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A systematic investigation of the crane fly subfamily Limoniinae (Tipuloidea: Limoniidae)

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A systematic investigation of the crane fly subfamily
Limoniinae (Tipuloidea: Limoniidae)

by

Matthew Jon Petersen

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

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CHAPTER 6. GENERAL CONCLUSIONS
CHAPTER 1: DISSERTATION OVERVIEW

Systematics provides the knowledge base from which all biology is based, and the subdivisions of this science provide many fundamental methodological criteria by which we investigate the natural world. Far from simply a service science that provides a reference system for study by other disciplines (Ebach & Holdrege 2005), systematics is a dynamic science that involves many facets such as the discovery and delineation of species and other taxa (taxonomy), defining current and historical distributional patterns (biogeography), and the study of evolutionary patterns (phylogenetics). Systematics allows researchers to answer the questions of what and how many organisms inhabit the Earth (Agnarsson & Kuntner 2007).

The importance of basic taxonomic research is now greater than ever, as deterioration of taxonomic expertise coupled with an increased rate of species extinction, the so called “taxonomic impediment” (Rodman & Cody 2003) or “taxonomic crisis” (Taylor 1976) threatens to eliminate diversity even before it is identified. For the study of insects this is particularly true as taxonomic revisions occur on average once every hundred years (Wheeler, 2004). The impact of a depleting knowledge base has the power to affect multiple aspects of related biological disciplines such as ecological studies (Gotelli 2004) and conservation planning (Golding & Timberlake 2003; Godfrey & Knapp 2004). In the absence of taxonomy, the language by which we interpret and identify life disappears.

The acknowledgement of the importance of taxonomic research has led to a recent resurgence of basic taxonomic work that incorporates traditional aspects of systematic investigations, such as the study of morphology, species descriptions, and classification, with new technologies of molecular biology (DNA taxonomy) and electronic resources (“new
taxonomy” (Wheeler, 2008). With this resurgence comes the opportunity to rapidly disseminate taxonomic resources and world species catalogs, thus greatly decreasing the time spent researching records and searching for taxonomic tools.

Within the Diptera (Insecta) the general descriptor of crane fly has been used for the Ptychopteridae (phantom crane flies), Trichoceridae (winter crane flies), Tanyderidae (primitive crane flies), and the Tipuloidea (true crane flies), having been loosely applied to those groups of flies that show a tendency for the elongation of the legs, wings, and abdomen, often in a delicate form. Since the advent of modern cladistic approaches (Henning 1966) and subsequent phylogenetic analyses of the Lower Diptera (Wood & Borkent 1989; Griffith 1990; Oosterbroek & Courtney 1995), a consensus has been reached that the term crane fly in fact represents a paraphyletic or polyphyletic group of independently derived lineages that have convergence on this delicate body form. Of the groups that have had this descriptor attached, the true crane flies of the superfamily Tipuloidea represent the largest and most diverse assemblage of Diptera. The 15,000 described crane fly species account for over 10% of all fly diversity and are placed in 700 genera and subgenera (Oosterbroek 2008).

The chapters included in this dissertation examine the systematics of the true crane flies of the superfamily Tipuloidea. This large and diverse group is taxonomically rich in terms of described species, but suffers from an inadequate classification and lack of available and complete taxonomic tools. Although the knowledge of species identity is broad and not limited to any particular region, the effect of inadequate taxonomic tools is largely felt in areas outside of the Nearctic and Western Palearctic where they are limited or often nonexistent. As a result, the biogeographic, phylogenetic, and ecological knowledge is
lacking, especially in those groups and regions where basic taxonomy has been insufficiently studied.

Some basic biological information can be learned from the few studies on widespread taxa in North America and Europe. The developmental histories of the majority of crane flies are quite similar, with most of the lifecycle spent in the larval stage. Feeding takes place in the larval stage where a variety of feeding types occur, including predation, detritivory, herbivory, and omnivory (Pritchard 1983). Adult feeding is uncommon and rare. While most of the life span is spent in the larval life stage, this is where the least is known. The larval preferences of crane flies are generally thought to be either aquatic, semi-aquatic, or terrestrial (Young & Gelhaus 2000), however the great majority of species occupy habitats that are neither aquatic nor terrestrial but are areas that are either an interface between the two, or occupy both areas in different times of immature development. Examples of intermediate aquatic / terrestrial habitats include algae growing in splash zones, saturated dead wood in aquatic areas, partially saturated soils, and partially aquatic mosses. Species that occupy by terrestrial and aquatic habitats will occupy aquatic habitats in the larval stage but move to terrestrial areas to pupate. While these examples illustrate the diversity of habitats utilized by crane fly larvae, our knowledge of larval behavior and habitat preference is still in its infancy, with life stage associations made for less than 4% of the world species and 16% of the genera and subgenera.

The crane fly adult, more specifically restricted to the adult male, is in almost every case the life stage in which the knowledge of species identity is maintained. The adult lifespan is short, ranging from about a day to not more than a week. Feeding is rare in adult flies and generally restricted to the intake of water, however a few genera are adapted for
nectar feeding (e.g., *Elephantomyia* Osten Sacken, *Helius* Lepeletier & Serville, *Toxorhina* Loew, and *Geranomyia* Haliday) and may be important in pollination (e.g., *Toxorhina*, Singer 2001). Additional attributes of adult behavior are poorly studied.

The goal of this dissertation is to incorporate new technologies and resources that can be utilized by modern taxonomists around the world to examine the systematics of the true crane flies of the superfamily Tipuloidea. Several approaches of systematics utilized here are novel procedures for the Tipuloidea. These approaches include Bayesian analysis for the estimation of phylogeny (Chapter 2), species delineation by ordination techniques (Chapter 5), distribution projections using ecological niche modeling (Chapter 5), and species richness estimation and community assemblage analysis (Chapter 4).

1.1 Dissertation Organization

This dissertation is organized into six chapters. Chapter one is an overview that outlines the components of my research and the motivation behind the formulation of this research program. Chapter two is a manuscript detailing research conducted in collaboration with Matthew A. Bertone (North Carolina State University), which involves a phylogenetic analysis of the Tipuloidea based on morphological and molecular datasets. The collaborative effort between Bertone and Petersen involved a joint effort in both: 1) gene choice and 2) the extraction, amplification, and processing of sequence data used in the molecular dataset. I was independently responsible for 1) the selection of taxa, 2) the formation of the morphological dataset, 3) the independent analysis of these datasets and 4) the interpretation of the results. This chapter is formatted for submission to *Systematic Entomology*. Chapter three details work that expands the results of Chapter two and defines the classification the subfamily Limoniinae. The genera and subgenera diagnosed in this chapter in order to
produce the diagnostic key utilized in Chapter four. A revised classification of the Limoniinae is provided. Chapter four examines the observed and predicted faunal diversity of Limoniinae crane flies in north and central Thailand, and investigates their geographic distribution across this region. This chapter is a manuscript formatted for submission to Biodiversity and Conservation. Chapter five provides a finer scale taxonomic investigation through a revision of the genus Lipsothrix. The taxonomic validity of the genus and inclusive species are examined in order to provide taxonomic resolution, detailed natural history information, and a phylogenetic hypothesis of the group. This chapter is prepared and formatted as a manuscript for submission to Zootaxa. The sixth and final chapter provides general conclusions of this research.
1.2 References


CHAPTER 2. A COMBINED MORPHOLOGICAL AND MOLECULAR PHYLOGENETIC ANALYSIS OF THE TRUE CRANE FLIES (DIPTERA; TIPULOIDEA)

Matthew J. Petersen

(in preparation for submission to SYSTEMATIC ENTOMOLOGY)

2.1 Abstract

The results of the first quantitative analysis of the true crane flies (Tipuloidea) based on combined adult and immature morphological characters and DNA sequence data from the 28S ribosomal gene are presented. Forty-five species from 38 genera were chosen to represent the four recognized families (Cylindrotomidae, Limoniidae, Pediciidae, Tipulidae) and five species represented two Lower Diptera (Trichoceridae, Ptychopteridae) and one Mecopteran (Nannochoristidae) outgroups. Parsimony and Bayesian analyses using individual morphological and molecular datasets resulted in unresolved topologies. Greater resolution and tree support was obtained when both datasets were combined in both total evidence parsimony and Bayesian analyses than when analyzed separately. The Pediciidae are recovered as the sister group to the remaining Tipuloidea, while Limoniidae is paraphyletic to a Tipulidae + Cylindrotomidae clade. The recovered phylogenetic hypothesis is not consistent with the current subfamily classification of the “Limoniiidae”, as all three subfamilies recovered as para- or polyphyletic groups. A revised classification is given for the true crane flies based on the results of these analyses.

Key Words: Tipuloidea, Limoniidae, Tipulidae, Cylindrotomidae, Pediciidae, phylogeny, morphology, 28S rDNA
2.2 Introduction

Studies of the morphological attributes of organisms have provided the initial framework for how we view and delineate the many diverse components of the biological world and have helped to formulate our early views on how life has evolved over time. Just as the utilization of more powerful scanning electron microscopes and cytological approaches have increased the resolution to which morphological attributes can be examined, the advent of modern molecular techniques (Curtis & Cregg, 1984; Hillis, 1987; Rogers & Bendick, 1985) has allowed for new and independent characters to compare and often reevaluate long standing hypotheses. The role of molecular data in phylogenetic investigations continues to increase, however morphological characters are still used across many taxonomic groups (see Wortley & Scotland, 2006).

Subsequent to the expanded use of molecular tools, the role of morphological information in phylogenetic reconstructions has been strongly debated. Some have advocated the sole use of molecular data and the cessation of morphological character usage due to the limited number of highly subjective characters that can be drawn from morphology (Bateman, 1992), the supposed high level of homoplasy in morphological data (Hawkins, 2000; Scotland et al., 2003), and the difficulties in coding morphological characters and assessing homology (Pimental & Riggins, 1987; Smith, 1994; Wagner, 2001). Advocates of including morphological data in unison with molecular data point to the utility of including data that draws information from many different unaligned genes (Doyle, 1992; Hillis & Wiens, 2000), thereby drawing characters from across the genome and drawing information from multiple genes. In summarizing the effects of combined analysis from 1986 to 2003, both Baker et al. (1998) and Wortley and Scotland (2006) reached the same conclusion and
showed that when morphological and molecular data are combined, the resolution of
topologies, in number of resolved clades, significantly increases over that of analyses based
on independent datasets. While the utility of morphological data in combined analysis is
strongly supported, increased studies examining the synergistic effects of data combination
and the individual contributions of these data partitions are still needed.

Here we examine the phylogenetic relationships of the true crane flies (Diptera:
Tipuloidea) through a combined molecular (28S rDNA) and morphological (adult, pupae,
larvae) investigation. The taxonomic structure of this group is based solely on morphological
attributes, with the classification of the group based largely on qualitative assessments of
phylogeny. Only two cladistic analyses have explicitly coded morphological characters in
order to reconstruct phylogenetic relationships (Oosterbroek & Theowald, 1991; Stary,
1992). These studies were, however, both based on a single insect life stage and were
argumentative in construct and did not use quantitative analytical procedures. Through this
current investigation we aim to examine the phylogenetic relationships of the crane flies and
explore the phylogenetic signals of separate and combined morphological and molecular
analyses.

Dating to their original description, the true crane flies have had a history of
presenting a difficult, or at best muddled classification system. The systematic arrangement
was summarized by Hennig (1973) as “entirely unsatisfactory”. While widely believed to
represent a monophyletic group based on a set of both larval and adult characters (Hennig,
1973; Wood & Borkent, 1989; Oosterbroek & Theowald, 1991; Stary, 1992), systematic
research of the group has largely concerned species descriptions. Research on the
phylogenetic relationships and classification of the group has received considerably less
attention. Early works of Alexander (1919, 1927) and Savchenko (1966, 1979, 1983) are responsible for framing our understanding of the group, but were qualitative and provided classifications based on plesiomorphic or simply unstated criteria. The classification of the Tipuloidea may best be described as utilitarian, with divisions of the Linnaean taxonomic structure applied more toward specimen identification than with separating the diversity of the groups representing distinct evolutionary lineages.

Three alternative higher-level classifications are concurrently applied to the group, with usage alternatively divided between the Tipulidae, the Tipulomorpha, or the Tipuloidea. This resulting disagreement recognizes two systems that agree in four divisions that are divided into the: Tipuli-dae/nae, Limonii-dae/nae, Cylindrotomi-dae/nae, and Pedicii-dae/nae placed under Tipulidae (-nae ending) or Tipuloidea (-dae ending). The third classification, Tipulomorpha, is generally used to include the Trichoceridae with the Tipuloidea as a monophyletic group in higher classifications. The historical arguments concerning this debate were covered by Byers (1992). Taxonomists prior to 1900 treated the crane flies as the single family Tipulidae. This trend was continued in the United States after 1900 in large part due to the extensive influence of C.P. Alexander, and in England due to the influence of F.W. Edwards. The alternative position of a three-family concept, recognizing Tipulidae, Limoniidae, and Cylindrotomidae (Tipuloidea) apparently originated in Central Europe and was strengthened as a classification concept by P. Lackschewitz and E.N. Savchenko. A modification of the three-family concept to a four-family concept based on the elevation of Pediciidae was later made by Stary (1992). Subsequent usage of these alternative systems has been largely attributed to regional delineation. The range of influence of Alexander and Edwards was extensive, including the majority of true crane fly research conducted in Great
Britain, North America, Central America, South America, Asia, Africa, and Australia.
Within these areas the single-family concept was adopted. The influence of Alexander and
Edwards in Europe was much less, and here the three-family concept advocated in the
extensive publications of Lackschewitz and Savchenko was adopted. The superfamily
system of the Tipuloidea is employed here for consistency of terminology with other
phylogenetic studies (Oosterbroek & Theowald 1991; Stary 1992).

The taxonomic structure within the Tipuloidea has changed little since the inception
of the group, being largely divided between the Tipulidae (long-palped crane flies) and
Limoniidae (short-palped crane flies). The elevation of two former subfamilies by Stary
(1992) has resulted in the current four family system of: Tipulidae, Limoniidae, Pediciidae
(erected from Limoniinae), and Cylindrotomidae (erected from Tipulidae). The largest
family Limoniidae is further subdivided into four ill-defined subfamilies. The Limoniinae
are based on 1) the absence of tibial spurs (shared by Chioneinae), 2) two medial wing veins
to the wing margin (shared by Chioneinae), and 3) and three radial veins to the wing margin.
The Limnophilinae are defined by: 1) the presence of tibial spurs, 2) three medial wing veins
to the wing margin, and 3) four radial veins to the wing margin, all of which are shared by
Tipulidae and Pediciidae. The Chioneinae are based largely on 1) the absence of tibial spurs
(shared by Limoniinae), 2) two medial wing veins to the wing margin (shared by
Limoniinae), and 3) and three radial veins to the wing margin.

Recent phylogenetic studies have shown that neither classification system may
accurately capture the evolutionary relationships of the superfamily (Oosterbroek and
Theowald, 1991). The purpose of this work is to test the capacity of the current classification
system to adequately represent the evolutionary history of the group. While previous studies
have proposed phylogenetic hypotheses for the Tipuloidea, all utilized qualitative methods and were either based on the information of a single life stage or did not provide sufficient explanation of the characters used. The analysis presented here is the first analysis of Tipuloidea based on a coded matrix of characters derived from all live life-stages (adult, pupae, larvae), and the first analysis within the Tipuloidea to utilize DNA sequence information. The phylogenetic hypothesis produced from this work helps to provide insight into the evolution of the group and indicate which morphological attributes represent the plesiomorphic or derived conditions within the Tipuloidea, which may provide benefit in placing this diverse group within the greater Diptera phylogeny.

2.3 Material and Methods

2.3.1 Taxon sampling

Because of the weak taxonomic structure and lack of group defining characters for each of the subfamiliar units within the Limoniinae, taxon choice emphasized genera that showed both “high” and “low” taxonomic stability. Taxonomic stability was defined as the tendency of a genus to be moved between subfamiliar classifications, with “low” stability genera having weak taxonomic certainty and having been moved between subgenera units and “high” stability genera showing taxonomic certainty and having not been moved between subfamilies since the time of generic description. An exemplar species represented each genus in the molecular analysis (Table 1) except in the case of large cosmopolitan genera with multiple subgenera (*Limnophila* Macquart, *Erioptera* Meigen, *Tipula* Linnaeus) that were represented by multiple terminal units representing multiple subgenera or species. In order to ensure character scoring represented each genus / subgenus and was not restricted to being descriptive of the exemplar species, scoring of morphological terminal units was based
on both the exemplar molecular taxa as well as comparisons with multiple other species from each genus.

Genera served as the terminal taxonomic units to represent the 4 recognized Tipuloidea families (Cylindrotomidae, Limoniidae, Pediciidae, Tipulidae). All four families of Tipuloidea as well as all subfamilies of Limoniidae were represented in the analysis. Representation for each taxonomic level was chosen such that the number of terminal taxa corresponded to the proportion of diversity accounted for by each taxonomic level within the Tipuloidea.

2.3.2 Outgroup choice

The placement of the Tipuloidea within the phylogeny of the Diptera remains unresolved. Phylogenetic analyses of Rohdendorf (1974), Hennig (1973), Krzeminski (1992), and Oosterbroek and Courtney (1995) place the Trichoceridae as the sister group to the Tipuloidea, but are often based on weak or unresolved characters. Wood and Borkent (1989) considered the Tipuloidea (Tipulidae sensu lato) as the sister group to the Diptera, without a close relationship to the Trichoceridae, which they placed within the Psychodomorpha. Outgroup choice plays an important role in interpreting which state represents the plesiomorphic or derived state of a character and will affect the topology of the ingroup taxa (Nixon & Charpenter, 1994; Swofford et al., 1996; Sanderson & Shaffer, 2002). Outgroups should therefore represent the nearest ancestor to the ingroup in order to properly characterize ingroup character polarity. To account for the uncertainty of evolutionary placement of the Tipuloidea, we chose two sets of outgroups to represent both the most probable sister group (Trichocera: Trichoceridae) as well as additional Lower Diptera (Bittacomorpha, Ptychoptera: Ptychopteridae) and Mecoptera (Microchorista:...
Nannochoristidae). Each analysis was rooted separately with each group to observe any potential difference outgroup choice would have on the topology of the ingroup taxa.

2.3.3 DNA isolation, amplification, and sequencing

Specimens used for DNA extraction were collected either by hand collections (netting) and placed live into 95% EtOH or through Malaise trapping into 95% EtOH. Genomic DNA was extracted from single or multiple whole flies using Qiagen’s DNeasy Tissue kits using standard manufacturer protocols and stored at -80°C. Vouchers of specimens from which genomic DNA were extracted are deposited in the North Carolina State University insect collection. The 28s ribosomal DNA gene (28S) has been previously utilized in phylogenetic analyses of both insect and non-insect groups and offers conserved and variable units that are useful in recovering ancient and more recent divergences. Three sections of the 28S were amplified and sequenced using primers from Hamby et al. (1988) that were modified to the published sequence of Drosophila melanogaster Meigen (Hancock et al., 1988; Yang et al., 2000) for 28S. Primer sequences used to amplify the three sections of 28S are listed in Table 2. Three separate PCR fragments of 28S rDNA were generated: rc28Ab to 28C, rc28B to 28E, and rc28D to 28K. Protocols for gene amplification involved a reaction cycle with: 95°C (1 min); 30 cycles of 95°C (1 min), 45°C (1 min), 72°C (2 min); 72°C (7 min). Amplification products were visualized on standard agrose gels in TAE buffer before being cut and purified using a QIAquick Gel Extraction Kits.

Sequence reactions were carried out using PE applied Biosystems Big Dye Terminator sequencing kits (Perkin-Elmer Applied Biosystems, Forest City, CA) with the primers used in gene amplification (Table 2). Sequence data were obtained by analyzing samples on a ABI Prism™ 377 automated DNA sequencer (PE Applied Biosystems).
Sequencing electropherograms were edited and contigs assembled and proofed using Sequencher\textsuperscript{\textsc{tm}} 4.1 (GenCodes Corp., Michigan, USA).

2.3.4 Alignment

Amplified sequences were aligned using both automated and manual alignments techniques. Initial alignment was performed using ClustalX (Thompson et al., 1997) under default program parameters. Large unambiguous sequence regions remained after initial sequence alignment. To account for these regions the sequences were then fitted to the secondary structure model of Hancock et al. (1998) for the 28S rDNA gene of \textit{Drosophila melanogaster}. Conserved regions were matched to the conserved stem regions of the model while unambiguous regions corresponded to loop expansion regions. Loop sections of unambiguous sequence data were eliminated from further analysis.

2.3.5 Morphological characters

Eighty-five characters derived from all developmental life stages (larvae, pupae, adult) (Table 3; Appendix) were used in the phylogenetic analysis. Characters were chosen to sample the spectrum of morphological diversity of each life stage and to not focus on any particular aspect of adult or immature morphology. Because the associations between the adult and larval life stages for the great majority of crane fly species are not established, scoring of immature characters was based on available immature material, scored from closely related taxa from the same genus, or scored from the literature as provided by Oosterbroek and Theowald (1991). The majority of characters used in this analysis are novel, but many represent characters long used in crane fly classification as well as those used in other analyses (see Appendix). Characters were scored as discrete additive (unordered) and as either binary or multi-state.
2.3.6 Phylogenetic analyses and tree support

Phylogenetic analyses were conducted under both maximum parsimony criteria using PAUP* version 4.0b10 (Swofford, 2002) and Bayesian estimation using Mr. Bayes version 3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Unweighted parsimony analyses were conducted on morphological and molecular datasets in the following combinations in accordance with the recommendations of Wiens (1998) for analyzing different types of data: 1) parsimony analysis based on the morphological dataset, 2) parsimony analysis based on the 28S rDNA dataset, 3) total evidence parsimony analysis on a combined morphological (adult and immature) and molecular (28S) dataset, 4) Bayesian analysis using the morphological dataset, 5) Bayesian analysis using the 28S rDNA dataset, and 6) total evidence Bayesian analysis using the combined molecular and morphological analysis. For each parsimony analysis a heuristic search was performed with 1000 random addition sequences and repeated tree bisection-reconnection (TBR) branch swapping. In cases where more than one most parsimonious tree was recovered during the search, a strict consensus tree of all equally most parsimonious trees was calculated. Relative branch support was determined by bootstrapping based on 500 independent iterations as implemented in PAUP*, and with Bremer support (BS) indices (Bremer, 1994) for individual analysis, and partitioned Bremer support (PBS) for the combined analysis as calculated using TreeRot v3 (Sorenson, 1999; Sorenson & Franzosa, 2007). Partitioned Bremer support allows for the contributions of individual datasets to the overall BS of each node to be measured, thereby identifying areas of incongruence between the different data partitions (Baker & DeSalle, 1997; Lambkin et al., 2002). The Bayesian search was conducted on a partitioned morphological and molecular dataset. Model selection for use in the Bayesian
analysis was determined using Modeltest 3.07 (Posada & Crandall, 1998) and implemented using PAUP*. The GTR+I+G model was found to be most appropriate for the 28S dataset. The morphological dataset was run under the Mk model of Lewis (2001). Two simultaneous iterations of the Bayesian analysis were run using a Monte Carlo Markov Chain (MCMC) method with four simultaneous MCMC chains ran for 1,000,000 generations. Trees were sampled every 100 generations. The first 25% of trees saved, or those recorded prior to the MCMC chains attaining stationarity, were discarded during the burn-in phase. Posterior probabilities representing a measure of clade credibility were generated from the majority-rule tree composed from the remaining saved trees.

### 2.4 Results

#### 2.4.1 Parsimony analysis of morphological data

The parsimony analysis of the 50 taxa with characters scored for all life stages resulted in 146 equally most parsimonious trees with a score of 419 (consistency index [CI]=0.5561, retention index [RI]=0.7718, rescaled consistency index [RCI]=0.4292) (Figure 1). Characters were highly informative with 84 of the 85 scored characters being parsimony informative. Overall support for the preferred topology was low, but did show strong support for a monophyletic Tipuloidea. The Cylindrotomidae and Tipulidae were strongly supported as monophyletic groups with a strong sister group relationship. The Pediciidae and Limoniidae were recovered as paraphyletic groups. Pediciidae was not recovered as a monophyletic group due to a lack of synapomorphy to unite the three species used in the analysis. Limoniinae was seen to be paraphyletic in relation to Tipulidae+Cylindrotomidae and Pediciidae. The Limoniidae subfamilies (Limoniinae, Chioneinae, and Limnophilinae) were not recovered as monophyletic groups. The genera *Chionea* Dalman and *Cladura*
Osten Sacken were recovered as the sister group to all remaining taxa, while the Limnophilinae and Limoniinae were recovered in an unresolved clade with the Tipulidae+Cylindrotomidae. The placements of Limoniidae taxa defined by low taxonomic stability (Atarba Osten Sacken, Dactylolabis Osten Sacken, Dicranoptycha Osten Sacken, Helius Lepeletier and Serville, Elephantomyia Osten Sacken) were not resolved in this analysis.

2.4.2 Parsimony analysis of 28S rDNA sequence data

The parsimony analysis of the 50 taxa sequenced for 28S resulted in 30 equally most parsimonious trees with a score of 3816 (consistency index [CI]=0.4162, retention index [RI]=0.6116, rescaled consistency index [RCI]=0.3045) (Figure 2). Of the 3543 included characters, 2265 were constant (64%) and 809 were parsimony informative (23%). Relationships within the Tipulidae were shown to be weakly supported as in the morphological analysis. As with morphological data, the analysis of 28S rDNA recovered a monophyletic Tipuloidea. Within the Tipuloidea, a monophyletic Pediciidae was seen to be the sister group to all other ingroup taxa. A monophyletic Tipulidae and Cylindrotomidae were recovered and seen to be sister groups. The genus Brachypremna Osten Sacken is strongly supported as a primitive element in the Tipulidae phylogeny. Nodal support for the family Limoniidae was low with all subfamilies appearing as either paraphyletic or polyphyletic groups. Two strongly supported clades of Limnophilinae (Limnophila (A.) Alexander + Euphylidorea Alexander + Prolimnophila Alexander + Prionolabis Osten Sacken, Hexatoma Latreille + Limnophila + Pilaria Sintenis) were recovered. Each Limnophilinae clade was recovered with a weak sister group relationship to separate clades of Chioneinae taxa. The subfamily Chioneinae was polyphyletic with two major clades.
recovered. The relationships of Limoniinae were similar to those recovered with the morphological dataset. A weak *Lipsothrix* Loew + *Antocha* Osten Sacken clade is recovered as the sister group to a strongly recovered clade of Limoniinae (*Dicranomyia* Stephens, *Metalimnobia* Matsumura, *Geranomyia* Haliday, *Limonia* Meigen, *Libnotes* Edwards). The placements of Limoniidae taxa defined by low taxonomic stability (*Atarba*, *Dactylolabis*, *Dicranoptycha*, *Helius*, *Elephantomyia*) were not resolved in this analysis.

### 2.4.3 Parsimony analysis of combined dataset

The parsimony analysis of the combined morphological and 28S datasets for 50 taxa resulted in 9 equally most parsimonious trees with a score of 4229 (consistency index [CI]=0.4895, retention index [RI]=0.6265, rescaled consistency index [RCI]=0.3066) (Figure 3). Addition of the morphological dataset increased the CI, RI, and RCI scores over those of the 28S data alone but was lower than that of the morphological dataset alone. This analysis was based on 3629 characters, of which 2265 were constant (62%) and 893 were parsimony informative (25%). Molecular and morphological characters accounted for 91% and 9% of parsimony informative characters, respectively. The addition of morphology to the molecular data increased nodal support for most basal clades, increasing resolution over the topologies recovered in the separate analysis. The Pediciidae were recovered as the sister group to the remaining Tipuloidea. The monophyletic Tipulidae and Cylindrotomidae relationship seen in both separate analyses was recovered in the combined analysis. *Dactylolabis* was recovered as a sister group to the Tipulidae+Cylindrotomidae. The placement of the other Limoniidae taxa defined by low taxonomic stability (*Atarba*, *Dicranoptycha*) was not resolved in this analysis. The *Lipsothrix* as the sister group to the supported Limoniinae clade relationship present in individual analysis was recovered. The
combination of datasets resulted in the placement of the *Elephantomyia* + *Helius* clade as the sister group to the *Lipsothrix* + Limoniinae clade, a relationship not recovered with either independent analysis. The Chioneinae and Limnophilinae were recovered as polyphyletic groups.

### 2.4.4 Bayesian analysis

Bayesian analyses of individual morphological (Figure 4) and molecular (Figure 5) datasets resulted in tree topologies that were similar to those of the individual parsimony analyses. Relative node support, as measured by the posterior probability, was generally low in the morphological analysis (less than 0.95) and higher in the molecular analysis (greater than or equal to 0.95). Nodes with high levels of bootstrap support in the parsimony analysis were similarly well supported in the Bayesian analysis.

As with the parsimony analysis, Bayesian analysis based on combined morphology and molecular data (Figure 7) provided a different topology than those recovered by either of the two independent analyses. These differences, as in the combined parsimony analysis, involve incongruence between data types in both resolving the interfamilial relationships among the Limoniidae taxa and the placement of taxa with low taxonomic resolution. In the combined analysis, the Pediciidae was the sister group to the remaining Tipuloidea. All exemplars of Pediciidae showed a high degree of molecular differentiation as indicated by their long branches (Figure 6). The Tipulidae + Cylindrotomidae clade was strongly supported in this analysis. The Chioneinae and Limnophilinae were recovered as polyphyletic groups. Both the Limnophilinae, without the genus *Epiphragma* Osten Sacken, and Limoniinae, without the genus *Dactylolabis*, were recovered as monophyletic groups. The low taxonomic resolution genera *Atarba* and *Dicranoptycha* were placed at the base of
the Limoniinae while *Dactylolabis* was the sister taxon to the Tipulidae + Cylindrotomidae clade.

### 2.4.5 Influence of separate and combined datasets

Under both parsimony and Bayesian criteria, morphological and molecular datasets recovered similar clades and indicated high congruence between datasets at similar positions. Both data types supported monophyletic a Tipuloidea and supported the clades corresponding to the Tipulidae, Cylindrotomidae, and the Limoniidae clades Limoniinae, Chioneinae (partial), and Limnophilinae (partial). Partitioned Bremer Support indicated the separate data types (28S / adult morphology/ immature morphology) were largely congruent across these aspects of the tree topology. Similarly, the least resolved portions of the individual topologies were the same across analyses, indicating high congruence among unresolved areas. Irresolution in tree topology was greatest in the placement of the Tipulidae+Cylindrotomidae clade and among the Limoniidae subfamilies. Partitioned Bremer Support indicated the separate data types (28S / adult morphology/ immature morphology) were largely incongruent across these aspects of the tree topology.

In analyses under the parsimony criteria, the 28S dataset outperformed the morphological dataset in providing higher support for recovered clades, but the morphological data provided higher resolution. The higher support by the molecular dataset is not surprising as it provided nearly 10 times as many characters as did the morphological dataset. The greater number of characters present in the 28S data showed less total consistency and greater homoplasy than the morphological as indicated by the CI, HI, and RCI. When combined in a total evidence analysis, the number of equally most parsimonious trees decreased and the resolution and clade support of the consensus tree increased over that
of individual analyses. This result indicates that while morphology may provide only a small fraction of the total characters used in the analysis (9%), it has the ability to greatly influence the topology of phylogenetic reconstructions.

When analyzed under the Bayesian framework, molecular data outperformed the morphological data both in terms of overall resolution and node support. Both analyses recovered similar well-supported clades, but resolution within the morphological analysis was lower. When combined in a total evidence analysis the recovered topology was different than that of either independent analysis. Support for the morphological and combined topologies were lower than that of the molecular analysis, with PBS indicating conflict in data partitions among the arrangement of well-supported clades recovered in each separate analysis.

2.5 Discussion

Considerable debate surrounds the incorporation of morphology into molecular datasets in computer-based analytical phylogenetic reconstructions (Baker & Gatesy, 2002; Hillis & Wiens, 2000; Scotland et al., 2003; Wiens, 2003; Wortley & Scotland, 2006a, 2006b). To investigate the phylogenetic signal provided by our two independent datasets, we analyzed the morphological and 28s rDNA molecular datasets both separately and in combined total evidence analyses. By observing the individual and combined effects of character data on the phylogenetic reconstructions we were able to observe areas of congruence and incongruence between datasets and to detect how phylogenetic signals from each data source interact.

Under the parsimony search criterion our results were consistent with those recorded by Wortley and Scotland (2006) and Baker et al. (1998) in showing that the addition of
morphology to molecular data in a total evidence analysis strongly influences the final topology. This was true even when the percentage of morphological characters contributing to the analysis was very small. Our morphological dataset included only a fraction of the total combined dataset (9%) but contained a large proportion of characters that had low homoplasy and high consistency. When combined in a total evidence analysis, the recovered topology displayed both higher resolution and clade support for a preferred topology that was different from either tree recovered in independent analysis. We did not find such a result when the datasets were analyzed under Bayesian criteria. In the Bayesian analyses the highest resolution and support was recovered for the independent molecular dataset, and both resolution and support decreased with the addition of morphological data.

The synergistic effects of combining the two data types indicate that while both data sets are providing weak phylogenetic signal at similar aspect of the phylogeny, their combination provides an answer that is not evident in either independent dataset and is recovered regardless of the search criterion. The inability of these combined datasets to recover a fully resolved topology does not seem to be the result of shortcomings of the data due to conflicting phylogenetic signals, as we have shown the two data types were largely congruent. Instead we believe that sampling of additional taxa is needed to fully resolve the topology. As evidenced by Figure 6, the sampling of crane flies in this analysis show both recent radiations indicated by short branches (Limoniinae, Tipulidae) and highly divergent independent lineages indicated by long branches (*Dicranoptrycha, Epiphragma*). While there has been considerable debate surrounding the addition of more data or more taxa to provide better resolution in phylogenetic investigations, it is well documented that long branches in phylogeny reconstructions often contribute to poor resolution (Graybeal, 1998; Hillis, 1998;
Pollock et al., 2002; Hillis et al., 2003; Rokas & Carroll, 2005; Bergsten, 2005). We anticipate that an expanded taxon sampling with characters taken from all life stages will help bisect these long branches and help to provide greater resolution for the Tipuloidea phylogeny.

While our results at first appear at odds with some of the traditional classification of the Tipuloidea, this apparent incongruence is largely an artifact of what we consider a misapplication of Linnaean rank across much of the classification. The terminology used in classifying taxonomic groups should impart information about that group and be based on a monophyletic lineage (i.e. natural group), allowing the results of phylogenetic analyses to inform the classification process (*sensu* Kuntner and Agnarsson 2006), but not dictate it. Until the analysis of Oosterbroek and Theowald (1991), the monophyly of neither the crane flies families nor subfamilies had been tested in a cladistic manner. Our results are in agreement with those originally shown but not discussed in Oosterbroek and Theowald (1991) in illustrating the limited utility of the current subfamiliar classification of the Limoniidae to represent the evolutionary relationships of the Tipuloidea.

Based on our analysis, the following classification is proposed in order to provide a system that more adequately conveys the evolutionary history of the Tipuloidea (Figure 8; Table 4). These changes largely maintain the traditional four-family classification, but separate the subfamilies of “Limoniidae” to a greater degree than has been previously proposed.

### 2.5.1 Pediciidae

The Pediciidae are recovered as the sister group to the remaining crane flies and are supported by both the molecular and morphological datasets. Based on morphology alone
our results are similar to those of Oosterbroek and Theowald (1991) who placed the Pediciidae in a basal polytomy along with Chioneinae + Limnophilinae and Limoniinae + Tipulidae + Cylindrotomidae clades. The placement of the Pediciidae as the sister group to the remaining Tipuloidea within our analysis is based largely on the presence of plesiomorphic characters (chars 10; 15; 20; 24; 28; Appendix 1) shared with outgroup taxa, but is highly congruent with the 28S dataset in the placement of the Pediciidae.

2.5.2 Tipulidae

The Tipulidae are recovered as a strongly monophyletic group supported by both morphological and molecular datasets. The classification of the group as a distinct family unit is supported by our analysis and is seen to be a sister group to the Cylindrotomidae. Interfamilial relationships within the Tipulidae were poorly resolved and showed high incongruence between data types. The purpose of this investigation was not to recover the intrafamilial relationships of this group and it is apparent that our character sampling did not adequately address this issue.

The radiation of the Tipulidae is impressive, accounting for nearly 30% (4254 spp.) of all crane fly diversity. The molecular analysis reveals very short branches linking the included morphologically diverse taxa within the group (Fig. 6), indicating many taxa arising in a relatively rapid radiation. Future molecular analyses of this group will likely need to examine more quickly evolving genes than those utilized here in order to more adequately capture this recent radiation.

2.5.3 Cylindrotomidae

The Cylindrotomidae have alternatively been placed as a tribe of the Limoniinae, a subfamily of the Tipulidae, or as an independent family. The molecular and morphological
data in our analysis confirms the Cylindrotomidae are the sister group to the Tipulidae. This arrangement is in agreement with that of Oosterbroek and Theowald (1991) based on immature characters and that of Stary (1992) based on adult morphological characters.

2.5.4 “Limoniidae”

The definition of Limoniidae corresponds largely to the early division of the short-palped (Limoniidae) and long-palped (Tipulidae) crane flies, dividing the crane flies based on the length of the terminal maxillary palptomere. Stary (1992) proposed the monophyly of the Limoniidae based on the elongation and flattening of the antepronotum and the development of the subspiracular sclerites. We found both of these characters to be homoplasious within our taxon sampling. Both characters were removed from our analysis because they were not easily partitioned into distinct character states. Our results support those of Oosterbroek and Theowald (1991) in that the Limoniidae represents a paraphyletic group in relation to the Cylindrotomidae + Tipulidae clade. The subfamily divisions of Limoniidae were considerably less resolved. A topology consistent with the three-subfamily classification of the Limoniidae (Chioneinae, Limnophilinae, Limoniinae) (sensu Alexander & Byers, 1981; Stary, 1992; Oosterbroek, 2008) was not recovered in any of our phylogenetic analyses and does not appear to adequately represent the evolutionary relationships of the Limoniinae.

We advocate the maintenance of the family recognition of the “Limoniidae”, while recognizing the paraphyletic nature of the group. Based on relationships recovered in these analyses, we propose the following modifications to the classification of the Limoniidae.
These changes are offered in order to maintain monophyletic subfamiliar groups within the “Limoniinae”.

2.5.4.1 Eriopterinae

The Eriopterinae presented here removes the genera Chionea and Cladura and places them in the subfamily Chioneinae (see below). This concept of the Eriopterinae was well supported in this investigation based on morphological and molecular characters. A monophyletic Eriopterinae was recovered in all analyses; however, morphological and molecular data provided contrasting placements within the greater Tipuloidea phylogeny. The Eriopterinae consistently appeared as a primitive lineage and maintained a close relationship to the Limnophilinae, a position that supports the larval morphological phylogeny of Oosterbroek and Theowald (1991). analyses based on molecular data place the Eriopterinae as a sister group to part of the paraphyletic Limnophilinae, indicating that this subfamily may have originated either from within some part of the Limnophilinae or that the Limnophilinae originated from within the Eriopterinae.

2.5.4.2 Limnophilinae

The taxa corresponding to the traditional subfamily Limnophilinae (sensu Alexander & Byers, 1981; Stary, 1992; Oosterbroek, 2008) are not recovered as a monophyletic group, and are instead recovered in a similar fashion to that presented by Oosterbroek and Theowald (1991). We consistently recovered three clades of Limnophilinae taxa, although only one group (Epiphragminae) provided clear morphological characters for their division. The Limnophilinae, as presented by Oosterbroek and Theowald (1991), show a reduction in the larval head capsule (partially seen in Paradelphomyia Alexander and Pseudolimnophila Alexander), with the mandibles become increasingly sickle-shaped in a likely modification
for a predatory lifestyle. This reduction is not seen in the genera *Epiphragma* or *Austrolimnophila* Alexander. Both of these taxa closely adhere to the concept of Limnophilinae based on adult characters (three branches of *Rs* reaching the wing margin, vein *Sc₂* (*sc-r*) situated distal to the level of the origin of *Rs*, eyes bare, tibial spurs present; *sensu* Alexander & Byers, 1981; Stary, 1992). To account for this arrangement it is recommended that the subfamily Limnophilinae be interpreted in a more restrictive sense, with the removal of Epiphragminae (*see below*), based on support from both morphological and molecular data.

The larval states for a great majority of Limnophilinae taxa are still unassociated with the adult, but the characters from this life stage were seen to be more informative than the plesiomorphic adult characters. The recovery of a polyphyletic traditional Limnophilinae (*sensu* Alexander & Byers, 1981; Stary, 1992; Oosterbroek, 2008) indicates that associating the adult and larval life stages for a greater number of Limnophilinae taxa is clearly needed. In particular, more data on characters associated with the larval head capsule will be important in further resolving the classification and phylogeny of this group.

### 2.5.4.3 Chioneinae

Strong support for the *Chionea* + *Cladura* clade is seen in both larval morphology and molecular characters. This clade corresponds to the Cladurini of Savchenko (1989), which additionally included the genera *Neolimnophila* Alexander and *Crypteria* Bergr. (not included here). This clade is recognized as separate from the Eriopterinae and designated as the subfamily Chioneinae (confirming to the priority of Chioneinae over Cladurini, *see* Stary (1992)). The basal position and abundant plesiomorphic characters indicate that the
Chioneinae may represent either a basal lineage of the “Limoniidae”, or of the Eriopterinae + Limnophilinae clade.

### 2.5.4.4 Limoniinae

The organization of Limoniinae recovered in these analyses is identical to that of Savchenko (1989) and Oosterbroek and Theowald (1991) and was recovered as the most resolved subgenus of “Limoniidae”. The application of the term Limoniinae is restricted somewhat from that used by Alexander and Byers (1981) and Stary (1992). The two commonly recognized tribes, Antochiini and Limoniini, are recovered but with insufficient taxon sampling to test for their monophyly. It is expected that with expanded taxon sampling the arrangement provided by Oosterbroek and Theowald (1991), which depicts a paraphyletic Antochiini and monophyletic Limoniini, is likely to be recovered.

### 2.5.4.5 Elephantomyinae

The Elephantomyinae presented here is identical to that of the Elephantomyiini of Savchenko (1989), but is removed from the Limnophilinae and raised to the subfamily rank. The elevation of this group from tribe to subfamily is to emphasize its distinctness from the former group, and the apparent sister group relationship to the Limoniinae clade. The genus *Toxorhina* Loew (not included in this analysis), which similarly shares the elongation of the rostrum in an adaptation for nectar feeding, may additionally be placed in this subfamily.

### 2.5.4.6 Lipsothrixinae

The genus *Lipsothrix* has alternatively been placed within each of the three traditional Limoniidae subfamilies. The arrangement presented here is in agreement with Stary (1992) in placing the genus *Lipsothrix* as a sister group to the Limoniinae. The genus does not correspond to any of the “Limoniidae” subfamilies as presented in these analyses. We
advocate the placement of *Lipsothrix* within a new subfamily, Lipsothrixinae to account for its distinction from other subfamilies of “Limoniidae”. The genera *Rhabdomastix* Skuse and possibly *Limnophilomyia* Alexander should be placed within this subgenus based on wing venation (four branches of $R$, two branches of $M$) and the composition of the separated elongate interbase of the male hypopygium.

2.5.4.7 Epiphragminae

Both morphological and molecular data support the separation of the genus *Epiphragma* from the remaining taxa of Limnophilinae. *Epiphragma* is typically placed within the Limnophilinae based on plesiomorphic adult characters (three branches of $Rs$ reaching the wing margin, vein $Sc_2$ ($sc-r$) situated distal to the level of the origin of $Rs$, eyes bare, tibial spurs present). The separation of *Epiphragma* from the Limnophilinae was recovered in the analysis of Oosterbroek and Theowald (1991) and was advocated by Savchenko (1989) who placed *Epiphragma* along with *Austrolimnophila* Alexander and *Dactylolabis* Osten Sacken within the Epiphragmini. A relationship between *Epiphragma* and *Dactylolabis* is not recovered in our analysis, and we therefore restrict the Epiphragminae to the genera *Epiphragma* and *Austrolimnophila*.

2.5.4.8 Dactylolabinae

*Dactylolabis* is an anomaly in regards to other genera of the “Limoniidae” and has been placed as either within the Limnophilinae or as a separate monotypic subgenus, Dactylolabinae. The equivocal placement of *Dactylolabis* within the Tipuloidea is not definitively resolved in our analysis. The consensus of both combined analyses places the genus as the sister group to the Tipulidae + Cylindrotomidae clade, but with limited morphological and molecular support. We support the maintenance of a separate
Dactylolabinae due to the unresolved placement of *Dactylolabis* and apparent lack of association with other subfamiliar groups.

### 2.6 Conclusions

The phylogenetic hypothesis of the Tipuloidea presented in these analyses presents better resolution and support for a classification system that describes the evolutionary diversification of the group. Although these analyses did not incorporate all Tipuloidea taxonomic diversity, the framework provided by this research illustrates that the simple explanation of four major crane fly lineages does not adequately describe the evolutionary history of the group. Instead, a more complicated explanation of ancient lineages and recent radiations is observed. The novel application of molecular sequence data to the analysis of the Tipuloidea utilized new evidence that largely agreed with the phylogenetic signal provided by the morphological data. The incorporation of morphological data in the analysis did, however, provided a strong set of evidence and should be incorporated in any future study. The support and evidence provided by this phylogenetic hypothesis serves as the basis for a new classification system, one that will better define this diverse group and provide greater stability to future workers.
Figure 1. **Strict consensus cladogram resulting from a parsimony analysis based on the morphological dataset.** Bootstrap values are given above the branches and Bremer support values are given in parentheses. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 2. **Strict consensus cladogram resulting from a parsimony analysis based on the 28S rDNA molecular dataset.** Bootstrap values are given above the branches and Bremer support values are given in parentheses. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 3. Strict consensus cladogram resulting from a total evidence parsimony analysis based on the combined 28S rDNA molecular and morphological dataset. Bootstrap values are given above the branches and Partitioned Bremer support values (28S, adult morphology, immature morphology) are given in parentheses. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 4. Consensus cladogram resulting from a Bayesian analysis based on the morphological dataset. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 5. Consensus cladogram resulting from a Bayesian analysis based on the 28s rDNA dataset. Relative support for the given cladogram is given as posterior probability. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 6. Consensus phylogram resulting from a Bayesian analysis based on the 28s rDNA dataset.
Figure 7. Strict consensus cladogram resulting from a total evidence Bayesian analysis for the combined morphology and 28S rDNA datasets. Parsimony Bootstrap values and Bremer support values (28S, adult morphology, immature morphology) are given above the branches and below the branches in parentheses, respectively. The classification of the ingroup taxa based on Oosterbroek (2008) is given to the right of the cladogram.
Figure 8. Cladogram presenting consensus of total evidence analyses showing the phylogenetic relationships of the Tipuloidea. A proposed classification of the Tipuloidea is presented based on the phylogenetic relationships uncovered during this work.
Table 1. **Species selected as exemplar taxa.** The species selected to serve as exemplar taxa to represent their genera are presented. Species with associated adult and immature life stages are listed with a Y, N if not associated. The collection information for the exemplar taxa are given.

