G	A	G	T	G	G	C	C	G	A	T	T	A	A	T	G	G	A	G	G	C	A	C	A	T	T	A	T	C	C	G	A	T	A	G	C	
Cylindromyia TN	T	G	A	G	T	G	G	C	C	G	A	T	T	A	A	T	G	G	A	G	G	C	A	C	A	T	T	A	T	C	C	G	A	T	A	G	C	
Cylind. Ich. AZ	T	G	A	G	T	G	G	C	C	G	A	T	T	A	A	T	G	G	A	G	G	C	A	C	A	T	T	A	T	A	T	G	A	T	A	G	C	
Xysta	C	G	A	C	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Hermya	C	G	T	T	T	G	G	C	C	T	A	T	T	A	A	C	G	G	G	G	C	G	A	A	T	T	A	C	C	C	A	T	A	A	C	G		
Opesia	A	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	T	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Rondaniooestrus	C	G	A	C	T	G	G	C	C	T	A	T	T	A	A	T	G	G	T	G	G	C	A	T	A	T	T	G	C	C	C	A	C	A	T	C		
Strongygaster TN	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	G	G	G	C	A	T	C	T	T	G	C	C	C	A	T	A	C	C		
Strongygaster OH	C	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	G	G	G	C	A	T	C	T	T	G	C	C	C	A	T	A	C	C		
Catharosia	A	G	A	A	T	G	G	C	C	A	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	C	A	A	T		
Weberia	A	G	A	G	T	G	G	C	C	T	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Leucostoma AZ	A	G	A	C	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	C	A	T	T	G	C	C	T	G	A	G	A	A	T	
Leucostoma TN	A	G	A	C	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	C	A	T	T	G	C	C	T	G	A	G	A	A	T	
Clairvillia	A	G	A	G	T	G	G	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C			
Labigastera	A	G	A	G	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	G	C		
Elomya	C	G	A	C	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	T	G	A	T	A	A	C	
Phasia AZ	C	G	A	T	T	G	G	C	C	C	A	T	T	A	A	T	A	A	C	G	G	G	G	C	A	C	A	T	T	A	C	C	C	A	T	A	A	C
Phasia TN	C	G	A	T	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Phasia SA	C	G	A	T	T	G	G	C	C	C	A	T	T	A	A	T	G	G	A	G	G	Y	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Euclytia	G	G	A	T	T	G	G	C	C	C	A	T	T	A	A	T	G	G	C	G	G	C	A	T	W	T	T	A	C	C	C	A	T	A	A	C		
Ellozeta	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Clytiomya	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Ectophasia	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Gymnosoma AZ	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	G	A	C		
Gymnosoma TN	T	G	A	T	T	G	G	C	C	G	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	A	A	C		
Gymnoclytia	T	G	A	T	T	G	G	C	C	T	A	T	T	A	A	T	G	G	C	G	G	C	A	T	A	T	T	A	C	C	C	A	T	G	A	C		
Xanthomel. AZ	T	G	A	G	T	G	G	C	C	T	G	T																										

VITA

Jeremy Blaschke was born in Santa Fe, New Mexico and spent many hours of his childhood collecting insects in his southwest backyard. Jeremy was home-educated throughout high school and after graduating in 2006 left the plains and deserts of New Mexico for the hills and forests of Tennessee where he attended Bryan College in Dayton. Jeremy earned a Bachelor of Science degree in Biology with a minor in Origins Research and graduated *cum laude* in 2010. After college, Jeremy worked at TestAmerica (an environmental testing company) in Knoxville, TN as a chemical analyst for eighteen months. Scientific research and teaching have always been his passions and while employed, Jeremy pursued various graduate programs in Paleontology, Ecology, Evolutionary Biology, Genetics, and Entomology. In 2011 he accepted a position in the Entomology and Plant Pathology department at the University of Tennessee to study molecular systematics under the mentoring of Dr. Kevin Moulton. Currently, Jeremy is studying the phylogenetics of the subfamily Phasiinae (Diptera: Tachinidae) and expects to receive his Master's degree in August 2013.