<table>
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<th>Taxon</th>
<th>Genbank Accession No.</th>
<th>Immature Association</th>
<th>Collection information</th>
</tr>
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<td>Y</td>
<td>USA: North Carolina, 11 May 2005; M Petersen</td>
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</tbody>
</table>

^1 scored from reared larvae; ^2 partial life stage association; ^3 scored for closely related taxon
Table 1 cont’. Species selected as exemplar taxa.

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^1 scored from reared larvae; ^2 partial life stage association; ^3 scored for closely related taxon
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*not investigated in this analysis
2.8 References


2.9 Appendix

Morphological characters and character states used in the morphological analyses.

Characters are presented as scored in the character matrix (Table 3). In cases where characters correspond to those of previous phylogenetic investigations of the Tipuloidea, the number of the corresponding character from that investigation is given (Oosterbroek and Theowald, 1991 [OT]; Stary, 1992 [S]).

1. Ocelli: present (0), absent (1) (S: 3)
2. Arolium: present (0), absent (1) (*questionable character*; see Wood and Borkent 1989))
3. Wing vein A2: present (0), absent (1)
4. Larval head capsule: cephalic (0), hemicephalic (1)
5. Spiracular state: polypneustic (holo-, peri-, or hemipneustic) (0), amphipneustic (1), metapneustic, apneustic (2)

**Adult head**

6. Nasus: absent (0), present (1)
7. Rostrum: smaller than remaining head (0), subequal or greater than remaining head (1)
8. Dorsal vertex: present as raised posterior element (0), present as a raised anterior element (1), absent or vertex flattened (2)
9. Ventral margin between genae: wide and membranous (0), full or partial fusion of genae or as a thin strip genae (1), fused into a single sclerite (2)
10. Stipes: separate (0), fused (1) (S: 10)
11. Adult tentorium: 0) complete rods between pits (0), rods absent or incomplete between pits (1)
12. Terminal palpomere: subequal about 2.5 greater than penultimate (0), greater than 2.5X penultimate palpomere (1) (S: A)

13. Ratio of scape to pedicel: subequal (0), scape greater than 1.5X the length of pedicel (1)

14. Number of flagellomeres: 0) sixteen or more (0), fifteen (1), fourteen (2), thirteen (3), twelve (4), eleven (5), ten (6), nine (7), eight (8), seven (9), six (10)

15. Setulae between ommatidia: present (0), absent (1)

Adult thorax

16. Meron 1: absent (0), present (1)

17. Meron 2: triangular sclerite (0), medially reduced into two lobes (1), inapplicable (a-c)

18. Meron 3: width greater than height (“potbelly”) (0), width subequal to height (1), height greater than width (2), inapplicable (a-c)

19. Metasternal furca: dorsal projections as in mesosternal furca, with cup-like apex (0), dorsal projections as in mesosternal furca, apex blunt (1), without dorsal projection (2)

20. Meso- and metafurca connection: absent (0), present (1)

21. medial fusion of metasternal furca: 0) separate (0), fused (1)

22. Trochanter spike: 0) absent (0), present (1), inapplicable (2)

23. Sclerotized ring of the trochanters (femur and trochanter connection): inner ring connection absent (0), inner ring present without medial division (1), inner ring present with medial break (2)

24. Tibial spurs: present (0), absent (1) (S: 9)

Adult wing

25. Number of branches of Rs to wing margin: four or more (0), three (1), two (2), inapplicable (3)
26. Wing vein $R_1$: vein to margin (may be as $R_{1+2}$) (0), vein captured by $R_2$, not attaining wing margin (1), inapplicable (2)

27. Wing crossvein $R_2 (r-r)$: absent (0), present (1), inapplicable (2-4)

28. Number of medial veins to the wing margin: three (0), two (1), one (2), inapplicable (3) (S: 11)

29. Setiforms on "calypter" (lobe of wing base): absent (0), present (1), inapplicable (2)

30. Relationship of anal veins: parallel or slightly divergent (0), strongly convergent (1)

31. Subcostal wing vein $Sc_1$: ending into costal vein (0), $Sc_1$ with atrophied tip (1), entering into radius (2), inapplicable (3)

32. Wing crossvein $Sc_2 (sc-r)$: near free tip of $Sc_1$ (0), far basal of free tip of $Sc_1 (>5 \times length,$ often much more) (1), absent (2), inapplicable (3)

33. Wing vein secondary $m-cu$: present (0), absent (1)

34. Wing folds through $CuA$ crossvein (through cells $bm$ and $cua_1$): absent (0), present (1)

35. Wing fold crossing through cells $br$, $dm$, and $m_3$: absent (0), present (1)

36. Wing fold crossing through veins near or at split of $Rs$: absent (0), present (1)

37. Relationship of veins $r-m$ and basal section of $M_{1+2}$: $r-m > M_{1+2}$ or veins subequal (0), $r-m < M_{1+2}$ (1), $r-m$ atrophied (2), inapplicable (a-d)

Adult male hypopygium

38. 9th abdominal segment: tergite and sternite fused (0), 9t and 9s separate (1)

39. Reduction of 9th tergite: absent (0), present (1)

40. Ventro-medial expansion of 8th sternite: absent (0), expanded into broad lobes (often equipped with strong setiforms) (1)
41. Ejaculatory apodeme: laterally flattened blade (0), dorso-ventrally flattened blade (1),
    absent (a-f)
42. Gonostylus: absent (0), singular (1), bifid (2)
43. Gonostyli: joined at base (0), base of styles separate (1), widely separated (2),
    inapplicable (a-p)
44. Gonostyli arrangement: 0) anterior/posterior (0), dorsal/ventral (0), a-p) inapplicable
45. Gonostylus articulation: grasping with gonocoxite (0), horizontal (1), vertical (2)
46. Ventral gonostylus ("lobe of gonostylus"): thin fleshly lobe (0), broad fleshy lobe (1),
    sclerotized lobe (2), bulbous lobe (3)
47. Interbase: connected to aedeagus apex (0), separate from aedeagus apex (1)
48. Form of interbase: simple lobe (0), cupped lobe with dorsal and ventral spikes (1),
    adhered to 9th tergite (2), fused to dorsal parameres (3), inapplicable (a-h)
49. Bridge of interbase: interbase medially linked (bridge present) (0), interbase separate
    (bridge absent) (1)
50. Separation of dorsal parameres from aedeagus: absent (0), present (1)
51. Raised dorsal parameres: absent (1), present as raised structures (2)
52. Articulation of interbase on dorsal parameres: absent (0), present (1)
53. Setation of interbase: absent (0), present (1)
54. Rostral spines of ventral gonostylus: absent (0), present (1)
55. Ventral division of gonocoxites: divided (0), basal pivot or small fusion (1), membranous
    fusion (2), sclerotized fusion (3)
56. Ventromedial lobe of gonocoxite: absent (0), present (1)
57. Membranous folds of gonocoxite: absent (0), present (1)
58. Orientation of sperm pump of aedeagus: horizontal to 90° rotation (0), 90°-180° rotation (1), greater than 180° rotation (2)

59. Aedeagal guide: absent (0), present (1)

60. Secondary aedeagal guide: absent (0), present (1)

61. Number of terminal aedeagus openings: three (0), two (1), one (2)

**Adult female genitalia**

62. Spermathecae: spherical and sclerotized (0), membranous and sac-like (1)

63. Number of spermathecae: three (0), two (1), one (2)

**Immature**

64. Fleshy lobes on larval abdomen and thorax: absent (0), present (1)

65. Postgenal incisions: absent (0), shallow incisions (1), deep incisions (2) (OT: 3; 8)

66. Maxillae: small lobe (0), bulbous lobe (1)

67. Maxillary palpus: flush with maxilla (0), raised stem or chitinous ring (1) (OT: 12)

68. Maxillary lobe: bulbous (0), elongate (1) (OT: 27)

69. Hypopharyngeal skeleton: absent (complete head capsule) (0), present (reduced to skeleton) (1) (OT: 67)

70. Statocysts: absent (0), present (1) (OT: 54, 68)

71. Elongation of labrum: not produced (0), compressed and elongate (1)

72. Compression of labrum: no compression (0), compressed laterally (1) (OT: 13 in part)

73. Orientation of mandibles: oblique (0), vertical (1), horizontal (2) (OT: 10)

74. Teeth of hypostoma: absent (0), present (1) (OT: 11, 23, 85, 93)

75. Hypostomal bridge: absent (0), present (1) (OT: 11, 23, 67, 86)

76. Dorsal bridge of larval head: fused (0), divided (1) (OT: 72)
77. Hypostoma with push-button connection: absent (0), present (1) (OT: 86)
78. Premaxillary suture and side plates: absent (0), present (1) (OT: 21)
79. Prostheca on a separate sclerite: absent (0), present (1) (OT: 22)
80. Spiracular lobes (4th instar): zero lobes (0), six lobes (1), five lobes (2), four lobes (3),
    two lobes (4), more than 6 lobes (5) (OT: 20, 41, 43, 87, 104)
81. Ventral larval creeping welts on segment 5: absent (0), present (1) (OT: 29, 79, 103)
82. Ventral larval creeping welts on segments 8-10: absent (0), present (1) (OT: 29, 48, 79,
    84, 103)
83. Ventral larval creeping welts on segments 2-4: absent (0), present (1) (OT: 29, 103)
84. Dorsal larval creeping welts on segments 5-10: absent (0), present (1), naked transverse
    swelling (2) (OT: 30)
85. Dorsal pupal creeping welts: absent (0), present (1) (OT: 32, 45, 96)
CHAPTER 3: A CLASSIFICATION OF THE LIMONIINI CRANE FLY GENERA
(“LIMONIIDAE”: LIMONIINAE)

As defined in Chapter 2 the Limoniinae clade of the “Limoniidae” was recovered with strong support and defined by two adult synapomorphies: 1) lateral separation of the male ninth sternite and tergite and 2) separation of the dorsal parameres from the aedeagus on the male genitalia. The revised classification based on this analysis presents the Limoniinae in a restrictive sense that is representative of the recovered monophyletic group. Two tribes are recognized within the Limoniinae, the Antochiini and the Limoniini, which are separated by the number of adult flagellomeres (12 in Limoniini, 14 in Antochiini) and the presence of ventral larval creeping welts on segments 2-4 in the Limoniini (sensu Oosterbroek and Theowald 1991). Of the two tribes, the genera of the smaller tribe Antochiini are well defined and the separation between generic units is easily diagnosable. The Limoniini, conversely, present taxonomic difficulty due to a high degree of morphological homogeneity. Additionally the genus level descriptions provided for the majority of genera are lacking detail or based on subjective criteria such as “complex” or “enlarged”, or based on coloration.

3.1 Introduction

The purpose of this chapter is three-fold. First it is to establish the classification of the Limoniinae to the framework of Petersen and Bertone (Chapter 2). Second, the genera and subgenera of the Limoniini are diagnosed in order to better establish the boundaries between the generic and subgeneric divisions. This revised taxonomic structure is then used to construct a multi-access taxonomic key to the Limoniinae crane flies of the Oriental
Region. It should be stressed that this process does not represent a revision of the Limoniinae, rather a diagnosis of the tribe to present the current understanding the group.

3.2 Methods

Designation of levels of taxonomic hierarchy are distinguished using the Linnaean taxonomy system as presenting in the International Commission on Zoological Nomenclature (ICZN, 2000). The prior taxonomic classification of the Limoniini presented a system of generic units that are subdivided into many subgeneric groups. Under this system, the group defining characters of each genus were largely lacking or based on subjective characteristics.

The system presented here places a greater emphasis on the generic unit. A genus is here defined as an evolutionary lineage comprised of individual metapopulations (species) that share one or many group defining synapomorphies and are separable from other such lineages based on these shared synapomorphies. This genus concept is used to eliminate genera that represent polyphyletic and paraphyletic groups. This genus concept approximates the species concept of de Queiroz (1998, 2005) in assigning taxonomic identity to evolutionary lineages.

Subgenera designations are used to describe patterns within a genus. A subgenus is regarded as a questionable taxonomic unit that is defined by subjective characters that may or may not represent a distinct evolutionary lineage, but does not maintain characters by which it is clearly separated from other taxonomic units. In cases where previously recognized subgenera were defined by clear synapomorphy, they were raised to genus. If no such character was detected they were maintained as subgenera and not elevated to the generic level.
The generic and subgeneric taxonomic divisions discussed here are those listed in the Catalogue of the Craneflies of the World (Oosterbroek, 2008). The validity and definition of each group was investigated using the following process: 1) identify the original intent of the descriptor based on original descriptions and define characters proposed to designate the group, 2) observe type material or type illustrations, 3) observe congruence between generic definitions and the species placed in these genera to see if they adhere to the generic concept, and 4) provide a written diagnosis to define the current concept of each taxonomic unit. All units determined to represent valid genera are provided with a detailed diagnosis of adult morphology. Morphological terminology follows that of McAlpine (1981) and Sinclair (1998) except where noted in the text.

Valid taxonomic units were used to create the Key to the Adult Limoniinae Crane Flies of the Oriental Region, version 2.0 (Petersen, 2007). The key was constructed from a coded character matrix using Lucid© taxonomic key building software for all genera and subgenera currently known from or with a high probability of occurring in the Oriental Region. Characters used for specimen identification were based primarily on wing venation and characteristics of the male hypopygium.

3.3 Results and Discussion

The Limoniinae crane flies (sensu Stary, 1991; Oosterbroek, 2008) are now divided between the Limoniinae (Limoniini [Table 1]; Antochiini [Table 2]), Elephantomyinae (Table 3), and Lipsothrixinae (Table 4). The following subgenera of Dicranomyia Stevens are elevated to a generic designation: Alexandriaria Garrett, Doaneomyia Alexander, Erostrata Alexander, Euglochina Alexander, Peripheroptera Schiner, Pseudoglochina Alexander, Sivalimnobia Alexander, and Zelandoglochina Alexander. The following

The genera *Dicranomyia*, *Libnotes*, and *Rhipidia* Meigen all maintain subgeneric units that correspond to groups that do not clearly delineate the limits of the group or maintain a clear morphological character for separation from other taxonomic units. One genus, *Amphilimnobia* Alexander, is maintained as a questionable member of the Limoniini.

### 3.3.1 Genera of Limoniini

**ACHYROLIMONIA** Alexander 1965

Reference: Alexander 1965a

Type species: *Achyrolimonia trigonia* Edwards (as *Limnobia*)

Diagnosis. **Head**: Anterior vertex of head present as a thin strip between eyes; rostrum greatly reduced, its length less that that of the maxillary palpus; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus length reduced, two or fewer subequal palpomeres present. **Antennae**: 14 articles, flagellomeres oval to cylindrical. **Wings**: Subhyline commonly patterned with clouds of brown located along veins; wing cells typically without macrotrichia, uncommonly with sparse trichation in the stigma and in distal
wing cells. Wing Venation: $S_{c_1}$ not removed from $S_{c_2}$, both elements ending near or after split of $Rs$; $Rs$ long, its origin near or before wing midlength, strongly angled at its base and subparallel to $R$; $R_{1+2}$ in near alignment with $R_2$; two branches of $Rs$ ($R_{3+4}$, $R_3$) attaining wing margin; two medial veins attaining wing margin ($M_{1+2}$, $M_3$); cell $dm$ present or absent; $CuA$ crossvein intersection with $M$ at split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two anal veins ($A_1$, $A_2$) attaining wing margin; anal angle of the wing present. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, remnants of 9s adhered to aedeagus and without further setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal gonostyle heavily sclerotized, falcate with microscopic scabrous points over the outer face, ventral gonostyle bulbous with a long, sclerotized basal rostral prolongation its length nearly equaling the length of the remainder of the style; one or two rostral spines present, when two spines present they are widely separated with one placed near the base of the projection on a long tubercle, the other placed at or beyond the midlength of the projection; apex of the aedeagus simple, with two subterminal openings; parameres weakly to strongly pointed and falcate at apex; proctiger simple, without modification.

Discussion: Achyrolimonia is defined by: 1) the long $Sc$ wing vein ending near the split of $Rs$, along with a long $Rs$ vein that is typically angled at its base and 2) mouthparts that show a great reduction of the rostrum and labial palpus to a nearly absent condition. The maxillary palpus is similarly reduced and present as two or fewer segments. This reduction in mouthparts is similarly seen in the genus Erostrata. The male genitalia ha a long and narrow sclerotized rostral projection that is variably adorned with long rostral spines. These spines are typically greatly separated and placed at the tips of long tubercles. This sclerotized
rostral projection and widely separated spines of the male genitalia most closely resembles that of Lasiolimonia of the Afrotropical Region, some species of Dicranomyia (s.l.) from the Neotropical Region, and Dicranomyia (Hesperolimonia) of the Nearctic.

**AFROLIMONIA Alexander 1965**

**Reference:** Alexander 1965a

**Type species:** Afrolimonia rhizosema Speiser (as Limonia)

**Diagnosis:** _Head_: Anterior vertex present, width variable; rostrum subequal to less than head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length subequal to less than that of remaining head; first palpomere reduced, remaining palpomeres subequal. _Antennae_: 14 articles; flagellomeres oval to elongate-oval. _Wings_: Subhyline, commonly patterned with clouds of brown and tawny located along veins and in cells; cells without macrotrichia; wing base not narrowed at wing base, anal angle of wing present. _Wing Venation_: $S_c^2$ not removed from $S_c^1$, both elements ending prior to or slightly after the split of $R_s$; $R_s$ beginning after wing midlength, its length greater than that of $m-cu$; $R_{1+2}$ in near alignment with $R_2$, $R_2$ infrequently longer than $R_{1+2}$ by the movement of $R_{1+2}$ toward the wing base; two branches of $R_3$ ($R_{3+4}, R_5$) attaining wing margin; two medial veins ($M_{1+2}, M_3$) attaining wing margin; cell $dm$ present; distal wing chord in general alignment in distal 1/3 of wing; two cubital veins ($CuA_1, CuA_2$) attaining wing margin; two anal veins ($A_1, A_2$) attaining wing margin. _Male Hypopygium_: 9th tergite (9t) and sternite (9s) separate by lateral division, remnants of 9s adhered to aedeagus and not showing setation; ventromedial lobe of gonocoxite a prominent simple lobe; gonostylus bifid; dorsal style a decurved sclerotized rod, from midlength to apex adorned with scabrous points; ventral bulbous with a slender basal rostral projection that is
equipped with a basal tubercle adorned with 2-4 rostral spines; face of style with a accessory lobe equipped with abundant setiforms and 2-3 strong setiforms; aedeagus simple with two terminal openings, often with two terminal aedeagal lobes; parameres weakly to strongly pointed and falcate at apex; proctiger simple, without modification.

Discussion: Afrolimonia does not possess a strong synapomorphy or combination of characters by which the group is defined. It was originally based on the bright coloration of the wing and body, however this is a difficult character by which to maintain the distinctness of the group and delineate it from similarly colored taxa.

The presence of an accessory lobe on the dorsal face of the ventral gonostylus that is shared by all known species indicates a relationship to Dapanoptera Westwood, Gressittomyia Alexander, Laosa Edwards, and Libnotes Edwards, but is separated from these by the lack of additional supernumerary wing crossveins (present in Dapanoptera, Gressittomyia, and Laosa) and the lack of the elongate and greatly modified wing of Libnotes.

ALEXANDRIARIA Garrett 1922

Reference: Garrett 1922

Type species: Alexandriaria suffusca Garrett

Diagnosis: Head: Anterior vertex present, width about twice the diameter of the scape of the antennae; rostrum present, its length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less than remaining head, basal palpomere reduced, remaining palpomeres subequal.

Antennae: 14 articles. Wings: Typically subhyline, infrequently suffused with darker, additional patterning of wing uncommon; anal angle of wing slightly reduced. Wing
Venation: $Sc_2$ ending near tip of $Sc_1$, both elements ending near the origin of $Rs$ at about wing midlength; $Rs$ long, its base near wing midlength; $R_{1+2}$ in alignment with $R_2$; two branches of $Rs$ ($R_{3+4}$, $R_5$) attaining wing margin; one medial vein ($M_{1+2}$) attaining wing margin; discal cell ($dm$) absent; $CuA$ crossvein intersection with $M$ near or before the split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two anal veins ($A_1$, $A_2$) attaining wing margin.

Male Hypopygium: 9th tergite ($9t$) and sternite ($9s$) divided, separated by lateral division, $9s$ present as a small patch with setation; gonocoxite with ventromedial lobe weakly produced; gonostylus divided; dorsal style a sclerotized falcate rod; ventral appearing as a bulbous lobe adorned with two additional lobes, the first a narrow lobe on the dorsal face (may be split into two lobes) equipped with abundant setiforms, and the second a basal rostral projection; 0-2 rostral spines present; aedeagus with two terminal openings; parameres weakly to strongly pointed and falcate at apex; proctiger simple, without modification.

Discussion. *Alexandriaria* was originally described as genus by Garrett (1922) and later placed as a subgenus of *Dicranomyia*. Although considered a valid genus here, delineating characters are limited and addition examination is needed. This genus is very similar to *Nealexandriaria* Alexander, separated on the composition of the male gonostylus, however this character is not clearly delineated.

**ATYPOPHTHALMUS** Brunetti 1911

Reference: Brunetti 1911

Type species: *Atypophthalmus umbratus* de Meijere

Diagnosis: Head: Eyes holoptic or subholoptic, divided dorsally and ventrally by a thin vertex; rostrum length subequal or shorter than that of the remaining head; labial palpus weakly present or absent; maxillary palpus five segmented, length subequal to remaining
head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles; flagellomeres oval to cylindrical. Wings: Subhyline; wing cells without macrotrichia; stigma typically present; veins brown; anal angle of wing present. Wing Venation: $S_{C1}$ short, not removed from $S_{C2}$; both elements ending between origin and split of $Rs$; $Rs$ long, its origin near wing midlength; $R_{1+2}$ in near alignment with $R_2$; two branches of $Rs$ ($R_{3+4}$, $R_5$) attaining wing margin; two medial veins ($M_{1+2}$, $M_3$) attaining wing margin; discal cell ($dm$) present or absent; $CuA$ crossvein intersection with $M$ near the split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two anal veins ($A_1$, $A_2$) attaining wing margin. Male Hypopygium: 9th tergite ($9t$) and sternite ($9s$) separated by lateral division, $9s$ adhered to aedeagus, without setation; $9t$ variably produced; ventromedial lobe of gonocoxite present, variously produced and multiple lobes common; gonostylus variable, a variable number of lobes may be present; dorsal gonostyle typically absent, if present a falcate sclerotized lobe; ventral gonostyle bulbous, variously produced; aedeagus variable, apex simple, with two subterminal openings, two terminal lobes of aedeagus common; parameres variable; proctiger variable, typically strongly and complexly produced.

Discussion: Atypophthalmus is a diverse and variously produced genus that is based on the adult holoptic condition and the highly variable and “complex” male genitalia. The holoptic condition is approached by many genera through the reduction of the dorsal vertex, with the genus Microlimonia attaining a holoptic condition most similar to that seen here (the two separated by the rounded eye margins and singular gonostylus of Microlimonia to the parallel eye margins and complex gonostylus of Atypophthalmus). The “complex” configuration of the male genitalia is only vaguely defined and it is not clear if this truly represents a synapomorphy for this group. The designation of a “complex” hypopygium is additionally
approached in the genus *Idiopyga* Savchenko, but separated on the holoptic condition of *Atypophthalmus*. Further work is needed to clearly delimitate the boundaries of this genus.

**DAPANOPTERA** Westwood 1881

Reference: Westwood 1881

**Type species:** *Dapanoptera plenipennis* Walker (as *Limnobia*)

**Diagnosis:** *Head:* Anterior vertex narrow, present as a thin strip; rostrum length subequal to remaining head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than or subequal to remaining head length; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles, flagellomeres oval to elongate-oval. *Wing:* Subhyline, additional coloration common; cells without macrotrichia; anal angle of wing present. *Wing Venation:* *Sc*₂ not removed from *Sc*₁, *Sc*₁ ending near or after the split of *Rs*; *Rs* long, its origin near wing midlength; *R*₁⁺₂ in near alignment with *R*₂; two branches of *Rs* (*R*₃⁺₄, *R*₅) attaining wing margin, their tips generally drawn ventrally at wing margin; a single supernumerary crossvein present in cell *r*₅; two medial veins (*M*₁⁺₂, *M*₃) attaining wing margin; cell *dm* present; two cubital veins (*CuA₁, CuA₂*) attaining wing margin; two anal veins (*A₁, A₂*) attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separate by lateral division; 9s adhered to the aedeagus, without setation, ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid; dorsal style a decurved sclerotized rod; ventral style bulbous with a small basal rostral projection that is equipped with 2 or more rostral spines placed at its base; face of ventral style with an accessory lobe that is equipped with numerous long setiforms; aedeagus variable, simple to equipped with lateral flanges, narrowed at the apex with two
terminal openings; parameres not narrowed to apex, not strongly falcate; proctiger simple, without modification.

**Discussion:** *Dapanoptera* possesses the characteristic accessory lobe of the ventral gonostylus shared by *Gressittomyia* Alexander, *Laosa* Edwards, and *Libnotes* Westwood. It is separated from *Laosa* by the presence of only a single crossvein, and from *Gressittomyia* by in possession crossvein *r-m*. The wing venation does not show the enlargement of wing cell *r₃* to the extremity of *Libnotes*. The supernumerary crossvein in cell *r₂* is shared with *Laosa* and may indicate a close relationship between these groups.

**DEGENEROMYIA** Alexander 1956

**Reference:** Alexander (1956)

**Type species:** *Dicranomyia thais* Alexander (as *Limonia*)

**Diagnosis:** *Head:* Anterior vertex very narrow; rostrum length shorter than or subequal to remaining head length; labial palpus weakly two segmented, length less than that of rostrum, infrequently equal to length of remaining head; maxillary palpus five segmented, length less than or subequal to remaining head length; basal palpomere reduced, remaining palpomeres variable. *Antennae:* 14 articles, flagellomeres oval. *Wing:* Subhyline, patterned with brown along wing veins, additional coloration in distal wing cells; cells without macrotrichia; anal angle of wing present. *Wing Venation:* *Sc₂* removed from *Sc₁*, *Sc₁* ending midlength of *Rs*; *Rs* length variable, its origin often near wing midlength; *R₁+₂* in near alignment with *R₂*; two branches of *Rs* (*R₃+₄*, *R₅*) attaining wing margin; supernumerary crossveins present in cell *r₄*, *r₅*, and *a₁*; two medial veins (*M₁+₂*, *M₃*) attaining wing margin; cell dm present; two cubital veins (*CuA₁*, *CuA₂*) attaining wing margin; two anal veins (*A₁*, *A₂*) attaining wing margin.

**Male Hypopygium:** 9th tergite (*9t*) and sternite (*9s*) separate by lateral division; *9s* adhered to
the aedeagus as a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe, but may be highly modified in some groups; gonostylus bifid, rarely single, dorsal style a decurved sclerotized rod, uncommonly with scabrous points on posterior face, ventral style bulbous with a variable rostral projection that is equipped with 2 rostral spines; aedeagus with two terminal openings; parameres broad, weakly to strongly falcate; proctiger simple, rarely with modification.

**Discussion.** *Degeneromyia* was originally described as a subgenus of *Limonia* for a single species, *D. thais*, known from Fiji. The group is separated from other *Dicranomyia* based on the presence of supernumerary crossveins in wing cells *r3*, *r5*, and, *a1*.

**DICRANOMYIA** Stevens 1829

**Reference:** Stephens 1829

**Type species:** *Dicranomyia modesta* Meigen

**Diagnosis:** *Head:* Anterior vertex variable, narrow to widely separated; rostrum length shorter than or subequal to remaining head length; labial palpus weakly two segmented, length less than that of rostrum, infrequently equal to length of remaining head; maxillary palpus with variable segmentation, length less than or subequal to remaining head length; basal palpomere reduced, remaining palpomeres variable. *Antennae:* 14 articles, flagellomeres oval to elongate-oval. *Wing:* Subhyline, additional coloration common; cells with or without macrotrichia; anal angle of wing present. *Wing Venation:* *Sc*₂ removed from *Sc₁* or in near alignment with *Sc₁*, *Sc₁* ending from well before to near the split of *Rs*; *Rs* length variable, its origin often near wing midlength; *R₁+₂* in near alignment with *R₂*; two branches of *Rs* (*R₃+₄*, *R₅*) attaining wing margin; supernumerary crossveins sometimes present in cell *r₄* or *r₅*; two medial veins (*M₁+₂*, *M₃*) attaining wing margin; cell *dm* present or
absent; two cubital veins \((CuA_1, CuA_2)\) attaining wing margin; two anal veins \((A_1, A_2)\) attaining wing margin. *Male Hypopygium*: 9th tergite (9t) and sternite (9s) separate by lateral division; 9s adhered to the aedeagus as a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe, but may be highly modified in some groups; gonostylus bifid, rarely singular, dorsal style a decurved sclerotized rod, uncommonly with scabrous points on posterior face, ventral style bulbous with a variable rostral projection that is equipped with 0-4 rostral spines; aedeagus with two terminal openings; parameres broad, weakly to strongly falcate; proctiger simple, rarely with modification.

**Discussion**: The genus *Dicranomyia* has been highly problematic in the classification of the Limoniinae. Under the view of Edwards (1938) or what is known as the “European” system, *Dicranomyia* is applied to species with wing vein \(Sc_2\) separated from \(Sc_1\) and ending before or at the origin of \(Rs\), with numerous subgeneric divisions. The alternative “North American” system (attributed to Charles Alexander) places nearly all genera of Limoniinae covered in this report as subgenera of the genus *Limonia* Meigen. Under this North American system, the limits of the subgenus *Dicranomyia* are broadened to include numerous species that do not adhere to the original \(Sc_1\) and \(Sc_2\) group defining characteristic.

The current status of the genus, as evidenced by the above diagnosis, is very loosely defined and weakly bounded. An exhaustive revision of *Dicranomyia* is outside the bounds of this current report, however taxonomic groups previously contained as subgenera of *Dicranomyia* but not conforming to the current concept of the genus (\(Sc_1\) slightly or greatly removed from \(Sc_2\), both elements ending at or before the origin of \(Rs\)) have been removed and elevated to a generic standing. The following synopsis of subgenera listed under the heading of *Dicranomyia* are groups that are maintained as questionable units that may or may
not represent monophyletic lineages. Most are based on weak group defining characters or are provided with incomplete or confusing descriptions that do not allow for clear delineation. Further revision is needed to determine the validity of these groups.

**Dicranomyia subgenus Caenoglochina Alexander**

Reference: Alexander (1964)

Type species: *Dicranomyia apicata* Alexander

Discussion: Erected as a subgenus for a group of Neotropical species based on the combination of antennal, wing, and male genitalic characteristics. The antennae of the male (female unknown) have the apical flagellomere reduced to an acute pedicel, much as in the serrate condition of some *Rhipidia* Meigen. The wing venation is not of the strict *Dicranomyia* type in that $Sc_1$ and $Sc_2$ are closely proximated and end at about the midlength of vein $Rs$, which itself is long and has its origin near wing midlength. The male genitalia has a single gonostylus, as in *Limonia*, that is narrowed to an acute tip. Characteristics such as a variable dorsal vertex of the head and the common condition of reduction of the gonostylus to a single styli indicate that this group may not represent a monophyletic group.

**Dicranomyia subgenus Caenolimonia Alexander**

Reference: Alexander (1967a)

Type species: *Limonia neorepanda* Alexander

Discussion: This is a variable group that is based the elongation of the labial palpus to one-half the length of the maxillary palpus. This is seen as a weak character because the elongation of labial palpus has been seen in many addition taxonomic groups (*Geranomyia* Haliday, *Zelandoglochina* Alexander, *Limonia*) and is likely a phenotypical adaptation for intake of fluids, possibly an adaptation for nectar feeding. Additional characteristics of the
group include the occurrence of an occasional supernumerary crossvein in cell $r_4$, a long and strongly angled basal $Rs$, and veins $Sc_1$ and $Sc_2$ ending in close proximity near the origin of $Rs$. Dicranomyia hypopygium.

Dicranomyia subgenus Cygnomyia Theischinger

Reference: Theischinger (1994)

Type species: Dicranomyia youngoloy Theischinger (as Limonia)

Diagnosis: This subgenus is based on a single species from north-eastern Australia. The subgenus is differentiated from other Dicranomyia because it differs from all other subgenera of Limonia in wing venation and structure of the male hypopygium (Theischinger 1994). Although not directly stated by Theischinger (1994), it is assumed that the thin rostral projection of the ventral gonostylus is the distinguishing synapomorphy of this group. The unclear description and weak differentiation of this species from other Dicranomyia make this a tenuous subgenus at best. Additional characteristic of the group include an elongate $Sc$ (ending at midlength of $Rs$), the absence of rostral spines, and the reduced anal lobe of the wing.

Dicranomyia subgenus Dicranomyia Stephens

Reference: Stephens (1829)

Type species: Dicranomyia modesta Meigen (as Limnobia)

Discussion: The subgenus Dicranomyia is reserved for species that conform to the strict interpretation of the genus, namely having a combination of 1) $Sc_1$ removed from $Sc_2$ and both elements ending before the origin of $Rs$, 2) wing base not strongly petiolate and cuneiform, and 2) male genitalia with a sclerotized falcate dorsal gonostylus and bulbous ventral gonostylus with a basal rostral projection adorned with 0-2 rostral spines.
Dicranomyia subgenus Glochina Meigen

Reference: Meigen (1830)

Type species: Glochina sericata Meigen

Diagnosis. The subgenus is maintained as a distinct group in the catalog of Oosterbroek (2008) based on the classification of Savchenko et al. (1992). A group defining character of the group is unknown.

Dicranomyia subgenus Hesperolimonia Alexander

Reference: Alexander (1966)

Type species: Dicranomyia infuscate Doane

Discussion: The subgenus Hesperolimonia is maintained for a single species from western North America based on the presence of abundant scabrous points on the broad face of the dorsal gonostylus. The wing venation is not of the strict Dicranomyia type and the presence on this subgenus within Dicranomyia is questionable.

Dicranomyia subgenus Idioglochina Alexander

Reference: Alexander (1921b)

Type species: Idioglochina tusitala (Alexander) (as Rhipidia)

Discussion: The subgenus Idioglochina is based on the antennal structure of the adult fly, which is produced into a subserrate condition. The original description of Idioglochina states that the flagellomeres have the inner face strongly produced into flattened disks that give a subserrate appearance to the antennae, the periphery of each disk equipped with about six strong setiforms (Alexander, 1921). The male genitalia is generally of the typical Dicranomyia type with a bulbous ventral gonostylus and a sclerotized falcate dorsal
gonostylus. The rostral projection is variable ranging from bulbous to less commonly short and slender.

**Dicranomyia subgenus Idiopyga Savchenko**

Reference: Savchenko (1987)

Type material: *Dicranomyia stigmatica* Meigen (as *Limnobia*)

Discussion: The subgenus Idiopyga is based primarily on the “complex” or “complicated” nature of the male gonostylus, especially the ventromedial lobe and the occasional medial expansion of 9t. Wing venation is that of standard *Dicranomyia* with *Sc*₁ and *Sc*₂ moderately divided and ending before origin of *Rs*. The strong modification of the male genitalia differentiates this group from other species of *Dicranomyia*, however the weak group-defining characteristic of “complex” does not easily delineate the boundaries of the group and is therefore left as a subgenus. Similar derivations to the male genitalia are seen in *Atypophthalmus*, though can be separated from this group by the long *Sc* that ends near split of *Rs* and holoptic condition of *Atypophthalmus* that is not seen in *Idiopyga*.

**Dicranomyia subgenus Melanolimonia Alexander**

Reference: Alexander (1965b)

Type species: *Dicranomyia morio* (Fabricius) (as *Tipula*)

Discussion: The *Melanolimonia* group likely corresponds to a distinct monophyletic group based on the overall melanistic coloration and silvery pleura of the adult flies. It is however based largely on coloration, which presents difficulty when attempting to separate these species from other darkly colored species. Further revision is needed to better define the boundaries of this group.
**Dicranomyia subgenus Neoglochina Alexander**

Reference: Alexander (1967a)

Type species: *Dicranomyia felix* (Alexander) (as *Limonia*)

Discussion: *Neoglochina* was established for a group of Neotropical flies that deviate from the *Dicranomyia* wing in having Sc long, ending between the origin and split of Rs, the antennae ending in short abrupt pedicels (as in *Rhipidia* and *Zelandoglochina*), the adult mouthparts (rostrum and maxillary palpus) “reduced”, some species with trichation in the distal wing cells, and the male hypopygium with the rostral projection small and without spines. This variable group is weakly defined and may represent a polyphyletic grouping of species that have a closer relationship to *Rhipidia* than to *Dicranomyia*.

**Dicranomyia subgenus Neolimnobia Alexander**

Reference: Alexander (1928)

Type species: *Dicranomyia diva* (Schiner) (as *Limnobia*)

Discussion: The subgenus *Neolimnobia* is based on the presence of a supernumerary vein in cell r₄. The presence of a supernumerary crossvein in this wing cell is shared with other species of *Dicranomyia*, so it is unclear if this subgenus is different from those other species.

**Dicranomyia subgenus Nesciomyia Theischinger**

Reference: Theischinger (1994)

Type species: *Dicranomyia durroon* (Theischinger) (as *Limonia*)

Discussion: *Nesciomyia* was established by Theischinger (1994) for a single species based on unclear criteria. The venation shows Sc long and Sc₂ not separated from Sc₁, the male hypopygium with rostral spines absent, and the apex of wing rounded. The etymology of the
name would lead to a diagnosis that the author was unsure of the status of this as a distinct
group: nescio= “I don’t know”, myia= “fly”.

**Subgenus Dicranomyia subgenus Numantia Bigot**

Reference: Bigot (1854)

**Type species:** *Dicranomyia fusca* (Meigen) (as *Limonia*)

**Discussion:** *Numantia* is used as a name synonymized with *Dicranomyia* by some
(Savchenko 1989; Theischinger 1994) but maintained by others (Oosterbroek 2008) as a
distinct subgenus of *Dicranomyia* based on the presence of macrotrichia in all wing cells.
The presence of macrotrichia in wing cells is seen throughout other subgenera of
*Dicranomyia* and therefore this is a questionable characteristic to define a subgenus.

**Dicranomyia subgenus Pandamyia Theischinger**

Reference: Theischinger (1994)

**Type species:** *Dicranomyia nowankareena* (Theischinger) (as *Limonia*)

**Discussion:** The subgenus *Pandamyia* was established based on the combination of two
characters: 1) male flagellomereres produced (apical pedicels not narrowed), and 2) a
supernumerary veins in cell *r₄*. This group is a maintained as a subgeneric group because the
presence of a supernumerary vein in *r₄* is common in *Dicranomyia* (shared *Pandamyia*, and
*Caenolimonia*) as well as in the genera *Laosa* and *Degeneromyia*. This may represent a
monophyletic genus, but revision is needed to delineate it from other similar groups.

**Subgenus Dicranomyia subgenus Zalusa Enderlein**

Reference: Enderlein (1906)

**Type species:** *Dicranomyia falklandica* (Enderlein) (as *Zalusa*)
Discussion: Zalusa was established for a single species, *D. falklandica* (Enderlein), from Port Darwin, Falkland Islands. The male hypopygium is of the general *Dicranomyia* type with a bulbous ventral gonostylius, falcate dorsal gonostylius, and two widely spaced rostral spines. The wings of both the male and female are greatly reduced so small pads while the wing venation shows a reduction by the atrophy of *m-cu* and the medial veins to reduced to 2 veins. The female ovipositor is characteristic of the group, being long and about 2/3 the length of the abdomen. The distinct female ovipositor and geographic isolation indicated that this may represent a true monophyletic group.

**DISCOBOLA** Osten Sacken 1865

Reference: Osten Sacken (1865)

Type species: *Discobola argus* (Say) (as *Limnobia*)

Diagnosis: Head: Anterior vertex suppressed, produced as a thin strip; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less then or subequal to that of the remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles; flagellomeres cylindrical. Wing: Subhyline, patterned with darker areas forming ocelliform or ring-like patterning; stigma absent; anal angle of wing present. Wing Venation: *Sc*1 slightly removed from *Sc*2; both elements ending near split of *Rs*; *R*1+2 greater than 2 times the length of *R*2; two branches of *Rs* (*R*3+4, *R*5) attaining wing margin; two medial veins (*M*1+2, *M*3) attaining wing margin; discal cell (*dm*) present; *CuA* crossvein near split of *M*; two cubital veins (*CuA*1, *CuA*2) attaining wing margin; two anal veins (*A*1, *A*2) attaining wing margin; a supernumerary crossvein present between *A*1 and *A*2. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without
setation; gonocoxite with ventromedial lobe present as a simple lobe; gonostylus divided, dorsal gonostyle heavily sclerotized and falcate, ventral gonostyle bulbous with a fleshy basal rostral prolongation; base of projection with or without one or two hyaline spines; aedeagus with two terminal openings, its apex simple; parameres weakly to strongly pointed and falcate at apex; proctiger simple, without modification. 

Discussion: *Discobola* is based primarily on the presence of a supernumerary crossvein connecting the two anal veins of the wing. The species are typically brightly colored and maintain a characteristic occelate patterning of the wing. The gonostylus of the male differs from other genera in possessing a short, weakly produced rostral projection that has two nearly clear stout spines at its base.

**DOANEOMYIA** Alexander 1921

Reference: Alexander (1921)

Type species: *Doaneomyia tahitiensis* Alexander

Diagnosis: Head: Anterior vertex present, not strongly reduced or widened; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less than or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles; flagellomeres oval, at times elongate, commonly with prominent basal pedicels on basal flagellomeres; ultimate flagellomere commonly elongate, constricted at midlength. 

Wings: Subhyline, commonly patterned with clouds of brown located along veins; cells without macrotrichia; anal angle of wing weakly present, at times greatly restrictedly. Wing Venation: *Sc*₂ removed from *Sc*₁, both elements ending prior to or slightly after the origin of *Rs*; *Rs* short, less than twice the length of *m-cu*; *R₁₂* in alignment with *R₂*; *R₂* infrequently
longer than $R_{1+2}$; two branches of $Rs$ ($R_{3+4}$, $R_5$) attaining wing margin; two medial veins ($M_1$, $M_3$) attaining wing margin; cell dm present or absent; $CuA$ crossvein intersection with $M$ near the split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; one anal vein ($A_2$) attaining wing margin. *Male Hypopygium*: 9th tergite (9t) and sternite (9s) separated by lateral division; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal gonostyle a sclerotized and falcate rod, ventral gonostyle bulbous with a basal fleshy rostral prolongation equipped with either one or two spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple two terminal openings; proctiger simple, without modification.

**Discussion**: *Doaneomyia* was originally described as a subgenus by Alexander (1921) based on the possession of a single anal vein of the wing. The reduction of the wing venation to such a state is not known to exist in other limoniid flies and is used here to distinguish this as valid genus. A similar reduction of the anal field of the wing is also seen in *Pseudoglochina* Alexander where a small remnant of $A_2$ is clearly present. The reduction seen in these two groups likely indicates a close relationship.

**EROSTRATA** Alexander 1976

**Reference**: Savchenko and Krivolutskaya (1976)

**Type species**: *Erostrata globithorax* (Osten Sacken) (as *Dicranomyia*)

**Diagnosis**: *Head*: Anterior vertex present, wide; rostrum length less than that of the remaining head; labial palpus weakly two segmented; rostrum reduced to a very short element; maxillary palpus apparently three-segmented; basal palpomere reduced, remaining palpomeres subequal. *Antennae*: 14 articles; flagellomeres oval. *Wings*: Subhyline; cells without macrotrichia; anal angle of wing present. *Wing Venation*: $Sc_2$ not removed from $Sc_1$. 
both elements ending at midlength of $Rs$; $R_{1+2}$ in alignment with $R_2$; two branches of $Rs$ ($R_{3+4}$, $R_3$) attaining wing margin; two medial veins ($M_{1+2}$, $M_3$) attaining wing margin; cell dm present or absent; CuA crossvein intersection with $M$ near the split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; one anal vein ($A_2$) attaining wing margin. 

**Male Hypopygium:** 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus singular, style bulbous without a rostral prolongation; two clear stout spines present on the dorsal face of the style; parameres weakly to strongly pointed and falcate at apex; aedeagus simple two terminal openings; proctiger simple, without modification.

**Discussion:** *Erostrata* does not conform to the characteristics of *Dicranomyia* and is here elevated to a genus. Two characters are offered as a strong set of group defining characters: 1) greatly reduced mouthparts including the rostrum and maxillary and labial palpus (also seen in *Atypophthalmus*), and 2) a singular male gonostylus that is equipped with two hyaline spines placed on the dorsal face of the style. The spines present on the male genitalia are similar to those of *Discobola* and are often very difficult to detect and may actually be absent in some species. This genus needs addition revision work to better delineate its boundaries.

**EUGLOCHINA Alexander 1921**

**Reference:** Alexander (1921b)

**Type species:** *Euglochina cuneiformis* (de Meijere) (as *Dicranomyia*)

**Diagnosis:** Head: Anterior vertex of present, not strongly reduced or produced; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than to subequal to remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14
articles; flagellomeres elongate, narrowed at both ends; ultimate flagellomere elongate, constricted at midlength. *Wing*: Subhyline to suffused with darker; further patterning of wing uncommon; wings cuneiform, anal angle of wing greatly reduced or absent. *Wing Venation*: \( Sc_2 \) removed from \( Sc_1 \), both elements ending before the origin of \( Rs \); \( Rs \) very short, subequal or slightly longer than \( m-cu \); \( R_{1+2} \) in general alignment with \( R_2 \); two branches of \( Rs \) \((R_{3+4}, R_5)\) attaining wing margin; one or two medial veins \((M_{1+2}, M_3)\) attaining wing margin; cell dm present or absent; distal wing chord in general alignment, compressed in distal 1/4 of wing; two cubital veins \((CuA_1, CuA_2)\) attaining wing margin; two anal veins \((A_1, A_2)\) attaining wing margin. *Male Hypopygium*: 9th tergite \((9t)\) and sternite \((9s)\) divided, separated laterally, \( 9s \) reduced to a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, ventral style much longer than dorsal style, dorsal gonostyle a sclerotized falcate rod, ventral gonostyle bulbous with a variably produced basal rostral prolongation equipped with two (less commonly one) spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings, two terminal lobes of aedeagus may be present; proctiger simple, without modification.

**Discussion**: *Euglochina* was established as a subgenus of *Dicranomyia* by Alexander (1921) and is raised to generic designation based on the compression of the apical elements of the wing to the extreme margins of the wing. The cuneiform wing shape caused by the reduction of the anal margin of the wing gives *Euglochina* a superficial similarity to both *Doaneomyia* and *Pseudoglochia*, however the presence of a complete vein \( A_2 \) along with the compression of the distal wing elements differentiates this group.
**GERANOMYIA Haliday 1883**

**Reference:** Haliday (1883)

**Type species:** *Geranomyia unicolor* Haliday

**Definition:** *Head:* Anterior vertex variable, from wide to narrow; rostrum length subequal head; labial palpus and labella greatly expanded, their length greater than or equal to the remaining head; maxillary palpus at tip or rostrum, number variable but typically less than five segmented, length less than that of the remaining head; palpomeres subequal. *Antennae:* 14 articles; basal flagellomeres oval, distal segments becoming elongate. *Wing:* Subhyline to suffused with darker, additional darker coloration along wing veins and in wing cells common; stigma present or absent; anal angle of wing present. *Wing Venation:* *Sc*$_1$ short, not or slightly removed from *Sc*$_2$; both elements ending between origin and split of *Rs*; a variable supernumerary vein present in cell *sc* (may be absent); *R$_{1+2}$* in near alignment with *R$_2$*; two branches of *Rs* (*R$_{3+4}$, *R$_5$*) attaining wing margin; two medial veins (*M$_{1+2}$, *M$_3$*) attaining wing margin; cell *dm* present; *CuA* crossvein near split of *M*; two cubital veins (*CuA$_1$, *CuA$_2$*) attaining wing margin; two anal veins (*A$_1$, *A$_2$*) attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separated by lateral division, 9s present as a small patch with setation; posterior margin of 9th tergite simple to medial excavated by the expansion of lateral margins; ventromedial lobe of gonoxonte present as a simple lobe; gonostylus bifid; ventral style generally much larger than dorsal style dorsal style a slender falcate sclerotized rod, ventral style a bulbous lobe with a basal rostral projection equipped with one or two (rarely more) rostral spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.
**Diagnosis:** The genus *Geranomyia* is based on the elongation of the labial palpus, with the degree of elongation ranging from between equaling over one-half the length of the adult body to subequal the length of the rostrum. This single characteristic creates difficulties in delimiting this genus because a lengthened labial palpus is shared by species of *Rhipidia*, *Zelandoglochina*, *Limonia*, and *Dicranomyia* (*Caenolimonia*). This group is in need of revision to adequately define its boundaries. Under the current concept it may be separated from the above mentioned genera based on the lack of pectinate or otherwise produced flagellomeres (present in *Rhipidia*), a rostrum that is subequal to the length of the head (shorter in *Zelandoglochina*), and a bifid male gonostylus (singular in *Dicranomyia* (*Caenolimonia*)).

**GONIODINEURA** van der Wulp 1895

**Reference:** van der Wulp (1895)

**Type species:** *Goniodineura nigriceps* van der Wulp

**Diagnosis:** *Head:* Anterior vertex presented as a thin strip between eyes; rostrum subequal to less than length of remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, it length subequal to less than that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles; flagellomeres oval to elongate-oval. *Wings:* Subhyline, additional coloration common; cells without macrotrichia; anal angle of wing present. *Wing Venation:* *Sc*$_2$ removed from *Sc*$_1$, *Sc$_1$ ending prior to or slightly after the split of *Rs*, *Sc* at midlength of *Rs*; *Rs* long, its origin at or before wing midlength; *R*$_{1+2}$ in near alignment with *R*$_2$; two branches of *Rs* (*R*$_{3+4}$, *R*$_5$) attaining wing margin, their tips with a weak tendency for ventral deflection; cell *r*$_3$ large; two medial veins (*M*$_{1+2}$, *M*$_3$) attaining wing margin; discal cell (*dm*) present; *CuA* crossvein
typically in distal 2/3 of wing, ranging from wing midlength to about distal 1/3 of wing; two
cubital veins (CuA1, CuA2) attaining wing margin; two anal veins (A1, A2) attaining wing
margin. *Male Hypopygium*: 9th tergite (9t) and sternite (9s) separate by lateral division, 9s
adhered to aedeagus without setation; posterio-lateral edges of 9t produced; ventromedial
lobe of gonocoxite present as simple lobes; gonostylus bifid, dorsal style a decurved
sclerotized rod narrowing to a slender apex, ventral style bulbous with a small basal rostral
projection; rostral projection equipped with 2 unequal rostral spines, the outer spine strongly
produced and blackened the outer spine only weakly differentiated from the remaining
setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus with long
lateral flanges, narrowed at the apex with two terminal openings; proctiger simple, without
modification.

**Discussion**: *Goniodineura* presents a combination of characters not seen in any other genus.
The wing venation approaches that of *Libnotes*, with the decurved and elongated cell $r_3$,
however several wing venation characteristics ($Sc_1$ and $Sc_2$ separated and long $Rs$) do not
correspond to the *Libnotes* type and more approximate the genus *Dicranomyia*. The male
genitalia possess a bulbous ventral style with two rostral unequally sized spines on a short
rostral projection. This combination of wing venation and male genitalic characters should
be sufficient to delineate this group from others.

**GRESSITTOMYIA** Alexander 1936

**Reference**: Alexander (1936)

**Type species**: *Gressittomyia xenoptera* (Alexander) (as *Limonia*)

**Diagnosis**: *Head*: Anterior vertex present as a thin strip; rostrum subequal to less than head
length; labial palpus weakly two segmented, length less than that of rostrum; maxillary
palpus five segmented, its length less than or subequal to remaining head; basal palpomere reduced, remaining palpomeres subequal. **Antennae:** 14 articles; flagellomeres oval to elongate-oval. **Wing:** Subhyline, cells typically with clouds of coloration and veins lined with darker coloration; cells without macrotrichia; wing not narrowed at wing base, anal angle of wing present. **Wing Venation:** $Sc_2$ not removed from $Sc_1$, both elements ending between origin and split of $Rs$; $Rs$ short, about twice $m-cu$; $R_{1+2}$ in near alignment with $R_2$, $R_2$ less than $1/2$ length of $R_{1+2}$; two branches of $Rs$ ($R_{3+4}$, $R_5$) attaining wing margin, their tips slightly convergent at wing margin; a supernumerary vein present in cell $r_3$; two medial veins ($M_{1+2}$, $M_3$) attaining wing margin, strongly directed ventrally; $r-m$ crossvein atrophied resulting in the fusion of $R_{4+5}$ and $M_{1+2}$ for a short distance; discal cell ($dm$) present; $CuA$ crossvein near split of $M$; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two anal veins ($A_1$, $A_2$) attaining wing margin. **Male Hypopygium:** 9th tergite (9t) and sternite (9s) separate by lateral division; 9s adhered to aedeagus with setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal style a decurved sclerotized rod, ventral style bulbous with a long slender basal rostral projection that is equipped with 2 long rostral spines, face of ventral style with an accessory lobe that is equipped with a large tubercle and long setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Discussion:** *Gressittomyia* is established for a single species from the Oriental Region. The genus is morphologically similar to *Libnotes*, *Laosa*, and *Dapanoptera* in the possession of an accessory lobe on the ventral gonostylus. *Gressittomyia* is separated from other genera that share this lobe by the presence of a supernumerary crossvein in cell $r_3$ (also seen in
Laosa and Neolimnobia) and the atrophy of crossvein r-m (seen rarely in Laosa). The similar genus Laosa has a supernumerary vein in cell r₅, which is absent in Gressittomyia.

**LAOSA Edwards 1926**

Reference: Edwards (1926)

Type species: Laosa gloriosa Edwards

Diagnosis: Head: Anterior vertex suppressed, present as a thin strip; rostrum length subequal to remaining head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than or subequal to remaining head length; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles, flagellomeres oval to elongate-oval. Wing: Subhyline, additional coloration common; cells without macrotrichia; anal angle of wing present. Wing Venation: Sc₂ short, not removed from Sc₁, Sc₁ ending near or after the split of Rs; Rs short, origin near wing midlength, length less than twice m-cu; R₁+₂ in near alignment with R₃; two branches of Rs (R₃+₄, R₅) attaining wing margin, their tips generally drawn ventrally at wing margin; supernumerary crossveins present in cells r₄ and r₅; two medial veins (M₁+₂, M₃) attaining wing margin; cell dm present; distal wing chord in general alignment in distal 1/3 of wing; two cubital veins (CuA₁, CuA₂) attaining wing margin; two anal veins (A₁, A₂) attaining wing margin. Male Hypopygium: 9th tergite (9t) and sternite (9s) separate by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal style a decurved sclerotized rod, ventral style bulbous with a small basal rostral projection that is equipped with 2 or more rostral spines placed at its base, face of ventral style with an accessory lobe that is equipped with numerous long setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus variable, simple to
equipped with lateral flanges, narrowed at the apex with two terminal openings; proctiger simple, without modification.

**Discussion:** The genus *Laosa* is established for a group of ornate Oriental and East Palearctic crane flies that have an accessory lobe on the ventral gonostylus (shared by *Libnotes*, *Gressittomyia*, and *Dapanoptera*) and supernumerary veins in cells $r_4$ and $r_5$. The combination of these two character separates these species from all other genera. The closest genus to *Laosa* in morphology is *Gressittomyia*, which lacks the supernumerary vein in cell $r_4$.

**LASIOLIMONIA** Alexander 1976

**Reference:** Alexander (1976)

**Type species:** *Lasiolimonia tigripes* (Alexander) (as *Limonia*)

**Diagnosis:** *Head:* Anterior vertex present as a thin strip; rostrum subequal to less than head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than or subequal to that of head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles, flagellomeres oval to elongate-oval.

*Wings:* Subhyline, additional coloration in wing cell and along veins common; cells with macrotrichia in stigma, infrequently in the outer ends of apical wing cells; wing not narrowed at wing base, anal angle of wing present. *Wing Venation:* $Sc_2$ not removed from $Sc_1$, $Sc_1$ ending between origin and split of $Rs$; $Rs$ long, its origin at wing midlength, angulated at origin; $R_{1+2}$ typically drawn toward the wing base, $R_2$ subequal to $2x$ the length of $R_{1+2}$; two branches of $Rs$ $(R_{3+4}, R_5)$ attaining wing margin, their tips generally drawn ventrally at wing margin; two medial veins $(M_{1+2}, M_3)$ attaining wing margin; discal cell ($dm$) present; $CuA$ crossvein near wing midlength; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two
anal veins ($A_1$, $A_2$) attaining wing margin. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal style a decurved sclerotized rod, ventral style bulbous with a small basal rostral projection that is equipped with zero to numerous rostral spines placed at its base, face of ventral style with a variable accessory lobe that is typically equipped with numerous long setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus simple or equipped with lateral flanges, narrowed at the apex with two terminal openings; proctiger simple, without modification.

Discussion: Lasiolimonia was described by Alexander (1976) as one of numerous subgenera of Limonia. The group is based on the presence of macrotrichia in the stigma (infrequently distal wing cells) of the wing, a characteristic shared by Tricholimonia Alexander, also of the Afrotropical Region. The description of Lasiolimonia is very short (two sentences), and is meant to separate a number of species from Tricholimonia based on hypopygial characters (Alexander 1976). It is not directly stated but is assumed that these differences are a lack of both a tooth on the parameres and the down-turned rostral spines on the projection of the ventral gonostylus in Lasiolimonia, both of which are present in Tricholimonia. The catalog of Oosterbroek (2008) places Lasiolimonia as a subgenus of Metalimnobia, however this recommendation was based on the presence of macrotrichia in the stigma, likely a homoplasious character as it is present in other genera. Lasiolimonia is here placed as a separate genus but in need of revision to better delineate its boundaries.

**LIBNOTES Westwood 1876**

Reference: Westwood (1876)

Type species: Libnotes thwaitesiana Westwood
**Diagnosis:** *Head:* Anterior vertex as a thin strip; rostrum subequal to less than head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than or subequal to that of head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles, flagellomeres oval to elongate-oval. *Wings:* Subhyline, additional coloration common; cells without macrotrichia; wing not narrowed at wing base, anal angle of wing present. *Wing Venation:* $Sc_2$ short, not removed from $Sc_1$, $Sc_1$ ending after the split of $Rs$; $Rs$ short, origin at wing midlength; $R_{1+2}$ typically drawn toward the wing base, $R_2$ subequal to 2x the length of $R_{1+2}$, an additional spurious element infrequently present; two branches of $Rs$ ($R_{3+4}, R_5$) attaining wing margin, their tips generally drawn ventrally at wing margin; two medial veins ($M_{1+2}, M_3$) attaining wing margin; discal cell ($dm$) present; $CuA$ crossvein near wing midlength; two cubital veins ($CuA_1, CuA_2$) attaining wing margin; two anal veins ($A_1, A_2$) attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal style a decurved sclerotized rod, ventral style bulbous with a small basal rostral projection that is equipped with zero to numerous rostral spines placed at its base, face of ventral style with a variable accessory lobe that is typically equipped with numerous long setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus simple or equipped with lateral flanges, narrowed at the apex with two terminal openings; proctiger simple, without modification.

**Discussion:** The genus *Libnotes* is considered here in a strict sense, based on the combination of: 1) the elongation of the wing resulting in the lengthening of the distal wing elements, and
2) the presence of a supplemental lobe on the dorsal face of the ventral gonostylus (also present in *Afrolimonia, Dapanoptera*, and *Laosa*).

Other genera that share the supplemental lobe on the dorsal face of the ventral gonostylus and show an expansion of cell *r₃* (*Afrolimonia, Dapanoptera*, and *Laosa*) have been included as subgenera of Libnotes by Oosterbroek (2008). As in the classification of *Dicranomyia* presented here, taxonomic groups with strong group defining characters and are delineated from other such groups are defined as generic units, therefore the genus *Libnotes* is treated in a strict sense and these other units are treated as separate genera. The similar lengthening of cell *r₃* and shared presence of the supplemental lobe may indicate a close evolutionary link among these genera. Additional revision is need with this genus.

Three groups are maintained as subgenera of *Libnotes*. Each group maintains characters that do not adhere to the strict interpretation of *Libnotes* presented here, but do share a similar wing venation in having cell *r₃* elongate. They are maintained here as subgenera, but additional revision is needed to determine if they represent distinct genera or merely variation from the strict *Libnotes* type.

*Libnotes subgenus Metalibnotes Alexander*

Reference: Alexander (1972)

Type species: *Libnotes (Metalibnotes) fijiensis* Alexander (as *Teucholabis*)

Discussion: This is a problematic group that may not possess a clear synapomorphy.

Alexander designated this group as separate from *Libnotes* and as a subgenus of his large encompassing genus *Limonia*. As described in the original description the genus us based on an elongate *Sc*, ending ⅔ the length of *Rs*, longitudinal veins beyond cord not decurved apically, *m-cu* beyond fork of *M*, parallel anal veins, a conspicuous ventromedial lobe that is
narrowed outwardly (another subset of species have a broad ventromedial lobe that is bi-lobed), single gonostylus (a weak indication of dorsal gonostylus at base of style may be present), and parameres with a mesal-apical tooth-like extension. This tooth-like extension is not known from other genera and may represent a true synapomorphy for the group.

**Libnotes subgenus Neolibnotes Alexander**

**Reference:** Alexander (1972)

**Type species:** *Libnotes (Neolibnotes) samoensis* Alexander

**Discussion:** A weak group of 6 species that were removed from *Libnotes* and erected by Alexander as a subgenus of *Limonia*. A true synapomorphy is not clear for this group and the original description of Alexander bases the subgenus on the absence of characteristics of the typical *Libnotes*, namely the lobe of the ventral gonostylus. This genus can be identified by the small gonosytlus of the male hypopygium that have a short stout rostral projection of the ventral gonostylus that lacks rostral spines. The apex of the aedeagus is variable, but often adorned with a dorsal bilobed projection. Additional revision work is needed for this group.

**Libnotes subgenus Paralibnotes Alexander**

**Reference:** Alexander (1972)

**Type species:** *Paralibnotes bidentata* (Alexander) (as *Limnobia*)

**Discussion:** *Paralibnotes* is similar in composition to *Metalibnotes* and *Neolibnotes* in possess in a single gonostylus. The long narrow aedeagus is the characteristic that may be used to separate this group from others.
**LIMONIA Meigen 1803**

Reference: Meigen (1803)

Type species: *Limonia phragmitidis* (Schrank) (as *Tipula*)

Diagnosis: Head: Anterior vertex variable, not reduced to a thin strip; rostrum length subequal or less than that of the remaining head, infrequently longer than remaining head; labial palpus weakly two segmented, length less than that of rostrum, infrequently longer than rostrum; maxillary palpus five segmented, length less than that of remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles, flagellomeres suboval to cylindrical. Wing: Color variable, typically patterned with darker areas; stigma present or absent; anal angle of wing present. Wing Venation: Sc1 short, only slightly removed from Sc2; both elements ending between origin and split of Rs; Rs long, its origin near wing midlength; R1+2 removed from R2, about twice the length of R2; two branches of Rs (R3+4, R5) attaining wing margin; two medial veins (M1+2, M3) attaining wing margin; cell dm present, rarely absent; CuA crossvein near split of M; two cubital veins (CuA1, CuA2) attaining wing margin; two anal veins (A1, A2) attaining wing margin. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s reduced and adhered to aedeagus without setation or with weak setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus single, variable in construction, typically bulbous with interior face with strong setiforms or with apex narrowed to an acute tip; anterior face of parameres typically absent; aedeagus simple with two terminal openings; proctiger simple, without modification.

Discussion: The classification of *Limonia* has been problematic. The classification of Alexander and Byers (1981; followed by Theischinger 1994; 1996) treated nearly all of what is considered here the tribe Limoniini as the genus *Limonia*. The character for inclusion in
*Limonia* in the catalog of Oosterbroek (2008) is unclear, but appears to be based on the singular gonostylus of the male hypopygium, a highly convergent characteristic within the Limoniinae. The genus *Limonia* is here defined in a strict sense represented by taxa that have: 1) \( R_{1+2} \) straight to the wing margin and about 2x the length of \( R_2 \), and 2) a single gonostylus. The configuration of \( R_{1+2} \) and \( R_2 \) is shared only in the genus *Discobola*, and is otherwise produced with \( R_{1+2} \) and \( R_2 \) in a near vertical alignment or with \( R_{1+2} \) drawn to the wing base.

**METALIMNOBIA** Matsumura 1911

**Reference:** Matsumura (1911)

**Type species:** *Metalimnobia vittata* Matsumura

**Diagnosis:** *Head*: Anterior vertex variable, not reduced to a thin strip; rostrum less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less than or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae*: 14 articles; flagellomeres variable, oval, cylindrical, or moniliform. *Wings*: Subhyline, extensively patterning common with clouds of brown located along veins and in cells; stigma typically present; macrotrichia may be infrequently present in stigma area, other wing cells without macrotrichia; anal angle of wing present. *Wing Venation*: \( Sc_2 \) not removed from \( Sc_1 \), both elements between origin and split of \( Rs \); \( Rs \) long, its origin near wing midlength, many times greater than \( m-cu \); \( R_l \) in near alignment with \( R_2 \), or with \( R_{1+2} \) straight to wing margin (>2x \( R_2 \)); two branches of \( Rs \) (\( R_{3+4}, R_5 \)) attaining wing margin; two medial veins (\( M_{1+2}, M_3 \)) attaining wing margin; cell \( dm \) present; two cubital veins (\( CuA_1, CuA_2 \)) attaining wing margin; two anal veins (\( A_1, A_2 \)) attaining wing margin. *Male Hypopygium*: 9th tergite (9t)
and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus highly variable, commonly divided but may be present as a single style or several lobes present may be present; when divided, dorsal gonostyle a heavily sclerotized, falcate rod, ventral gonostyle a divided bulbous lobe with a long basal rostral prolongation; rostral spines absent; parameres with posterior face elongate, tipped apically with setation; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Diagnosis:** *Metalimnobia* is a group of large, highly ornate flies based largely on characteristics of the male hypopygium. While there is variability in the production of the male genitalia, the parameres are consistently produced into long lobes that are apically tipped with setation, a characteristic not seen in other genera. The variable gonostylus are produced as one to three lobes. The various lobes typically observed in the gonostylus of *Metalimnobia* are a result of a division of the ventral gonostylus into two or three lobes, while retaining the sclerotized rostral projection and dorsal sclerotized gonostylus. In some species this modification is further transformed by a complete fusion of these elements into a single fused style.

**MICROLIMONIA** Savchenko 1976

**Reference:** Savchenko and Krivolutskaya (1976)

**Type species:** *Microlimonia inelegans* (Alexander) (as *Limonia*)

**Diagnosis:** *Head:* Eyes nearly holoptic, dorsal vertex reduced to a thin strip; rostrum length less than that of the remaining head; maxillary palpus five segmented, length less than that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles; flagellomeres oval to cylindrical. *Wings:* subhyline; wing cells without
macrotrichia; stigma typically present; veins brown; anal angle of wing present. **Wing**

Venation: *Sc₁* short, not removed from *Sc₂*; both elements ending between origin and split of *Rs*; *R₁+₂* in near alignment with *R₂*; two Radial veins (*R₃+₄*, *R₅*) attaining wing margin; two medial veins (*M₁+₂*, *M₃*) attaining wing margin; cell dm present; *CuA* crossvein intersection with *M* near the split of *M*; two cubital veins (*CuA₁*, *CuA₂*) attaining wing margin; two anal veins (*A₁*, *A₂*) attaining wing margin; anal angle of the wing present. **Male Hypopygium**: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; 9t strongly produced; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus single, bulbous with a long slender sclerotized rostral projection; parameres with posterior variously produced; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Discussion**: *Microlimonia* is considered a genus based on the near holoptic condition of the adult and the single gonostylus of the male genitalia. *Microlimonia* has been placed as a subgenus of *Atypophthalmus* due to the near holoptic condition shared by the two. That position is not shared here as the reduction of the dorsal and ventral margins of the head are approached by numerous genera and it is not believed that this is a strong synapomorphy by which to join the two groups.

**NEALEXANDRIARIA** Alexander 1967

**Reference**: Alexander (1967b)

**Type species**: *Nealexandriaria tecta* (Alexadner) (as *Limonia*)

**Diagnosis**: **Head**: Anterior vertex of head narrow; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less that or subequal to that of remaining head;
basal palpomere reduced, remaining palpomeres subequal. *Antennae*: 14 articles; flagellomeres oval to cylindrical. *Wing*: Subhyline to suffused with darker; stigma present or absent; anal angle of wing present. *Wing Venation*: Sc variable, ending before or rarely at origin of Rs; Sc₂ present or absent, if present removed from tip of Sc₁; R₁+₂ alignment with R₂ variable; Rs short, length less than three times length of m-cu; two branches of Rs (R₃+₄, R₅) attaining wing margin; one medial vein (M₁+₂+₃) attaining wing margin; cell dm absent; CuA crossvein near entering M near the split of M; two cubital veins (CuA₁, CuA₂) attaining wing margin; two anal veins (A₁, A₂) attaining wing margin. *Male Hypopygium*: 9th tergite (9t) and sternite (9s) divided, separated by lateral division; gonocoxite with ventromedial lobe present as a simple lobe; gonostylus divided; dorsal gonostyle heavily sclerotized, falcate; ventral gonostyle bulbous with a basal rostral prolongation equipped with two or one variable spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two subterminal openings; proctiger simple, without modification.

**Discussion**: *Nealexandriaria* was erected by Alexadner (1965) for a group of species that shared with the genus *Alexandriaria* the characteristic wing venation, where the medial field is reduced to a single vein attaining the wing margin, but lacking the two distinctive V-shaped lobes of the ventral gonostylus. This single genitalic characteristic separating the two groups, along with the distinctive wing venation that is not shared by any other genus indicates a close relationship between these two. They are here left as separate units, but further revision is needed to determine whether these two groups should remain separated or combined into a single generic unit.
**NEOLIMONIA Alexander 1964**

Reference: Alexander (1964)

**Type species:** *Neolimonia eiseni* (Alexander) (as *Furcomyia*)

**Diagnosis:** *Head:* Anterior vertex of head narrow; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less that or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles; flagellomeres cylindrical, verticils shorter than segment. *Wing:* Subhyline; stigma absent or obscured by additional coloration; wing cells and veins commonly colored with addition coloration; anal angle present. *Wing Venation:* $Sc_1$ near $Sc_2$, both elements ending from before origin to after split of $Rs$; $Rs$ long, its origin at wing midlength, strongly to weakly angulated at its base; $R_{1+2}$ in near alignment with $R_2$; two branches of $R_s$ ($R_{3,4}, R_5$) attaining wing margin; two medial veins ($M_{1+2}, M_3$) attaining wing margin; discal cell ($dm$) present; $CuA$ crossvein near split of $M$; two cubital veins ($CuA_1, CuA_2$) attaining wing margin; two anal veins ($A_1, A_2$) attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separated by lateral division, 9s present as a weak patch without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, rarely singular by loss of dorsal style; dorsal style a sclerotized rod, typically falcate and ending in an acute tip, ventral style bulbous with an enlarged basal rostral projection that nearly equals the length of style, rostral projection equipped with two peg-like spines surrounded by delicate setiforms; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.
**Discussion:** *Neolimonia* represents a variable group that is based on the presence of small hyaline peg-like rostral spines on the rostral projection of the ventral gonostylus. The variable production of the dorsal vertex of the head (wide to narrow), the wing venation (*Rs* and *Sc* variable), and male hypopygium (ventral gonostylus showing similarity to *Discobola* to *Erostrata*) along with a weak group defining characteristic indicate that this may represent a polyphyletic grouping of species in need of further revision.

**PERIPHEROPTERA** Schiner 1868

**Reference:** Schiner (1868)

**Type species:** *Peripheroptera nitens* Schiner

**Diagnosis:** *Head:* Anterior vertex present, not narrowed; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less that or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles; basal flagellomeres subglobular to suboval, distal flagellomeres more elongate. *Wing:* Subhyline to suffused with darker, additional coloration uncommon; stigma present or absent; wing cuneiform, anal angle of wing absent. *Wing Venation:* *Sc* 1 short, removed from *Sc* 2, both elements ending before or at origin of *Rs*; *Rs* short, typically less than twice the length of *m-cu*; *R* 1+2 variable, typically in general alignment with *R* 2, a spurious element infrequently present; two (*R* 3+4, *R* 5) branches of *Rs* attaining wing margin; two medial veins (*M* 1+2, *M* 3) attaining wing margin; discal cell (*dm*) present rarely absent; *CuA* crossvein entering *M* near wing midlength; two cubital veins (*CuA* 1, *CuA* 2) attaining wing margin; two anal veins (*A* 1, *A* 2) attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separate, 9s reduced to a small patch with setation; ventromedial lobe of gonocoxite present as a simple
lobe; gonostylus bifid, dorsal gonostyle a long narrow sclerotized rod ending in an acute tip; ventral gonostyle a bulbous fleshy lobe with a basal rostral projection equipped with two small rostral spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Discussion:** *Peripheroptera* is separated from other taxonomic groups based on the distinctive wing venation, namely the cuneiform wing base with an enlarged prearcular cell and broadly rounded apex of the wing. The retracted vein $Sc$ with $Sc_1$ and $Sc_2$ widely separated shows similarities to many *Dicranomyia* subgenera, as well as the genus *Thrypticomyia*, however the broad wing apex should separate *Peripheroptera* from other groups.

**PSEUDOGLOCHINA** Alexander 1921

**Reference:** Alexander (1921b)

**Type species:** *Pseudoglochina pulchripes* (Alexander) (as *Libnotes*)

**Diagnosis:** *Head*: Anterior vertex present, not strongly reduced; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less that or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae*: 14 articles; flagellomeres oval to cylindrical. *Wing*: Subhyline to suffused with darker, patterning of wing uncommon; wings cuneiform, anal angle of wing lacking. *Wing Venation*: $Sc_1$ removed from $Sc_2$, $Sc_1$ 2-3 times as long as $Sc_2$, both elements ending near the origin of $Rs$; $Rs$ short, its origin near wing midlength; $R_{1+2}$ in near alignment with $R_2$; two branches of $Rs$ ($R_{3+4}, R_3$) attaining wing margin; two medial veins ($M_{1+2}, M_3$) attaining wing margin; cell $dm$ absent; $CuA$ crossvein entering $M$ near the split of $M$; two cubital veins ($CuA_1, CuA_2$) attaining wing
margin; two anal veins ($A_1, A_2$) attaining wing margin, vein $A_2$ at times basally fused with wing margin resulting in only one anal vein ($A_1$) attaining wing margin. **Male Hypopygium:** 9th tergite (9t) and sternite (9s) separate, 9s reduced to a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal gonostyle a long narrow sclerotized rod ending in an acute tip; ventral gonostyle a bulbous fleshy lobe with a basal rostral projection equipped with two small rostral spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Discussion:** *Pseudoglochina* shows a cuneiform wing with a reduced anal lobe. A similar reduction of the wing is seen in the genera *Euglochina, Doaneomyia, Peripheroptera,* and *Thrypticomyia* Skuse. It is separated from these genera based on the anterior wing cord occurring at about $\frac{3}{4}$ the wing length and not compressed as in *Euglochina,* the presence of vein $A_2$ which is absent in *Doaneomyia,* the acute apex and the absence of cell *dm* which is present in *Peripheroptera* with a broadly rounded wing apex, and the non-alignment of the anterior wing cord which is aligned in *Thrypticomyia* (*Thrypticomyia* also with cell *dm* present).

**Rhipidia** Meigen 1818

**Reference:** Meigen (1818)

**Type species:** *Rhipidia maculata* Meigen

**Diagnosis:** **Head:** Anterior vertex of head present, not as thin strip; rostrum length less than that of the remaining head, infrequently longer than head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, uncommonly reduced, its length less that or subequal to that of remaining head; basal palpomere reduced,
remaining palpomeres subequal. Antennae: 11-14 articles; flagellomeres variably produced, bipectinate, unipectinate, or subpectinate (female flagellomeres less-developed), distal section of flagellomeres reduced to thin petiole. **Wing:** Subhyline, typically patterned with darker areas; stigma present or absent; anal angle of the wing present. **Wing Venation:** $Sc_1$ only slightly removed from $Sc_2$; both elements ending between origin and split of $Rs$, a supernumerary crossvein cell $sc$ may be present; $Rs$ long, its origin near wing midlength; $R_{1+2}$ in near alignment with $R_2$; two branches of $Rs$ ($R_{3+4}$, $R_5$) attaining wing margin; two medial veins ($M_{1+2}$, $M_3$) attaining wing margin; cell $dm$ present or absent; two cubital veins ($CuA_1$, $CuA_2$) attaining wing margin; two anal veins ($A_1$, $A_2$) attaining wing margin. **Male Hypopygium:** 9th tergite (9t) and sternite (9s) separated by lateral division, 9s reduced to a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostyle bifid, dorsal gonostyle heavily sclerotized falcate rod, ventral gonostyle bulbous with a basal rostral prolongation equipped with a variable number of spines, typically 1-8; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

**Discussion.** The genus *Rhipidia* is based on the pectinate condition of the adult antennae. This character is a weak group defining character as it is shared by other genera with produced flagellomeres. An additional character that may separate *Rhipidia* from other genera with produced antennae is the presence of greater than three rostral spines placed on the rostral projection of the ventral gonostylus. The genus is most similar to *Zelandoglochina* Alexander of the Neotropical Region with whom it is separated by the length of the rostrum. Further revision is needed to better define the limits of this genus.
**Rhipidia subgenus Eurhipidia Alexander**

Reference: Alexander (1965a)

**Type species:** *Rhipidia rostifera* Edwards

**Discussion:** The species of *Rhipidia (Eurhipidia)*, like *R. (Rhipidia)*, are generally similar in structure to *Dicranomyia*. The males have produced flagellomeres into a bipectinate condition. *Rhipidia (Eurhipidia)* is separated from *R. (Rhipidia)* by: 1) the variable number of antennal articles, 11-14 in *R. (Eurhipidia)* and 14 in *R. (Rhipidia)*, 2) a generally smaller size, 3) the absence of the discal cell (*dm*), and 4) rostral projection of the ventral gonostyle with two spines arising from a common enlarged basal tubercle.

**Rhipidia subgenus Rhipidia Meigen**

Reference: Meigen (1818)

**Type species:** *Rhipidia maculata* Meigen

**Discussion:** *Rhipidia (Rhipidia)* is a group of 189 species that are characterized by the elongation on the flagellomeres into a serrate to pectinate condition. The flagellomeres lateral extension at its extreme has a length that exceeds that of the corresponding segment, but may be suppressed to a condition where it is hardly serrate, much as in *Dicranomyia*. The characteristics of wing venation and male genitalia are similar to those of *Dicranomyia*, differing in the highly variable number of rostral spines found on the rostral projection of the ventral gonostyle, which commonly number between 3-8. *Rhipidia (Rhipidia)* is separated from *R. (Eurhipidia)* by the number of flagellomeres, 14 in *R. (Rhipidia)* and 11-14 in *R. (Eurhipidia)*, and presence of the discal cell, present in *R. (Rhipidia)* and absent in *R. (Eurhipidia)*.
**SIVALIMNOBIA** Alexander 1963

Reference: Alexander (1963)

Type species: *Sivalimnobia fortis* (Brunetti) (as *Dicranomyia*)

**Diagnosis:** Head: Anterior vertex reduced to a thin strip; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less that or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles; basal flagellomeres oval, distal segments becoming elongate. Wing: Coloration of cell and veins variable; stigma present or absent; anal angle of wing present, slightly constricted. Wing Venation: *Sc*₁ aligned or slightly removed from *Sc*₂; both elements ending at or after the origin of *Rs*; *Rs* origin near wing midlength; *R₁+₂* in near general alignment with *R₂*; two branches of *Rs* (*R₃+₄, R₅*) attaining wing margin; two medial veins (*M₁+₂, M₃*) attaining wing margin; discal cell (*dm*) present; *CuA* crossvein entering *M* near split of *M*; two cubital veins (*CuA₁, CuA₂*) attaining wing margin; two anal veins (*A₁, A₂*) attaining wing margin. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s present as small patch with setation; posterior margin of 9th tergite simple to medially excavated by the expansion of lateral margins; ventromedial lobe of gonocoxite present; gonostylus bifid, styles subequal; dorsal style a slender falcate sclerotized lobe, ventral style typically a bulbous lobe, equipped with two accessory lobes, a slender basal spine and a slender rostral projection that has a triangularly produced apex equipped with a single stout spine; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.
**Discussion:** The genus *Sivalimnobia* is based solely on a male genitalic character, namely the production of the rostral projection of the ventral gonostylus into a narrow elongate arm that is equipped with a basal spine and an apical spine that give the apex of the projection a triangular appearance. The separation of rostral spines is similar to that of *Achyrolimonia*, however the two genera are separated by the reduction of mouthparts (rostrum, labial palpus, maxillary palpus) in *Achyrolimonia*, with the mouthparts fully produced in *Sivalimnobia*.

**THRYPITICOMYIA Skuse 1890**

**Reference:** Skuse (1890)

**Type species:** *Thrypticomyia aureipennis* Skuse

**Diagnosis:** *Head:* Anterior vertex wide; rostrum length less than that of the remaining head; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, its length less than or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. *Antennae:* 14 articles; flagellomeres variable (oval, cylindrical, or moniliform); verticils of flagellomeres long. *Wings:* Subhyline, coloration of wings variable; cells without macrotrichia; wing base cuneiform, anal angle of wing greatly reduced. *Wing Venation:* Basal crossveins in near alignment with arculus (*ma*); *Sc*₂ removed from or in alignment with *Sc₁*, both elements ending before origin of *Rs*; *Rs* origin near wing midlength; *R₁₂* variable, typically subequal to *R₂*; tip of *R₁₂* may be atrophied to a spurious element; two branches of *Rs* (*R₃₄*, *R₅*) attaining wing margin; two medial veins (*M₁₂*, *M₃*) attaining wing margin; cell *dm* present; distal wing cord not in alignment; two cubital veins (*CuA₁*, *CuA₂*) attaining wing margin; two anal veins (*A₁*, *A₂*); attaining wing margin. *Male Hypopygium:* 9th tergite (9t) and sternite (9s) separated by lateral division, 9s present adhered to aedeagus without setation; posterior edge of 9t
commonly excavated medially; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid; dorsal gonostyle a heavily sclerotized falcate rod, ventral gonostyle bulbous with a basal rostral prolongation equipped with two spines; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

Discussion: *Thrypticomyia* is based on the cuneiform wing base and near alignment of interanal crossveins with the wing arculus (*ma*). The remaining genera of Limoniinae do not show such an alignment and instead have the internal crossveins in non-alignment and typically located basal to the arculus. *Thrypticomyia* is additionally separated from other genera that possess a cuneiform wing base (*Euglochina, Doaneomyia, Peripheroptera*, and *Pseudoglochina*), in lacking the distal wing elements compressed as in *Euglochina*, the presence of vein *A*₂ which is absent in *Doaneomyia*, not having a broadly rounded wing apex as in *Peripheroptera*, and the presence of cell *dm* which is absent in *Pseudoglochina*.

**TRICHOLIMONIA** Alexander1965

Reference: Alexander (1965a)

Type species: *Tricholimonia congensis* (Alexander) (as *Limnobia*)

Diagnosis: Head: Anterior vertex; rostrum subequal to less than head length; labial palpus weakly two segmented, length less than that of rostrum; maxillary palpus five segmented, length less than or subequal to that of head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles, flagellomeres oval to elongate-oval. Wings: Subhyline, additional coloration in wing cell and along veins common; cells with macrotrichia in stigma, infrequently in the outer ends of apical wing cells; wing not narrowed at wing base, anal angle of wing present. Wing Venation: *Sc*₂ not removed from *Sc₁, Sc₁* ending between origin
and split of $Rs$; $Rs$ long, its origin at wing midlength; $R_{1+2}$ and $R_2$ subequal in near alignment; two branches of $Rs$ ($R_{3+4}, R_3$) attaining wing margin, their tips generally drawn ventrally at wing margin; two medial veins ($M_{1+2}, M_3$) attaining wing margin; discal cell ($dm$) present; $CuA$ crossvein near wing midlength; two cubital veins ($CuA_1, CuA_2$) attaining wing margin; two anal veins ($A_1, A_2$) attaining wing margin. **Male Hypopygium:** 9th tergite (9t) and sternite (9s) separated by lateral division, 9s adhered to aedeagus without setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostylus bifid, dorsal style a decurved sclerotized rod, ventral style bulbous with a small basal rostral projection that is equipped with two rostral spines placed on the ventral face of projection; parameres weakly to strongly pointed and falcate at apex; aedeagus simple or equipped with lateral flanges, narrowed at the apex with two terminal openings; proctiger simple, without modification.

**Discussion:** *Tricholimonia* is a small group of species from Africa and Madagascar based at least in part by the ornate appearance of the adult fly. Morphologically the group is based on the presence of setation in the wing stigma (shared with *Lasiolimonia, Metalimnobia*, and some *Dicranomyia*) and the structure of the male hypopygium, namely the two rostral spines of the ventral gonostylus placed on the ventral face of the rostral projection. The wing venation of the group is similar to many other genera of Limoniinae in having $Sc_1$ and $Sc_2$ in close proximity and ending at the midlength of $Rs$.

**ZELANDOGLOCHINA Alexander 1924**

**Reference:** Alexander (1924)

**Type species:** *Zelandoglochina huttoni* (Edwards) (as *Dicranomyia*)

**Diagnosis:** *Head:* Anterior vertex of head present, not as thin strip; rostrum length less than that of the remaining head, infrequently longer than head; labial palpus weakly two
segmented, length variable often much longer than remaining head; maxillary palpus two to five segmented, its length less that or subequal to that of remaining head; basal palpomere reduced, remaining palpomeres subequal. Antennae: 14 articles; flagellomeres variably produced, bipectinate, unipeptinate, or subpectinate (female flagellomeres less-developed), distal section of flagellomeres reduced to thin petioles. Wing: Subhyline, typically patterned with darker areas; stigma present or absent; anal angle of the wing present. Wing Venation: \( Sc_1 \) only slightly removed from \( Sc_2 \); both elements ending near origin of \( Rs \); \( Rs \) origin near wing midlength; \( R_{1+2} \) in near alignment with \( R_2 \); two branches of \( Rs \) \(( R_{3+4}, R_5 \)) attaining wing margin; two medial veins \(( M_{1+2}, M_3 \)) attaining wing margin; cell \( dm \) present, rarely absent; two cubital veins \(( CuA_1, CuA_2 \)) attaining wing margin; two anal veins \(( A_1, A_2 \)) attaining wing margin. Male Hypopygium: 9th tergite (9t) and sternite (9s) separated by lateral division, 9s reduced to a small patch with setation; ventromedial lobe of gonocoxite present as a simple lobe; gonostyle bifid, dorsal gonostyle heavily sclerotized falcate rod, ventral gonostyle bulbous with a variable basal rostral prolongation equipped with a variable number of spines, typically 1-4; parameres weakly to strongly pointed and falcate at apex; aedeagus simple with two terminal openings; proctiger simple, without modification.

Discussion: Zelandoglochina is a variable group that holds similarities to the genera Rhipidia, Dicranomyia, and Geranomyia, with the exact limitations of the genus questionable. The wing venation is of a general type with \( Sc_1 \) placed near \( Sc_2 \), and ending at or near the origin of \( Rs \). Zelandoglochina generally resembles Geranomyia in the having their labial palpus produced to a length subequal to longer than the head length, but is separated by having the rostrum shorter than the remaining head (subequal to the remaining head in Geranomyia). The antennae of Zelandoglochina show similar variation to Rhipidia,
with the apical flagellomeres reduced to a slender petiole. Additional revision is need on this genus to better delineate its boundaries.

3.3.2 Questionable Limoniini genera

AMPHILIMNOBIA Alexander 1920

Reference: Alexander (1920)

Type species: Amphilimnobia leucopeza Alexander

Discussion: The subgenus Amphilimnobia was erected and is maintained for a single species, D. leucopeza, from Africa based on a damaged holotype specimens. The basis for the group are 1) the small, subterminal, and untoothed claws, 2) features of the male and female genitalia (not explicitly stated), and 3) very long Sc1 which ends opposite crossovein R2. I have not viewed this holotype specimen, but a lack of complete antennae in this specimen raises questions of whether this genus is truly within the Limoniini, especially with the comment in the description that compares the male genitalia to the genera Dicranoptycha and Helius.
Table 1. Genera and subgenera of the tribe Limoniini (Limoniinae; Limoniidae).
Taxonomic changes are made by elevation to genus from subgenus of Atypophthalmus (1), Dicranomyia (2), Libnotes (3), and Metalimnobia (4).

<table>
<thead>
<tr>
<th>Genus</th>
<th>Subgenus</th>
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<td>Zelandoglochina</td>
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1. Chang et al., 2012.
2. Laosa et al., 2014.
3. Theischinger et al., 2015.
4. Savchenko et al., 2016.
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<th>Genus</th>
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Table 3. Genera and subgenera of the Subfamily Elephantomyinae (Limoniiidae)

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Table 4. Genera and subgenera of the Subfamily Lipsothrixinae (Limoniidae)

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Table 5. Unplaced genera of Limoniidae (Tipuloidea).

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<td>(Trentepohlia) Bigot</td>
</tr>
<tr>
<td><em>Trichoneura</em></td>
<td>Loew</td>
</tr>
<tr>
<td><em>Trichoneura</em></td>
<td>(Ceratolimnobia) Alexander</td>
</tr>
<tr>
<td><em>Trichoneura</em></td>
<td>(Trichoneura) Loew</td>
</tr>
<tr>
<td><em>Trichoneura</em></td>
<td>(Xipholimnobia) Alexander</td>
</tr>
<tr>
<td><em>Xenolimnobia</em></td>
<td>Alexander</td>
</tr>
</tbody>
</table>
3.5 References

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CHAPTER 4: EVALUATING CRANE FLY (DIPTERA; TIPULOIDEA)

TAXONOMIC RICHNESS AND COMMUNITY ASSEMBLAGE IN A

BIODIVERSITY HOTSPOT

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(for submission to BIODIVERSITY AND CONSERVATION)

4.1 Abstract

Crane flies (Limiioniidae; Limoniinae) were sampled at national parks across central to
northern Thailand to observe patterns of species richness and turnover in this southeast Asian
biodiversity hotspot. Sixty-six morphospecies from 28 genera were collected with light
trapping and Malaise trapping and identified with the multi-access taxonomic key designed
for this project. Eighty total species are projected to be collected using richness estimators
with mountainous northern Thailand projected to have the highest diversity. The fauna of
Thailand was stratified between the north and the south, with the north generally composed
of more typically temperate genera and the south composed of more tropical genera. The
increased diversity in northern Thailand was influenced by topology, with faunal
assemblages changing across the latitudinal gradient of the north and providing more similar
faunas at elevation between mountain ranges than within national park regions.

Key Words: Tipuloidea, Limoniinae, Thailand, inventory, species diversity, community
assemblage
4.2 Introduction

Tropical insect faunas are known to be extraordinarily diverse, but remain largely under-sampled for a majority of taxonomic groups (Godfray et al. 1999). Within well-studied tropical insect faunas there exists a tendency for increased attention for either pestiferous taxa or charismatic entomofauna, that is insects which are large, ornate, and typically with well known taxonomy. Even for these well-studied groups, there is a general lack of fundamental biological and ecological information pertaining to natural history and geographic distribution (Novotny et al. 2002; Lewis and Basset 2007). The species diversity of the remaining non-charismatic tropical entomofauna likely dwarfs that of these better-studied groups and includes many insects that play integral ecological roles in environmental processing and food web dynamics (Kremen et al 1993; Nee 2004; Rohr et al. 2007).

Estimating species richness and understanding the impact of biotic and abiotic factors on the observed richness are critical in conservation biology, and especially important in biodiversity hotspots where elevated richness is coupled with increased rate of habitat destruction (Myers 1988; Myers et al. 2000). With this in mind, a goal of tropical insect research should be to document patterns in diversity and community structure (Basset et al. 1998). Understanding the ecological and distributional dynamics of hyperdiverse taxa will allow for monitoring of critical components of ecosystem functioning and may more efficiently detect environmental impact due to anthropogenic causes (Hilty and Merenlender 2000; Rohr et al. 2007).

Adequate taxonomic information is of primary importance when utilizing insects for ecological monitoring and conservation planning (Hilty and Merenlender 2000; Isaac et al. 2004; Mace 2004). The inventory of insect faunas across much of the tropics, especially the
non-charismatic fauna, is limited due to a lack of taxonomic tools and a decrease in taxonomic expertise. This loss of taxonomic integrity is greatly accelerated in large part due to the current taxonomic impediment (Taylor 1976). This taxonomic inadequacy greatly limits our ability to identify many insect groups to a meaningful level of resolution, resulting in incomplete food web reconstructions (Godfray et al. 1999) and the danger of species being lost before they have been documented (Lawton and May 1995).

This study examines the taxonomic richness and community assemblage of crane flies (Diptera; Tipuloidea) as a step towards elucidating potential determinants of species distribution and biogeographic affinities. With over 15,000 described species, crane flies represent the most species rich family of Diptera, itself being one of the four hyperdiverse insect orders (Lepidoptera, Hymenoptera, Diptera, Coleoptera). This globally distributed family occupies a wide range of habitats, both terrestrial and aquatic, that range from tundra to tropical forest, and often play an important role in environmental processing and nutrient cycling (Pritchard 1983). Outside of well-studied areas (North America and Europe), the diversity of this group is largely contained as point locality data with further distributional information lacking due to a paucity of taxonomic tools for species identifications. Although the biological affinities and geographic distributions remain poorly understood for the great majority of crane fly taxa, species with restrictive biology (Godfrey 2000, 2001; Rotheray 2000) or strict habitat associations with unique habitats (Salmela & Ilmonen 2005) indicate that some species may represent important indicator taxa. Within the tropics, however, the study of this ecologically diverse group is hindered because of its notorious reputation for taxonomic difficulty at all levels of classification and a lack of basic taxonomic tools for specimen identification (see Papp et al. 2006).
Here we examined the richness and community assemblage of Limoniinae crane flies (Diptera; Limoniidae) in Thailand while producing taxonomic tools for this and future specimen identifications. The subfamily Limoniinae represents one of the largest monophyletic crane fly clades (>5,000 spp.) and is made up largely of detritivorous species with aquatic or semi-aquatic larval forms. The fauna of Thailand, like much of the Oriental Region, is poorly studied and prior to this study was represented by only 18 species in 10 genera (Oosterbroek 2007). Other systematic crane fly inventories of equally sized or smaller temperate areas have shown much greater diversity (42 spp. Tennessee/North Carolina, USA [Petersen et al. 2005]; 55 spp. Pennsylvania, USA [Young & Gelhaus 2000]; 22 spp. Ohio, USA [Foote 1956]) and indicate that the crane fly faunal diversity of Thailand is undoubtedly greatly underestimated. The purpose of this project was to estimate the potential species richness for Thailand, examine the efficiency of different collection methodologies, and characterize the community assemblages and distributional patterns of crane flies across a network of protected forests in Thailand.

4.3 Methods and Materials

4.3.1 Study area

Thailand represents an area of increased faunal biodiversity and endemism that is coupled with high rates of habitat degradation and forest loss (Wilson 1988; Mittermeier et al. 1998; Meyers et al. 2000). Located in the Indo-Burma Hotspot, which ranges from Nepal to Malaysia, Thailand’s diverse geologic and biogeography history has resulted in a flora and fauna that represents a biotic interface between major biogeographic regions. This project focused on collections made adjacent to lotic habitats located in protected national parks throughout central and northern Thailand (Figure 1; Table 1). These national parks are
situated around the central Chao Phraya River basin, along the Thanon Thongchai Range of northeastern Thailand (Doi Suthep, Khlong Lan, Doi Intanion, Mae Ping National Parks), the Phetchabun Range of north-central Thailand (Na Heaw and Phu Hin Rong Kla National Parks), and Dongrak Range of the central Thailand (Khao Yai National Park).

4.3.2 Sampling methods

Collections were made using both light traps and Malaise flight intercept traps. Light trap sampling was conducted at dusk adjacent to target streams using mercury vapor and black light methods. Mercury vapor lamps were run at dusk with the light source placed over a suspended white sheet. Mercury vapor lamps were operated for 2 hours with attracted flies collected off of the sheet and into vials of 70% ethanol. Standard wand black lights were placed over a pan of soapy water and operated overnight. Collected contents were later rinsed and transferred into 70% ethanol. Malaise trap collections were using 2-meter standard wet head Malaise traps placed alongside target streams. Insects were collected into jars of 70% ethanol with collected samples emptied on average every two weeks. Samples were grouped into three different categories, those originating from light trapping (NLT; northern light trapping), those originating from only Malaise trapping (KYMT; Khao Yai Malaise traps), and one site with samples from both collection types (COMB; combined sampling) (Table 1). The NLT sites were used to characterize the community assemblage of the mountainous northern region of Thailand, the KYMT were used to categorize the community assemblage of a mountainous region of central Thailand, and the COMB site was used to offer comparisons between sampling methods. The combination of all sampling sites (NLT, KYMT; COMB) is coded as ALL.
4.3.3 Sample processing

Insects were sorted to the family level at either Chiang Mai University or Kasetsart University in Thailand, with final sorting of crane fly specimens to genus and morphospecies at Iowa State University. The subfamily Limoniinae used here is as defined by the World Catalog of Crane flies (Oosterbroek, 2007) except for the inclusion of the genera Atarba Osten Sacken and Atarbodes Alexander and changes to the taxonomic nomenclature used for generic and subgeneric levels of resolution. Specimens were identified to genus and subgenus using the Key to the Adult Limoniinae Crane Flies of the Oriental Region, version 2.0 (Petersen, 2007) constructed for this project. The key was constructed from a coded character matrix using Lucid© taxonomic key building software. Characters used for specimen identification were based primarily on wing venation and characteristics of the male hypopygium. Many taxonomic divisions are based on traits of the male and are not found in the corresponding female, resulting in a number of female specimens not being identified during this investigation. Specimens were identified to morphospecies based on the recommendations of Krell (2004) by M.J. Petersen and are housed at the Department of Entomology collection at Iowa State University. Morphospecies are here described as separation of specimens into discrete recognizable groups based on morphological and/or coloration patterns.

4.3.4 Data analysis

Potential richness was estimated for NLT, KYMT, and Thailand (ALL) using both parametric estimators (ICE, Chao 2) and an asymptotic model (MMMeans) using EstimateS 8.0.0 (Colwell, 2006), with sample input order randomized 100 times. Different individual sampling events (blacklight, pan trap, Malaise trap) do not produce equal sampling effort per
collected sample and were expected to accumulate specimens at equal rate. Therefore a
measure of accumulated individuals was utilized as the index of accumulation. Sampling
completeness was determined by estimating the number of additional species needed for the
constructed collection curve to reach an asymptote.

Individual NLT sampling locations received different sampling intensities in the form
of total sampling events per site (Table 1). All sites received at least two sampling events
each occurring during the peak on adult fly emergence (February-June; September-
December), but some sites received up to 6 total sampling events. Biased sampling may
skew the observed community assemblage of a site by either artificially inflating or under-
representing the morphospecies from a site. An ANOVA as implemented using JMP 6.0©
was performed in order to address any potential effect of number of samples taken per site on
the number of morphospecies collected. Significance was tested at the P=0.05 level.

Nonmetric multidimensional scaling (NMDS) in R-project (R Development Core
Team 2004) with the vegan package was used to examine relationships among the
community assemblages of northern Thailand (NLT sites) and for all sites combined (ALL)
at both the morphospecies and generic level. The similarity matrix used in NMDS was
constructed using the Canberra index based on morphospecies and generic levels of
taxonomic resolution. Abiotic factors (latitude, longitude, elevation) were fit to the
constrained ordination using the envfit option and run with 9999 permutations. Significant
correlations between factors and community structure were determined at P < 0.05 level.

We first evaluated whether sampling protocol affected the trap composition at either the
specific or generic level of taxonomic resolution using the COMB sampling location. The
COMB sampling utilized both collection protocols from a common location and allowed for
comparison of the two different sampling protocols from a common faunal pool. It would be expected that two different sampling methods would collect a similar subset of a shared fauna if there were no sampling bias between the methods. A sampling bias would be observed if the trap composition from either method were more similar to that of the same method from another location. Effects of sampling protocols were evaluated by conducting a cluster analysis utilizing the Canberra similarity index and Ward's linkage criteria using R-project (R Development Core Team 2004). All sites (NLT, KYMT, COMB) were included in the cluster analysis and individual analysis runs were conducted for both morphospecies and generic data. If either morph-species or generic data resulted in the COMB sites being separated and grouped by methodology rather than location a bias was recorded and not analyzed further at that level.

4.4 Results

4.4.1 Observed diversity

Collections from all sampling techniques resulted in a total of 647 specimens representing 66 morphospecies from 28 genera/subgenera. Twenty genera were collected from Thailand for the first time and eight previously known genera from Thailand were recollected during this sampling (Table 2). One genus of Limoniinae, *Limonia* Meigen, which was previously recorded from Thailand was not recollected. Details of morphospecies lists for individual sites are available through the corresponding author. Light trapping resulted in greater diversity than Malaise trapping and was responsible for 70% of all collected morphospecies. The number of morphospecies collected during the NLK sampling was not significantly influenced by number of sampling events per site ($P=0.1128$; $R^2=0.2554$). The proportion of unique morphospecies at each site was positively correlated
with elevation ($P=0.007; R^2=0.6175$), with high elevation sites containing a greater proportion of total morphospecies as unique to that site (Table 3).

**4.4.2 Estimated Diversity**

Collection curves from individual sampling protocols and ALL (Figure 2) each failed to reach asymptotes. Asymptotic estimators indicate that ALL (94% complete) and the KYMT sampling (95% complete) are very near completion while the NLT light sampling was 88% complete (Table 4). Non-parametric estimators, which are partially influenced by the presence of species represented by one or two specimens, provided higher estimates of potential richness (Table 4). All sampling events did show a reduction of singleton numbers with increased sampling, including a marked decrease at KYMT. Singleton morphospecies represented 30% of total collected morphospecies in NLT sampling and 25% of morphospecies for both KYMT and ALL samplings.

**4.4.3 Collection methods**

Cluster analyses based on specific and generic data provided different topologies (Figure 3). The two sampling techniques from COMB, 2.1 (Malaise trap) and 2.2 (light trap), were separated in the morphospecies analysis, grouping the 2.1 trap with the Malaise traps from KYMT sampling (Figure 3a) and 2.2 trap with other light-trapping locations. When analyzed based on the generic data, the two sampling techniques used at the COMB site clustered together and not by sampling technique (Figure 3b). The differential clustering likely indicates a sampling bias between the two protocols, with each technique retrieving different subsets of morphospecies from a common faunal pool. A similar bias is not observed when viewed at the coarser generic level of taxonomic resolution. This result
indicates that the generic level is a more appropriate level by which to compare the community assemblage collected using different sampling methodologies.

### 4.4.4 Regional faunas

Observation of the Thailand fauna (ALL) showed a separation of KYMT collections from all other sites (Figure 5) and indicated the presence of distinct northern and central faunas. Changes in generic community assemblage were significantly correlated with latitude \( (P=0.006) \) and longitude \( (P=0.049) \) but was not correlated with elevation \( (P=0.488) \) (Table 5). Northern sites (BLK) were generally dissimilar in community assemblage caused by a large number of morphospecies unique to individual sites. The BLK sites did not group strictly by geographic distance or national park, but instead responded to the landscape and altitudinal profiles of the region (Figure 5) showing significant correlations with both elevation \( (P=0.0002) \) and latitude \( (P=0.034) \) (Table 4). Locations were strongly divided between sites located above 1000 m and less than 1000 m elevation. The BLK sites showed a homogenous generic composition, with no significant correlations observed among abiotic variables and community assemblage (Table 5).

### 4.4.5 Biogeographic affinities

The majority of collected taxa were from genera with widespread global distributions that find their highest species richness in the lower latitudes (Oriental and Neotropical) (Table 2). The remaining genera were divided into two patterns of distribution, those that are either strongly represented in the Holarctic and weakly in the lower latitudes (‘temperate’), or those strongly represented in the Australian/Oceanic Region and weakly in other biogeographic regions (‘tropical’) (Table 2). Northern Thailand is largely comprised of both widespread and ‘temperate’ genera, while central Thailand is comprised of widespread and
‘tropical’ genera. Most evident in the north of Thailand is an influence of genera such as *Geranomyia* Haliday and *Antocha* Osten Sacken that are more typical to the Holarctic Region. Although not limited to the higher latitudes, their presence in the lower latitudes is typically limited to higher elevations. In central Thailand, a ‘tropical’ influence can be seen in the presence of genera such as *Laosa* Edwards, *Libnotes* Westwood, *Neolibnotes* Alexander, and *Pseudoglochina* Alexander. These groups are largely limited to lower latitudes and rapidly become less diverse at both higher latitudes and elevations.

**4.5 Discussion**

This is the first systematic inventory of a tropical crane fly community and provides valuable insight into the taxonomic diversity of a tropical environment and the causative agents acting to produce this diversity. When compared to other structured inventories, we discovered a richer crane fly fauna than any temperate survey that covered either similarly sized sampling areas (Young & Gelhaus 2000) or was comprised of more intensive sampling protocols (Petersen et al 2005). Uncovering a pattern of increased biotic diversity within the lower latitudes is not unexpected and has been reported for many taxonomic groups (Rozenweig 1995; Brown & Lomolino 1998; Willig et al 2003). By comparing the faunal assemblages of similar habitats within the protected forested areas of disjunct national park fragments we found that the assemblage of species in central and northern Thailand are affected by both landscape and the position of Thailand in an area of biotic interface that crosses biogeographic regions. Both factors produce gradients that influence the observed biota, with changes in altitude and topography creating a rapid change over short distances and changes in latitude creating gradual changes over long distances (Hodkinson 2005).
It is unexpected that a regional inventory will recover the entire pool of potentially available species within the study area. Therefore the ability to provide estimates of collection success and identify sampling success or bias will benefit future endeavors (Lewis and Basset 2007). The richness estimates offered here, while greater than those of previous studies, are still low-end approximations for Thailand that are likely to underestimate its true species richness because of geographic, biological, and methodological criteria. From a geographic standpoint, it is important to note that this sampling was limited to: 1) areas adjacent to aquatic systems and 2) central and northern Thailand. The estimates provided here apply only to this portion of the Thailand, meaning the exclusion of large expanses of southern peninsular Thailand and eastern Thailand that are likely to contain unrecorded species and genera. From a biological standpoint, the known immature life stages of Limoniinae crane flies are predominantly aquatic or semi-aquatic, but do contain species that occupy purely terrestrial habitats. The terrestrial genus *Limonia*, which was previously known from Thailand, was not recollected in this study and provides indication that the terrestrial fauna was not strongly sampled in this project. The objective of this project was collections in riparian habitats, and terrestrial areas not in close proximity to aquatic resources are likely to provide new unrecorded taxa. Finally, the indication that the two sampling protocols employed here yielded different morphospecies compositions suggests that the use of either technique alone may underestimate total richness. The enhanced richness shown in COMB sampling provides evidence that a combination of sampling techniques will provide a better estimate of taxonomic richness and both techniques should be used in future studies.
While the Thai fauna is largely dominated by genera with widespread distributions, the protected areas sampled in this study show separation of two faunal components along a longitudinal gradient. These faunas correspond to both a ‘tropical’ southern fauna and a ‘temperate’ northern fauna. Local community assemblages will be comprised of elements of surrounding regional species pools, which are in turn, affected by large-scale biogeographic processes (Ricklefs and Schluter 1993; Morin 1999; Webb et al. 2002; Wiens and Donoghue 2004). The incorporation of surrounding taxa pools into these two faunal types corresponds to landscape variables largely explained by the complex geologic history of this Southeast Asia (Hall 1998), resulting in the confluence of two fauna corridors. The mountainous north of the country is an extension of a continuous mountain range extending from Nepal through southwest China, northeastern India, and Myanmar into northern Thailand. This range acts as a faunal corridor incorporating Holarctic elements into a region of tropical rain forest that extends farther north ($26^\circ N$) than any place on earth (Whitmore 1990). This meeting of these faunal assemblages has subsequently influenced the overall fauna of the region and resulted in the elevated diversity seen for the country as a whole.

An influence of elevation on insect richness and community assemblage has been illustrated for many insect groups (McCoy 1990; Hodkinson 2005; Petersen el al. 2005). The altitudinal gradient of northern Thailand, acting in a similar fashion to the longitudinal gradient of the country, filters the availability of species into the local community assemblage by altering climatic and habitat types with increasing altitude. The resulting fauna is more similar at comparable elevations than by geographic location. This change in community assemblage may help to explain the trend of increased taxonomic richness in northern Thailand observed in many different groups (owls, hawkmoths, tiger beetles, ...
Kitching 1996; *Lepidoptera*, Beck et al. 2007). When compared to other areas of southeast Asia, Beck et al. (2007) found that hawkmoths (*Lepidoptera; Sphingidae*) and other Lepidopteran families reached their greatest diversity in northern Thailand due to habitat heterogeneity and the mixing of temperate and tropical faunas. Because of inadequate sampling across much of southeast Asia, similar landscape comparisons can not be made for crane flies, however the high richness and change in community assemblages across this gradient when compared to that of central Thailand does indicates that a similar southeast Asian taxonomic hotspot could be found here.

The biological and physiological constraints and requirements of the vast majority of crane flies remain unknown. However both altitudinal and longitudinal gradients would be expected to exert a differential force on the immature and adult life stages both directly through a change in thermal profile, and through an indirect influence on vegetative assemblage and soil profile. The range limit of an insect species is determined by the capacity of the species to match its thermal tolerance range to the altitudinal temperature profile of its habitat (Hodkinson 1999). Although short lived and typically non-feeding, the adult life stage of crane flies perform the essential duties of reproduction and deposition of fertilized eggs in suitable larval habitat. These gradients affect survivorship in numerous ways, including the abilities of the adult fly to thermoregulate, reach flight potential, locate mates, and in some cases obtain floral resources (Mani 1962; 1968). Without adult survivorship the incorporation of any species into the local community assemblage is impossible. Because the majority of crane fly life span is contained in the larval stage, it is expected that climatic factors would act largely here. In a terrestrial setting, increased elevation has been shown to influence microhabitat in the form of soil composition, soil
moisture, and organic content, all of which provide a more favorable crane fly larval habitat and increase species richness (Coulson & Whittaker 1978). A similar change in semi-aquatic and aquatic characteristics across an altitudinal gradient could be expected to act on habitat suitability within these systems. With very little known about the habitat and climatic requirements of crane flies, increased attention should be aimed at better understanding the biotic and abiotic factors acting to determine species distributions.

A major limitation to the cataloging of many faunal groups is the disparity between the location of taxonomic expertise and the epicenters of taxonomic richness presented by their group of study. Such taxonomic “hotspots” are often areas of conservation importance where the ability to identify the flora and fauna are most limited due to the absence of adequate taxonomic tools. This dichotomy stagnates our ability to adequately infer ecological niches, community assemblage, and faunistic distribution. The investigation of sampling methodology and factors influencing community assemblages as well as the production of easily disseminated taxonomic resources will serve to bridge this taxonomic divide by providing a framework that will benefit future taxonomic endeavors in this region. This increase of data flow will help to further conservation efforts by offering a better understanding of diverse faunas by identifying areas of increased taxonomic richness, endemism, and causative effects that determine the observed community structure.
Figure 1. Sample locations in Thailand. National parks and research centers where sampling was conducted, with designation of sampling type (NLT=light trapping, KYMT=malaise trap, COMB=light trapping and malaise trapping): Khao Yai NP (1: KYMT), Phu Hin Rong Kla (2: COMB, NLT), Na Heaw NP (3: NLT), Doi Luang NP (4: NLT), Chiang Dao Research Center (5: NLT), Doi Inthanon (6: NLT), Wieng Ko Sai NP (7: NLT), and Khlong Lan NP (8: NLT).
Figure 2. Accumulation curve for crane fly sampling in Thailand. A species accumulation curve created using EstimateS is plotted showing accumulated morphospecies (ALL) plotted against accumulated specimens. Also plotted are curves for nonparametric estimators (ICE; Chao2) and morphospecies collected as singletons (S) and doubletons (D).
Figure 3. Cluster analyses of all sampling sites using morphospecies and genera/subgenera. Dendograms are shown for analysis run on morphospecies (A), and genus (B) data. Sites from combined sampling (COMB) are designated with an asterisk (*).
Figure 4. Non-Metric Multidimensional Scaling (NMDS) projection of sampling sites in northern Thailand based on morphospecies community composition. Collection codes refer to Khao Yai NP (1), Phu Hin Rong Kla (2), Na Heaw NP (3), Doi Luang NP (4), Chiang Dao Research Center (5), Doi Inthanon (6) Wieng Ko Sai NP (7), Khlong Lan NP (8).
Figure 5. Non-Metric Multidimensional Scaling (NMDS) projection of all sites and based on generic community composition. Collection codes refer to Khao Yai NP (1), Phu Hin Rong Kla (2), Na Heaw NP (3), Doi Luang NP (4), Chiang Dao Research Center (5), Doi Inthanon (6) Wieng Ko Sai NP (7), Khlong Lan NP (8).
Table 1. Malaise trap collections from Thailand, 2000-2003. Details for sites used as collection locations are given along with collection type (MT=Malaise trap; LT=Light trap) and dates of activity when specimens were collected.

<table>
<thead>
<tr>
<th>Site</th>
<th>Trap Type</th>
<th>Collection Details</th>
<th>Lat / Long</th>
<th>Elevation (m)</th>
<th>Active Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>MT (KYMT)</td>
<td>Khao Yai National Park: Creek 2 km up Khao Khieo Road</td>
<td>14°22'N 101°24'E</td>
<td>950</td>
<td>vi.2000 – x.2001</td>
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<tr>
<td>1.2</td>
<td>MT (KYMT)</td>
<td>Khao Yai National Park: Huai Patabak (km29)</td>
<td>14°19'N 101°21'E</td>
<td>505</td>
<td>vi.2000 – x.2001</td>
</tr>
<tr>
<td>1.3</td>
<td>MT (KYMT)</td>
<td>Khao Yai National Park: Huai 'TaDapoo' above Namtok</td>
<td>14°24'N 101°22'E</td>
<td>745</td>
<td>vi.2000 – x.2001</td>
</tr>
<tr>
<td>2.1</td>
<td>MT (COMB)</td>
<td>Phu Hin Rongkla National Park; Huai Man Daeng Noi @ trail</td>
<td>16°57'N 101°03'E</td>
<td>1600</td>
<td>vi.2002 – v.2003</td>
</tr>
<tr>
<td>3.1</td>
<td>LT (NLT)</td>
<td>Na Heaw National Park; Namtok Tat Huang</td>
<td>17°33'N 100°59'E</td>
<td>500</td>
<td>9-10.iii.2002; 22.x.2002</td>
</tr>
<tr>
<td>5.1</td>
<td>LT (NLT)</td>
<td>Creek @ Chiang Dao Wildlife Research Center</td>
<td>19°21'N 98°55'E</td>
<td>520</td>
<td>26.i.2003; 24.xii.2002; 27.ii.2003; 27-28.xii.2002; 13.x.2002</td>
</tr>
<tr>
<td>6.2</td>
<td>LT (NLT)</td>
<td>Doi Inthanon National Park; Namtok Siripum (lower)</td>
<td>18°32'N 98°35'E</td>
<td>650</td>
<td>16-17.x.2002; 3.iii.2002</td>
</tr>
</tbody>
</table>
Table 2. Genera and subgenera found during sampling. Genera discovered during sampling of northern and central Thailand are listed. Listed below each sampling location are the number of species of each genus found at that location (KY= Khao Yai NP; PHR=Phu Hin Rongkla NP; NH=Na Heaw NP; DL= Doi Luang NP; CDW= Chaing Dao Wildlife Center; DI= Doi Inthanon NP; WKS= Wieng Ko Sai NP; KL= Khlong Lan NP)

<table>
<thead>
<tr>
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<th>CDW</th>
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<td>0</td>
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<td>Antocha*</td>
<td>0</td>
<td>6</td>
<td>2</td>
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<td>4</td>
<td>1</td>
<td>1</td>
</tr>
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* genera discovered for the first time in Thailand
1 genera that find their greatest species richness in the lower latitudes of the tropics but strongly represented in other biogeographic regions
2 genera found throughout the Oriental region but more common in northern latitudes or at higher elevations
3 genera more common in the Australian/Oceanic region but less common in the Oriental and Eastern Palearctic
Table 3. Morphospecies collected at light trap locations. The number and percentage of morphospecies collected by light trapping in northern Thailand as species unique to that location are given.

<table>
<thead>
<tr>
<th>Site</th>
<th>Morphospecies</th>
<th>Uniques</th>
<th>% Uniques</th>
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<td>2.2</td>
<td>17</td>
<td>8</td>
<td>47%</td>
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<td>2.3</td>
<td>6</td>
<td>2</td>
<td>33%</td>
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<tr>
<td>2.4</td>
<td>12</td>
<td>3</td>
<td>25%</td>
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<tr>
<td>3.1</td>
<td>5</td>
<td>1</td>
<td>20%</td>
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<tr>
<td>4.1</td>
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<td>5.1</td>
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<tr>
<td>7.1</td>
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<td>25%</td>
</tr>
<tr>
<td>8.1</td>
<td>5</td>
<td>0</td>
<td>0%</td>
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</tbody>
</table>
**Table 4. Estimated and realized morphospecies richness.** The number of observed (Sobs) morphospecies collected during light trap sampling (NLT), combined sampling at Phu Hin Rongkla (MT=Malaise trap; BLT=black light trap) and Malaise trap (KYMT) sampling are presented. Potential richness is estimated using asymptotic (MMMeans) and nonparametric (ICE; CHAO2) estimators.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Sobs</th>
<th>MMMeans</th>
<th>ICE</th>
<th>CHAO2</th>
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<tr>
<td>NLT</td>
<td>46</td>
<td>52</td>
<td>57</td>
<td>57</td>
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<tr>
<td>COMB</td>
<td>28</td>
<td>33</td>
<td>37</td>
<td>41</td>
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<tr>
<td>KYMT</td>
<td>20</td>
<td>21</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>All Sampling Combined</td>
<td>66</td>
<td>70</td>
<td>81</td>
<td>80</td>
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Table 5. Nonmetric multidimensional scaling correlations of abiotic factors with community composition. P

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<tr>
<th></th>
<th>$R^2$</th>
<th>$Pr(&gt;r)$</th>
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<td>Elevation</td>
<td>0.544</td>
<td>0.002**</td>
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<tr>
<td>Latitude</td>
<td>0.148</td>
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<td>Longitude</td>
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<td>Latitude</td>
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<td>Longitude</td>
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4.8 References


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CHAPTER 5: SYSTEMATICS OF THE CRANE FLY GENUS

*LIPSOThRIX* LOEW (DIPTERA; TIPULOIDEA)

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(in preparation for submission to ZOOTAXA)

5.1 Abstract

The life history, morphological attributes, and phylogenetic relationships of the genus *Lipsothrix* Loew are evaluated. Several novel characters are used to redescribe the adult life stage of the genus and define morphological variation within the group. The revised genus contains 31 valid species, including one new species description for *L. nullusarma* from India. The natural histories of *Lipsothrix* species are similar across the recognized taxa. European and North America species have broad geographic distributions while species outside of Europe and North American are poorly collected and represented in collections by few specimens. A phylogenetic hypothesis for the group is derived from a parsimony analysis using a matrix of coded adult morphological characters. The phylogenetic analysis recovered three major monophyletic groups, the basal Oriental *assamica* clade, a Western Palearctic *nobilis* clade, and a Western Palearctic and Nearctic clade (WP+N). The WP+N clade indicates that there has been significant faunal exchange between the two biogeographic regions and is hypothesized that exchange across the trans Beringian land bridge has occurred more than once.
5.2 Introduction

The world crane fly (Diptera; Tipuloidea) fauna may be described as well studied as a whole, due in large part to the expansive publications of Charles P. Alexander. This work resulted in over 11,000 of the 15,290 presently recognized described species (Oosterbroek 2008). While the alpha taxonomic knowledge and descriptions of individual species has greatly benefited from this work on the Tipuloidea, other aspects of basic taxonomy including higher-level classification, placement within the greater Diptera phylogeny, and adequate and complete specific and generic definitions remain under studied.

The problem of inadequate species and genus descriptions is increasingly important when species are used in conservation planning and environmental monitoring. One such genus, Lipsothrix Loew, has received increased attention in Great Britain where three species are used to assess woodland stream health (Godfrey 2003; UK Biodiversity Partnership 2008). Similar mandates of conservation status may be possible for the other species of this genus, however as with many crane fly species incomplete species descriptions and inadequate tools for species identification limit their potential.

The purpose of this taxonomic revision is to diagnose and redescribe the species of Lipsothrix. The generic and species resolution in this revision will provide details of the genus that will better facilitate placement of the genus within the Tipuloidea, provide descriptions by which to better delineate the valid species, summarize the natural history of the genus based on all valid species, and explore the phylogenetic relationships among these species.
5.2.1 Taxonomic history

The first species of *Lipsothrix* to be described were *L. errans*, *L. ignota* (later synonymized with *L. remota*), and *L. remota* by Walker (1848) as species of the now defunct genus *Limnobia*, and *L. icterica* (later synonymized with *L. errans*) as a species of *Trichostigma* by Egger (1863). The designation of the genus *Lipsothrix* did not appear until Loew (1873) offered the description of the female of *L. nobilis*, designating the genus on the presence of four Radial veins reaching the wing margin but only two medial veins reaching the wing margin, along with details of adult coloration. The genus was not immediately recognized, as Alexander (1916) described *L. sylvia*, Tonnoir (1921) described *L. clara* (later synonymized with *L. remota*), and Doane (1900) described *L. nigrilinea* all as species of the genus *Limnophila* Macquart. Usage of the generic descriptor *Lipsothrix* was later stabilized by Alexander (1928) with the transfer of *L. sylvia* to *Lipsothrix* from *Limnophila* and the description of *L. taiwanica* based on the elongate interbase of the male hypopygium. The subsequent concept of the genus has come to be defined by a suite of adult characteristics: 1) 14-segmented antennae, 2) tibial spurs lacking, 3) a reduced meron, 4) four Radial veins to the wing margin, 5) two medial wing veins to the wing margin, and 6) presence of an elongate interbase of the male hypopygium.

5.2.2 Taxonomic placement

*Lipsothrix* clearly belongs within the Limoniidae, being differentiated from the Cylindrotomidae by the absence of the prominent larval projections and four-branched Radial sector, from the Pediciidae by the lack of setiforms between the ommatidia and two branched medial sector, and from the Tipulidae by the number of antennal flagellomeres (14) and two branched medial sector (additional details in Alexander & Byers 1981; Oosterbroek
The placement of *Lipsothrix* within the classification of the Limoniidae has been problematic, having been placed in the Limoniinae, Limnophilinae, or Chioneinae subfamilies by separate authors. Early classifications of Edwards (1938) and Alexander (1916) noted similarities of the wing venation to that of Limnophilinae flies, indicating a close relationship. Later placements by Alexander (1942; 1967; 1981), Dienske (1987), and Savchenko (1989) placed *Lipsothrix* within the Chioneinae based on presence of 14 flagellomeres, $Sc_2$ lacking, four Radial veins the wing margin, and tibial spurs lacking. Later phylogenetic analysis of Oosterbroek and Theowald (1991) based on larval and pupal characters, and by Stary (1992) based on adult characters found a closer relationship of *Lipsothrix* to either the Limoniinae or to a clade consisting of Limoniinae, Cylindrotomidae, and Tipulidae. Recent work of Petersen and Bertone (*detailed in* Chapter 2) based on molecular (28S) and adult and larval morphological characters confirms the placement of *Lipsothrix* as a sister group to the Limoniinae (Limoniidae).

### 5.3 Methods and Materials

#### 5.3.1 Specimens

Specimens used in this revision originated from the author’s personal collections (2002-2005: east coast of the United States; 2007: west coast of the United States) and through generous loans. The following institutions provided valuable loaned materials used in this revision: The Natural History Museum, London (BM), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (MK), Academy of Natural Sciences, Philadelphia, Pennsylvania (ANSP), Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM),
California Academy of Sciences, San Francisco, California (CAS), Personal collection of Jaroslav Stary (JS), Personal collection of Andrew Godfrey (AG), University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ), and University of Kansas, Snow Entomological Museum, Lawrence, Kansas (KU).

Morphological terminology (Figs. 1-3) follows that of McAlpine (1981), Sinclair (1998), and Kotrba (1998) except where noted in the text. Descriptions of non-genitalic features of coloration, setation, and size were derived from research specimens available for each species. Material was limited to only the existing type material for a number of valid species, in these cases details of morphological attributes were derived from the type materials. Non-genitalic attributes were designated from the original published descriptions in instances where the body of the described specimen no longer exists and the type material is maintained on a mounted slide.

Illustrations were produced from cleared specimens stored in glycerin. Specimens were cleared in warm 10% KOH for a period of 5-10 minutes, rinsed with distilled water, and transferred into 50% alcohol before being moved through an alcohol series until brought up to 95%. Specimens in alcohol were then transferred to a mixture of 50% glycerin and 50% alcohol and allowed to sit until the alcohol had evaporated and the glycerin had permeated the specimen, after which specimens were transferred to clean glycerin.

5.3.2 Measurements

*Body length:* Measured from the tip of the rostrum to the apex of the abdomen. In instances where material was distorted, individual body sections (head, thorax, abdomen) were measured and summed. Description lengths are given as the mean length of all specimens with the observed range given in parentheses.
**Wing length:** Straight line measurement from the connection of the wing to the thorax to the wing apex. Description lengths are given as the mean length of all specimens with the observed range given in parentheses.

**Wing width:** Measured at the widest part of the wing, typically located at or in close proximity to the intersection of wing vein A₁ with the wing margin. Description lengths are given as the mean length of all specimens with the observed range given in parentheses.

**Antennal length:** Measured from the connection of the scape and head to the apex of the final flagellomere. The length of individual flagellomeres is given as a ratio of the flagellomere width to length. Description lengths are given as the mean length of all specimens with the observed range given in parentheses.

**Maxillary palpomere ratio:** Measured on palpomeres 2-5 and listed as a ratio of length to the shortest palpomere.

### 5.3.3 Genus and species concept

The concept employed here defines a genus as a group of evolutionary lineages, themselves comprised of individual species that share one or many group defining synapomorphies and are separable from other such lineages based on these shared traits. The goal of this approach is to create generic entities that represent monophyletic groups of independently evolving lineages that share a common ancestor and are distinguishable based on shared group traits. This definition is employed to eliminate the occurrence of genera comprising polyphyletic and paraphyletic groups. The genus *Lipsothrix* is here defined as a monophyletic evolutionary lineage defined by a combination of characters that are not shared by any other taxonomic groups within the Diptera or Tipuloidea. The species maintained
within the boundaries of this generic concept share the combination of characters as defined in the diagnosis of the genus.

The species concept adopted here is that of de Queiroz (1998; 2005) in which species represent separately evolving segments of metapopulation lineages. A metapopulation is defined as an inclusive population made up of a set of connected or separated subpopulations. A lineage, as defined at the population level, is a population extended through time or an ancestral-descendant series of time-limited populations. Speciation, or the process of new species formation, is then defined as the process of separation of the independent metapopulation lineages (de Queiroz 2005).

5.3.4 Species delineation

The methodology of species separation used here is based on a modified morphological species concept that separates species as specimens grouped on the shared possession of strong morphological attributes (e.g., number of aedeagal branches; wing vein configuration). Species were delineated into discrete groups based on the presence of defined morphological characters. In revising the species of this genus, previously identified specimens first had species identification labels covered and/or effectively removed in order to bring all material to a state of non-identification. Material was then separated into groups based on shared repeatable traits observed in the material. All specimens representing previously designated type material of existing species were then identified and the specific epithet of the type material was applied to the specimens in the group associated with each type material. The written descriptions of all previously recognized species of Lipsothrix were then evaluated to determine if the morphological attributes designated in the original description could be used to separate the groups formed in this revision. Groups that did not
correspond to any previously described species were established as new species. Groups that
maintained morphological attributes analogous to the original description were retained as
species and were provided with a redescription including a diagnosis of group defining
characteristics, a species description, and discussion. In cases where specimens of previous
species could not be separated from each other species were either combined and
synonymized, or in cases were substantial morphological variation occurred specimens were
grouped into species complexes.

Specimens from species complexes were then evaluated to determine if they could be
delineated into groups using both hierarchical clustering using Wards distance and average
linkage, and non-meteric multidimensional scaling (NMDS) using a dissimilarity matrix
computed using the Canberra index in R project (R Development Core Team 2004). The
dissimilarity matrix used in the ordination and clustering procedures was derived from
morphological characters gathered from all available specimens within species complexes
and scored as continuous quantitative characters. Characteristics of coloration were
measured using Adobe Photoshop based on images captured using a SPOT RT Slider camera
mounted on a Olympus SZX12 stereo microscope under identical camera settings. All body
measurement characters were standardized for differences in body size by dividing each
measurement by the total length of the specimen.

Specimens forming distinct groups using clustering and ordination methods were
categorized as potential species. The difference between the characters used to separate
groups during clustering and NMDS analyses were tested for significance using a
permutation test in Poptools (Hood 2000) by running 999 replicates of randomly assigning
group membership to a specimen and then testing for significant differences among group means for each character.

5.3.5 Seasonal emergence

The seasonal emergence of adult flies is determined from a consensus of all known collection dates. The presented adult distribution pattern is indicative of when adults have been collected and may not be representative of the entire emergence cycle of each species. In cases where only a single or two specimens have been collected for a species, the emergence for that species is presented as those dates.

5.3.6 Species distributions

The geographic distribution of each species was determined by gathering all known distributional records for all species. All georeferenced data records were mapped for each species. In cases where 10 or more georeferenced specimen locations existed, the potential distribution of the species was created with ecological niche modeling using DIVA-GIS v.5.4 (Hijmans et al. 2001), utilizing the WORLDCLIM 1.4 ecological dataset (Hijmans et al. 2005). Ecological niche modeling uses the ecological characteristics of the locations where specimens have been collected to extrapolate to areas that share similar ecological conditions and offer a similar ecological niche. This analysis uses the ecological constraints of a species to create a model that projects a potential range, this range may include areas both in which the species has and has not been previously been collected. The distribution mapped from this analysis is interpreted as all areas that offer at least 10% chance of species occurrence based on known collection locations. While the projection offered in this analysis likely displays an overestimate of the actual range of the species, it does provide inference into additional areas in which to focus future collection efforts.
5.3.7 Phylogenetic analysis

A cladistic analysis of *Lipsothrix* was conducted on the species determined to represent valid species units during the revision process (Table 1). Taxa that were represented by incomplete morphology (see *Species of Uncertainty*) were removed from the analysis due to a limited ability to score characters and the uncertainty of taxonomic validity. A character matrix that consisted of non-ordered discrete binary and multi-state coded characters was derived from adult male and female morphological characters (Table 5). Incomplete life stage association for the majority of species limited the ability to score all taxa for larval or pupal characters and these were therefore omitted from the analyses. The placement of *Lipsothrix* within the greater phylogeny of the Tipuloidea is unclear, and the most recent common ancestor of the genus is unknown. Three genera, *Rhabdomastix* Skuse, *Elephantomyia* Osten Sacken, and *Limnophilomyia* Alexander, which share similarities in both adult and larval morphology, as well as ecological natural history (larvae occurring in sodden wood) were chosen as outgroups to polarize the ingroup taxa.

Two separate analyses were run to evaluate the phylogenetic relationships between the species of *Lipsothrix*. The first analysis was conducted using the parsimony algorithm in PAUP* v4.0 (Swofford 1998) using Fitch optimization and an unweighted heuristic search with 100 addition sequence replicates followed by repeated tree-bisection reconnection (TBR). All additional criteria were left under default factory settings. A second analysis was conducted to limit the effect of homoplasious characters by downweighting their input on the analysis using successive weighting (Farris 1969) based on the rescaled consistency index (RC). After the initial (first) replicated search, characters were weighted according to the RC, and a second replicated search was conducted. This process was repeated until two
consecutive searches resulted in the same tree score. In cases where more than one optimal
tree was found after tree searching, a strict consensus tree was derived from the most
parsimonious trees recovered during tree searching. Relative node support for the consensus
trees was determined through bootstrap analysis with 500 addition sequence replicates in
PAUP* and Bremer support (Bremer 1988) using TreeRot v.3 (Sorenson & Franzosa 2007).

5.4 Results and Discussion

Thirty-two valid species, including one newly described species, *L. nullusarma*, are
recognized as species of the genus *Lipsothrix* (Table 1). Of these recognized species, twenty-
nine species are determined to represent distinct and valid species while three species are
listed as species of uncertainty due to inadequate material to definitively delineate them.
*Lipsothrix nigristigma* is synonymized with *L. nobilis*, *L. mirifica* is synonymized with *L.
mirabilis*, and *L. apicifusca* is synonymized with *L. fenderi* due to a lack of diagnostic
characteristics. One species complex, the *shasta* species complex (*L. shasta, L. fulva, L.
nigrilinea*), was recognized and further delineated using additional analyses.

Specimens corresponding to *L. shasta, L. nigrilinea*, and *L. fulva* were separated from
all other species based on the possession of two shared characteristics (macrotrichia in wing
cells, enlarged basal interbase with edge scalloped), but lacked additional fixed
morphological characters by which to separate them from each other. Eight continuous
quantitative characters (length of flagellomere 1, length of flagellomere 2, coloration of
dorsal thorax, coloration of lateral thorax, coloration of dorsal abdomen, coloration of lateral
abdomen, femur coloration, macrotrichia in cell $m_1$, macrotrichia in cell $r_3$) were found to be
variable in this group and were used to further separate specimens. Cluster analysis and
NMDS ordination separated the species into two distinct groups (Fig. 4). Eight characters
were significantly (p<0.01) different between the two groups (Table 4), while one character, lateral abdominal coloration, was not significant (p=0.55). Based on these techniques two species, *L. nigrilinea* and *L. shasta*, are recognized with the third species, *L. fulva*, synonymized with *L. shasta*.

### 5.4.1 Diagnosis of the genus *Lipsothrix*.

*Reference.* Loew 1873.

*Type species.* *Lipsothrix nobilis* Loew

*Diagnosis.* **Head:** Variable coloration, yellow, tan, to mottled with brown; anterior vertex prominent, eyes widely separated; rostrum short, variably colored; maxillary palpus variable, five palpomeres present, the basal palpomere greatly reduced so that palpus appears four segmented. **Antenna:** 16 articles; typically concolorous; scape length about twice that of pedicel; flagellomere length 2x width; ultimate flagellomere variable; flagellomeres with a whorl of verticils present. **Thorax:** Variably colored; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 10-40 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum anterior edge with 10-20 setiforms. **Halteres:** Base long and slender. **Legs:** Coxae and trochanters variably colored; femur and tibia typically yellow; tarsal claws slender with 0-4 teeth. **Wing:** Subhyline, may be suffused with brown in wing cells or along wing veins; stigma present or absent. **Wing venation:** *Sc* ending near split of *Rs*; *Sc*₂ ending at *Sc*₁, subequal; basal section of *Rs* long, 2x length of *R₂+₃; *R₂* present; *R₁+₂* and *R₂* subequal; *R₃* and *R₄* parallel, may be divergent at margin; cell *dm* present or absent; two medial branches attaining wing margin; crossvein *m-cu* intersecting *M* ranging from prior to or to the midlength of *dm*; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. **Wing**
Chaetotaxy: Veins basal to origin of Rs glabrous; Sc with or without setation; veins A₁ and A₂ with or without trichation; radial and medial cells with or without macrotrichia. Abdomen: Tergites and sternites 1-7 variably colored, dorsal abdomen often with a medial dark stripe, or tergites ringed with darker coloration; abdominal segments 8-9 of male ranging from black to concolorous to remaining abdomen. Male Hypopygium: Ninth tergite (9t) and sternite (9s) a fusion segment; gonocoxite subequal in length to 9t; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed between 1/2-4/5 the length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; base of gonocoxite with an elongate interbase, the length and base of which being variable, typically 1/3 the length of the gonocoxite and bent medially; aedeagal complex with elongate dorsal parameres, the interbase resting on and articulating the apex of the paramere; ejaculatory apodeme present or absent; aedeagus with one or two terminal openings, length of aedeagal branches variable, may be equipped with dorsal or ventral lobes on the aedeagal branches. Female Ovipositor: Terga 8-9 similar in composition to proceeding abdominal tergites, with abundant setation; tergite 10 with restricted setation, more sclerotized than abdominal tergites, tapered at base and increasing in width at juncture of cerci; cerci length subequal to tergite 10, heavily sclerotized, with a weak to strongly produced medial ridge at juncture with tergite 10, length of cerci gradually curved dorsally into an acute apex; sternite 9 separated from the genital fork, very weakly joined or medially divided dorsally, laterally adjoined to the ventral side of sternite 9; bursa inseminalis situated between the separated branches of sternite 9; genital fork deeply forked, Y-shaped; infra-anal plate (sternite 10)
fleshy, medially divided into two separate lobes; hypogynial valves heavily sclerotized, their apex becoming desclerotized and white in color, apex modified into a characteristic shape such that when at rest the apex of the hypogynial is situated into the ventral side of the cerci.

5.4.2 Redescription of valid species

*Lipsothrix assamica* Alexander


*Type Material.* **Holotype.** Assam, Cherrapunji, 4,000 ft. elevation, May 1936 [adult male (pointed, slide: wing & antennae)] (USNM).

*Diagnosis.* Body coloration uniformly amber; femur widely ringed with brown distally; wing cells and veins yellow/amber, stigma absent; $R_2$ at or near split of $R_{2+3+4}$; cell $dm$ open by atrophy of basal $M_{1+2}$; anal veins glabrous or with 1-5 setiforms each; hypopygium amber, not strongly darkened; interbase with base weakly enlarged, arm of interbase slender; aedeagus of male hypopygium with two terminal openings, length of individual arms exceeding the length of aedeagal complex or length of interbase, confluence of aedeagal arms leading to a basal single tube equipped with a strong ventral lobe.

*Description.* **Adult.** Measurements: MALE (N= 2): Body length: 5.8 mm (5.2 – 6.2), wing length: 6.4 mm (6.0 – 6.8), wing width: 3.6 mm (3.5 – 3.7), antennal length: 1.3 mm; FEMALE (N=1): Body length: 6.9 mm, wing length: 7.0 mm, wing width: 3.8 mm, antennal length: 1.2 mm. **Head:** Amber; rostrum short amber; maxillary palp brown; palpomere ratio 1.0–1.4–1.4–1.6. **Antenna:** 16 articles; scape and pedicel amber; flagellum amber; flagellomeres length twice the width; ultimate flagellomere 2/3-equal to penultimate flagellomere; flagellum covered with golden prunosity; flagellomeres with a whorl of 2-3 weak verticils at 1/2 length of flagellomere; verticils shorter than flagellomere. **Thorax:**
Amber; interspaces amber. *Thoracic Chaetotaxy*: Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with anterior edge with 10-15 setiforms. *Halteres*: Yellow. *Legs*: Femur amber, fading to brown beyond midlength, remaining segments missing on all specimens. *Wing* (Fig. 5.1): Subhyline; stigma absent; veins yellow. *Wing Venation* (Fig. 5.1): Sc ending before split of Rs; Sc₂ ending at Sc₁, subequal; basal section of Rs longer than R₃; R₂ nearly split of R₂₊₃ and R₄; R₂ and R₁₊₂ subequal; three branches of Rs attaining wing margin; R₃ and R₄ strongly divergent; cell dm open by atrophy of m-m; two medial branches attaining wing margin; m-cu intersecting at split of M; two cubital branches of attaining wing margin; two anal branches attaining wing margin, veins divergent. *Wing Chaetotaxy*: Wing cells without macrotrichia; Veins beyond midlength of wing with trichation, crossveins glabrous; Sc glabrous; A₁ and A₂ each with 2-3 setiforms. *Abdomen*: Tergite 1 yellow, tergites 2–9 brown; sternites 1–7 yellow, sternites 8–9 brown; abdomen with sparse golden randomly arranged setiforms. *Male Hypopygium* (Figs. 7.1; 15.1; 18.1): Amber; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex, basal 2/3 equipped with micro setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a slender rod curved at midlength and tapering to a pointed apex, the base of interbase moderately enlarged; aedeagus strongly bifid, branches of aedeagus arising from a common duct, common duct of aedeagus with a large ventral lobe; individual arms of aedeagus elongate; dorsal parameres wide based and narrowing at apex; ejaculatory apodeme present. *Female Ovipositor*: Sternites, tergites, ceri
and hypogynial valves amber in color, apex of hypogynial valves white; cerci and tenth
tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial
valves extending to slightly after origin of cerci, valves broad based and narrowing to an
acute apex. **Imatures.** Unknown.

*Other material examined.* INDIA: Sikkim: 3,700 ft. elevation, July 1959, Schmid [1
adult male (pointed)] (USNM); Assam: Khasid: Nongrim, 7-Schmid, 3,500 ft. elevation, 11
October 1930 [1 adult female (pointed)] (USNM); Sikkim: Singhit, 3,700 ft. elevation, June
1959, Schmid [1 adult female (pointed)] (USNM); Kumaon, Pauri garhwal, Khumyara,
4,300-5,000 ft. elevation, 28 May, 1958 [adult male (slide: wing, antennae, & hypopygium)]
(USNM).

*Geographic Distribution* (Fig. 20.1). Distributed across northern India through the
Sikkim, Assam, and Uttarakhand districts and has been collected at elevations ranging from
1,067 m to 1,524 m.

*Seasonal Emergence* (Table 2). Adults have been collected in late May, June, July
and from a single female taken in early October.

*Discussion.* *Lipsothrix assamica* is a member of the *assamica* clade (Fig. 28), defined by the
possession of a bifid male aedeagus. The presence of a strong ventral lobe of the aedeagus
shows similarity to *L. chettri* and *L. orthotenes*. The absence of cell *dm* will separate *L.
assamica* from all species of this group.

*Lipsothrix babai* Alexander

*Reference.* Alexander 1938

*Type Material. Holotype:* JAPAN: Honshu, Kurokawa, 17 June 1955 [adult male
(adult male pointed, slide: wing, antennae, hind leg, & hypopygium)] (USNM). *Allotype:*
JAPAN: Echigo, Mt. Anaka, 25 June 1955 [adult female (pointed)] (USNM). **Paratypes:**

*Diagnosis.* Melanistic dark brown body coloration, interspaces lighter in coloration; apical wing cells with macrotrichia, crossvein *m-cu* present near midlength of cell *dm*; base of IB enlarged and prominent; aedeagus simple with a single terminal opening, ejaculatory apodeme complete and with a medial ridge.

*Descriptions. Adult.* Measurements: MALE (N= 4): Body length: 7.7 mm (7.0–8.5), wing length: 8.8 mm (8.4–9.3), wing width: 2.6 mm (2.5–2.8), antennal length: 2.4 (2.3–2.5); FEMALE (N=1): Body length: 7.7 mm (7.0–8.5), wing length: 8.8 mm (8.4–9.3), wing width: 2.6 mm (2.5–2.8), antennal length: 2.4 mm. *Head:* Tan, molded with brown; vertex prominent; rostrum short, tan; maxillary palpus dark brown, palpomere ratio 1.75-1.75-1.0-1.0. *Antenna:* 16 articles; scape, pedicel, and flagellum brown, length 2x width; ultimate flagellomere 1/3 penultimate flagellomere; flagellomeres with a whorl of 3-4 verticils at 1/3 length of flagellomere, verticils less than length of flagellomere; flagellomeres with a uniform golden prunosity. *Thorax:* Uniformly brown; interspaces yellow. *Thoracic Chaetotaxy:* Pronotum with 30-40 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 15-20 setiforms. *Halteres:* Amber. *Legs:* Coxae and trochanters yellow; femur and tibia yellow, posterior tips of femur and tibia weakly and narrowly tipped with brown; setiforms of legs brown; tarsal claws slender with 0-1 prominent basal teeth and 2 much reduced basal teeth. *Wing* (Fig. 5.2): Suffused with brown; stigma absent; wing veins brown. *Wing Venation* (Fig. 5.2): Sc ending slightly before split of Rs; Sc₂ ending at Sc₁, subequal; basal section of
Rs long, 2x length of R_{2+3}; R_2 present, near split of R_{2+3} and R_4; R_{1+2} and R_2 subequal; R_3 and R_4 parallel, may be divergent at margin; cell dm present, rectangular; two medial branches attaining wing margin; crossvein m-cu intersecting M midlength of dm; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. Wing

Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins glabrous; Veins basal to origin of Rs glabrous; Sc with setation; A_1 and A_2 with 10-15 macrotrichia; radial and medial cells containing macrotrichia. Abdomen: Tergites and sternites 1-7 brown, tergites and sternites 8-9 dark brown.  

Male Hypopygium (Figs. 7.2; 15.2; 18.2): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase basal stem slender and widening at 3/4 length, interbase sinuous after midlength, apex acute; aedeagus singular, short, bent strongly ventrally with dorsal face weakly divided, apex blunt; dorsal parameres wide; ejaculatory apodeme present. Female Ovipositor: Sternites and tergites amber in color, cerci and hypogynial valves brown; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

Immatures. Unknown.

Distribution (Fig. 20.2). Distributed across the Japanese island of Honshu.

Seasonal emergence (Table 2). Adults have been collected in mid June.
Discussion. *Lipsothrix babai* is part of the *sylvia* clade (Fig. 25). *Lipsothrix babai* along with *L. shasta* and *L. nigrilinea* are the only known species that have macrotrichia in the apical cells of the wing. Both *L. shasta* and *L. nigrilinea* are from the Nearctic while *L. babai* is known from the Eastern Palearctic Region (Japan). *Lipsothrix babai* is separable from *L. shasta* and *L. nigrilinea* based on its complete melanistic coloration of the thoracic sclerites and abdominal sclerites and tergites. In *L. shasta* the abdomen and thorax are primarily amber with the darker coloration restricted to the thoracic and abdominal dorsum, while in *L. nigrilinea* the thorax and abdomen are mottled with amber and dark brown melanistic coloration but never completely melanistic as in *L. babai*. All three share a simple aedeagus with a single terminal opening and similar interbase shape, including an enlarged basal lobe (additionally shared with *L. sylvia* without macrotrichia in wing cells).

*Lipsothrix chettri* Alexander

Reference. Alexander 1959

Type material. Holotype. NEPAL: Simbhanjang Pass, 8,197 ft. elevation, 24 June, 1957 [adult female (pointed; slide: wing, antennae, & leg)] (USNM).

Diagnosis. Wing with cell dm small, length of cell equal to or less than height; male aedeagus bifid, the two branches elongate and exceeding the length of the entire aedeagal complex or about twice the length of the interbase; ventral aedeagus with a prominent lobe.

Descriptions. Adult. Measurements: MALE (N=1): Body length: absent, wing length: 7.1 mm, wing width: 2.1 mm, antennal length: 1.9 mm; FEMALE (N=1): Body length: 7.2 mm, wing length: 7.6 mm, antennal length: 1.8. Head: Absent from holotype. Antenna: 16 articles; scape and pedicel yellow, flagellomeres tan, becoming darker apically; flagellomeres oval, length about twice the width; ultimate flagellomere 1/2 penultimate
flagellomere; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 1-2 medial verticils. Thorax: Absent from holotype. Thoracic Chaetotaxy: Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with anterior edge with 10-15 setiforms. Halteres: Absent from holotype. Wing (Fig. 5.4): Subhyline; stigma absent; veins yellow. Wing Venation (Fig. 5.4): Sc ending near split of Rs; Sc₂ ending before end of Sc₁; Rs subequal or shorter than R₃; R₂ present, subequal to R₁₂, near split of R₂ and R₄; three branches of R attaining wing margin; R₃ and R₄ parallel; cell dm present, small, square shaped with height equal to width; two medial branches attaining wing margin; crossvein m-cu at split of M; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. Wing Chaetotaxy: Costal vein with setation to arculus, other veins before midlength of wing glabrous, beyond midlength of wing with macrotrichia; crossveins glabrous; Sc glabrous; A₁ and A₂ glabrous or with 1-2 setiforms; wing cells without macrotrichia. Abdomen: Abdomen prior to 6th segment absent. Tergite and sternite 6 yellow, remainder of abdomen dark brown; abdomen with sparse golden randomly arranged setiforms. Male Hypopygium (Figs. 7.3; 15.3; 18.3): Dark brown; gonocoxite and gonostyli subequal in length; gonostylus bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a slender sickle-shaped rod, base weakly enlarged, apex flattened before attaining a narrow apex; aedeagus bifid with individual arms long, length greater than that of remaining aedeagal complex, shaft directed ventrally and bent near midlength so that
opening is directed posteriorly, base of aedeagal arms with a strongly produced ventral lobe, dorsum with or without a strongly produced lobe (not discernable); dorsal parameres slender; ejaculatory apodeme apparently absent on holotype slide. *Female Ovipositor*: Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. **Immatures.** Unknown.

*Other Material Examined.* INDIA: Kumaon, Pauri garhural, Ugsara, 4,500 ft elevation, 29 May 1958 [adult male (slide: antennae, wing, and male hypopygium)] (USNM).

*Geographic Distribution* (Fig. 20.3). *Lipsothrix chettri* is known from northern India and Nepal. Although limited collections have been made, records indicate this species is likely to be found at high elevations, having been collected at 2,500 m elevation from Simbhanjag Pass in Nepal.

*Seasonal Emergence* (Table 2). Adults have been collected in late June.

*Discussion.*** Lipsothrix chettri* was originally based on general coloration (thorax yellow, dorsum more fulvous yellow; head reddish brown; pronotal scutum dark brown; halteres yellow; legs darkened, wings pale yellow, veins yellow) and wing venation (*Sc*₁ ending opposite fork *Rs*; *dm* very small) of the female of the species. The male of the species is described here from an unidentified slide mounted specimen in the Alexander Collection in the USNM. It is associated with the female here based on the similar construction of the wing, namely the reduced wing cell *dm.*** Lipsothrix chettri* is a member of the *assamica* clade (Fig. 28), defined by the possession of a bifid male aedeagus. *Lipsothrix chettri* has the ventral lobe of the male aedeagus present and dorsal lobe absent as in *L. assamica* and *L.*
orthotenes. Coloration within this group is generally fulvous/yellow and is not sufficient to separate them. The species defining character of the reduced cell $dm$ is however sufficient to separated this species from all species of this group.

**Lipsothrix decurvata Alexander**


*Paratypes,* same information as holotype [4 adult males (pinned)] (USNM).

*Diagnosis.* Wing with stigma weakly present; aedeagus bifid, individual arms about equaling length of interbase, dorsum of each arm equipped with a strong prominent lobe, individual aedeagal branches with degenerating tips.

*Description. Adult.* Measurements: MALE (N=5): Body length 6.0 mm (5.5–6.5); wing length 7.2 mm (7.0–7.4); wing width 2.3 mm (2.1–2.4); antennal length 2.3 mm (2.1–2.5); FEMALE. Unknown. *Head:* Brown; rostrum short, amber/brown; maxillary palpus dark brown, palpomeres ratio 1.4–1.4–1.0–1.0. *Antennae:* 16 articles; scape, pedicel, and flagellomeres brown; flagellomeres cylindrical, length 3x width; ultimate segment 1/4 length of penultimate segment; flagellomeres with a whorl of 1-2 short verticils at 1/2 length of flagellomere; ultimate flagellomere with 3 apical setiforms; flagellomeres with a uniform golden prunosity. *Thorax:* Pronotum dark brown; prescutum amber to brown laterally with a dark brown dorso-medial stripe; lateral sclerites amber; anatergite dark brown. *Thoracic Chaetotaxy:* Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum anterior edge with 15-20 setiforms. *Halteres:* Base yellow, stem and knob brown. *Legs:* Femur, tibia and tarsomere 1
amber, the apex of each widely tipped with brown; tarsomeres 2-4 brown; tarsal claws slender with a single basal tooth. *Wings* (Fig. 5.5): Suffused with brown; stigma absent or faintly indicated; veins brown. *Wing Venation* (Fig. 5.5): Sc ending at split of Rs, Sc₁ subequal to Sc₂; R₂ very faint; R₂ and R₁₊₂ subequal; three branches of Rs attaining wing margin; R₃ and R₄ parallel, divergent at wing margin, R₄ strongly deflected ventrally at wing margin; cell dm present, square shaped; m-cu near split of M; two medial branches attaining wing margin; two cubital branches attaining with margin; two anal branches attaining wing margin, veins divergent. *Wing Chaetotaxy*: Veins glabrous basal to origin of Rs; Sc glabrous; anal veins with 1-2 setiforms; wing cells without macrotrichia. *Abdomen*: Tergites and sternites 1-6 brown; tergites and sternites 7-9 dark brown. *Male Hypopygium* (Fig. 15.4; 18.4): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase weakly enlarged basally, remainder a slender rod, narrowing to a blunt apex; aedeagus bifid, dorsal face expanded into two large lobes; dorsal parameres slender; ejaculatory apodeme present. *Imatures*. Unknown.

*Other material examined*. INDIA: Assam [adult male (slide: hypopygium)] (USNM); Assam, Manipur, Sirhoi, Kashong, 6,000 ft. elevation, 06 June, 1960 [adult male (slide: wing, antennae, 2 legs, & hypopygium)] (USNM); Assam, Manipur, Mattiyang, 2,800 ft. elevation, 17 June, 1960 [adult male (slide: wing, antennae, 2 legs, & hypopygium)] (USNM); Assam, Kameng, Nakhu, 4,800 ft. elevation, 03 July, 1961 [adult male (slide:
Distribution (Fig. 20.4). Distributed across northeastern India in the Sikkim and Assam regions. This species is known from an altitudinal range of between 1,463 and 2,362 meters.

Seasonal Emergence (Table 2). Adults have been collected from late May to July.

Discussion. Lipsothrix decurvata is a member of the assamica clade (Fig. 28), defined by the presence of a bifid aedeagus of the male hypopygium. Within this species group, three additional species (L. kraussiana, L. malla, and L. flavissima) share a common attribute of an enlarged dorsal face on each branch of the aedeagus. Lipsothrix kraussiana is separated from these other three species of this dorsally lobed group by lacking the squared basal interbase (Figs. 18, 19). Lipsothrix decurvata is further separated from L. malla and L. flavissima in the possession of the stigma in the radial sector of the wing.

Lipsothrix ecucullata Edwards

Reference. Edwards 1938


Diagnosis. Overall body coloration yellow, dorsal thorax and abdomen not darkened, male hypopygium and female ovipositors amber to tan, wing cells and veins yellow stigma absent; tarsal claws with 2-3 basal teeth; wing vein $R_{2+3}$ shorter than $R_{2+3+4}$, vein $R_5$ to wing
margin or ending in vein $M_1$; aedeagus with a single terminal opening, directed posteriorly with a weakly produced ventral lobe.

**Description.** **Adult.** Measurements: MALE (N=11): Body length 7.5 mm (6.5–8.9), wing length 8.1 mm (7.8–9.1), wing width 2.3 mm (2.1–2.5), antennal length: 2.1 mm (2.1–2.2); FEMALE (N=12). Measurements: Body length 8.3 mm (7.8–9.4), wing length 7.5 mm (7.4–7.9), wing width 2.3 mm (2.2–2.6), antennal length: 2.1 mm (2.1–2.2). **Head:** Amber; rostrum short, amber; palpomeres brown; palpomere ratio: 1.0-1.0-1.0-1.4. **Antennae:** 16 articles; scape, pedicel, and flagellum amber; flagellomeres suboval, length 2x width; ultimate flagellomere length 1/2–2/3 penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 4-5 verticils placed at midlength, verticils shorter than segments; flagellomeres with a pubescent covering of golden setiforms. **Thorax:** Sclerites uniformly yellow/amber; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 15-20 setiforms. **Halteres:** Amber, knobs lightly infumed. **Legs:** Coxae and trochanters yellow; femur and tibia yellow, widely tipped with brown; tarsomeres 1-3 yellow, tergite 4-5 brown amber, tips widely ringed with dark brown; tibia and tarsomeres 1-3 amber, tarsomeres 4-5 brown; tibial spurs absent; tarsal claws with 2-3 major teeth placed at the base of claw, if 2 major teeth present then basal claw reduced to 1/2 length remaining teeth. **Wings** (Fig. 5.6): Subhyline; stigma absent; veins tan. **Wing Venation** (Fig. 5.6): Sc ending near split of Rs; free tips of $Sc_1$ and $Sc_2$ subequal; Rs moderately long, subequal to $R_3$; $R_2$ faintly indicated, near split of $R_3$ and $R_4$; $R_{1+2}$ about twice $R_2$; three branches of Rs attaining wing margin; $R_3$ and $R_4$ parallel, both deflected ventrally at wing margin; cell $dm$ present, rectangular; $m-cu$ close to the fork of $M$; two medial braches
reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. Wing Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with trichation; A\textsubscript{1} with \sim 20 setiforms, A\textsubscript{2} with 4-6 setiforms; wing cells without macrotrichia. Abdomen: Tergites 1-6 yellow/amber; tergite 7 anterior half yellow/amber, posterior half dark brown; tergite 8-9 dark brown; sternites amber. Male Hypopygium (Figs. 8.1; 15.5; 18.5): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with base weakly enlarged, remainder long and slender, bending near apex, narrowing to apex; aedeagus singular, weakly bent ventrally near base, bent dorsally near apex, ventral face with a medial lobe; dorsal parameres slender; ejaculatory apodeme present. Female Ovipositor: Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. Immatures. Collected and known, but as yet remain undescribed.

Other Material Examined. SCOTLAND: Perthshire nr. Rannoch, Ballagan, 23 June 1967 [adult male (pinned)] (BM); NORWAY: Hoylandet, Tverraa 1 Opp, 1-9 July 1986 [1 adult male, 1 adult female (alcohol)] (MK). CZECH REPUBLIC: Moravia, Rohatec u Hodonina, 10 June 1976 [1 adult male, 1 adult female (pinned)] (JS). AUSTRIA:
Vorarlberg, Moutatou, Silbertal, 25 May-03 June 1982 [1 adult male, 1 adult female (alcohol)] (MK). SWEDEN: Kaltisjokk/Messaure, May-June 1966 [1 adult male (alcohol)] (MK); Kaltisjokk/Messaure, 5-12 July 1970 [1 adult female (alcohol)] (MK); Kaltisjokk, Wasserfall im Wald, 07-28 July 1971 [2 adult males, 1 adult female (alcohol)] (MK).


**Geographic Distribution** (Figs. 20.5,6). Broadly distributed across Europe in the Czech Republic, Denmark, Finland, France, Germany, Great Britain, Lithuania, Romania, and Slovokia. The projected distribution of *L. ecucullata* (Fig. 20.6) indicates that is more likely to be found in northern Europe or at higher elevations in southern Europe.

**Seasonal Emergence** (Table 2). Adults of *L. ecucullata* emerge from early June to the middle of August.

**Discussion.** *Lipsothrix ecucullata* is a member of the weakly supported *nobilis* clade (Fig. 28) based on the possession of a weakly produced ventral lobe of the aedeagus and a sinuous S-shaped aedeagus. *Lipsothrix ecucullata* is quite similar to many species in this group in terms of coloration and wing venation. It is separated from both *L. nobilis* and *L. nervosa* in the absence of the stigma of the wing, and additionally from *L. nervosa* in having the antennal flagellomeres short and not elongate as in *L. nervosa*. *Lipsothrix remota* is most similar in overall appearance to *L. ecucullata*, but is separated based on its darkened femoral
tips and posteriorly directed aedeagus that has a weakly produced ventral lobe in *L. ecucullata*. The phylogenetic relationships between these species are largely unresolved.

*Lipsothrix errans* Alexander

**Reference.** Walker 1848.

**Type Material.** Holotype, Great Britain.

**Diagnosis.** Overall body coloration yellow/amber, femur and tibia amber and variably tipped with brown, wing cells and veins yellow, stigma absent, male hypopygium dark brown; tarsal claws with prominent teeth; wing venation with *Sc*1 and *Sc*2 ending near or after split of *Rs*, *R*2+3 shorter than *R*2+3+4; aedeagus with a single terminal anteriorly directed opening, dorsum of aedeagus with a greatly enlarged lobe, dorsal lobe weakly divided medially; interbase long and slender, its base simple.

**Description.** Adult. Measurements: MALE (N=20): Body length 8.4 mm (7.4–9.8), wing length 9.0 mm (8.3–10.1), wing width 2.5 mm (2.0–2.7), antennal length: 2.4 mm (2.1–2.8); FEMALE (N=15): Body length 10.2 mm (9.2–11.3), wing length 10.3 mm (9.2–11.5), wing width 3.1 mm (2.9–3.4), antennal length: 2.2 mm (2.1–2.3). **Head:** Amber; rostrum short, brown; palpomeres dark brown; palpomere ratio: 1.1–1.0–1.2–1.6. **Antennae:** 16 articles; scape and pedicel amber; flagellomeres 1-7 amber, flagellomere 8-14 brown; flagellomeres cylindrical, length 2x width; ultimate flagellomere length 1/2–3/4 penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 4 black verticils placed at midlength, verticils shorter than segments; flagellomeres with a pubescent covering of golden setiforms that are about 1/4 length of associated flagellomere. **Thorax:** Uniformly amber; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 30-40 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with
two anterior edge with 12-16 setiforms. Halteres: Yellow, knobs lightly infumed. Legs:
Coxae and trochanters amber; femur, and tibia amber, each widely tipped anteriorly and
posteriorly with brown; tarsomere 1 brown, tipped anteriorly with dark brown; tarsomeres 2-5 brown; tibial spurs absent; tarsal claws basally enlarged, equipped with 2-3 major teeth and
1-2 basal minor teeth. Wing (Fig. 5.7): Subhyline; stigma absent; veins brown. Wing
Venation (Fig. 5.7): Sc ending near split of Rs; free tips of Sc₁ and Sc₂ subequal, Sc₂ rarely
longer; Rs moderately long, subequal to R₃; R₂ placed beyond split of R₃ and R₄; R₁₊₂ and R₂
subequal; three branches of Rs attaining wing margin; R₂ and R₄ parallel, deflected ventrally
at wing margin; cell dm present, rectangular; m-cu close to the fork of M; two medial
branches reaching wing margin; two cubital branches attaining wing margin; two anal
branches reaching wing margin, veins divergent. Wing Chaetotaxy: Veins beyond midlength
of wing with trichation, crossveins glabrous; Sc with setiforms; A₁ and A₂ with abundant
setiforms; wing cells without macrotrichia. Abdomen: Tergites 1-6 amber, t₂ may have a
dorsal brown spot; tergite 7-9 ranging from amber to dark brown; sternites 1-6 amber,
sternite 7 posteriorly dark brown, anteriorly amber. Male Hypopygium (Figs. 8.2; 15.6;
18.6): Dark brown; gonoxoite and gonostyli subequal in length; gonostyli bifid, subequal;
dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a
single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing
to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of
style, distally glabrous, equipped with setiforms along entire length, more abundant at apex;
interbase with base weakly enlarged, remainder long and slender, bending near apex,
narrowing to apex; aedeagus singular, apex bent ventrally, dorsal face with a greatly enlarged
lobe that is weakly divided medially; dorsal parameres slender; ejaculatory apodeme present.
Female Ovipositor: Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. Immatures. Descriptions provided by Beling (1886), Brindle (1967), Krivosheina (1969), and Savchenko (1982; 1986).

Other Material Examined. DENMARK: Silkeborg, 08 July 1918 [1 adult (pinned, abdomen removed)] (BM). GERMANY: Rheinland, Siebangebirge, 24 June 1960 [1 adult male (pinned)] (MK); Lux a Kreuzbach, Kreuzthal/Westeallgau, 31 May-30 June 1971 [2 adult males, 1 adult female (alcohol)] (MK); Birgsau, Allg Alpen, Ringaug, 900 m elevation, 23 June – 25 July 1973 [10 adult female (alcohol)] (MK); Traufbachtal, Quellbang, Allgauer Alpen, elevation 1,250 m, 22 June 1971 [3 adult males, 1 adult female (alcohol)] (MK); Oberunzburg, Allg. Teufelskuche, 24 July 1971 [1 adult male (alcohol)] (MK); Ochsentobel, Kurnach, westl. Kempter/Allg., 10 June 1971 [2 adult males (alcohol)] (MK); Kreuzthal/West., Allgau lux, 26 June-22 July 1972 [3 adult males, 7 adult females (alcohol)] (MK). CZECH REPUBLIC: Moravia, Kosanska, Beskydy Mtns., 08 June 1965 [1 adult male (pinned)] (JS). UNITED KINGDOM: Perthshire, Loch Rannoch, vi.1931 [adult male (pinned)] (BM); Perthshire, Killin District, Glen Lochay, elevation 500-1500 feet, 03-18 June 1932 [1 adult female (pinned)] (BM); Dolgellau, 24 July 1888 [1 adult female (pinned)] (BM); Angus, River Isla, Den of Airlie, 04 July 1977 [1 adult male (pinned)]; Avon, 18 October 1903 [adult (pinned)] (BM); Great Britian: Seaton Hole, Seaton, Devon, 21.vi.1905 [adult (slide: wing)] (BM). YUGOSLAVIA: Slovenich, Jelendol, 29 June 1981 [adult female (alcohol)] (MK). AUSTRIA: Lunz, NO, 21 Sept 1981 [adult male (alcohol)] (MK);

**Geographic Distribution** (Figs. 21.1; 21.2). Distributed across central Europe through Austria, Belgium, Bulgaria, Czech Republic, Denmark, Finland, France, Germany, Great Britain, Italy, Lithuania, Poland, Romania, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, and Russia. The projected distribution of *L. errans* (Fig. 21.2) shows a broad latitudinal and elevational European distribution.

**Seasonal Emergence** (Table 2). Adult emergence occurs from late May through late July or early August. Infrequent collections show some emergence events in late September.

**Discussion.** *Lipsothrix errans* is weakly placed within the greater *Lipsothrix* phylogeny and not associated with any species groups (Fig. 25). *Lipsothrix errans* is defined by the enlarged dorsal lobe of the aedeagus of the male hypopygium. No other species of *Lipsothrix* possesses such a structure, however a similar lobe was described for *L. heitfeldi* in its original description. The slide preparation of the type of *L. heitfeldi* is damaged and no other specimens of this species have been collected. These two species are widely separated geographically, *L. heitfeldi* in China and *L. errans* in Europe, and both differ in body coloration with *L. errans* yellow and weakly mottled with tan or brown and *L. heitfeldi* with the body entirely suffused with dark brown.

**Lipsothrix fenderi** Alexander

**Reference.** Alexander 1946.

**Type Material.** **Holotype.** USA: Oregon: Yamhill County, Peavine Ridge near McMinnville, 23 October 1945 [adult male (pinned, slide: wing, antennae, leg, & hypopygium)] (USNM). **Allotype.** Same information as holotype. **Paratypes.** Same
information as holotype except: 24 October 1945 [4 adult males, 1 adult female (pinned)] (USNM); 03 October 1945 [1 adult male, 1 adult female (pinned)] (USNM); 12 October 1945 [2 adult males, 1 adult female (pinned)] (USNM).

**Diagnosis.** Wing and body coloration pale yellow to obscure white; wing vein basal \( R_{2+3+4} \) subequal to \( R_{2+3} \), cell \( dm \) elongate with width greater than twice the height; male aedeagus with a single opening, the posterior face widely split; dorsal gonostylus beyond medial tooth elongate and bluntly tipped.

**Description.** **Adult.** Measurements: MALE (N=18): Body length: 8.6 mm (7.8–9.5), wing length” 10.2 mm (9.2–10.8), wing width: 2.8 mm (2.5–3.2), antennal length: 1.4 mm (1.2–1.5); FEMALE (N=4): Body length: 10.4 mm (8.4–11.2), wing length: 9.4 mm (9.0–10.3), wing width: 2.9 mm (2.8–3.0), antennal length: 1.5 mm (1.4–1.5). **Head:** Yellow, faintly mottled with tan dorsally; rostrum small, dusty yellow; maxillary palpus yellow/tan, palpomere ratio: 1.0-1.1-1.0-1.3. **Antennae:** 16 articles; scape, pedicel, and flagellum golden yellow; flagellomeres length twice the width, oval shaped; ultimate flagellomere subequal to penultimate flagellomere; flagellomeres with a whorl of 5-8 medial verticils; verticils greater in length than corresponding flagellomere. **Thorax:** Sclerites of thorax yellow; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 10-15 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 10-15 setiforms. **Halteres:** Yellow. **Legs:** Coxae and trochanters yellow; femora and tibia tan, posteriorly ringed with brown; tarsi tan; tarsal claw toothed with 2-3 major teeth. **Wing** (Fig. 5.8): Subhyline; stigma absent; veins tan. **Wing Venation** (Fig. 5.8): \( Sc \) ending at split of \( Rs \); \( Sc_2 \) at tip of \( Sc_1 \), subequal; \( Rs \) long, equal to \( R_{2+3} \) and \( R_3 \); \( R_2 \) subequal to \( R_{1+2} \), placed near wing margin far removed from split of \( R_{2+3} \) and \( R_4 \); three branches of R
attaining wing margin; \( R_3 \) and \( R_4 \) divergent at wing margin; cell \( dm \) present; \( m-cu \) near split of M; two medial branches attaining wing margin; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. Wing Chaetotaxy: Veins with long conspicuous macrotrichia, especially on the veins beyond the origin of \( Rs \); veins glabrous before origin of \( Rs \); \( A_1 \) with 6-10 setiforms, \( A_2 \) with 6-10 setiforms; wing cells without macrotrichia. Abdomen: Tergites and sternites 1-6 pale yellow, \( t7 \) and \( s7 \) pale brown, \( t8-9 \) and \( s8-9 \) mottled with golden tan and brown. Male Hypopygium (Figs. 8.3; 15.7; 18.7): Tan; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a simple sclerotized rod, enlarged at 3/4 length and narrowing to an acute point; aedeagus singular, short, bent strongly ventrally with dorsal face divided, apex blunt; dorsal parameres wide; ejaculatory apodeme absent or weakly present. Female Ovipositor: Sternites and tergites pale yellow in color, cerci and hypogynial valves amber, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. Immatures. Described by Hynes (1965).

Other Material Examined. JAPAN: Kurokawa, Echigo, 10 September 1954 [adult male (pointed), as \( L. \) apicifusca] (USNM). USA: Oregon: Yamhill County, Siuslaw National Forest, McMinnville, 20 July 1965 [6 adult males, 1 adult female (pinned)] (CM); Tillamook County, Wilson River, 26 September 1964 [2 adult males (pinned)] (CM); S. Santiam,
Tombstone Mas., 17 August 1947 [2 adult males (pinned)] (USNM); Benton County, Berry Creek, 9 miles N of Corvallis, 30 September, 1959 [adult male (pinned)] (SM); Peavine Ridge, near McMinnville, 01 October, 1946 [7 adult males, 1 adult female (pinned)] (USNM); Peavine Ridge, near McMinnville, 03 October, 1946 [2 adult males (pinned)] (USNM); 12 October, 1946 [5 adult males, 1 adult female (pinned)] (USNM); Humbug Mountain, 05 August, 1950 [1 adult male (pinned)] (USNM); Washington: East Port Orchard, 25 September, 1946 [5 adult males (pinned)] (USNM); 23 September, 1946 [1 adult male (pinned)] (USNM); Washington: Lewis & Clark State Park, 28 September, 1946 [1 adult male (pinned)] (USNM).

**Geographic Distribution** (Figs. 21.3; 21.4; 21.5). *Lipsothrix fenderi* has a disjunct distribution that is split between Japan and the west coast of North America. The distribution projected from known collection points (Fig. 21.5) indicates a broad distribution in North America ranging from northern California through the Coastal and Cascade Ranges of Oregon and Washington, into British Columbia in Canada. The distribution from Japan is poorly known.

**Seasonal Emergence** (Table 2). Adults have been collected from late July through early October.

**Discussion.** *Lipsothrix fenderi* is placed within a large clade of Nearctic and East Palearctic species (Fig. 28) which is partially defined by the simple aedeagus without lobes and the split of the face of the aedeagus of the male hypopygium. The two most similar species of this group, *L. leucopeza* and *L. taiwanica*, are separable from *L. fenderi* based on wing venation (restricted basal $R_5$ in *L. fenderi*, lengthened in *L. leucopeza* and *L. taiwanica*) and male genitalia (restricted aedeagus, expanded and directed apically in *L. leucopeza* and
L. taiwanica). Lipsothrix fenderi is separated from L. hynesiana, L. pluto, and L. mirabilis by the lack of coloration along the wing cord and the lack of teeth on the tarsal claws. The formerly recognized species L. apicifusca is here synonymized with L. fenderi.

**Lipsothrix flavissima Alexander**


*Type Material.* **Holotype.** BURMA: Kambaiti, 7,000 ft. elevation, 25 May 1934 [adult female (slide: wing)] (USNM).

*Diagnosis.* Wing and body yellow/amber, rarely showing darker thoracic coloration, dorsal abdomen may possess darker coloration; aedeagus bifid with two terminal openings, each aedeagal branch equipped with a strongly produced dorsal lobe, aedeagal branches subequa to length of aedeagal complex; interbase with a squared origin and narrowing after midlength, apex of interbase bluntly rounded.

*Description.* **Adult.** Measurements: MALE (N= 6): Body length: 5.5 mm (5.2–5.7), wing length: 7.3 mm (7.0–7.5), wing width: 1.9 mm (1.8–2.1), antennal length: 1.5 (1.3–1.7); FEMALE (N= 5): Body length: 5.5 mm (5.2–5.7), wing length: 7.3 mm (7.0–7.5), wing width: 1.9 mm (1.8–2.1), antennal length: 1.5 (1.3–1.7). *Head:* Yellow/tan; rostrum short, tan; maxillary palponeres 2-3 brown, palpomeres 4-5 dark brown, palpomere ratio: 1.2-1.2-1.0-1.0. *Antenna:* 16 articles; scape and pedicel yellow, flagellomeres 1-7 yellow, flagellomeres 8-14 brown; flagellomeres cylindrical, length 2x width; ultimate flagellomere 1/4 penultimate flagellomere; flagellomeres with 4 verticils placed at midlength; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 2-3 medial verticils. *Thorax:* Tan/yellow; interspaces yellow. *Thoracic Chaetotaxy:* Pronotum with 15-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits.
to the scutellum, scutellum with two anterior edge with 10-15 setiforms. *Halteres:* Yellow. *Legs:* Coxae and trochanters yellow; femur and tibia yellow, posterior tips narrowly tipped with brown; tarsomeres amber; tarsal claws slender with no or a single basal tooth. *Wing* (Fig. 5.9): Suffused with yellow; stigma absent; veins brown. *Wing Venation* (Fig. 5.9): Sc ending before split of Rs; Sc2 ending at Sc1, subequal; basal section of Rs long, greater than length of R3, less then R5; R2 present, near split of R2+3 and R4; R2 and R1+2 subequal; three branches of Rs attaining wing margin; R2+3 and R4 strongly divergent; cell r3 long petiolate; cell dm present; two medial branches attaining wing margin; crossvein m-cu intersecting M near split of M; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. *Wing Chaetotaxy:* Veins beyond midlength of wing with setiforms, crossveins glabrous; Sc glabrous; A1 and A2 glabrous, infrequently with 1-5 setiforms; wing cells without macrotrichia. *Abdomen:* Tergite 1 tan, tergites 2-6 brown, tergite 7 brown to tan, tergites 8-9 dark brown; sternites 1-7 tan, sternites 8-9 dark brown. *Male Hypopygium* (Figs. 8.4; 15.8; 18.8): Golden tan; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a simple sclerotized rod narrowing to an acute point, base with a weak dorsal enlargement, basal half of interbase thicker than apical half; aedeagus bifid arising from a common base, branches bent ventrally near base, splitting near midlength, dorsal face of aedeagus with a divided lobe; dorsal parameres narrow; ejaculatory apodeme present. *Female Ovipositor:* Sternites and tergites pale amber in color, cerci and hypogynial
valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. **Imatures.**

Unknown,

*Other Material Examined.* INDIA: Assam: Rupa, Kameng Frontier Division, Northwest Frontier Division, elevation 5,200-5,500 feet, 02-03 May 1961 [6 adult males (pinned), 2 adult females (pinned)] (USNM).

*Geographic Distribution* (Fig. 21.6). *Lipsothrix flavissima* has been recorded from two collections, one from northern Myanmar at 2,134 m elevation and a second from northwestern Assam region of India from between 1,585 to 1,676 m elevation.

*Seasonal Emergence* (Table 2). Adults have been collected from early to late May.

*Discussion.* *Lipsothrix flavissima* is a member of the *assamica* clade (Fig. 28), defined by the presence of a bifid aedeagus of the male hypopygium. Within this species group, three additional species (*L. kraussiana, L. malla, and L. decurvata*) share a common attribute of an enlarged dorsal face on each branch of the aedeagus. *Lipsothrix kraussiana* is separated from the other species of this dorsally lobed group by lacking the squared basal interbase (Fig. 15). *Lipsothrix flavissima* is separated from *L. decurvata* in lacking a stigma in the radial sector of the wing and from *L. malla* in the coloration of the thorax (*L. malla* possess a dark brown medial stripe on the thorax while *L. flavissima* does not).
Lipsothrix hynesiana Alexander


Type Material. Holotype. USA: California: Monterey Co., Salmon Creek, 26 October 1962 [adult male (pinned, slide: wing, antennae, legs, & hypopygium)] (USNM).

Paratype, same information as holotype [adult male (pinned)] (USNM).

Diagnosis. Base coloration of body amber, dorsal thorax and abdomen each with brown coloration (variably produced), lateral thoracic sclerites variably colored with amber, brown, and dark brown; wing veins $Sc_1$ and $Sc_2$ ending after wing cord, $R_{2+3+4}$ subequal to $R_{2+3}$, cell $dm$ elongate with width greater than twice the height; wing stigma absent, darker wing coloration along wing cord, distal cell $dm$, and $Sc_1/Sc_2$; aedeagus with a single terminal opening; interbase a simple blunt tipped rod, its base weakly enlarged.

Description. Adult. MALE. Measurements (N= 2): Body length: 8.9 mm (8.7–9.0), wing length: 9.7 mm (9.6–9.8), wing width: 2.8 mm (2.7–2.9), antennal length: 3.9 mm (3.7–4.0); FEMALE. Unknown. Head: Mottled with amber and brown; rostrum short, brown; maxillary palpus brown, palpomere ratio: 1.0–1.2–1.0–1.0. Antenna: 16 articles; scape and pedicel tan, flagellum brown; flagellomeres length 5-6x width; ultimate flagellomere 1/4 penultimate flagellomere; flagellomeres with a whorl of 4-5 verticils at 1/4 length of flagellomere; f14 with 4 terminal verticils; verticils 1/4–1/3 length of corresponding flagellomere; flagellomeres with a uniform golden prunosity. Thorax: Pronotum dark brown dorsally; scutellum yellow; prescutum suffused yellow with a brown dorso-medial stripe, divided in anterior half; scutellum suffused yellow with darker markings; interspaces yellow. Thoracic Chaetotaxy: Pronotum with 20-30 setiforms, scutellum with 2 parallel rows of pale setiforms, scutum with 2 loose posterior clusters of 6-7 setiforms. Halteres: Amber, knob
suffused. **Legs:** Coxae and trochanters tan; Femur and tibia amber, tarsomeres brown; tarsal claws with 2 prominent basal teeth, one placed at midlength and one placed basally. **Wing** (Fig. 5.11): Suffused with tan; clouds of faint brown along cord and outer end of *dm*; stigma lightly indicated; veins brown. **Wing Venation** (Fig. 5.11): *Sc* ending beyond origin of *Rs*; free tips of *Sc*₁ and *Sc*₂ subequal; *Rs* moderately long, subequal to *R*₄; *R*₂ far beyond split of *R*₂₊₃ and *R*₄; *R*₁₊₂ subequal to *R*₂; three branches of *Rs* attaining wing margin; *R*₃ and *R*₄ parallel, *R*₄ strongly deflected ventrally at wing margin; cell *dm* present, rectangular, length 3x *m-m*; *m-cu* close to the fork of M; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. **Wing Chaetotaxy:** Veins beyond midlength of wing with trichation, crossveins glabrous; *Sc* with trichation; *A*₁ with 15-20 setiforms, *A*₂ with ~20 setiforms; wing cells without macrotrichia. **Abdomen:** Tergites 1-6 brown, tergites 7-9 dark brown; sternites 1-7 amber, sternites 7-9 dark brown. **Male Hypopygium** (Figs. 9.1; 15.9; 18.9): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase simple sclerotized rod narrowing to an blunt rounded point, base with a dorsal enlargement; aedeagus short with a single opening, shaft directed ventrally; dorsal parameres slender; ejaculatory apodeme present. **Immatures.** Described by Hynes (1965).
**Geographic Distribution** (Fig. 22.2). Collection records show a patchy distribution along coastal southcentral California in the United States. All known collections have been made from streams in steep coastal or inland canyons.

**Seasonal Emergence** (Table 2). Adults have been collected in late October.

**Discussion.** *Lipsothrix hynesiana* is placed near the base of a large clade of Eastern Palearctic and Nearctic species (Fig. 28) which is partially defined by the simple aedeagus without lobes and the split face of the aedeagus of the male hypopygium. *Lipsothrix hynesiana* is easily distinguished from the other Nearctic species based on the coloration of the wing (darkened along the cord), a state shared with *L. pluto* and *L. mirabilis* of the Eastern Palearctic. *Lipsothrix hynesiana* is separated from *L. mirabilis* by having wing vein $R_{2+3+4}$ not greatly shortened and from *L. pluto* in not possessing a stigma in the Radial sector of the wing.

**Lipsothrix iranica Alexander**


**Type Material.** Holotype. IRAN: Ardehyan, 11 September 1956 [adult female (pointed)] (USNM).

**Diagnosis.** Base coloration of body amber/tan, head tan, prescutum and scutum with a broad medial dark brown stripe that continues after the transverse suture, dorsal thorax dark brown; femur and tibia amber and tipped with brown, wing cells amber, wing veins brown, stigma strongly present, abdomen with sclerites and tergites amber and ringed posteriorly with dark brown, coloration of lateral abdomen variable, typically brown, male hypopygium dark brown; tarsal claws with teeth, wing venation with $R_{2+3}$ shorter than $R_{2+3+4}$, vein $A_2$
glabrous; aedeagus with a single terminal opening, arm of aedeagus with a prominent ventral lobe, apex of aedeagus directed dorsally; ejaculatory apodeme absent or weakly present.

**Description.** **Adult.** Measurements: MALE (N= 8): Body length: 8.8 mm (8.2 – 9.6), wing length: 10.2 mm (10.0 – 10.8), wing width: 2.8 mm (2.6 – 3.0) antennal length: absent; FEMALE. Measurements (N= 1): Body length: 7.2 mm, wing length: 7.6 mm, wing width: 2.7 mm, antennal length: 1.8 mm. **Head:** Variable coloration, amber to brown; rostrum short, dark brown; palpomeres dark brown; palpomere ratio: 1.0-1.2-1.1-1.3. **Antennae:** 16 articles; ranging from amber to brown; flagellomeres suboval, length 2x width; ultimate subequal to penultimate flagellomere; flagellomeres with 5-6 verticils placed at midlength, subequal to flagellomere length; flagellomeres with a weak pubescent covering of golden setiforms. **Thorax:** Thoracic ground color amber; pronotum laterally amber, dorsally with a medial dark brown stripe; prescutum amber with a dorsomedial broad, dark brown stripe; intensity of scutum coloration variable, base coloration amber, dorsomedial dark brown stripe continues beyond the transverse suture; scutellum and mediotergite dark brown; lateral sclerites amber, rarely dark brown; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with ~20 setiforms. **Halteres:** Amber, knobs lightly infumed. **Legs:** Coxae and trochanters amber; femur amber, tips widely ringed with dark brown; tibia and tarsomeres 1-3 amber, tarsomeres 4-5 brown; tibial spurs absent; tarsal claws with 2-3 major teeth placed at the base of claw. **Wing** (Fig. 5.12): Subhyline, weak brown coloration along cord; stigma present, prominent; veins brown. **Wing Venation** (Fig. 5.12): Sc ending near split of Rs; free tip of Sc2 2x free tip of Sc1; Rs moderately long, subequal to R4; R2 present, at end of stigma; R1+2 subequal to R2; three branches of R
attaining wing margin; $R_3$ and $R_4$ parallel; cell $dm$ present, rectangular; $m-cu$ close to the fork of $M$; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, divergent. **Wing Chaetotaxy:** Veins beyond midlength of wing with trichation, crossveins glabrous; $Sc$ with trichation; $A_1$ with ~3 setiforms, $A_2$ glabrous; wing cells without macrotrichia. **Abdomen:** Tergites 1-2 dark brown; tergite 3-6 with posterior half dark brown with an occasional dorsomedial stripe that continues to the anterior edge, anterior end yellow; tergite 7-9 dark brown; sternite 1 yellow; sternites 2-6 narrowly ringed with dark brown that continues to the lateral edge of the segment; sternite 7-9 dark brown. **Male Hypopygium** (Fig. 15.10): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt spatulate apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with dorsal base enlarged, deeply excavated, arm slender, bent at 3/4 length, narrowing to an acute tip; aedeagus with a single opening, curved ventrally near base, directed dorsally before apex, anterior edge of aedeagus with margin enlarged into an acute lobe; dorsal parameres slender; ejaculatory apodeme present. **Female Ovipositor:** Sternites and tergites mottled with brown and amber, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. **Immatures.** Unknown.
Other Material Examined. TURKEY: Rize, Camlihemsin, 1,400 m elevation, 28 July 1967 [8 adult males (pointed)] (MK).

Geographic Distribution (Fig. 23.5). Known from Ardehyan, Iran and from eastern Turkey.

Seasonal Emergence (Table 2). Emergence is known to occur in July and August.

Discussion. Lipsothrix iranica was originally described as a species by Alexander (1975) based on a single female specimen taken from Iran. The lack of an associated male of the species and the similarity of coloration to L. nobilis led to the designation of L. iranica as a subspecies of L. nobilis. It is here treated as a distinct species based on the association of the male of the species based on the dark dorsal stripe of the thorax that is not divided as in L. nobilis. The male genitalia of L. iranica is similar to that of L. nobilis, differing in the more dorsally directed apex of the aedeagus.

Lipsothrix kashmirica Alexander


Type material. Holotype. INDIA: Kashmir, Kai-Nap, 9,000 ft elevation, 30 May 1934 [adult male (pointed)] (USNM). Allotype. same label data as holotype [adult female (pointed)] (USNM). Paratypes. same label data as holotype [adult male (pointed)] (USNM); INDIA: Kashmir, Kai-Nap, 8,000 ft elevation, 25 May 1934 [adult male (pointed)] (USNM); Kashmir, Kai-Nap, 8,000 ft elevation, 22 May 1934 [3 adult males (pointed)] (USNM); Kashmir, Kai-Nap, 8,000 ft elevation, 24 May 1934 [1 adult male, 1 adult female (pointed)] (USNM).

Diagnosis. Wing and body yellow/amber; wing with stigma absent; dorsal abdomen tergites with a medial brown stripe; hypopygium dark brown; dorsal gonostylus nearly
subequal to gonocoxite; interbase with base compressed into an acute point, arm of interbase equipped with dorsal spines; aedeagus with a single terminal opening, ventral face of aedeagus with a weak lobe.

Description. Adult. Measurements: MALE (N=9): Body length: 7.5 mm (6.4–8.8), wing length: 8.6 mm (7.6–9.3), wing width: 2.3 mm (2.1–2.6), antennal length: 3.3 mm (2.9–3.7); FEMALE (N=1): Body length: 9.1 mm, wing length: 9.8 mm, wing width: 2.7 mm, antennal length: 1.6 mm. Head: Uniformly golden yellow coloration; rostrum small, amber; maxillary palpus amber; palpomere ratio 1.0–1.1–1.1–1.3. Antenna: 16 articles; scape and pedicel yellow, flagellomeres 1-4 yellow, remaining flagellomeres becoming tan; flagellomeres length twice the width; ultimate flagellomere 1/3 penultimate flagellomere; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 4-5 basal verticils. Thorax: Golden yellow; interspaces golden yellow. Thoracic Chaetotaxy: Pronotum with 10-14 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterolateral groups of 4-5 setiforms. Halteres: Golden yellow. Legs: Coxae and trochanters golden yellow; femur and tibia golden yellow, each tipped narrowly with brown, tarsomeres suffused tan; tarsal claws with 3-4 teeth, a major tooth at 1/3 distance from base and 2-3 descending smaller teeth to claw base. Wing (Fig. 5.13): Subhyline; stigma absent; veins yellow. Wing Venation (Fig. 5.13): Sc ending at split of Rs; Sc₂ ending at Sc₁, subequal; Rs subequal to Rₛ; R₂ present, subequal to R₁⁺₂; far removed from split of R₃ and R₄, positioned beyond m–m; three branches of R attaining wing margin; R₂⁺₃ and R₄ parallel; cell dm present, rectangular; two medial branches attaining wing margin; crossvein m-cu at split of M; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. Wing
Chaetotaxy: Veins before midlength of wing glabrous, beyond midlength of wing with macrotrichia; crossveins glabrous; $A_1$ and $A_2$ with 13-15 setiforms; wing cells without macrotrichia. Abdomen: Tergite 1-6 brown, posterior of tergite narrowed to a broad dorsal stripe bordered by tan; tergites 7-9 uniformly brown; sternites 1-6 tan; sternites 7-9 brown; abdomen with sparse golden randomly arranged setiforms. Male Hypopygium (Fig. 9.2; 16.1; 18.10): Dark brown; gonoxicite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a slender sickle-shaped rod equipped with 2-3 basal dorsal spines, narrowing to a pointed apex, dorsal base a greatly enlarged broad spine, ventral apodeme suppressed; aedeagus short with a single opening, shaft directed ventrally and bent near apex so that opening posteriorly, anterior face of shaft with margin enlarged to form a weak lobe, posterior face weakly enlarged; dorsal parameres slender; ejaculatory apodeme present.

Female Ovipositor: Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to midlength of cerci, valves broad based and narrowing to an acute apex. Immatures. Unknown.

Other Material Examined: PAKISTAN: Shardi, NW7P, 6,130 ft. elevation, 05 August 1953 [3 adult males (pinned)] (USNM); PAKISTAN: Kashmir, Shardi, 6,130 ft. elevation, 19 June, 1954 [adult male (slide: hypopygium)] (USNM).
Geographic Distribution (Fig. 22.3). Known only from the Kashmir region of India and Pakistan from 1,868 to 2,438 m elevation.

Seasonal Emergence (Table 2). Adults have been collected from late May through late August.

Discussion. Lipsothrix kashmirica is not strongly placed in the phylogeny of the genus (Fig. 28), but it shares morphological similarities to many other clades along with L. nullusarma and L. tokunagai. The wing venation of L. kashmirica has R\textsubscript{2} separated from the split of R\textsubscript{2+3+4}, and width of cell dm about twice the height, similar to that of the Nearctic / Eastern Palearctic group of species. The male hypopygium has a singular aedeagus equipped with a weak ventral lobe, similar to that of the nobilis clade, but does not possess the characteristic S-shaped sinuous aedeagus. The interbase is long and slender, similar to those of the nobilis clade, but with a characteristic compressed base which results in a blunt, spike-like appearance that is shared with L. nullusarma and absent in L. tokunagai. Lipsothrix kashmirica is most similar in morphology to L. nullusarma, separated by the presence of spines on the interbase in L. kashmirica, which is bare in L. nullusarma.

Lipsothrix kraussiana Alexander


Type Material. Holotype, MALAYSIA: Cameron’s Highlands, 4,800 ft elevation, July 1940 [adult male (pointed, slide: wing, legs, & hypopygium)] (USNM). Paratypes, same information as holotype [5 adult males (pointed)] (USNM); Pakasy, Frarers Hill, October 1948 [adult male (pointed)] (USNM).

Diagnosis. Base coloration of body amber, head mottled with brown, dorsal thorax with a variably produced weak brown stripe, mediotergite brown, abdomen tan; posterior
abdominal tergites and sternites conspicuously ringed with dark brown, hypopygium dark brown; wing cells and veins pale yellow, stigma present but weakly so, clouds of coloration along cord, distal end of cell \(dm\), and origin of vein \(Rs\); cell \(dm\) small, width about equal to height, vein \(R_{2+3+4}\) short not exceeding cell \(dm\) in length; male hypopygium with aedeagus bifid, each aedeagal arm with a strongly produced dorsal lobe.

**Description.**  **Adult.** Measurements: MALE (\(N=6\)): Body length: 5.7 mm (5.6–5.8), wing length: 6.8 mm (6.2–7.0), wing width: 2.0 mm (1.9–2.1), antennal length: absent; FEMALE: Unknown.  **Head:** Amber, mottled with brown; rostrum short, amber; maxillary palpus brown, palpomere ratio: 1.0–1.0–1.1–1.2.  **Antenna:** Scape and pedicel yellow; flagellum missing.  **Thorax:** Base tan/yellow base; dorsal scutum ranging from tan to brown; anterior section of postscutural area brown; mediotergite brown; interspaces yellow.  **Thoracic Chaetotaxy:** Pronotum with 15-20 setiforms, scutellum with 2 parallel rows of setiforms, scutum with 2 loose posterior clusters of 4-5 setiforms.  **Halteres:** Bases yellow, knobs suffused brown.  **Legs:** Coxae and trochanters amber; femur and tibia tan/yellow, posterior tips of femur and tibia narrowly tipped with brown; setiforms black; tarsal claws with a single elongate basal tooth.  **Wing** (Fig. 5.14): Subhyline; stigma present, may be faintly indicated; faint clouds of brown at origin of \(Rs\) and along cord, coloration more evident on wing veins; veins yellow, brown at clouds of coloration.  **Wing Venation** (Fig. 5.14): \(Sc\) ending near split of \(Rs\); \(Sc_2\) ending at \(Sc_1\), subequal; basal section of \(Rs\) subequal to free branches of \(R_5\); \(R_2\) near the split of \(R_{2+3}\) and \(R_4\), 1/2 length of \(R_{1+2}\); three branches of \(R\) attaining wing margin; \(R_3\) and \(R_4\) parallel, \(R_4\) deflected ventrally at wing margin; cell \(dm\) present, square, height subequal to width; two medial branches attaining wing margin, crossvein \(m-cu\) variable, intersecting \(M\) near split to middle \(dm\); two cubital branches
attaining wing margin, two anal branches attaining wing margin; veins divergent. **Wing**

**Chaetotaxy:** Veins beyond midlength of wing with trichation, crossveins glabrous; setiforms brown; Sc with setiforms to wing base; A₁ and A₂ with 10-15 setiforms each; wing cells without macrotrichia. **Abdomen:** Tergites and sternites tan/yellow, abdomen ringed with 5-6 dark brown rings that encompass the thoracic tergites and sternites; tergites and sternites 8-9 dark brown. **Male Hypopygium** (Figs. 9.3; 16.2; 18.11): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a slender sickle-shaped rod narrowing to a obtuse pointed apex, base simple; aedeagus short, bifid, bent ventrally near base, splitting near midlength, curving dorsally near apex, posterior face with marginal enlargement on each arm of aedeagus; dorsal parameres slender; ejaculatory apodeme present. **Immatures.** Unknown.

**Geographic Distribution** (Fig. 22.3). Collected from a small areas of Malaysia. The elevation of only one collection is known, with specimens collected at 1,463 m elevation.

**Seasonal Emergence** (Table 2). Adults have been collected from two dates, one in mid July and the other in early October.

**Discussion.** *Lipsothrix kraussiana* is placed within the *assamica* clade (Fig. 28) which is defined by the presence of two aedeagal branches of the male hypopygium. The strongly produced dorsal lobes of the aedeagus indicate a relationship to the *L. decurvata-flavissima-malla* clade (Fig. 28), but differs in: 1) the short aedeagal arms that do not exceed
the length of either the interbase or the entire aedeagal complex, and 2) in wing venation where cell \( dm \) is reduced to a small square, its width about equal to its height. The reduction of cell \( dm \) is similar to that of \( L. \) chetri, but is separated from this species by the coloration of the wing cord and ring-like coloration of the abdomen in \( L. \) kraussiana. The remaining species of this group, \( L. \) assamica, is separated based on wing venation, namely the opening of cell \( dm \) by the loss of basal \( M_{1+2} \) in \( L. \) assamica.

**Lipsothrix leucopeza Alexander**


**Type Material**: **Holotype**, JAPAN: Sikoku, Myanase, 400 m elevation, 02 May 1951 [adult male (pointed, slide: wings, antennae, & leg)] (USNM). **Allotype**, same information as holotype [adult female (pointed w/ holotype)] (USNM).

**Diagnosis**. Body and wing uniformly pale tan to suffused white; wing venation with cell \( dm \) length more than twice its height, \( R_5 \) shortened by increase in length of veins basal \( R_5 \) and \( R_{2+3+4} \); tarsomeres white; dorsal gonostylus of male hypopygium with tooth place near apex of style, base of interbase moderately enlarged, aedeagus with a single terminal opening with apex of aedeagus directed anteriorly, dorsal face of aedeagus with a medial split.

**Description**. **Adult**. Measurements: MALE (N= 7): Body length: 5.1 mm (4.8–5.4), wing length: 7.2 mm (6.6–7.5), wing width: 2.0 mm (1.8–2.1), antennal length: 1.1 mm (1.1–1.2); FEMALE (N=2): Body length: 6.0 mm (5.9–6.1), wing length: 6.7 mm, wing width: 2.8 mm, antennal length: 1.0 mm. **Head**: Pale tan mottled with brown; rostrum small, yellow; maxillary palpus tan, palpomere ratio: 1.0–1.0–1.1–1.1. **Antenna**: 16 articles; scape pale yellow; pedicel and flagellum brown; flagellomeres oval, length about twice the width; ultimate and penultimate flagellomere subequal; flagellomeres with a whorl of 5–6 verticils
at midlength of flagellomere; verticils longer than corresponding flagellomere; ultimate flagellomere tipped with 4–5 setiforms. *Thorax*: Sclerites and interspaces uniformly tan.

*Thoracic Chaetotaxy*: Sparse group of 20–30 setiforms on Pronotum, 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two groups of 5-10 setiforms. *Halteres*: Yellow. *Legs*: Coxae and trochanters tan; femur, tibia, and tarsi pale yellow; tarsal claws with a single small suppressed basal tooth, or untoothed. *Wing* (Fig. 5.15): Lightly suffused with brown; stigma absent; veins tan. *Wing Venation* (Fig. 5.15): Sc attaining wing margin after split of Rs; Sc₂ ending at Sc₁, subequal; basal section of Rs long, subequal to R₄; R₂ present, placed near split of R₂₊₃ and R₄; R₂ and R₁₊₂ subequal; three branches of R attaining wing margin; R₂₊₃ and R₄ weakly divergent; basal R₅ elongate, about 5 times r-m crossvein; dm present; two medial branches attaining wing margin; crossvein m-cu near split of M; two cubital branches attaining wing margin; two anal branches attaining wing margin, divergent. *Wing Chaetotaxy*: Veins beyond midlength of wing with setiforms, crossveins glabrous; Sc glabrous; A₁ and A₂ with 2-3 setiforms; all other wing veins glabrous before wing midlength; wing cells without macrotrichia. *Abdomen*: Tergites and sternites 1-9 uniform tan, tergites and sternites 8-9 tan to brown; with randomly arranged sparse golden setiforms. *Male Hypopygium* (Fig. 10.1; 16.3; 18.12): brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt spatulate apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender, weakly curved rods narrowing to a obtuse pointed apex, base weakly enlarged; aedeagus of moderate length,
singular, curved ventrally, the apex directed anteriorly; dorsal parameres slender; ejaculatory apodeme present. **Female Ovipositor:** Sternites and tergites brown in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci about one-half to three-fourths the length of the tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. **Im matures.** Unknown.

**Other Material Examined.** JAPAN: Honshu, Aomori, Towada, 30 June 1957 [5 adult males, 1 adult female (pointed)] (USNM); Kyushu, Kunimidake, altitude 1,200-1,500 m [1 adult male (pointed)] (USNM); Kyushu, Kunimidake, altitude 1,000 m [adult male (pointed)] (USNM); Shikoku, Tosa, Kuroson, 300-400 m elevation [adult male (pointed)] (USNM).

**Geographic Distribution** (Fig. 22.4). Recorded from the Japanese islands of Shikoku, Honshu, and Kyushu from 91 to 457 m elevation.

**Seasonal Emergence** (Table 2). Adults have been collected from early May to late June.

**Discussion.** *Lipsothrix leucopeza* is the sister taxa to *L. taiwanica* (Fig. 28) with whom it shares the split dorsal face of the strongly anteriorly directed aedeagus. The two species are very similar, differing in wing venation, with *L. leucopeza* having crossvein *m-cu* near the base of the split of *M*, while *L. taiwanica* has *m-cu* near the midlength of cell *dm*. *Lipsothrix taiwanica* possesses a small terminal tooth on the dorsal gonostylus, however this is very weakly present in some *L. leucopeza* specimens. With *L. taiwanica* represented by only a single specimen, additional specimens are needed to adequately separate the two species and prove that these represent distinct species and not clinal variation.
Lipsothrix malla Alexander


Type Material. Holotype, NEPAL: Simbhanjang Pass, 2,499 m elevation, 24 June 1957 [adult male (pointed, slide: wing, leg, antennae, & hypopygium)] (USNM).

Paratopotype: same label information [adult male (pointed)] (USNM).

Diagnosis. Body golden yellow/amber base coloration, dorsal thorax and abdomen with a broad brown stripe of coloration; wing weakly suffused with brown, stigma spot absent though may be indicated by a faint outline; \( R_2 \) at or near split of \( R_{2+3+4} \), male hypopygium dark brown; interbase with base weakly produced, in a rectangular form; aedeagus with two terminal openings, length of each arm about equal to interbase or aedeagal complex length, dorsal face of each aedeagal branch with a strongly produced lobe.

Description. Adult. Measurements: MALE (N= 5): Body length: 6.0 mm (5.4–7.3), wing length: 6.9 mm (6.4–7.5), wing width: 1.8 mm (1.7–1.9), antennal length: 2.2 mm (1.8–2.5); FEMALE: Unknown. Head: Variable, ranging from yellow to brown; rostrum small, tan; maxillary palpus dark brown, palpomere ratio: 1.0–1.1–1.0–1.1. Antenna: 16 articles; scape and pedicel tan/brown, flagellum dark brown; flagellomeres filiform, length 2.5-3.3x width, f1 wider medially; ultimate flagellomere length 1/5 penultimate flagellomere length; flagellomeres with a whorl of 2-4 verticils on basal half, f12 with 3 apical setiforms; flagellomeres with a uniform golden prunosity. Thorax: Golden yellow base, Pronotum dark brown, prescutum with dorsal medial brown stripe, scutum and scutellum brown-dark brown; interspaces yellow. Thoracic Chaetotaxy: Sparse group of 10-18 setiforms on Pronotum, scutellum with 2 parallel rows of setiforms, scutum with 2 loose posterior clusters of 4-5 setiforms. Halteres: Bases yellow, knobs suffused brown. Legs: Coxae and trochanters
golden yellow, femur and tibia yellow, posterior tips narrowly tipped with brown; setiforms black; tarsal claws with a single basal tooth. **Wing** (Fig. 5.16): Lightly suffused; stigma faint, outline indistinct; veins brown. **Wing Venation** (Fig. 5.16): $Sc$ attaining wing margin at split of $Rs$; $Sc_2$ ending at $Sc_1$, subequal; basal section of $Rs$ long, subequal to $R_4$; $R_2$ present, positioned beyond the split of $R_{2+3}$ and $R_4$; $R_2$ 1/2 length of $R_{1+2}$; three branches of $Rs$ attaining wing margin; $R_3$ and $R_4$ weakly divergent; cell $dm$ present, width about twice the length of height; two medial branches attaining wing margin; crossvein $m$-cu intersecting $M$ near split; two cubital branches attaining wing margin; two anal branches attaining wing margin, divergent. **Wing Chaetotaxy**: Veins beyond midlength of wing with trichation, crossveins glabrous; setiforms brown; $Sc$ glabrous; $A_1$ and $A_2$ with 2-3 setiforms; wing cells without macrotrichia. **Abdomen**: Tergites with a medial dark brown stripe, may encompass the entire segment; sternites tan to brown. **Male Hypopygium** (Figs. 10.3; 16.4; 18.13): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt spatulate apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender, bent apically before acute tip, base simple; aedeagus elongate, bifid, curved ventrally near base, directed dorsally before apex, posterior edge of basal aedeagal arm with margin enlarged; dorsal parameres slender; ejaculatory apodeme present. **Immatures.**

 unknown.

**Other Material Examined.** INDIA: Assam, Manipur, Hviahu, 4,900 ft elevation, 1311 m elevation, 01 July 1960 [3 adult males, 2 adult females (pinned)] (USNM).
Geographic Distribution (Fig. 22.5). Lipsothrix malla has been recorded from Nepal at 762 m elevation, and from the Assam Region of India (not mapped) at 1,494 m elevation.

Seasonal Emergence (Table 2). Adults have been collected from late June to early July.

Discussion. Lipsothrix malla is a member of the assamica clade (Fig. 28), defined by the presence of a bifid aedeagus of the male hypopygium. Within this species group, three additional species (L. decurvata, L. kraussiana, and L. flavissima) share a common attribute of an enlarged dorsal face on each branch of the aedeagus. Lipsothrix kraussiana is separated from the other species of this group by possessing short aedeagal branches and lacking the squared basal interbase. Lipsothrix decurvata is separated from L. malla in the possession of the stigma in the radial sector of the wing. Lipsothrix malla is weakly separated from L. flavissima based on the yellow overall coloration of the wing and thorax in L. flavissima and the tan mottled thorax and brown wing veins in L. malla. The apex of the interbase in L. flavissima is more bluntly produced as opposed to the feathered apex of L. malla. Additional specimens will be needed to more adequately separate these two species.

Lipsothrix mirabilis Alexander


Type material. Holotype. CHINA: Szechwan, Omei, White Cloud Temple, 9,000 ft elevation, 07 June 1938 [adult male (pointed, slide: wing, leg, antennae, & hypopygium)] (USNM).

Diagnosis. Head and body dark brown, dorsal thorax with a dark brown stripe; wings suffused with brown, darker coloration along the anterior wing cord, Sc1 and Sc2, R2, and distal edge of cell dm (present or absent); wing venation with R2+3+4 reduced, subequal to
basal $R_5$; $R_{2,3}$ elongate, subequal to length of cell $dm$; cell $dm$ elongate, width greater than twice its height; male hypopygium dark brown; base of interbase moderately enlarged, its arm long and slender; aedeagus with a single terminal opening, face of aedeagus split; ejaculatory apodeme reduced, appearing as two lateral arms.

**Description.** **Adult.** Measurements: MALE (N= 2): Body length: 8.1 mm (7.6-8.6), wing length: 9.9 mm (9.4-10.4), wing width: 2.7 mm (2.6-2.8), antennal length: 3.5 mm (3.2-3.7); FEMALE: Unknown. **Head:** Tan variously mottled with dark brown; rostrum short, brown; maxillary palpus dark brown; palpomere ratio: 1.0–1.1–1.2–1.4. **Antenna:** 16 articles; scape, pedicel, and first flagellomere tan, remainder of flagellomeres brown-dark brown; flagellomeres subcylindrical, length greater than twice width; ultimate flagellomere 1/3 penultimate flagellomere; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-5 verticils on basal half. **Thorax:** Pronotum dark brown, prescutum with dorsal medial brown stripe, scutum and scutellum brown-dark brown; interspaces brown. **Thoracic Chaetotaxy:** Scutellum with 2 parallel rows of setiforms, scutum with 2 loose posterior clusters of 4-5 setiforms. **Halteres:** bases yellow, knobs suffused brown. **Legs:** Brown, anterior tips of femur narrowly yellow; setiforms black; tarsal claws with two prominent basal teeth. **Wing** (Fig. 6.1): Suffused with brown; stigma absent; weakly indicated brown clouds along cord, split of $Sc_1$ and $Sc_2$, $R_2$, and posterior $dm$; veins brown. **Wing Venation** (Fig. 6.1): $Sc$ ending after split of $Rs$; $Sc_2$ ending at $Sc_1$, subequal; basal section of $Rs$ long, subequal to $R_d$; $R_2$ present, far removed from split of $R_{3+4}$, in alignment with $m-m$; three branches of $R$ attaining wing margin; $R_3$ and $R_4$ parallel, divergent at wing margin; basal $R_5$ short, subequal to $r-m$ crossvein; crossvein $r-m$, basal $R_5$, and basal $R_{2+3+4}$ all subequal; cell $dm$ present, elongate rectangle; two medial branches attaining wing margin;
crossvein \( m-cu \) near split of \( M \); two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. *Wing Chaetotaxy*: Wing cells without macrotrichia; setiforms brown; \( Sc \) with trichation; \( A_1 \) and \( A_2 \) with 2-3 setiforms; all other wing veins glabrous before wing midlength. *Abdomen*: Tergites 1-6 uniform brown, tergites 7-9 dark brown; sternites 1-7 brown, sternites 8-9 dark brown yellow; abdomen with randomly arranged sparse golden setiforms. *Male Hypopygium* (Figs. 10.2; 16.5; 18.14): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, a single tooth placed 1/2 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with ventral apodeme moderately enlarged, arm of interbase slender, widening slightly at midlength, bent at midlength and narrowing to a much narrowed tip, base enlarged dorsally; aedeagus with a single opening, directed posteriorly; dorsal parameres slender; ejaculatory apodeme absent. *Immatures*. Unknown.

*Other Material Examined*: INDIA: Sikkim, Chachu, 9,950 ft elevation, 17 May 1959 [adult male (pointed, slide: head, wing, legs, & hypopygium) as *L. mirifica*] (USNM); Sikkim, gey(?), 11,650 ft elevation, 18 May 1959 [adult male (pointed) as *L. mirifica*] (USNM).

*Geographic Distribution* (Fig. 22.5). *Lipsothrix mirabilis* is known from three high elevation collections (2,743-3551 m) made in the Eastern Palearctic Region from China and India.
Seasonal Emergence (Table 2). Adults have been collected from early May to late June.

**Discussion.** *Lipsothrix mirabilis* is a part of a large clade of Nearctic and Eastern Palearctic species (Fig. 28) defined by the elongation of vein $R_{2+3}$ and the split of the face of the aedeagus. *Lipsothrix mirabilis* is separated from all other species on the composition of the wing veins, namely the elongation of cell $dm$ (shared by *L. fenderi*, *L. pluto* and *L. hynesiana*) and the reduction of vein $R_{2+3+4}$ to a length subequal to the length of vein basal $R_5$ or crossvein $r-m$. *Lipsothrix mirifica* Alexander is here synonymized with *L. mirabilis* due to lack of compelling evidence to separate the two.

**Lipsothrix neotropica** Alexander

*Reference.* Alexander 1940b.

*Type Material.* **Holotype**, PANAMA: Potrerillos, 3,000 ft elevation, 07 May 1935 [adult male (pointed, slide: wing, leg, & hypopygium] (USNM).

*Diagnosis.* Body and wing pale yellow to nearly white in color; wing veins pale yellow, stigma absent; wing vein $R_{2+3}$ ending near split of $R_{2+3+4}$, crossvein $m-cu$ meeting cell $dm$ in distal end of cell; male hypopygium not darkened, pale brown in color; interbase long a sinuous, becoming degenerate at apex; aedeagus with a single terminal opening, a weak ventral lobe present.

*Description.* **Adult.** Measurements: MALE (N=1): Body length: 6.5 mm, wing length: 7.3 mm, wing width: 1.9 mm, antennal length: absent; FEMALE: Unknown. **Head:** Head pale yellow; rostrum, short, pale yellow; maxillary palpus reduced, a little darker than rostrum. **Antennae:** 16 articles; scape and pedicel pale yellow, flagellum brown; flagellomeres length twice the width; ultimate flagellomere 1/4 penultimate flagellomere;
flagellomeres with a whorl of 3-4 basal verticils; flagellomeres oval shaped, length about 2x width; verticils of flagellum exceeding flagellomere length; flagellum with a weak golden prunosity. **Thorax:** Uniformly pale yellow, nearly white; katepisternum darkening slightly ventrally; interspaces pale yellow. **Thoracic Chaetotaxy:** Sparse group of 20–30 setiforms on pronotum, 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two groups of 5-10 setiforms. **Legs:** Coxae and trochanters pale yellow; femur yellow, fading to white distally; tibia and tarsi very pale yellow/white; tarsal claw long and narrow, a single major tooth placed at the base of the claw, two minor teeth basal of major tooth placed at base. **Halteres:** Base light yellow, knobs lightly infumed. **Wing** (Fig. 6.2): Subhyline; stigma absent; veins faintly indicated. **Wing Venation** (Fig. 6.2): $Sc$ ending slightly beyond fork of $Rs$; $Sc_2$ slightly removed from $Sc_1$, $Sc_2$ 2.5x the length of $Sc_1$; $R_2$ faintly indicated; $R_{1+2}$ 2x the length of $R_2$; three branches of $Rs$ attaining wing margin; $R_3$ deflected slightly dorsally; $R_4$ deflected ventrally; cell $dm$ present, rectangular; $m-cu$ placed at 2/3 the length of cell $dm$; two medial branches attaining wing margin; two cubital branches attaining wing margin; two anal branches attaining wing margin. **Wing Chaetotaxy:** Wing veins glabrous before origin of $Rs$, crossveins glabrous; $Sc$ glabrous except for a single setiforms placed near the arculus; $A_1$ with 12 setiforms, $A_2$ with 18 setiforms; wing cells without macrotrichia. **Abdomen:** Abdominal tergites uniformly pale brownish yellow; sternites paler than tergites, white. **Male Hypopygium** (Figs. 11.1; 16.6; 19.1): Pale yellow to white; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base, narrowing at midlength, apically bulbous spatulate apex; basal 2/3 equipped with weak setiforms, more abundant on
inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender, base not greatly dorsally enlarged, apodeme present, length of interbase sinuous and thin beyond midlength before an acute tip; aedeagus with a single wide opening, a weak ventral lobe present; dorsal parameres wide; ejaculatory apodeme present. **Immatures.** Unknown.

*Geographic Distribution* (Fig. 22.6). *Lipsothrix neotropica* was described from a single male specimen collected from Potrerillos, Panama at 914 m elevation.

*Seasonal Emergence* (Table 2). The single adult specimen of *L. neotropica* was collected in early May.

*Discussion.* *Lipsothrix neotropica* is known from a single pointed holotype specimen with the wing and genitalia mounted on a slide. *Lipsothrix neotropica* was not grouped into any clade in the greater *Lipsothrix* phylogeny, but most closely resembles *L. tokunagai* of Japan in the presence of white tarsomeres and degeneration of the apex of the interbase of the male hypopygium. The two geographically separated species are separated morphologically based on the position of wing crossvein *m-cu*, located in the distal end of cell *dm* in *L. neotropica* and in the apical end of cell *dm* (near split of *M*) in *L. tokunagai*, and the presence of the basal apodeme of the interbase and the ejaculatory apodeme in *L. neotropica*, these being absent in *L. tokunagai*.

*Lipsothrix nervosa* Edwards


*Type Material.* **Holotype**, UNITED KINGDOM: East Devon, Rousdon, June 1937 [adult male (pinned)] (BM). **Paratypes**, UNITED KINGDOM: South Devon, Rousdon, 08 June 1937 [1 adult male (pinned, hypopygium removed), 1 adult female (pinned)] (USNM).
**Diagnosis.** Base body coloration amber, head brown, dorsal thorax with a variably produced brown stripe, femur and tibia amber and tipped with brown, wing cells yellow, wing veins amber, stigma present, abdominal tergites variably produced but always with darker coloration ranging from a wide brown stripe to the tergite ringed posteriorly with brown, male hypopygium brown; antennae elongate, if bent posteriorly ending near base of halter; basal tarsal claws with teeth; wing venation with $R_{2+3}$ shorter than $R_{2+3+4}$; aedeagus with a single terminal opening, aedeagal arm with a narrow compressed ventral lobe.

**Description.** Adult. Measurements: MALE (N=3): Body length 7.1 mm (6.7–7.4), wing length: 7.8 mm (7.6–8.0), wing width: 2.1 mm (2.1–2.2), antennal length: 3.3 mm (3.2–3.5); FEMALE (N=2): Body length 8.5 mm (8.1–8.9), wing length: 8.9 mm, wing width: 2.1 mm, antennal length: 1.9 mm (1.7–2.0). **Head:** Dark brown; rostrum short, dark brown; palpomeres dark brown; palpomere ratio: 1.0–1.5–1.5–2.4. **Antennae:** 16 articles; scape dark brown, pedicel tan, flagellomeres 1-3 tan, flagellomeres 4-14 becoming dark; flagellomeres elongate, cylindrical, length 4x width in basal flagellomeres, length 3x width in apical flagellomeres; flagellomere 3-11 with anterior face slightly expanded; ultimate flagellomere length 1/3 penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 4 verticils placed at midlength, verticils shorter than segments; flagellomeres with a pubescent covering of golden setiforms that are about 1/4 length of associated flagellomere. **Thorax:** Pronotum and prescutum dark brown, anterior prescutum and scutum amber with a dorsal dark brown medial stripe, width of stripe variable, posterior scutum dark brown, scutellum and mediotergite dark brown; interspaces brown. **Thoracic Chaetotaxy:** Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with ~20 setiforms. **Halteres:** Brown,
knobs dark brown. Legs: Coxae and trochanters amber; femur amber, widely tipped with brown; tibia yellow, faintly tipped with brown; tarsomeres 1-3 yellow, tergite 4-5 brown amber, tips widely ringed with dark brown; tibia and yellow/amber; tibial spurs absent; tarsal claws basally enlarged, equipped with 2-3 major teeth. Wing (Fig. 6.3): Lightly suffused with brown; stigma faintly indicated; veins brown. Wing Venation (Fig. 6.3): Sc ending near split of Rs; free tips of Sc1 and Sc2 subequal; Rs moderately long, subequal to R3; R2 faintly indicated, near split of R3 and R4; R1+2 subequal to R2; three branches of Rs attaining wing margin; R3 and R4 parallel, R4 strongly deflected ventrally at wing margin, R3 weakly deflected ventrally; cell dm present, rectangular, length 3x m-m; m-cu close to the fork of M; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. Wing Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with setation; A1 with >30 setiforms, A2 with ~17 setiforms; wing cells without macrotrichia. Abdomen: Tergites 1-6 brown; tergite 7-0 dark brown/black; sternites 1-6 amber, posterior margin lined with brown; sternite 7-9 dark brown/black. Male Hypopygium (Figs. 11.2; 16.7; 19.2): Amber; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, a single tooth placed 1/2 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase base moderately enlarged dorsally, deeply excavated, basal stem of interbase stouter than apical half, falcate beyond midlength; aedeagus with a single opening, directed posteriorly with a weak ventral deflection, ventral face of aedeagal arm with a basal expansion, dorsum of lobe...
roughly textured; dorsal parameres slender; ejaculatory apodeme present. **Female**

**Ovipositor:** Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

**Immatures.** Collected but undescribed at this time. Diagnostic characters for separation for *L. remota* given by Hinton (1955).


**Geographic Distribution** (Figs. 23.1; 23.2). *Lipsothrix nervosa* is distributed across northern Europe and has been collected from Great Britain, Switzerland, Germany, and Austria (Fig. 20.1). The projected distribution (Fig. 23.2) shows a patchy European distribution but likely under represents the actual potential distribution as georeferenced collection points outside of Great Britain are largely unavailable.
Seasonal Emergence (Table 2). Adults have been collected from early May to late July.

Discussion. Lipsothrix nervosa is a member of the weakly defined nobilis clade (Fig. 28) based on the possession of a ventral lobe of the S-shaped sinuous aedeagus. Lipsothrix nervosa is separated from all other members of this group based on: 1) the elongate flagellomeres, and 2) the compressed ventral aedeagal lobe of the adult male.

Lipsothrix nigrilinea (Doane)

Reference. Doane 1900.

Type Material. Holotype, [adult female (pinned)] USA: Washington, Olympia [adult female (pointed)]. Allotype, USA: Oregon, Alsen Mount, 02 June 1929 [adult male (pointed)] (USNM).

Diagnosis. Base coloration of body amber, dorsal thorax and abdomen with a broadly produced dark brown stripe, lateral thorax and abdomen showing various patterning and intensities of darker coloration; wing vein \( R_2 \) at or near split of \( R_{2+3+4} \); apical wing cells with macrotrichia; male hypopygium dark brown; interbase base enlarged, dorsal face scalloped; aedeagus with a single terminal opening, dorsal face of aedeagus with a weak split.

Description. Adult. Measurements: MALE (N= 3): Body length: 11.7 mm (10.0–13.0), wing length: 12.5 mm (12.2–12.9), wing width: 3.4 mm (3.2–3.5), antennal length: 4.0 mm (3.9–4.1); FEMALE (N= 3): Body length: 11.7 mm (10.0–13.0), wing length: 12.5 mm (12.2–12.9), wing width: 3.4 mm (3.2–3.5), antennal length: 4.0 mm (3.9–4.1). Head: Amber, scattered brown setiforms; rostrum short, amber; maxillary palpus tan; palpmere ratio: 1.0–1.4–1.6–1.8. Antenna: 16 articles; flagellomeres 1–4 yellow, flagellomeres 5–14 becoming brown; flagellomeres cylindrical, length more than twice the width; ultimate
flagellomere 1/3 penultimate flagellomere; flagellomeres with a uniform golden prunosity and a whorl of 3-4 verticils placed at midlength. **Thorax:** Prescutum, scutum, and scutellum dark brown dorsally, fading to amber laterally; lateral sclerites amber; interspaces amber. **Thoracic Chaetotaxy:** Pronotum with 10-14 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with anterior edge with 10-15 setiforms. **Halteres:** Amber. **Legs:** Coxae and trochanters amber; femur amber fading to brown at midlength, tibia and tarsi brown; tarsal claw with 3-4 major teeth. **Wing** (Fig. 6.4): Suffused with brown; stigma absent; wing veins brown. **Wing Venation** (Fig. 6.4): Sc ending near split of Rs; Sc2 ending at Sc1, subequal; basal section of Rs subequal to R5; R2 crossvein present, subequal to R1+2, positioned near split of R2+3 and R4; three branches of Rs attaining wing margin; R3 and R4 parallel, divergent at wing margin; cell dm present, length about 1.5x width; two medial branches attaining wing margin; crossvein m-cu near split of m; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. **Wing Chaetotaxy:** Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with trichation; A1 and A2 with 13-15 setiforms each; radial and medial wing cells with central streaks of macrotrichia, becoming more extensive near wing margin. **Abdomen:** Tergites 1-6 amber with a broad dorsal stripe bordered; tergites 7-9 uniformly brown; sternites 1-6 tan; sternites 7-9 brown; abdomen with sparse golden randomly arranged setiforms. **Male Hypopygium** (Figs. 11.3; 16.8; 19.3): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt spatulate apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with
setiforms along entire length, more abundant at apex; interbase with base enlarged dorsally, ventral apodeme bulbous, base of arm slender becoming enlarged at midlength, bent at 3/4 length, narrowing to an acute tip; aedeagus with a single opening, curved ventrally near base; ventral parameres fused, anterior margin produced; dorsal parameres narrow; ejaculatory apodeme present. **Female Ovipositor:** Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

**Immatures.** Described by Hynes (1965).

**Other Material Examined.** USA: Oregon, Yamhill County, Bald Mt., 04 July 1958 [adult male (pointed)] (USNM); Oregon, Marion County, Silver Falls State Park, 23 June 1974 [adult male (pointed)] (CA); Washington, Olympic National Park, Boulder L. Trail, 21 July 1953 [adult male (pointed)]; Washington, King County, Snoqualmie Pass, 22 July 1950 [adult male (pointed)] (USNM); California, Mt. Shasta, foot hills, 22 May 1944 [adult male (pointed)] (ANSC); 30 May 1944 [adult female (pointed)] (ACNS); California, Marin County, Sausalito, 20 June 1964 [2 adult males (pointed)] (CA).

**Geographic Distribution** (Figs. 23.3; 23.4). Distributed along the west coast of North America. The projected distribution (Fig. 23.4) indicates a coastal distribution across northern California, that expands into the Coastal and Cascade Ranges of Oregon and Washington states, into southern British Colombia of Canada. Additional collection records of Dudley (1982) indicate the potential for *L. nigrilinea* in eastern Oregon.

**Seasonal Emergence** (Table 2). Adults have been collected from late May to early August.
Discussion. *Lipsothrix nigrilinea* is part of the *sylvia* clade (Fig. 28). *Lipsothrix nigrilinea*, along with *L. babai* and *L. shasta*, is separated from all other species by the presence of macrotrichia in the apical wing cells. The three species are extraordinarily similar in morphology and difficult to separate based on any synapomorphy. *Lipsothrix nigrilinea* (western North America) is separable from *L. babai* (Japan) based largely on coloration, with *L. babai* strongly melanistic with the entire body dark brown. Separating *L. shasta* from *L. nigrilinea* is difficult based on both morphological and coloration characters. The two species are easily separable based on coloration at the edges of their ranges, but are similar where their ranges converge in northern California and southern Oregon.

*Lipsothrix nobilis* Loew

Reference. Loew 1873.

Type material. Holotype.

Diagnosis. Base coloration of body amber/tan, head tan, prescutum and scutum with a broad medial dark brown stripe that is divided into two separated stripes after the transverse suture; femur and tibia amber and tipped with brown, wing cells amber, wing veins brown, stigma strongly present, abdomen with sclerites and tergites amber and ringed posteriorly with dark brown, coloration of lateral abdomen variable, may be contiguously brown, male hypopygium dark brown; tarsal claws with teeth, wing venation with $R_{2+3}$ shorter than $R_{2+3+4}$; vein $A_2$ glabrous; aedeagus with a single terminal opening, arm of aedeagus with a prominent ventral lobe; ejaculatory apodeme absent or weakly present.

Description. Adult. Measurements: MALE (N=9): Body length: 8.5 mm (7.1–9.5), wing length: 9.6 mm (8.5–10.4), wing width: 2.7 mm (2.1–3.1), antennal length: 1.7 mm (1.5–1.9); FEMALE (N=16): Body length: 11.4 mm (10.8–12.0), wing length: 11.5 mm
(10.8–12.1), wing width: 3.3 mm (3.2–3.4), antennal length: 2.1 mm (2.0–2.2). **Head:** Variable coloration, amber to brown; rostrum short, dark brown; palpomeres dark brown; palpomere ratio: 1.0-1.0-1.0-1.3. **Antennae:** 16 articles; ranging from amber to brown; flagellomeres suboval, length 2x width; ultimate subequal to penultimate flagellomere; flagellomeres with 5-6 verticils placed at midlength, subequal to flagellomere length; flagellomeres with a weak pubescent covering of golden setiforms. **Thorax:** Thoracic coloration variable; pronotum laterally amber, dorsally with a medial dark brown stripe; prescutum amber with a medial broad, dorsal dark brown stripe; intensity of scutum coloration variable, base coloration amber with a dorsomedial dark brown stripe that is divided into two separated stripes after the transverse suture; scutellum and mediotergite dark brown; lateral sclerites amber, rarely dark brown; interspaces yellow. **Thoracic Chaetotaxy:** Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with ~20 setiforms. **Halteres:** Amber, knobs lightly infumed. **Legs:** Coxae and trochanters amber; femur amber, widely tips widely ringed with dark brown; tibia and tarsomeres 1-3 amber, tarsomeres 4-5 brown; tibial spurs absent; tarsal claws with 2-3 major teeth placed at the base of claw, basal claw may be reduced to 1/3 the length of remaining claws. **Wing (Fig. 6.5):** Subhyline, weak brown coloration along cord; stigma present, prominent; veins brown. **Wing Venation (Fig. 6.5):** Sc ending near split of Rs; free tip of Sc2 2x free tip of Sc1; Rs moderately long, subequal to R4; R2 present, at end of stigma; R1+2 subequal to R2; three branches of R attaining wing margin; R3 and R4 parallel; cell dm present, rectangular; m-cu close to the fork of M; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, divergent. **Wing Chaetotaxy:** Veins beyond
midlength of wing with trichation, crossveins glabrous; Sc with trichation; A₁ with ~3
setiforms, A₂ glabrous; wing cells without macrotrichia. *Abdomen:* Tergites 1-2 dark brown;
tergite 3-6 with posterior half dark brown with an occasional dorsomedial stripe that
continues to the anterior edge, anterior end yellow; tergite 7-9 dark brown; sternite 1 yellow;
sternites 2-6 narrowly ringed with dark brown that continues to the lateral edge of the
segment; sternite 7-9 dark brown. *Male Hypopygium* (Figs. 12.1; 16.9; 19.4): Dark brown;
gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle
glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed
3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt spatulate
apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally
glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with
dorsal base enlarged, deeply excavated, arm slender, bent at 3/4 length, narrowing to an acute
tip; aedeagus with a single opening, curved ventrally near base, directed posteriorly before
apex, anterior edge of aedeagus with margin enlarged; dorsal parameres slender; ejaculatory
apodeme present. *Female Ovipositor:* Sternites and tergites mottled with brown and amber,
cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite
subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided
into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves
broad based and narrowing to an acute apex. **Im matures.** Collected but undescribed at this
time. Pupae illustrated by Godfrey (2001; as *L. nigristigma*).

**Other Material Examined.** CZECH REPUBLIC: Moravia, Adamov U jelinka, 26
May 1973, J. Stary [2 adult males, adult female (pointed)]; Moravia, Adamor u Brua, 26 May
1973 [adult male (pointed)]; Moravia, Lazniky nr. Prerov, 17 May 1992 [adult female
Lipsothrix nobilis is widely distributed across Europe, with records from Austria, Bulgaria, Czech Republic, France, Germany, Great Britain, Hungary, Lithuania, Macedonia, Romania, Slovakia, Ukraine, and Georgia. The limited availability of accurate georeferenced collection locations for L. nobilis (Fig. 23.6) creates a projected distribution that likely underestimates the true geographic distribution.

Seasonal Emergence (Table 2). Lipsothrix nobilis shows an emergence from May to June, however emergence records from September indicate a longer emergence period.

Discussion. Lipsothrix nobilis is a member of the weakly supported nobilis clade (Fig. 28) based on the presence of a ventral lobe of the aedeagus and the sinuous S-shaped aedeagus. Within this group, L. nobilis is distinguishable by the dark coloration of the dorsal thorax, dark coloration of the abdominal sternites and tergites, and the prominent stigma of
the wing. *Lipsothrix nervosa* is separated from *L. nobilis* based on the long antennae of the male and the presence of setation on wing vein \( A_2 \). *Lipsothrix iranica* is very similar to *L. nobilis* in all morphological attributes, but is separated from *L. nobilis* based on the more upturned apex of the aedeagus of the male and the coloration of the dorsal thorax where *L. iranica* has a continuous dark stripe and *L. nobilis* has the dorsal thoracic strip divided after the transverse suture.

**Lipsothrix nullusarma** new species

*Type Material. Holotype.* INDIA: Kumaon, Pauri garhural, Manghu Chatti, 9,270 ft. elevation, 01 June 1958 [adult male (slide: wing, head, leg, & hypopygium)] (USNM).

*Paratype.* INDIA: Kumaon, Pauri garhural, Tungnath, 9,000 ft. elevation, 20 May 1958 [adult male (slide: wing, antennae, leg, & hypopygium)] (USNM).

*Diagnosis.* Wing cells and veins yellow/amber, stigma absent; interbase of male hypopygium with base compressed into an acute point; interbase narrowing to narrow apex; aedeagus with a single terminal opening, ventral face of aedeagus with a weak lobe.

*Etymology.* *Lipsothrix nullusarma* is named for the lack of spines on the male interbase, a trait that distinguishes it from its sister taxon *L. kashmirica*.

*Description. Adult.* Measurements: MALE (N=2): Body Length: absent, wing length: 8.1 mm, wing width: 2.0 mm, antennal length: 1.9 mm; FEMALE: Unknown. *Head:* Uniformly golden yellow coloration; rostrum small, amber; maxillary palpus amber; palpomere ratio 1.5–1.0–1.5–2.0. *Antenna:* 16 articles; scape and pedicel yellow, flagellomeres 1-4 yellow, remaining flagellomeres becoming tan; flagellomeres length twice the width; ultimate flagellomere 1/2 penultimate flagellomere; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 4-5 basal verticils. *Thorax:* Absent in
holotype. **Halteres:** Absent in holotype. **Legs:** Coxae and trochanters absent on holotype; femur and tibia yellow, each tipped narrowly with brown, tarsomeres yellow tan, tipped with brown apically; tarsal claws with 3-4 teeth, a major tooth at 1/3 distance from base and 2-3 teeth at claw base. **Wing** (Fig. 6.6): Subhyline; stigma absent; veins yellow. **Wing Venation** (Fig. 6.6): Sc present at apex of R_{1+2}, both elements removed from split of R_3 and R_4, positioned beyond m–m; three branches of R attaining wing margin; R_{2+3} and R_4 parallel, convergent at wing apex; cell dm present, rectangular; two medial branches attaining wing margin; crossvein m-cu near split of M; two cubital branches attaining wing margin; two anal branches attaining wing margin, veins divergent. **Wing Chaetotaxy:** Costal vein with setiforms to arculus, other veins before midlength of wing glabrous, beyond midlength of wing with macrotrichia; crossveins glabrous; A_1 with 13-15 setiforms, A_2 with 6-8 setiforms; wing cells without macrotrichia. **Abdomen:** Segments 1 and 2 absent from holotype; tergites 3-6 yellow, with a wide medial brown stripe; tergites 7-9 uniformly brown; sternites 3-6 tan; sternites 7-9 brown; abdomen with sparse golden randomly arranged setiforms. **Male Hypopygium** (Fig. 16.10; 19.5): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender sickle-shaped rods, narrowing to a narrowed pointed apex, dorsal base a greatly enlarged broad spine, ventral apodeme suppressed; aedeagus short with a single opening, shaft directed ventrally and bent near apex so that opening posteriorly, anterior face of shaft with margin enlarged to form a weak lobe,
posterior face weakly enlarged; dorsal parameres slender; ejaculatory apodeme present.

**Immatures.** Unknown

*Geographic Distribution* (Fig. 24.1). *Lipsothrix nullusarma* is known from two collections made in northern India, one at 2,743 m and the other at 2,825 m elevation.

*Seasonal Emergence* (Table 2). Adult emergence occurs in late May.

*Discussion.** *Lipsothrix nullusarma* is described from two previously unidentified slides in the Alexander Collection at the USNM. The limited material limits the description of coloration for this species, however the morphological distinctness in the absence of armament on the interbase observed in these specimens warrents their separation as a distinct species. *Lipsothrix nullusarma* is most similar to *L. kashmirica* with whom it shares the characteristic compression at the base of the interbase in the male hypopygium. *Lipsothrix nullusarma* is separated from *L. kashmirica* by the absence of spines on the interbase of the male hypopygium.

**Lipsothrix orthotenes Alexander**


*Type Material.** **Holotype.** INDIA: Assam, Manipur, Hkayam Boum, 8,500 ft elevation, 23 June 1960 [adult male (slide: wing, legs, antennae, & hypopygium)] (USNM).

*Diagnosis.** General coloration of body yellow, prescutum light amber, posterior sclerites of notum pale brown; legs yellow, femoral tips narrowly pale brown; wings pale brown, stigma lacking; aedeagus of male hypopygium bifid with two terminal openings, arms of aedeagus nearly as long as the gonocoxite.

*Description.** **Adult.** Measurements: MALE (N=1): Body length: ~7.5 mm, wing length: ~7.5, antennal length: ~3.0 mm; FEMALE. Unknown. *Head:* Brown; rostrum
yellow, maxillary palpus black. **Antennae**: 16 articles; scape yellow, pedicel and flagellum dark brown; basal flagellomeres 1 1/2 length of distal segments; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-5 verticils at or before 1/2 length of flagellomere; verticils shorter than flagellomere; flagellomeres subcylindrical, length more than twice the width; ultimate flagellomere 1/3 penultimate flagellomere. **Thorax**: Mesonotal prescutum light fulvous, sides and the humeral region yellow; remainder of notum pale brown, central region of scutum, posterior border of scutellum light yellow; pleura and pleurotergite clear light yellow; scutellum and pretergites light yellow. **Thoracic Chaetotaxy**: Unknown. **Halteres**: Stem pale yellow, knob light brown. **Legs**: Coxae and trochanters light yellow; femur, tibia and tarsomeres more obscure yellow, tips of femora and tibia narrowly pale brown; tarsal claw with a single basal tooth. **Wing** (Fig. 6.7): Lightly suffused with light brown; stigma absent; veins pale brown. **Wing Venation** (Fig. 6.7): $Sc$ ending at split of $Rs$, $Sc_1$ equal to $Sc_2$; $R_2$ present, faintly indicated; $R_{1+2}$ about 2x length of $R_2$; three branches of $Rs$ attaining wing margin; $R_3$ not strongly deflected at wing margin; cell $dm$ present, height subequal to width; $m-cu$ at split of $M$; two medial branches attaining wing margin; two cubital branches attaining wing margin; two anal branches attaining wing margin. **Wing Chaetotaxy**: Veins basal to origin of $Rs$ glabrous; $Sc$ glabrous; $A_1$ with 2 macrotrichia, $A_2$ with 1; wing cells without macrotrichia. **Abdomen**: tergites light brown, sternites yellow, tergites and sternites 8-9 darker brown to form a weak ring. **Male Hypopygium** (Figs. 12.3; 17.1; 19.6): Amber; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex, basal 2/3 equipped with weak setiforms, more abundant on inner face of
style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase not expanded at base, its length a slender sickle-shaped rod, apex blunt; aedeagus bifid, directed ventrally and splitting into two arms at its midlength, dorsal face prominently enlarged; dorsal parameres narrow; ejaculatory apodeme present. **Immatures.** Unknown.

*Geographic Distribution* (Fig. 21.2). *Lipsothrix orthotenes* was described from a single male specimen taken at Jkayam Boum in the Manipur region of Assam, India at an elevation of 2,600 m.

*Seasonal Emergence* (Table 2). Adult emergence occurs in July.

*Discussion.* All that remains of this type specimen are the antennae, 3 legs, a haltere, and the male hypopygium mounted on slide in Canadian balsam. Because neither the remainder of the holotype nor additional specimens are available for observation, the coloration offered in this redescription is based largely on the original description offered by Alexander (1971). *Lipsothrix orthotenes* is placed within the *assamica* clade (Fig. 28) based on the bifid aedeagus of the male hypopygium, group with *L. chettri* and *L. assamica* in the possession of a strong ventral lobe. *Lipsothrix orthotenes* is best separated from these two species based on the composition of cell *dm*, it being atrophied in *L. assamica* and greatly reduced in *L. chettri* to a square, while having the width about twice the height in *L. orthotenes*.

* Lipsothrix pluto Alexander

*Reference.* Alexander 1929.

*Type Material.* **Holotype**, TAIWAN: Shorei, 7,000 to 8,000 ft elevation, October 25, 1928 [adult male (pointed, slide: wing, leg, antennae, & hypopygium)] (USNM).
**Diagnosis.** Head and body dark brown to black in coloration, lateral pretergites with obscure yellow coloration, dorsal thorax polished black; legs with femora black, base narrowly ringed with yellow; wing brown, stigma present; wing vein $R_2$ removed from $R_{2+3+4}$; hypopygium dark brown; base of interbase moderately enlarged; aedeagus with a single terminal opening, face of aedeagal arm split; ejaculatory apodeme reduced, seen as two lateral processes.

**Description.** **Adult.** Measurements: MALE (N=1): Body length: 7.5 mm, wing length: 8.5 mm, antennal length: 3.3 mm; FEMALE: Unknown. **Head:** Dull black; rostrum small, black; palpus black, palpomere ratio: 1.2–1.4–1.0–1.5. **Antennae:** 16 articles; scape, pedicel, and flagellum black; flagellomeres cylindrical with verticils that are shorter than the segments; flagellomeres subcylindrical, length gradually decreasing in length outwardly, ultimate flagellomere 1/3 that of penultimate segment; flagellomeres subglobular; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-5 verticils at 1/2 length of flagellomere; verticils shorter than flagellomere. **Thorax:** shining black, anterior lateral pretergites very restrictedly obscure yellow; dorsopleural membrane black. **Thoracic Chaetotaxy:** Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with ~20 setiforms. **Halteres:** obscure white, knobs infused with darker. **Legs:** Coxae and trochanters yellow; femora black, the extreme bases obscure yellow; tibia and tarsi black; tarsal claw toothed, a large tooth present at midlength of claw; basal to this tooth are 3-4 small teeth that range for 1/3 to 1/2 the length of the major tooth. **Wing** (Fig. 6.8): Suffused with brown; stigma darker brown; veins dark brown. **Wing Venation** (Fig. 6.8): Sc ending near split of Rs, Sc$_2$ and Sc$_1$ subequal; Rs subequal to $R_3$; $R_2$ equal to $R_{1+2}$; three branches of
Rs attaining wing margin; $R_3$ and $R_4$ parallel; cell $dm$ present, rectangular, length 3x width; $m-cu$ about one-half its length beyond the fork of $M$; two cubital branches attaining wing margin; two anal branches attaining wing margin, divergent. **Wing Chaetotaxy:** All veins beyond midlength of wing with trichation, crossveins glabrous; $Sc$ with trichation; $A_1$ with 20 setiforms, $A_2$ with 14 setiforms; wing cells without macrotrichia. **Abdomen:** Tergites and sternites black. **Male Hypopygium** (Figs. 12.2; 17.2; 19.7): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/4 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase yellow, base moderately enlarged dorsally, excavated, ventral apodeme enlarged to a slender knob, basal stem of interbase slender widening at 3/4 length at strong bend of interbase, apex acute; aedeagus with a single opening, short, strongly curved ventrally, posterior margin enlarged; dorsal parameres narrow; ejaculatory apodeme weakly present or absent. **Immatures.** Unknown.

**Geographic Distribution.** *Lipsothrix pluto* is known from a single male specimen from Taiwan at between 2,133 m to 2,438 m elevation.

**Seasonal Emergence** (Table 2). Adult emergence occurs in October.

**Discussion.** *Lipsothrix pluto* was originally described from a single male specimen collected from Taiwan in 1928. The holotype is preserved as a pointed specimen, an antennae, leg, wing, and hypopygium have been removed and mounted on a slide in Canadian balsam. *Lipsothrix pluto* is part of the large Nearctic / East Palearctic clade (Fig. 28). The genitalic structure, especially the 3/4 expansion of the interbase is similar to that of
the *sylvia* clade, but is separated by the absence of macrotrichia in the wing cells and not having the basal interbase enlarged. *Lipsothrix pluto* is darkly colored as in *L. mirabilis*, but is separated from *L. mirabilis* by the longer wing vein $R_{2+3+4}$ and from *L. hynesiana* in having the wing stigma present.

**Lipsothrix propatula** Alexander


*Type Material. Holotype,* BURMA: Kambaiti, 7,000 ft elevation, 30 April 1934 [adult male (slide: wing, leg, antennae, & partial gonostylus)] (USNM).

*Diagnosis.* Head coloration brownish black, body dark brown; femur yellow, tips narrowly colored with brown; tarsal claws with a single basal tooth; wing weakly darkened, stigma very faintly present; $R_{2+3}$ placed near split of $R_{2+3+4}$; cell $dm$ open by atrophy of basal section of $M_3$; male hypopygium dark brown.

*Description. Adult.* Measurements: MALE (N=1): Body length: 7.0 mm, wing length 7.7 mm, antennal length: 2.0 mm; FEMALE: Unknown. *Head:* Uniform brownish black. *Antennae:* 16 articles; scape brownish yellow, pedicel and flagellomeres brown; flagellomeres suboval, the outer ones more narrowed at ends; ultimate flagellomere small, about one-half as long as penultimate flagellomere; verticils relatively inconspicuous, shorter than segments; flagellomeres with a pubescent covering of golden setiforms that are about 1/4 length of associated flagellomere; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 2-3 verticils at 1/2 length of flagellomere; verticils shorter than flagellomere. *Thorax:* Cervical region and pronotum infuscated; mesonotum almost uniformly dark brown, the prescutum with three paler stripes, the interspaces brown; humeral portion of prescutum pale; dorsal pleurotergite darkened, the remainder, together with the
pleura, yellow. *Halteres*: Pale, the knobs weakly infuscated. *Thoracic Chaetotaxy*: Unknown. *Legs*: Coxae and trochanters yellow; femora yellow, the tips narrowly dark brown, the amount subequal on all legs; tibiae yellow, the tips narrowly infuscated, the bases weakly darkened; tarsi yellow, the outer segments darker; tibial spurs absent; tarsal claws with a single tooth at the base of claw. *Wing* (Fig. 6.9): with a faint brownish gray tinge; stigma pale to scarcely indicated; veins pale yellowish brown. *Wing Venation* (Fig. 6.9): Sc short, Sc₁ ending just before the level of the fork of Rs, Sc₂ at its tip and subequal; Rs moderately long, less than twice R₂₊₃₊₄; three branches of Rs attaining wing margin; R₁₊₂ subequal to R₂; R₂ weakly indicated; two medial branches reaching wing margin; cell dm open by the atrophy of the basal section of M₃; cell m₂ being about three times as long as its petiole; m-cu close to the fork of M; two cubital branches attaining wing margin; two anal branches reaching wing margin. *Wing Chaetotaxy*: All veins beyond midlength of wing, except Sc, with trichation, crossveins glabrous; Sc glabrous, A₁ and A₂ each with two macrotrichia placed at distal end of vein; wing cells without macrotrichia. *Abdomen*: dark brown, the pleural region yellowed. *Male Hypopygium*: Dark brown; gonocoixite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex. Aedeagus absent from holotype.

**Immatures.** Unknown.

*Geographic Distribution* (Fig. 24.2). *Lipsothrix propatula* is known from a single specimen taken from Kambaiti, Myanmar, at 2,133 m elevation.
Seasonal Emergence (Table 2). Adult emergence occurs in April.

Discussion. *Lipsothrix propatula* was described from a single male specimen collected in alcohol, all that remains of this holotype specimen is a slide mount in Canada balsam containing the dissected antennae, wing, leg, and partial hypopygium. The description of coloration presented here is based on the original description from a specimen collected into alcohol, which may have altered the actual body coloration. The wing venation with cell *dm* open by the atrophy of basal *M*_3 is not seen in any other known specimen of *Lipsothrix*, therefore this species is based largely on this one characteristic. Additional specimens will need to be collected to validate this species further.

*Lipsothrix remota* Walker

Reference. Walker 1848.

Type Material. Holotype, unknown locality (BM).

Diagnosis. Overall body coloration yellow, wing cells and veins yellow, stigma absent, femur yellow, tibia yellow with tips may be tipped with brown, male hypopygium variable, ranging from tan to brown; tarsal claws with teeth; wing venation with *R*_2+3 shorter than *R*_2+3+4; vein *A*_2 with weak setation at juncture of wing margin; aedeagus of male hypopygium with a single terminal opening, ventral lobe of aedeagus arm with a low lobe; ejaculatory apodeme present.

Description. Adult. Measurements: MALE (N=20): Body length: 8.3 mm (7.0–9.4), wing length: 10.0 mm (8.8–10.5), wing width: 2.8 mm (2.5–3.1), antennal length: 2.2 mm (1.8–2.4); FEMALE (N=15): Body length: 10.7 mm (12.0–9.8), wing length: 9.9 mm (8.9–11.8), wing width: 2.5 mm (2.1–2.7), antennal length: 2.0 mm (1.8–2.1). Head: Yellow; rostrum short, suffused yellow; maxillary palptomere 2 yellow, palptomere 3-4 brown,
palpomere ratio 1.2–1.0–1.1–1.4. Antennae: 16 articles; scape and basal flagellomeres may be bicolorous; flagellomeres subcylindrical, length 2x width; ultimate segment 1/2 length of penultimate segment; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-4 verticils at 1/2 length of flagellomere; verticils shorter than flagellomere. 

Thorax: Yellow, thoracic sclerites uniformly colored; interspaces yellow. Thoracic Chaetotaxy: Pronotum with 20-40 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 15-20 setiforms. Halteres: Yellow. Legs: Femur yellow, tibia and tarsomere 1-3 yellow with distal ends weakly ringed with brown, tarsomeres 3-5 dark brown; tarsal claws with base enlarged, with 2-3 major teeth and 1-2 minor basal teeth. Wing (Fig. 6.10): Suffused with yellow; stigma absent; veins golden yellow. Wing Venation (Fig. 6.10): Sc ending at split of Rs, Sc₂ slightly longer than Sc₁; R₂ present after split of R₃ and R₄; R₂ and R₁+₂ subequal; three branches of Rs attaining wing margin; R₃ and R₄ parallel, both curved ventrally at wing margin; cell dm present, rectangular; m-cu near split of M; two medial branches attaining wing margin; two anal branches attaining wing margin, divergent. Wing Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with setation; A₁ with 10-15 setiforms, A₂ with 0-5 setiforms; no macrotrichia in wing cells. Abdomen: Tergites and sternites 1-7 yellow; tergite 8-9 variably colored with yellow and brown; sternite 8 typically dark brown, but may be mottled with yellow. Male Hypopygium (Fig. 13.1; 17.3; 19.8): Yellow; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally
glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with base enlarged, deeply excavated ventrally, ventral apodeme broad based and suppressed, arm slender and weakly falcate; aedeagus short with a single opening, directed anteriorly at base and curving so opening is directed posteriorly at tip, anterior face of aedeagal arm expanded into a broad lobe; dorsal parameres slender; ejaculatory apodeme present. Female Ovipositor: Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

Immatures. Descriptions provided by Hinton (1955; 1967; 1968), and Brindle (1967).

Other Material Examined. GREAT BRITAIN: Derbyshire, Chee dale, Nr. Buseton, 27 June 1911 [adult male (pointed)] (BM); Sannox, Arron, 26-28 1919 [adult male (pointed)] (BM), [adult male (pointed)] (USNM); Brecon, Llangynidr, May 1937 [adult male (pointed)] (BM); S. Devon, Rousdon, 08 June 1937 [adult male (pointed)] (BM); Denbighshire, Llangollen, 30 June 1914 [adult male (pointed)] (BM); Corriegillils, Arran, 2-4 June 1919 [adult female (pointed)] (BM), [2 adult males (pointed)] (USNM); Yorks, Ingleton, 20 June 1924 [adult female (pointed)] (BM); Westmorland, Witherslack, 12 July 1923 [adult female (pointed)] (BM); Holker Moss, N. Lanes, 11-13 July 1923 [adult male (pointed)] (BM); Barton Beds, 8-9 July 1928 [adult male (pointed)] (BM); South Devon, Dartmouth, 28-31 May 1920 [adult male (pointed)] (BM); Bradenham 29 May 1949 [adult female (pointed)] (BM); Dovendal, 14 June 1988 [adult male (pointed)] (BM); Bramshaw, 05 July 1923 [adult male (pointed)]; Farlay, 06 June 1923 [adult male (pointed)]; Farlay, 10 July 1923 [adult male (pointed)]; Perthshire, Loch Rannoch, June 1931 [adult male (pointed)]; Isle of Wright,
Shanklin, 29 May 1929 [adult male (pointed)]; George Avon, 15 June 1940 [adult male (pointed)]. GREECE: Kallithea, Thrakien, 41°07’ N 25°04’ E, elevation 1000 m, 09 June 1973 [adult female (alcohol)] (MK); Pendayaia, 38°35’ N 22°04’ E, elevation 950 m, 03 June 1975 [adult female (alcohol)]; Dirtis, Dirtis-Gebirge, Euboa, Obern. Strapones, elevation 880 m, 24 May 1974 [2 adult males, 1 adult female (alcohol)] (MK); Diakopion, 25 km WNW Amphissa, 13-14 May 1978 [adult male, adult female (alcohol)] (MK); Euboa, Dirtis-Gebirge oberh. Stropones, 720 m elevation [adult male (alcohol)] (MK). ITALY: Laurino, Campania, Grava Di Vesolo, August 1970 [adult male, 2 adult females (alcohol)] (MK); Olymp – Prioni, 1000 m elevation, 03 June 1913., [adult male (pointed)] (MK); Ossa, 1,500 m elevation, 14 June 1917 [adult male, adult female (pointed)] (MK); Pertouli/trikalon, Pindos, 1,250 m elevation, 01 June 1968 [5 adult males, adult female (pointed)] (MK); Katara-Pass, 1,700 m elevation, 27 May-01 June 1964 [4 adult males (pointed)] (MK); Platamon Prov., Katerini, Castle-Camping lux, 07-14 June 1968 [adult female (pointed)] (MK). GERMANY: Bonn, am Rhein, 18 May 1965 [6 adult male, 1 adult female (pointed)] (MK); 02 June 1965 [adult male (pointed)] (MK); 04 June 1965 [adult male (pointed)] (MK); 07 June 1965 [2 adult male, 2 adult females (pointed)] (MK); 14 June 1965 [2 adult males (pointed)] (MK); 19 June 1965 [adult male, adult females (pointed)] (MK); 21 May 1965 [adult male, adult female (pointed)] (MK); 24 May 1969 [adult male (pointed)] (MK); Schwartzwald, b. Nagold, 20 July 1966 [2 adult males (pointed)] (MK); Kreuzbach, Kreuzthal/Westallgäu, 24 June-14 July 1971 [3 adult females] (MK); Teufelskueche, südlich Landsberg a. Lech., 30 May 1983 [adult male, adult female (alcohol)] (MK); Trautbachtal / Allg. Alpeau, 1,200 m elevation, 22 June 1971[3 adult males, adult female (alcohol)] (MK); Westerwald, Rengsdorf, 12 Aug 1948 [adult male (pointed)]. CZECHOSLOVAKIA:
Tatranska, Kotlina, 20 June, 1932, Bela Kalk Alpen 3,000 ft elevation [adult male (pointed)] (MK); Boh., nr Prague, Voznice, 10 June 1973 [2 adult female (pointed)] (BM); Moravia, Jeseniky Mtns., Branna Dembuda, 900 m elevation, 14 July 1999 [adult male (pointed)] (JS); FRANCE: B. Pyrenees, 10 September 1967 [adult female (pointed)] (MK).

ROMANIA: Retezatul Mtns., above Hobita, 2,500 ft. elevation, 28 June 1969 [7 adult males, 2 adult females (pointed)] (BM). LITHUANIA: Varena distr., Puvociai – Blindyne, 26 June 1998 [adult male (pointed)] (ANSC). YUGOSLAVIA: Slovenich, Jelendol [adult male (alcohol)] (MK); Cipari, 1,400 m elevation, 11 August 1955 [adult male (pointed)] (USNM).

Geographic Distribution (Figs. 24.3; 24.4). Widespread European species known from extensive collections from Albania, Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Czech Republic, Denmark, Estonia, France, Germany, Great Britain, Hungary, Ireland, Italy, Latvia, Lithuania, Macedonia, Netherlands, Poland, Romania, Slovakia, Slovenia, Spain, Sweden, Switzerland, and Ukraine. The predicted distribution projects a widespread range (Fig. 24.4).

Seasonal Emergence (Table 2). Adult emergence occurs from May to September.

Discussion. Lipsothrix remota is a member of a weakly supported nobilis clade (Fig. 28) based on the presence of a ventral lobe of the aedeagus the sinuous S-shaped aedeagus. Lipsothrix remota is separated from other species of this group based largely on coloration, namely the lack of darker coloration on the dorsal thorax, dorsal abdomen, or femur.
Lipsothrix shasta Alexander


Type Material. Holotype, USA: California, Shasta Co., Burney, 30 May 1939 [adult male (pointed)] (USNM). Paratype. Same information as holotype [adult male (pointed)] (USNM).

Diagnosis. Body coloration yellow to amber, prescutum with a variable dorsal brown stripe, lateral thoracic sclerites may be mottled with brown, wing suffused with brown, abdomen with a variable dorsal brown stripe, abdominal sternites amber, male hypopygium dark brown; wing venation with $R_2$ at or near split of $R_{2+3+4}$; apical wing cells with macrotrichia; aedeagus of male hypopygium with a single terminal opening, its dorsal face with a weak split; ejaculatory apodeme present; base of interbase enlarged, dorsal face of enlargement scalloped.

Description. Adult. Measurements: MALE (N=17): Body length: 8.5 mm (7.4 – 10.2), wing length: 9.8 mm (8.9 – 10.8), wing width: 2.8 mm (2.5 – 3.0), antennal length: 2.75 mm (2.65 – 3.1); FEMALE (N=17): Body length: 8.5 mm (7.4 – 10.2), wing length: 9.8 mm (8.9 – 10.8), wing width: 2.8 mm (2.5 – 3.0), antennal length: 2.75 mm (2.65 – 3.1).

Head: Rostrum short, amber (rarely brown); maxillary palpus brown, palpomere ratio 1.4–1.0–1.4–2.3. Antennae: 16 articles; scape and pedicel amber; flagellomeres 1-4 amber, flagellomere 5-12 brown (basal flagellomeres may be bicolorous); flagellomeres cylindrical, length 2x width; ultimate segment 1/2 length of penultimate segment; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-5 verticils at 1/2 length of flagellomere; verticils shorter than flagellomere. Thorax: Pronotum dorsally dark brown, laterally amber; scutum, scutellum, and mediotergite dark brown; interspaces pale brown to
yellow. *Thoracic Chaetotaxy*: Pronotum with 50-60 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 15-20 setiforms. *Halteres*: Amber, knobs infrequently infuscated. *Legs*: Femur, tibia and tarsomere 1 yellow with distal ends widely ringed with brown; tarsal claws with base enlarged, with 2-3 major teeth and 1-2 minor basal teeth. *Wing* (Fig. 6.11): Suffused with brown; stigma absent or faintly indicated; veins brown. *Wing Venation* (Fig. 6.11): Sc ending at split of Rs, Sc₁ subequal to Sc₂; R₂ present, near split of R₃ and R₄; R₂ and R₄₂ subequal; three branches of Rs attaining wing margin, R₃, R₄, and R₅; R₃ and R₄ parallel, R₄ weakly deflected ventrally; cell dm present; m-cu near split of M; two medial branches attaining wing margin. *Wing Chaetotaxy*: Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with setiforms until wing base; anal veins with 9-15 setiforms; macrotrichia in distal sections of cells R₂ to M₄. *Abdomen*: Tergites 1-6 variously colored with amber and brown, typically with a medial dorsal brown stripe and amber laterally; sternites 1-6 amber; tergites and sternites 7-9 dark brown. *Male Hypopygium* (Figs. 13.2; 17.4; 19.9): Amber; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase with base a large dorsal knob, narrowly excavated, basal stem slender, widening at 3/4 length at strong bend of interbase, apex acute; aedeagus with a single opening, short, strongly curved ventrally, margins simple; ventral parameres fused, anterior margin enlarged; lateral parameres long. *Female Ovipositor*: Sternites and tergites amber in color, cerci and
hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

**Immatures.** Described by Hynes (1965)

*Other Material Examined.* USA: California, Castle Crags State Park, elevation 2,000’, 08 July 1953, Alexander [9 adult males, 2 adult females (pointed)] (USNM); 06 July 1953 [3 adult males (pointed)] (USNM). Siskiyou Co., Mt. Shasta, 18 June 1959, Byers [2 adult females (pointed)]. Trinity Co., Little Bidden Creek, 25 June 1964, Hynes [3 adult males (pointed)] (CM); Sierra Co., Highway 49, creek @ Rosasco Ravine, 2.4 km west of Downieville, 04 July 1975, 890 m elevation [adult male (pointed)] (CA); Highway 49, creek in New York Ravine, on New Yuba River, 2.8 km east of Downieville, 05 July 1975, 940 m elevation [adult male (pointed)] (CA).

**Geographic Distribution** (Figs. 24.5; 24.6). Distributed along the southern Cascade Mountains in Northern California and southern Oregon, and the Sierra Nevada Range of California.

**Seasonal Emergence** (Table 2). Adult emergence occurs from May to July.

**Discussion.** *Lipsothrix shasta* is part of the *sylvia* clade (Fig. 28) and along with *L. nigrilinea* and *L. babai* are grouped by the presence of macrotrichia in the apical wing cells. *Lipsothrix shasta* (western North America) is separable from *L. babai* (Japan) largely based on coloration, with *L. babai* strongly melanistic with the entire body dark brown. Separating *L. shasta* from *L. nigrilinea* is difficult based on both morphological and coloration characters. The two species are easily separable based on coloration at the edges of their ranges, but are similar where their ranges converge in northern California and southern
Oregon. The ordination provided in the Species Delineation section illustrates the separation of these two species, while the provided key will adequately separate them based largely on coloration.

*Lipsothrix sylvia* (Alexander)


*Type Material.* Holotype. USA: New York, Fulton County, Woodworths Lake [adult male (pointed)] (USNM).

*Diagnosis.* Overall coloration amber, dorsal thorax and abdomen slightly darker, male hypopygium brown; wing vein $R_2$ near split of $R_{2+3}$ and $R_4$; stigma present, often weakly; base of interbase enlarged; aedeagus with a single terminal opening, the dorsal face split.

*Description.* Adult. Measurements: MALE (N=50): Body length: 6.1 mm (5.8 – 6.4), wing length: 7.0 mm (6.7 – 7.2), wing width: 2.0 mm (1.8 – 2.3), antennal length: 1.5 mm (1.3 – 1.6); FEMALE (N=50): Body length: 7.0 mm (6.2– 7.4), wing length: 7.1 mm (6.8 – 7.3), wing width: 2.0 mm (1.8 – 2.3), antennal length: 1.5 mm (1.4 – 1.6). *Head:* Rostrum short, amber (rarely brown); maxillary palpus brown, palptomere ratio 1.4–1.5–1.4–2.0. *Antennae:* 16 articles; scape and pedicel amber; flagellomeres 1-12 brown; flagellomeres cylindrical, length 2x width; ultimate segment 1/2 length of penultimate segment; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 3-5 verticils at 1/2 length of flagellomere; vertice length subequal or longer than flagellomere. *Thorax:* Pronotum dorsally brown, laterally amber; scutum, scutellum, and mediotergite variable, amber to brown, darker than lateral thoracic sclerites; interspaces pale brown to yellow. *Thoracic Chaetotaxy:* Pronotum with 20-30 setiforms, prescutum with 2 converging
rows of setiforms running from the prescutal pits to the scutellum, scutellum with two
anterior edge with 10-15 setiforms. Halteres: Yellow to amber, knobs infrequently
infuscated. Legs: Femur, tibia and tarsomere 1 yellow with distal ends weakly ringed with
brown; tarsal claws with base enlarged, with 1-2 minor basal teeth. Wing (Fig. 6.12):
Subhyline; stigma absent or faintly indicated; veins brown. Wing Venation (Fig. 6.12): Sc
eeding at split of Rs, Sc₁ subequal to Sc₂; R₂ present, near split of R₃ and R₄; R₂ and R₁+₂
subequal; three branches of Rs attaining wing margin, R₃, R₄, and R₅; R₃ and R₄ parallel, R₄
weakly deflected ventrally; cell dm present; m-cu near split of M; two medial branches
attaining wing margin; two anal veins to wing margin. Wing Chaetotaxy: Veins beyond
midlength of wing with trichation, crossveins glabrous; Sc with setiforms until wing base;
anal veins with 3-7 setiforms; wing cells without macrotrichia in distal sections of cells.
Abdomen: Tergites 1-6 brown, typically with a medial dorsal brown stripe and amber
laterally; sternites 1-6 amber; tergites and sternites 7-9 dark brown. Male Hypopygium (Figs.
13.3; 17.5; 19.10): Gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal;
dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a
single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing
to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of
style, distally glabrous, equipped with setiforms along entire length, more abundant at apex;
interbase with base a moderately enlarged, narrowly excavated, basal stem slender, widening
at 3/4 length, tip narrowed to an acute apex; aedeagus with a single opening, short, strongly
curved ventrally, margins simple; ventral parameres fused, anterior margin enlarged; lateral
parameres long. Female Ovipositor: Sternites and tergites amber in color, cerci and
hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal
in length; tenth sternite medially divided into two small lobes; hypogynial valves extending
to slightly after origin of cerci, valves broad based and narrowing to an acute apex.

**Imatures.** Described by Hynes (1965)

**Other Material Examined.** USA: Pennsylvania: Lebanon Co., State Game Lands
#211, 40° 28' 40.3" N 76° 37' 19" W, 04 June 1999, 04 June 1999 [adult male (pointed)]
(ANSC); Lycoming Co., 30 May 1932 [2 adult males (pointed). South Carolina: Greenville,
C4, 09 May 1932 [11 adult males (pointed)], 07 May 1932 [2 adult males (pointed)] [UM];
North Carolina: Black Mtms., 21 May 1912 [adult male (pointed)] (ANSC); Mt. Mitchell,
Seepage @ 5,000’, 22 May 1934 [2 adult males, adult female (pointed)]; Buncombe Co.,
Foot of Craggy, 30 May 1932 [adult male (pointed)]; Swaine Co., Great Smokey Mountains
National Park, 3 June 1952 [adult male (pointed)]; Haywood Co., Mt. Sterling, alt. 4,900’
29 July 1924 [2 adult males (pointed)]; Mt. Pisgah, 3,000’, 28 May 1934 [2 adult males
(pointed)]; Sharptop Mtn., alt. 3,400’, 28 June 1924 [adult male (pointed)]; Macon Co.,
Highlands, 11 June 1934 [3 adult males (pointed)], 12 June 1934 [3 adult males (pointed)],
13 June 1934 [adult male (pointed)], 30 June 1934 [6 adult males, adult female (pointed).
Transylvania Co., Camp Toxoway, alt. 3,200’, 09 June 1934 [3 adult males (pointed)], 10
June 1934 [adult female (pointed)]. New York: Helderberg Mtns., 5 June 1923 [adult male
(pointed)]. Massachusetts: Sunderland, 27 May 1923 [adult male (pointed)]; Orient Springs,
07 June 1924 [adult male (pointed)]. Kentucky: Whitely Co., 10 June 1934 [adult male
(pointed)]. Tennessee: Great Smokey Mountains National Park, Ramsey Cascades, 12 June
1946 [adult male (pointed)]; Fentress Co., Allardt, Buffalo Cove, alt. 1,400’, 24 June 1924 [3
adult males, 3 adult females (pointed)]. Virginia: Wise Co., Big Stone Gap, 02 July 1952
[adult male (pointed)]; Giles Co., Mountain Lake, 07 July 1943 [2 adult males, adult female

**Geographic Distribution** (Figs. 25.1; 25.2). *Lipsothrix sylvia* is widely distributed along the Appalachian Mountains of eastern United States and projects a widespread eastern US distribution (Fig. 25.2).

**Seasonal Emergence** (Table 2). Adult emergence occurs from May to July.

**Discussion.** *Lipsothrix sylvia* is a member of the *sylvia* clade within a larger Nearctic / Eastern Palearctic clade (Fig. 28). The *sylvia* clade is based on the presence of an enlarged base of the interbase of the male hypopygium and is separated from the other species of the Nearctic / Eastern Palearctic clade by the presence of wing vein $R_2$ near the split of $R_{2+3+4}$. *Lipsothrix sylvia* is separated from the other species of the *sylvia* clade by the absence of macrotrichia in the apical wing cells.

* Lipsothrix taiwanica Alexander

**Reference.** Alexander 1928.

**Type Material.** **Holotype.** Taiwan, west side of Mount Daibu, 3,000’-5,000’ elevation, March 1927 [location and condition of specimen unknown]; **Paratypes.** same as holotype [location and condition of specimens unknown].

**Diagnosis.** Body coloration pale yellow to nearly white, femur and tibia pale brown, tarsi white, wing cells pale yellow, wing veins pale tan, stigma absent, male hypopygium pale brown; antennal verticils long, exceeding flagellomere length; tarsal claws without teeth; wing venation with $R_2$ removed from split of $R_{2+3+4}$, crossvein $m-cu$ in distal end of cell $dm$; subcostal and anal veins without trichation; aedeagus of male hypopygium with a single
terminal opening, ventral side of aedeagal arm with a weak ventral lobe; ejaculatory apodeme present; base of interbase not produced, arm of interbase becoming degenerate after midlength.

**Description.** **Adult.** Measurements: MALE, (N=1): Body length: 5.75 mm (5.5-6.0), wing length: 6.4 mm (6.0-6.8); FEMALE: Unknown. **Head:** Yellow; rostrum short, pale brown; maxillary palpus pale brown. **Antennae:** 16 articles; scape, pedicel, and flagellum pale brown; flagellomeres cylindrical, length subequal to width; ultimate flagellomere subequal penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 5-7 long verticils placed at midlength, verticils longer than segments. **Thorax:** Thoracic sclerites obscure yellow. **Thoracic Chaetotaxy:** Unknown. **Halteres:** Pale yellow. **Legs:** Coxae and trochanters pale yellow; femur and tibia pale brown yellow; tarsi while; tarsal claws without teeth. **Wing** (Fig. 6.13): Lightly suffused with yellow; stigma absent; veins tan. **Wing Venation** (Fig. 6.13): Sc ending after split of Rs; Sc₁ subequal to Sc₂; Rs moderately long, subequal to R₄; R₂ beyond split of R₃ and R₄, R₂₊₃₊₄ subequal to R₂₊₃; R₂ subequal to R₁₊₂; three branches of Rs attaining wing margin; R₃ and R₄ parallel, divergent at wing margin; cell dm present, rectangular; m-cu close to the fork of M to midlength of cell; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. **Wing Chaetotaxy:** Veins beyond midlength of wing with trichation, crossveins glabrous; A₁ and A₂ glabrous; Sc without trichation; wing cells without macrotrichia. **Abdomen:** Tergites and sternites pale brown. **Male Hypopygium** (Figs. 14.1; 17.6; 19.11): Pale brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing
to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender and straight, the base a weakly enlarged; aedeagus bent gently ventrally, with a single terminal opening, dorsal face of style divided; dorsal parameres wide; ejaculatory apodeme present. **Immatures.** Unknown.

*Other Material Examined.* Formosa (Taiwan), Kanshirei, 13 May 1933, 1,500’ elevation [adult male (slide: wing, leg, antennae, male hypopygium)] (USNM).

*Geographic Distribution* (Fig. 25.3). *Lipsothrix taiwanica* is known from two collections made on the island of Taiwan. The collection records indicate a range in elevation of between 457 m to 1,524 m.

*Seasonal Emergence* (Table 2). Adult emergence occurs from March to May.

*Discussion.* *Lipsothrix taiwanica* was described in 1928 based on a male holotype and four paratype specimens listed as deposited in the personal collection of C.P. Alexander. Investigation of the collection of Alexander, now housed at the Smithsonian, did not uncover the types of *L. taiwanica* and it is unknown if they still exist. The redescription presented here is of a slide of a single male specimen from unidentified material from the USNM. The measurements and coloration presented in this redescription could not be determined from this slide and are based on the original 1928 description. *Lipsothrix taiwanica* is the sister taxon to *L. leucopeza* (Fig. 28). These species are grouped based on the anteriorly facing aedeagus of the male hypopygium. This trait is shared with *L. errans* (Western Palearctic) and possibly *L. heitfeldi* (Eastern Palearctic), however these two species are equipped with a strong dorsal lobe of the aedeagus (Fig. 15.6). *Lipsothrix taiwanica* is separated from *L.*
leucopeza based on the presence of a terminal tooth of the dorsal gonostylus and the reduced base of the interbase.

*Lipsothrix tokunagai* Alexander

*Reference.* Alexander 1933.

*Type Material. Holotype,* JAPAN: Daisen, Toxxori, Honshu, 02 July 1931 [adult male (pointed, slide: wing & hypopygium)].

*Diagnosis.* Overall body coloration pale yellow; tarsal claws with strong teeth; wing veins Sc and A₁ with trichation, A₂ glabrous; wing venation with R₂ near R₂+₃+₄, crossvein m-cu near spilt of M (basal cell dm); aedeagus of male hypopygium with a single terminal opening, and a weak ventral lobe; ejaculatory apodeme present; interbase narrowing after midlength and thinly produced.

*Description. Adult.* Measurements: MALE (N=10): Body length: 7.1 mm (6.6–7.6), wing length: 7.9 mm (7.8–8.0), wing width: 2.4 mm (2.3–2.6), antennal length: 2.6 mm (2.4–2.8); FEMALE (N=4): Body length: 8.7 mm (8.1–8.9), wing length: 8.1 mm (7.9–8.2), wing width: 2.3 mm (1.9–2.6), antennal length: 1.4 mm (1.0–1.8). *Head:* Yellow; rostrum short, yellow; maxillary palpus yellow; palpomere ratio: 1.0–1.5–1.1–1.9. *Antennae:* 16 articles; scape, pedicel, and flagellum yellow; flagellomeres subcylindrical, ends constricted, length 2x width; ultimate flagellomere length1/2 penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 3-4 verticils placed at midlength, verticils shorter than segments; flagellomeres with a thick pubescent covering of golden setiforms. *Thorax:* Thoracic sclerites yellow; interspaces yellow. *Thoracic Chaetotaxy:* Pronotum with 20-30 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 10-15 setiforms. *Halteres:* Yellow. *Legs:*
Coxae, trochanters, and legs yellow; tarsal claws equipped with 3-4 teeth, the largest at 1/3 length from base and 2-3 descending smaller teeth to base. **Wings** (Figs. 6.14): Lightly suffused with yellow; stigma absent; veins yellow. **Wing Venation** (Fig. 6.14): Sc ending near split of Rs; free tips of Sc2 twice the length of Sc2; Rs moderately long, subequal to R3; R2 beyond split of R3 and R4, R2+3+4 subequal to R2+3; R2 subequal to R2; three branches of Rs attaining wing margin; R3 and R4 parallel, divergent at wing margin; cell dm present, rectangular; m-cu close to the fork of M to midlength of cell; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. **Wing Chaetotaxy**: Veins beyond midlength of wing with trichation, crossveins glabrous; A1 with 10-15 setiforms, A2 glabrous; Sc with trichation; wing cells without macrotrichia. **Abdomen**: Tergites and sternites yellow. **Male Hypopygium** (Figs. 14.2; 17.7; 19.12): Yellow; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, a single tooth placed 1/2 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender, bent at 3/5 length and becoming slender after final bend, base moderately enlarged dorsally; aedeagus with a single wide opening, directed ventrally near base, anterior face of aedeagal arm with a suppressed marginal expansion; dorsal parameres wide; ejaculatory apodeme present. **Female Ovipositor**: Sternites and tergites pale yellow in color, cerci and hypogynial valves amber, apex of hypogynial valves white; cerci three-fourths the length of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial
valves brown, extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex. Immatures. Unknown.

Other Material Examined. JAPAN: Kurokawa, Echigo, elevation 300 m, 02 July 1955 [2 adult males, 1 adult female (pointed)] (USNM); Kurokawa, Echigo, elevation 350 m, 12 July 1955 [2 adult males (pointed)] (USNM); Sado Island, Mt. Donden. 600 m elevation. 19, July 1955 [3 adult males (pointed)] (USNM); Sado Island, Mt. Donden. 700 m elevation. 18, July 1955 [2 adult females (pointed)] (USNM); Echigo, Mt. Umakozari. 24, June 1955 [adult (pointed)] (USNM); Echigo, Mt. Naeha. 01, July 1956 [1 adult, 1 female (pointed)] (USNM); Shikoku, Sahea, Omogomura. 800 m elevation. 19, June 1955 [1 male, 1 female (pointed)] (USNM); Shikoku, Omogo Valley. 800 m elevation. 15, June 1956 [1 male (pointed)] (USNM).

Geographic Distribution (Fig. 25.4). Distributed across Japan at an elevation range of between 300 m to 800 m.

Seasonal Emergence (Table 2). Adult emergence occurs in June and July.

Discussion. Lipsothrix tokunagai is weakly placed in the phylogeny of Lipsothrix. It shares the trait of a prominent ridge of the aedeagus with L. kashmirica and L. nullusarma, but is separated from these two species by the presence of white tarsomeres. The presence of white tarsomeres is shared with L. taiwanica and L. leucopeza, and L. neotropica. Lipsothrix tokunagai is separated from these species based on the placement of wing crossvein m-cu, it being placed in the distal end of cell dm in L. neotropica and in apical end of cell dm (near split of M) in L. tokunagai, and the presence of the basal apodeme of the interbase and the ejaculatory apodeme in L. neotropica, these being absent in L. tokunagai.
Lipsothrix yamamotoana Alexander


Type Material. Holotype, JAPAN: Iwatekan, Funakoshi, 200 m elevation, 23 May 1947 [adult male (pointed)] (USNM). Paratypes, JAPAN: Iwatekan, Funakoshi, 200 m elevation, 23 May 1947 [adult male (pointed)] (USNM).

Diagnosis. Overall body coloration dark brown, pleural wing process and halteres yellow, wing lightly suffused with brown, wing veins amber, stigma present, femur and tibia yellow widely tipped with brown distally; tarsal claws with prominent teeth; wing venation with $R_{2+3}$ subequal or longer than $R_{2+3+4}$; length of cell $dm$ about twice height; interbase of male hypopygium falcate, its base not enlarged; aedeagus with a single terminal opening, directed dorsally, dorsal face of aedeagal arm with a weak dorsal lobe, ventral aedeagal face with a prominent lobe; ejaculatory apodeme present.

Description. Adult. Measurements: MALE (N=4): Body length: 6.8 mm (6.5–7.2), wing length: 8.4 mm (8.3–8.5), wing width: 2.4 mm (2.3–2.4), antennal length: 2.3 mm (2.2–2.4); FEMALE: Unknown. Head: Dark brown; rostrum short, dark brown; palpomeres dark brown; palpomere ratio: 1.0–1.2–1.2–1.3. Antennae: 16 articles; scape, pedicel, and flagellum dark brown; flagellomeres suboval, ventral face slightly enlarged, length 2x width; ultimate flagellomere length1/2 penultimate flagellomere length, tipped with 3-4 verticils; flagellomeres with 4-5 verticils placed at midlength, verticils shorter than segments; flagellomeres with a pubescent covering of golden setiforms. Thorax: Thoracic sclerites dark brown; interspaces brown, pleural wing process yellow. Thoracic Chaetotaxy: Pronotum with 10-15 setiforms, prescutum with 2 converging rows of setiforms running from the prescutal pits to the scutellum, scutellum with two anterior edge with 10-15 setiforms.
Halteres: Yellow. Legs: Coxae and trochanters amber; femur and tibia amber, widely tipped with brown; tarsomeres brown; tarsal claws equipped with 3-4 teeth, the largest at 1/3 length from base and 2-3 descending smaller teeth to base. Wing (Fig. 6.16): Lightly suffused with brown; stigma present; veins amber. Wing Venation (Fig. 6.16): Sc ending near split of Rs; free tips of Sc₁ and Sc₂ subequal; Rs moderately long, subequal to R₃; R₂ near split of R₃ and R₄; R₂ slightly longer than R₂; three branches of Rs attaining wing margin; R₃ and R₄ weakly divergent; cell dm present, rectangular; m-cu close to the fork of M; two medial branches reaching wing margin; two cubital branches attaining wing margin; two anal branches reaching wing margin, veins divergent. Wing Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins glabrous; Sc with trichation; A₁ with 2-5 setiforms, A₂ with 5-8 setiforms; wing cells without macrotrichia. Abdomen: Tergites and sternites dark brown. Male Hypopygium (Figs. 14.3; 17.8; 19.13): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long slender rod narrowing to a darkened acute apex, a single tooth placed 1/2 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase slender, falcate to a hair-like tip, the base enlarged dorsally; aedeagus with a single opening, directed ventrally near base with a strong poster bend near apex, a strong ventral lobe present; dorsal parameres wide; ejaculatory apodeme present. Female Ovipositor: Sternites and tergites brown in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length; tenth sternite medially divided into two small lobes; hypogynial valves brown, extending to
slightly after origin of cerci, valves broad based and narrowing to an acute apex.

**Immatures.** Unknown.

*Other Material Examined.* JAPAN: Sapari Mino, Sakauchi, 04 May 1958 [2 adult males, 2 adults with terminal abdomens removed (pointed)] (USNM).

*Geographic Distribution* (Fig. 25.6). Distributed across Japan and has been collected from an elevation of 200 m.

*Seasonal Emergence* (Table 2). Adult emergence occurs throughout May.

*Discussion. *Lipsothrix yamamotoana* one of many strongly melanistic species known from the Eastern Palearctic Region, but is differentiated by the possession of both a weak dorsal lobe and strongly produced ventral lobe of the aedeagus of the male hypopygium. No other species is known to possess such an aedeagus. The wing venation and general coloration of *L. yamamotoana* is very similar to that of *L. pluto*, with the females of both being difficult to separate.

**5.4.3 Species of Uncertainty**

The following species are weakly maintained as species due to a lack of available material for examination or damage to existing material that does not allow for comparisons with other species. These species are accepted as valid species, and redescribed to allow for separation from other species. They should be regarded, however, as species of uncertainty that are in need of additional study for determination of validity. These species are here re-described based on available material.
Lipsothrix burmica Alexander


Type Material. Holotype, MYANMAR: Kambaiti, 7,000 ft. elevation, 04 June, 1934 [adult male (slide: wing, antennae, hind leg & partial hypopygium)] (USNM).

Diagnosis. Overall body coloration dark brown, pleural wing process and halteres yellow, wing lightly suffused with brown, wing veins amber, stigma absent, femur and tibia yellow widely tipped with brown distally; tarsal claws weakly toothed; wing venation with $R_{2+3}$ subequal to $R_{2+3+4}$; length of cell $dm$ about twice height.

Description. Adult. Measurements. MALE (N= 1): Body length: 7.0 mm, wing length: 7.5 mm, antennal length: 2.0 mm; FEMALE: Unknown. Head: Head brown; vertex prominent; rostrum short, dark brown; maxillary palpus brown. Antenna: 16 articles; scape and pedicel brownish yellow, flagellum dark brown; basal flagellomeres subcylindrical, becoming oval apically; flagellomeres with 3-4 short verticils placed at midlength; ultimate flagellomere with 4 apical verticils, flagellomere length 1/3 the length of penultimate segment. Thorax: Pronotum brownish yellow, darker medially; mesonotum dark brown; pleura dark brown, the dorsopleural region paler. Halteres: Brown. Legs: Coxae dark brown; trochanters brownish yellow; femora and tibia light brown, the tips narrowly darkened; tarsi brownish yellow; tarsal claws with one major tooth located at 2/5 distance from base of claw; 2 to 3 minor teeth half the length of major tooth present between major tooth and base. Wing (Fig. 5.3): Suffused with brown; stigma absent; veins brown. Wing Venation (Fig. 5.3): $Sc$ attaining wing margin after split of $Rs$; $Sc_2$ ending at $Sc_1$; basal section of $Rs$ subequal $R_3$; $R_2$ present, near split of $R_{2+3}$ and $R_4$, $R_{1+2}$ twice length $R_2$; $R_3$ and $R_4$ parallel, divergent at wing margin; cell $dm$ present, rectangular; two branches of M attaining
wing margin, crossvein $m-cu$ intersecting at split of $M$; two cubital branches attaining wing margin, two branches of $A$ attaining wing margin; veins divergent. *Wing chaetotaxy:* Veins beyond midlength of wing with trichation, crossveins glabrous; Veins basal to origin of $Rs$ glabrous; $Sc$ glabrous; $A_1$ and $A_2$ each with 2-3 macrotrichia. *Abdomen:* Tergites and sternites 1-7 brown, tergites and sternites 8-9 dark brown. *Male Hypopygium* (Only partial hypopygium remains on holotype): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex. *Immatures.* Unknown.

*Geographic Distribution.* This species is known from a single specimen taken at 7,000’ elevation from Kambaiti, Myanmar.

*Discussion.* All that remains of this type specimen are the antennae, leg, and partial male hypopygium mounted on slide in Canadian balsam. Because neither the remainder of the holotype specimen nor any additional specimens are available for observation, the original male description and holotype information contained in the Alexander description for *Lipsothrix burmica* (Alexander 1952) is used here for the description of coloration. Alexander separated this as a species based on the combination of characters: closed $1^{st} M_2$, short $R_{2+3}$ (about as long as $r-m$), and aspects of coloration. Additional specimens are needed to confirm the status of this species.
Lipsothrix heitfeldi Alexander


Type Material. Holotype. CHINA: Fukien, Ta-chu-lan, 26 April 1948 [adult male (pointed, slide: wing, antennae, leg, & hypopygium)] (USNM).

Diagnosis. Overall body coloration dark brown, pleural wing process and halteres yellow, wing lightly suffused with brown, wing veins amber, stigma absent, femur and tibia yellow widely tipped with brown distally; tarsal claws with a single basal tooth; wing venation with \( R_{2+3} \) longer than \( R_{2+3+4} \); length of cell \( dm \) less than twice height, nearly square shaped.

Description. Adult. MALE. Measurements (N= 1): Body length: 6.0 mm, wing length: 8.2 mm, wing width: 2.4 mm, antennal length: 2.2 mm; FEMALE: Unknown. Head: Dark brown; rostrum short, dark brown; maxillary palpomeres dark brown. Antenna: 16 articles; scape, pedicel, and flagellomeres dark brown; flagellomeres cylindrical, length 3-4x width; ultimate flagellomere absent; flagellomeres with 4 verticils placed at midlength; flagellomeres with a uniform golden prunosity; flagellomeres with a whorl of 2-3 small medial verticils. Thorax: Dark brown; interspaces yellow. Thoracic Chaetotaxy: Pronotum with 6-10 setiforms, prescutum with 2 converging weak rows of setiforms running from the prescutal pits to the scutellum. Halteres: Brown, base yellow-brown. Legs: Coxae and trochanters yellow; femur and tibia tan, posterior tips narrowly suffused with brown; tarsomeres amber; tarsal claws slender with a single basal tooth. Wing (Fig. 5.10): Suffused with brown; stigma absent; veins brown. Wing Venation (Fig. 5.10): \( Sc \) ending near or after split of \( Rs; Sc_2 \) ending at \( Sc_1 \), subequal; basal section of \( Rs \) long, greater than length of \( R_3 \), less then \( R_5; R_2 \) present, well after split of \( R_{2+3} \) and \( R_4; R_2 \) and \( R_{1+2} \) subequal; three branches
of Rs attaining wing margin; $R_{2+3}$ and $R_4$ strongly divergent; cell $r_3$ long petiolate; cell $dm$ present; two branches of $M$ attaining wing margin; crossvein $m-cu$ intersecting $M$ after split of $M$; two cubital branches attaining wing margin; two branches of $A$ attaining wing margin, divergent. *Wing Chaetotaxy:* Veins beyond midlength of wing with setiforms, crossveins glabrous; $Sc$ with setation; $A_1$ and $A_2$ each with 2-6 setiforms; wing cells without macrotrichia. *Abdomen:* Tergites and sternites 1-9 dark brown. *Male Hypopygium* (partial hypopygium remains): Dark brown; gonocoxite and gonostyli subequal in length; gonostyli bifid, subequal; dorsal gonostyle glabrous, a long rod narrowing to a darkened acute apex, tipped with a single tooth placed 3/5 of length of style; ventral style with a bulbous base distally narrowing to a blunt apex; basal 2/3 equipped with weak setiforms, more abundant on inner face of style, distally glabrous, equipped with setiforms along entire length, more abundant at apex; interbase a simple sclerotized rod narrowing to an acute point, base with a weak dorsal enlargement, basal half of interbase thicker than apical half. **Immatures.**

Unknown.

*Geographic Distribution* (Fig. 22.1). This species is known from a single specimen taken from Ta-chu-lan in the Fukien region of China.

*Discussion.* This species was described by Alexander based on a combination of coloration and wing venation characteristics. The description of *L. heitfeldi* is most similar to *L. pluto* in the overall uniform liver-brown coloration, elongate male antennae (exceeding 1/3 the length of the wing), inconspicuous flagellomere verticals, and legs obscure yellow with tips darkened. Additional specimens are needed to confirm this is a valid species.
Lipsothrix yakushimae Alexander


Type Material. JAPAN: Kosugiani, Yakushima. 2,500 ft elevation. 29 April 1929 [adult female (pointed, slide: wing & leg)] (USNM).

Diagnosis. Overall body coloration amber, pleural wing process and halteres amber; rostrum of head greatly reduced, its length about subequal to that of the scape of antennae; tarsomeres white; tarsal claws without teeth; wings lightly suffused with brown; wing veins amber, stigma present; wing venation with basal $R_5$ extended toward wing base.

Description. Adult. MALE. Unknown; FEMALE. Measurements (N= 1): Body length: 8.5 mm, wing length: 8.2 mm; wing width 2.1 mm; antennal length: 2.0 mm. Head: amber; rostrum very short, reduced to length subequal to scape, amber; labial palpomeres greatly reduced; maxillary palpomeres present, palpomere ratio: 1.0-1.1-2.0-1.3. Antennae: 16 articles; ranging from amber to brown; flagellomeres suboval, length 2x width; ultimate subequal to penultimate flagellomere; flagellomeres with 5-6 verticils placed at midlength, subequal to longer than flagellomere length; flagellomeres with a weak pubescent covering of golden setiforms. Legs: Femora and tibia light brown; tarsi brownish yellow; tarsal claws without teeth. Wing (Fig. 6.15): Suffused with brown; veins dark brown. Wing Venation (Fig. 6.15): $Sc$ attaining wing margin after split of $Rs$; $Sc_2$ ending at $Sc_1$; $Rs$ split near wing midlength; basal section of $Rs$ subequal to $R_{2+3}$; $R_2$ present, after split of $R_{2+3}$ and $R_4$, $R_{1+2}$ subequal to $R_2$; $R_3$ and $R_4$ parallel, divergent at wing margin; cell $dm$ present, rectangular; two branches of M attaining wing margin, crossvein $m-cu$ intersecting at split of $M$; two cubital branches attaining wing margin, two branches of $A$ attaining wing margin; veins divergent. Wing Chaetotaxy: Veins beyond midlength of wing with trichation, crossveins
glabrous; veins basal to origin of Rs glabrous; Sc glabrous; \( A_1 \) and \( A_2 \) each with 2-3 macrotrichia.  

**Ovipositor:** Sternites and tergites amber in color, cerci and hypogynial valves brown, apex of hypogynial valves white; cerci and tenth tergite subequal in length, with a small ridge at apex of tenth tergite; tenth sternite medially divided into two small lobes; hypogynial valves brown, extending to slightly after origin of cerci, valves broad based and narrowing to an acute apex.  

**Imatures.** Unknown.

**Geographic Distribution** (Fig. 25.5). This species is known from a single specimen taken at 2,500 ft. elevation from Yakushima, Kosugiani Japan.

**Discussion.** *Lipsothrix yakushimae* is very similar to both *L. leucopeza* and *L. taiwanica* in wing venation and the white coloration of the tarsomeres. It differs most in the reduction of the mouthparts of the adult fly to a length that is much less than that of the remaining head. Because this species is known from only a single specimen, it is unknown if the holotype of this species represents an aberrant specimen of *L. leucopeza* or a separate species. Identification of the male of the species, which remains as yet undiscovered, and collection of additional material will validate this species.

### 5.4.4 Natural History

#### 5.4.4.1 Larvae

The larval stage has been identified and associated with the adult stage for 10 species of *Lipsothrix* (*L. ecucullata, L. fenderi, L. nigrilinea, L. shasta, L. hynesiana, L. nobilis, L. sylvia, L. errans, L. nervosa, L. remota*). The composition of habitat types utilized by these species is exceedingly similar. The following synopsis is summarized from the findings of Dudley and Anderson (1987), Dudley (1982), Rogers and Byers (1956), Godfrey (2000; 2001) and through personal observations.
The immature stages of *Lipsothrix* occur in saturated wood of various tree species (Table 3), however a preference for deciduous wood is evident. The decaying wood serves as a protected habitat, a food source, and a location for pupation. Larvae scour and ingest the sodden wood tissues in this habitat. Through this action they carve out and create the tunnel in which they live. Ingested wood in *L. nigrilinaea* is retained in the larval gut for up to 10 days and may be digested by the aid of filamentous bacteria found in a pouch attached to the larval hindgut. Similar filamentous bacteria have been discovered in the gut contents of both *L. sylvia* and *L. fenderi*. In general, larvae occupy the area 5-15 mm below the surface of the wood. Depth of larval penetration is somewhat variable and is dependent on decay class of the wood, with deeper penetration seen in wood of a greater decomposition stage. All species show a common pattern of tunneling parallel to the surface of the wood, though in smaller wood sources (20 mm diameter) *L. nigrilinaea* was seen to essentially mine through the center of the wood source. Tunneling and feeding generally occurs through the softer spring annual growth rings, with larvae passing through the denser winter rings only to move to additional spring growth rings.

A variety of aquatic situations ranging from seepages to third order streams provide adequate habitat for *Lipsothrix*. The type of aquatic system matters less than the ability of the aquatic system to maintain woody debris until it is of a suitable decay class (*sensu* Dudley & Anderson 1987; Triska and Cromak 1980; Dudley 1982). As with the aquatic system, the size class of woody substrates that maintain *Lipsothrix* populations vary greatly, with larvae recorded from wood sources ranging from 2-88 cm in diameter. Typically larger wood classes are found in larger aquatic systems and smaller diameter woody inputs (20-30 mm diameter) are found in small seepage, rills, and permanent boggy springs with infrequent
spate events. The most common aquatic environment in which *Lipsothrix* larvae are found is where woody input is gathered in debris dams or lodged into the stream bank.

It is not uncommon for more than one species to coexist within a single habitat. *Lipsothrix nigrilinea* and *L. fenderi*, and *L. shasta* and *L. fenderi* co-occur in the same woody substrate over a large portion of their ranges, while *L. errans*, *L. remota*, and *L. nervosa* have been documented to co-occur in Great Britain. Little is known about interspecific interactions between crane flies when 2 or more species co-occur within the same larval habitat. Barnes (1937) has documented competitive interactions between crane fly instars with later instars actively feeding on earlier instars, thus displacing them from the habitat. Dudley (1982) observed interspecific interactions between *L. fenderi* and *L. nigrilinea* where the larger *L. nigrilinea* would feed on the smaller *L. fenderi* in artificial laboratory situations. The degree to which these or other interactions affect the distribution of any species at either the landscape or microhabitat level remains unknown for the great majority of *Lipsothrix* species.

### 5.4.4.2 Pupa

Pupation occurs within the larval feeding chamber, with pupation behavior having been observed for *L. sylvia* (present study; Rogers & Byers 1956), *L. shasta* (present study) *L. fenderi* (Dudley & Anderson 1987), *L. nigrilinea* (Dudley & Anderson 1987), *L. hynesiana* (Hynes 1965), *L. nobilis* (Godfrey 2001), *L. remota* (Godfrey 2001), *L. errans* (Godfrey 2001), and *L. nervosa* (Godfrey 2000). Prior to the onset of pupation, a small circular section of wood is removed from larval chamber, exposing the chamber to the exterior. The larvae then retreats within the larval chamber before the final molt. Positioning of the pupa at the exit of the chamber occurs about an hour prior to eclosion of
the adult fly. During pupation the pupa is arranged parallel to the wood surface with the anterior section of the pupae bent dorsally so that the respiratory plastron is emergent through the removed chamber opening. Duration of pupation has not been recorded for all species, but was seen lasts 11 to 16 days for *L. nigrilinea* at 15°C (Dudley & Anderson 1987) and a minimum of 4 days for *L. sylvia* (Rogers & Byers 1956) in the laboratory.

### 5.4.4.3 Adult

Eclosion from the pupal skin may last from one to ten minutes. Upon eclosion, the teneral adults typically remain close to the site of emergence (within a few centimeters) for nearly 10 minutes until fully sclerotized. After complete sclerotization and inflation of wings with hemolymph, the adult fly will remain in the general vicinity of the larval habitat, rarely moving more than a few yards away from the larval habitat. Additional details of the adult behavior are poorly known, however because adults are not known to actively seek food, adult activity can be grouped into two major activities, those being dispersal and reproduction.

The flight potential and actual adult dispersal from the larval habitat is largely unknown. For the most part adult flies perch on woody substrates or within riparian vegetation where shade is provided and direct sunlight is limited. The collection of adult flies in close proximity to known larval habitat, and the fact that adults are rarely collected outside of a few meters from streams, indicate that adults infrequently venture from the site of larval habitat. Movement of adult flies within the stream course of the larval habitat is typically parallel to the stream course, with movement upstream more prevalent than downstream. While exact figures for duration of flight activity or the degree to which adults disperse from the larval habitats are unknown, it is assumed that the short life span of the
imago will greatly limit most long distance dispersal. In laboratory settings under ideal conditions, the life-span of unmated adult *L. nigrilinea* (Dudley 1982) and *L. sylvia* was 5 days for males and 8 days for females. Mated adults had a reduced life span at 3-4 days for both males and females. The short life span and relatively delicate and desiccation prone state of the adult is likely to restrict their dispersal. This will be especially true of species inhabiting aquatic areas that are restricted by inhospitable surroundings, such as *L. hynesiana* and *L. shasta*, which often occur in streams surrounded by highly xeric habitat.

Reproductive behavior is initiated by the male, often while the female is still teneral and unable to fly. No chemical or pheromone cues are known to be involved in mate location, copulation appears to be initiated by chance encounter. The male typically hovers near the larval habitat of the female, often resting and walking around the surface of the woody habitat. After contact with the female, the male quickly climbs onto female and initiates copulation, with mating occurring at all times of the day and evening. The amount of time spent coupled is variable, and may be disturbed by the interactions of other males. After fertilization, the female deposits eggs directly into the sodden wood that will serve as the larval habitat. Dudley (1982) observed no preference of wood species for oviposition, however eggs deposited in coniferous species did not survive past the first instar of development.

**5.4.5 Phylogenetic analyses**

The equally weighted character parsimony analysis of 28 ingroup and 3 outgroup taxa resulted in the recovery of 8 equally most parsimonious trees (tree score=107; CI=0.5648; RI= 0.7873; RC=0.4599). A single tree was derived from a strict consensus of all equally most parsimonious trees (Fig. 26). Bootstrap and Bremer support was generally low across
the tree (< 75 %), but did detect several highly supported clades. Reweighting of characters based on the rescaled consistency index followed by successive heuristic searches reached stabilization after two rounds of character reweighting, and resulted in 3 equally parsimonious trees (tree score= 49.89365; CI=0.7916; RI=0.9069; RC=0.7179) resulting in a single strict consensus tree (Fig. 27). The reweighted analysis improved overall tree resolution. Bootstrapping based on reweighted characters generally increased overall node support, but maintained a number of weakly supported clades similar to the unweighted analysis.

Phylogenetic analysis recovered a number of well-supported clades with the relationships between these clades weakly (<75) supported (Fig. 28). Well supported species clades include: 1) the Nearctic / Eastern Palearctic clade comprised of the strongly supported syl\text{\textit{via}} clade which is a sister clade to a weakly supported clade of Nearctic and Eastern Palearctic species, 2) the European nobilis clade, and 3) two well supported subclades in the paraphyletic assamica clade (Fig. 28).

The assamica clade is separated from all other taxa in the possession of a bifid aedeagus with two internal aedeagal branches visible to the sperm pump. A bifid aedeagus is found throughout the Tipuloidea but is very common among the Limoniinae as well as in several genera placed at the based of this subfamily clade (Petersen & Bertone Chapter 2). The transition between the primitive bifid aedeagus to the derived singular aedeagus is illustrated in a transformation series moving from the basal assamica clade, through L. kraussiana, to the singular aedeagus of L. yamamotoana (Fig. 28).

The nobilis clade is based on two weak characters, the sinuous curve of the male aedeagus and the presence of a ventral aedeagal lobe, which is additionally shared by L.
Additional characters of the larval and pupal life stages are needed to further examine this group.

The Nearctic / Eastern Palearctic group is morphological diverse and grouped based on the presence of the split dorsal face of the aedeagus. Within this clade the *sylvia* group is supported by the enlarged basal interbase while the remaining species are grouped based on the elongation of wing vein $R_{2+3+4}$. As with the *nobilis* clade, additional characters of the larval and pupal life stages are needed to further examine this group.

The high level of morphological conservation seen across the species of this genus resulted in low resolution for the phylogenetic hypothesis recovered during this investigation. This level of morphological conservation is not surprising as the ecology, climatic and habitat preferences of all known species are highly similar. The incorporation of additional characters from the larval and pupal life stages would be expected to greatly increase the resolution of any future analysis. The incorporation of these life stages, however, will only be possible with increased emphasis on the collection and association of life stages to the presently known adult life stage.

### 5.4.6 Biogeography

A complete discussion of the historic biogeographic relationships among the valid species of *Lipsothrix* is limited because the resolution of the phylogenetic reconstruction recovered during this investigation was low. It is possible however to discuss the evolution of the well resolved *assamica*, *nobilis*, and Nearctic / Eastern Palearctic clades, which illustrate the diversification of the genus within three different biogeographic regions.
5.4.6.1 *assamica* clade

The *assamica* clade, itself subdivided into two subclades, the *assamica* group and the paraphyletic *flavissima* group, is recovered as the sister group to the remaining *Lipsothrix*. The two subclades, with the exception of *L. kraussiana*, are found throughout the southern Himalayan Mountains through Pakistan, India, Nepal, and Myanmar. All species within this clade are represented in collections by fewer than 10 specimens and known largely from single locations. Until additional collections can be made and associated habitats described, little can be said about the true distribution of individual species as this inadequate sampling undoubtedly underestimates their true biogeographic ranges. This under sampling may in fact greatly under represent the true faunal diversity of this area, and the occurrence of as yet undescribed species is likely. Because this clade is greatly under sampled and may represent an area of underrepresented diversity, increased attention should be placed on collections from this region.

5.4.6.2 *nobilis* clade

The *nobilis* clade is broadly distributed across the Western Palearctic Region. Records for all species show widespread distributions mainly throughout the mountainous regions of central and southern Europe but becoming less restricted to mountainous regions at higher latitudes. The diversification of this clade is beyond the scope of this research due to the weak phylogenetic relationships recovered during this investigation. It is, however, possible to partially explain the widespread nature of these distributions due to both the historical occurrence of the genus within this region and the repeated climatic shifts that have occurred within this area. The earliest representation of *Lipsothrix* in the Eastern Palearctic is indicated by the occurrence of *L. radiata* Krzeminski (2001), described from the Baltic
amber of the Upper Eocene (30 mya). It is unclear whether this species represents a true member of the nobilis clade because it is described from a female specimens, however it does correspond to this clade in wing and antennal morphology and does show residency of this genus with this region. During this time the Western Palearctic has encountered repeated cycles of expanding and contracting glaciations (Hewitt 1996, 1999), and these shifts in climatic conditions have caused a subsequent shift in the distribution patterns of numerous taxa (Taberlet et al. 1998) into widespread disjunct European distributions. These areas of disjunct population are often characterized as areas of refugia, largely located throughout the mountains of southern Europe (Bennett et al. 1991). The occurrence of L. ecucullata, L. nobilis, and L. remota throughout much of these areas of refugia indicate that the cyclic action of climate may have greatly influenced the distributional patterns of the nobilis clade.

5.4.6.2 Nearctic / Eastern Palearctic clade

The presence of a North American – Asian disjunct distributional pattern has been commonly reported in a number of taxonomic groups (Suzuki et al. 1997; Patterson 1981; Anderson and Spence 1992; Enghoff 1993; Nordlander et al. 1996; Savage and Wheeler 1999; Sanmartin et al. 2001). The large Nearctic / Eastern Palearctic clade of species maintains multiple strongly supported independent sister group relationships that show similar vicariant distributions separated by the Pacific Ocean. The complex biogeographic relationships and weak underlying support of the area-cladogram for this clade (Fig. 29) make for an easy interpretation of the historic biogeographic relationships of this group, and multiple dispersal events are needed to adequately describe the observed patterns. Three historic connections are proposed to have connected the two landmasses and are discussed here as potential avenues for dispersal.
The first potential explanation for the current distributional pattern requires the occurrence of the genus during the Jurassic when all present continents were joined as the supercontinent Pangaea. This arrangement lasted until the Early-mid Jurassic (180 mya) with the breakup into Laurasia, consisting of North America and Eurasia, and Pangaea, consisting of the remaining southern continents. The absence of Mesozoic fossils and the relatively recent occurrence *Lipsothrix* in Baltic amber fossils along with the absence of *Lipsothrix* from the Southern Hemisphere would discourage this as a viable option.

The presence of the basal lineages of the genus within the Oriental and Palearctic regions indicate a likely origin of the genus within this region with subsequent dispersal into the Nearctic. The potential for post-Laurasian break-up faunal exchange (as summarized from Cox 1974; Raven and Axelrod 1974; Tangelner 1988; Sanmartin et al. 2001) would have been possible through two historic connections between the Palearctic and Nearctic regions. The first connection united eastern North American to Europe by way of Greenland through both the southern Thulean Bridge that existed from 80-50 mya, and the northern De Greer Bridge that persisted until about 39 mya. The De Greer land connection was thought to have minimal impact on terrestrial fauna movements as it was located at higher latitudes and maintained a harsher climate than the more southern Thulean connection. Conditions across the Thulean Bridge would have been favorable for faunal exchange between the areas that constitute the Nearctic and Western Palearctic regions. Sanmartin et al. (2001) concluded that this connection was highly important in the movement of numerous plant and animal groups. At the time of this connectivity, global temperatures were thought to be much warmer than current conditions (Greenwood and Wing 1995) and a rich boreotropical forest would have been present across much of the northern hemisphere. Such conditions would
provided favorable climatic and vegetative conditions needed for survival of both larval and adult *Lipsothrix*.

The second Nearctic – Palearctic connection was through the trans-Beringian route that connected western North America to Asia during at least two periods of time: 100-3.5 mya and repeatedly during the last 1my (as summarized from Cox 1974; Raven & Axelrod 1974; Tiffney 1985; Tangelner 1988; Sanmartin et al. 2001). Although this connection existed multiple times, each period of connectivity provided different climatic and vegetative conditions. Early faunal exchange across the first Beringian connection was likely minimal as the climate of the late Cretaceous and early Paleocene was greatly affected following the global cooling at the end of the Cretaceous. Warming in the early Eocene established a broad cover of boreotropical mesophytic forest across much of the Northern Hemisphere. Forest succession during the Eocene and Oligocene shifted forest types across the trans-Beringian area into a mixed mesophytic forest. During this much of the Northern Hemisphere was becoming more dominated by deciduous hardwoods (Wolfe 1987). The expansion of deciduousness during this time would have provided highly favorable habitat for *Lipsothrix* taxa, which may have facilitated successful colonization and diversification. Cooling in the Miocene to Pliocene across the trans-Beringian region led to a shift to coniferous-based forests until further climatic cooling resulted in a separation of forested elements between North America and Asia. Subsequent physical separation by a marine transgression occurred in the Late Pliocene. More recent trans-Beringian connections are thought to have occurred repeatedly during the Pleistocene. However, during this time the habitat of Beringia was essentially that of an extension of Siberia and dominated by tundra.
The current distributional patterns of the Nearctic- Eastern Palearctic clade supports the trans-Beringian connection rather than the Thulean Bridge due to the strong sister-taxon relationship across the area of Beringian connection and the lack of strong phylogenetic signal between the present Western Palearctic nobilis clade and Nearctic species of Lipsothrix. This concept is supported further by the occurrence of a diverse deciduous forest across the trans-Beringian connection during the Eocene and Oligocene (Wolfe 1987), after the disappearance of the Thulean Bridge.

The vicariance seen in the L. shasta-nigrilinea-babai species and the occurrence of L. fenderi in both the Western Nearctic and Japan would indicate that movement across the trans-Beringian connection must additionally have occurred more than once. The subsequent movement from the Western Nearctic to Eastern Palearctic is at odds with the prevailing idea that the trans-Beringian connection during the Pleistocene was thought to be dominated by tundra species, include minimal movement of temperate taxa, and be dominated by movement from the Palearctic to the Nearctic (Pielou 1979; 1991). Further resolution within this clade with additional phylogenetic support and divergence time estimation will be needed to resolve the complex biogeographic history of this clade.

5.5 Conclusions

The genus Lipsothrix is representative of the paucity of taxonomic knowledge of life-stage associations, biogeographic distributions, and phylogenetic placement within the greater Tipuloidea phylogeny that is observed in many Tipuloidea groups. As with a majority of crane fly species, our knowledge of species identity is maintained by the adult male, with few associations made with the larval or pupal life stages. As evidenced by this revision, this is more a result of location of taxonomic expertise, with Western Palearctic
(European) and Nearctic taxa that show a more extensive knowledge base of life stage associations and distributional records. Eastern Palearctic, Oriental, and Neotropical species remain poorly collected, which limits our knowledge of distribution and natural history. It is important to note that while this revision incorporates and synthesizes the current knowledge of *Lipsothrix*, many important life-stage associations, species distributions, and aspects of the evolutionary history of the group remain poorly understood.
Figure 1. Dorsal view of right wing of *Lipsothrix sylvia* Alexander showing venation. Wing venation: $A_1, A_2$: branches of anal veins; $C$: costa; $CuA$: anterior branch of cubitus; $CuA_1, CuA_2$: anterior branches of cubitus; $M$: media; $R$: radius; $R_{1+2}$: anterior branch of radius plus $R_2$ posterior branch of radius; $R_2$: $R_2$ posterior branch of radius connecting radial sector to radius; $R_3, R_4, R_5$: posterior branches of radius; $rm$: radial-medial crossvein; $Rs$: radial sector; $Sc$: subcosta, $Sc_1, Sc_2$ ($Sc-R$): subconstal veins. Wing cells: $a_1, a_2$: anal; $bm$: basal medial; $br$: basal radial; $c$: costal; $cua_1$: anterior cubital; $cup$: posterior cubital; $dm$: discal medial; $m_2, m_3$: medial; $r_1, r_2, r_3, r_4, r_5$: radial; $sc$: subcostal)
Figure 2. **Genitalic features of the female post-abdomen.** Abbreviations: t9: ninth tergite, t10: tenth tergite, ce: cerci, hv: hypogynial valves, ip: infraanal plate, sb: bursa seminalis.
Figure 3. Genitalic features of the male post-abdomen. Abbreviations (Hypopygium): 8t: eight tergite, 8s: eight sternite, 9s: ninth sternite, 9t; ninth tergite, aed: aedeagus, dg: dorsal gonostylus, gs: gonostylus, gxt: gonocoxite, ib: interbase, vg: ventral gonostylus. Abbreviations (aedeagus): as: aedeagal sheath, dp: dorsal parameres, ej: ejaculatory apodeme, vp: ventral parameres.
Figure 4. Delineation of the *Lipsothrix shasta* species complex. The relatedness of specimens of the *shasta* species complex are displayed (A) based on a cluster analysis based on Ward’s distance and average linkage, (B) in a two-dimensional display of non-metric multidimensional scaling (k=3) using a dissimilarity index based on the Canberra distance, and (C) by overlaying a cluster analysis based on Ward’s distance and average linkage on a two dimensional display of nonmetric multidimensional scaling (k=2) using a dissimilarity matrix based on the Canberra distance.
Figure 7. Illustrations of the male hypopygium of *Lipsothrix assamica*, *L. babai*, and *L. chettri*. Images not to consistent scale.
Figure 8. Illustrations of the male hypopygium of *Lipsothrix errans*, *L. fenderi*, and *L. flavissima*. Images not to consistent scale.
Figure 9. Illustrations of the male hypopygium of *Lipothrix hynesiana*, *L. kashmirica*, and *L. kraussiana*. Images not to consistent scale.
Figure 10. Illustrations of the male hypopygium of *Lipsothrix leucopez*, *L. mirabilis*, and *L. kraussiana*. Images not to consistent scale.
Figure 11. Illustrations of the male hypopygium of *Lipsothrix neotropica*, *L. nervosa*, and *L. nobilis*. Images not to consistent scale.
Figure 12. Illustrations of the male hypopygium of *Lipsothrix nigrilinea*, *L. pluto*, and *L. orthotenes*. Images not to consistent scale.
Figure 13. Illustrations of the male hypopygium of *Lipsothrix remota*, *L. shasta*, and *L. sylvia*. Images not to consistent scale.
Figure 14. Illustrations of the male hypopygium of *Lipsothrix taiwanica*, *L. tokunagai*, and *L. yamamotoana*. Images not to consistent scale.
Figure 15. Aedeagus plate of Lipsothrix species. Illustration of: (1) L. assamica, (2) L. babai, (3) L. chettri, (4) L. decurvata, (5) L. ecucullata, (6) L. errans, (7) L. fenderi, (8) L. flavissima, (9) L. hynesiana, (10) L. iranica. Images not to consistent scale.
Figure 17. Aedeagus plate of Lipsothrix species. Illustration of: (1) L. orthotenes, (2) L. pluto, (3) L. remota, (4) L. shasta, (5) L. sylvia, (6) L. taiwanica, (7) L. tokunagai, (8) L. yamamotoana. Images not to consistent scale.
Figure 20. Distribution of *Lipsothrix* species. Distributions of: (1) *L. assamica*, (2) *L. babai*, (3) *L. chettri*, (4) *L. decurvata*, (5) *L. ecucullata* - points, (6) *L. ecucullata* - projection. Locations of collection points from examined species are indicated by stars, open circles indicate countries where species have been collected but without latitude or longitude data.
Figure 21. Distribution of *Lipsothrix* species. Distributions of: (1) *L. errans* - points, (2) *L. errans* - projection, (3) *L. fenderi* - Japan points, (4) *L. fenderi* - North America points, (5) *L. fenderi* - projection, (6) *L. flavissima*. Locations of collection points from examined species are indicated by stars, open circles indicate countries where species have been collected but without latitude or longitude data.
Figure 22. Distribution of *Lipsothrix* species. Distributions of: (1) *L. heitfeldi*, (2) *L. hynesiana*, (3) *L. kashmirica* (circles) and *L. kraussiana* (stars), (4) *L. leucopoeza*, (5) *L. malla* (stars) and *L. mirabilis* (circles), (6) *L. neotropica*. Locations of collection points from examined species are indicated by stars or closed circles, open circles indicate countries where species have been collected but without latitude or longitude data.
Figure 23. Distribution of *Lipsothrix* species. Distributions of: (1) *L. nervosa* - points, (2) *L. nervosa* - projection, (3) *L. nigrilinea* - points, (4) *L. nigrilinea* - projection, (5) *L. nobilis* (stars) and *L. iranica* (triangle), (6) *L. nobilis* - projection. Locations of collection points from examined species are indicated by stars or triangles, open circles indicate countries where species have been collected but without latitude or longitude data.
Figure 24. Distribution of *Lipsothrix* species. Distributions of: (1) *L. nullusarma*, (2) *L. orthotenes*, (3) *L. remota* - points, (4) *L. remota* - projection, (5) *L. Shasta* - points, (6) *L. Shasta* - projection. Locations of collection points from examined species are indicated by stars or triangles, open circles indicate countries where species have been collected but without latitude or longitude data.
Figure 25. Distribution of *Lipsothrix* species. Distributions of: (1) *L. sylvia* - points, (2) *L. sylvia* - projection, (3) *L. taiwanica*, (4) *L. tokunagai*, (5) *L. yakushimae*, (6) *L. yamamotoana*. Locations of collection points from examined species are indicated by stars.
Figure 26. Equal weight parsimony analysis of the genus *Lipsothrix*. Relative branch support is indicated above each recovered clade (bootstrap support / Bremer support).
Figure 27. Reweighted parsimony analysis of the genus *Lipsothrix*. Relative branch support is indicated above each recovered clade (bootstrap support / Bremer support).
Figure 28. Reweighted parsimony analysis of the genus *Lipsothrix* showing strongly recovered clades. Recovered clades include: *assamica* clade (A), *assamica* group (B), *malla* group (C), *nobilis* clade (D), Western Nearctic / Eastern Palearctic clade (E), and the *sylvia* clade (F). Relative branch support is indicated above each recovered clade (bootstrap support / Bremer support).
Figure 29. Area cladogram based on the reweighted parsimony analysis of the genus *Lipsothrix*. Abbreviations: Eastern Palearctic (EP), Nearctic (NA), Neotropical (NO), Oriental (OR), Western Palearctic (WP).
Table 1. Checklist of *Lipsothrix* Loew species. Listed below are all presently and previously recognized species of *Lipsothrix*. Actions taken in this current revision are indicated for newly synonymized species (1).

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Table 2. Temporal distribution of adult *Lipsothrix* species. The collection date for all available specimens for all recognized species of *Lipsothrix* are plotted. Each month is divided into four quarters and the date of collection is assigned to the corresponding quarter.

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<tr>
<td><em>L. sylvia</em></td>
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<tr>
<td><em>L. taiwanica</em></td>
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<tr>
<td><em>L. tokunagai</em></td>
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<tr>
<td><em>L. yakushimae</em></td>
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<tr>
<td><em>L. yamamontana</em></td>
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</table>
**Table 3. Larval habitat type utilized by species of *Lipsothrix*.** The types of woody plant material that have been found to contain populations of *Lipsothrix* are listed along with the reference to the publication where the association was made.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wood type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. ecucullata</em></td>
<td>Ash (<em>Fraxinus</em> sp.); Birch (<em>Betula</em> sp.)</td>
<td>Rotheray, 2001</td>
</tr>
<tr>
<td><em>L. errans</em></td>
<td>Oak (<em>Quercus</em> sp.)</td>
<td>Hinton, 1955</td>
</tr>
<tr>
<td><em>L. fenderi</em></td>
<td>Alder (<em>Alnus rubra</em> Bong.); Maple (<em>Acer macrophyllum</em> Pursh.); Dougls fir (<em>Pseudotsuga</em> spp.)</td>
<td>Dudley and Anderson, 1987</td>
</tr>
<tr>
<td><em>L. hynesiana</em></td>
<td>Alder (<em>Alnus rubra</em> Bong.)</td>
<td></td>
</tr>
<tr>
<td><em>L. nigrilinea</em></td>
<td>Alder (<em>Alnus rubra</em> Bong.); Maple (<em>Acer macrophyllum</em> Pursh.); Western Red Cedar (<em>Thuja plicata</em> Donn) (marginally)</td>
<td>Dudley and Anderson, 1987</td>
</tr>
<tr>
<td><em>L. remota</em></td>
<td>Oak (<em>Quercus</em> sp.);</td>
<td>Hinton, 1955</td>
</tr>
<tr>
<td><em>L. sylvia</em></td>
<td><em>Rhododendron</em> spp.; Hickory (<em>Carya</em> spp.); Ash (<em>Fraxinus</em> spp.); Maple (<em>Acer</em> spp.)</td>
<td>Rogers and Byers, 1956</td>
</tr>
</tbody>
</table>
Table 4. Comparison of means between the two groups of the *shasta* species complex. Means for characters were compared using a permutation test running 999 replicates of randomly assigning group membership with significance tested at $P=0.001$. Character overlap is defined by whether or not there is a complete division between character expressions or whether values are shared by the two groups.

<table>
<thead>
<tr>
<th>Factor</th>
<th>P-value</th>
<th>Character overlap</th>
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</thead>
<tbody>
<tr>
<td>Flagellomere 1</td>
<td>0.007**</td>
<td>Yes</td>
</tr>
<tr>
<td>Flagellomere 2</td>
<td>0.005**</td>
<td>Yes</td>
</tr>
<tr>
<td>Dorsal thorax</td>
<td>0.001**</td>
<td>No</td>
</tr>
<tr>
<td>Lateral thorax</td>
<td>0.001**</td>
<td>Yes</td>
</tr>
<tr>
<td>Dorsal abdomen</td>
<td>0.001**</td>
<td>Yes</td>
</tr>
<tr>
<td>Lateral abdomen</td>
<td>0.550</td>
<td>Yes</td>
</tr>
<tr>
<td>Setiforms in $r_3$</td>
<td>0.001**</td>
<td>Yes</td>
</tr>
<tr>
<td>Setiforms in $m_1$</td>
<td>0.001**</td>
<td>Yes</td>
</tr>
<tr>
<td>Total body size</td>
<td>0.001**</td>
<td>Yes</td>
</tr>
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</table>
Table 5. Matrix of characters used in the phylogenetic investigation of the genus *Lipsothrix*.

<table>
<thead>
<tr>
<th>OUTGROUP</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>47</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Elephantomyia</em></td>
<td>00001A0003</td>
<td>0210000000</td>
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<tr>
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<td>0111011100</td>
<td>0000000000</td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>INGROUP</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>47</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. assamica</em></td>
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<td>0101001300</td>
<td>0000001001</td>
<td>0000000110</td>
<td>00101110</td>
</tr>
<tr>
<td><em>L. babai</em></td>
<td>0000101000</td>
<td>0001010013</td>
<td>0010010010</td>
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<td>00102110</td>
</tr>
<tr>
<td><em>L. chetri</em></td>
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<td>0101001300</td>
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<td>00101110</td>
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<tr>
<td><em>L. decurvata</em></td>
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<td>0011001411</td>
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<tr>
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<td>0000100000</td>
<td>0000111112</td>
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<tr>
<td><em>L. fenderi</em></td>
<td>0000111001</td>
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<td><em>L. flavissima</em></td>
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<td>0010001000</td>
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<tr>
<td><em>L. iranica</em></td>
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<tr>
<td><em>L. kashmirica</em></td>
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<tr>
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</tr>
<tr>
<td><em>L. mirabilis</em></td>
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<td>1000010013</td>
<td>0011010010</td>
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<td>00101110</td>
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<tr>
<td><em>L. malla</em></td>
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<td>00101110</td>
</tr>
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<td><em>L. nigirlinea</em></td>
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<tr>
<td><em>L. neotropica</em></td>
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<tr>
<td><em>L. nervosa</em></td>
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<tr>
<td><em>L. nobilis</em></td>
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<td>0000101000</td>
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<td>00101110</td>
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<tr>
<td><em>L. nullusarma</em></td>
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<td>0100010100</td>
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<tr>
<td><em>L. orthotenes</em></td>
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<td>0010013000</td>
<td>0000010010</td>
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<td>00101110</td>
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<tr>
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<tr>
<td><em>L. remota</em></td>
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<td><em>L. shasta</em></td>
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<td>0000000110</td>
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5.8 References


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Evolving Biosphere. London, British Museum of Natural History and Cambridge


5.9 Appendix

Characters used in the phylogenetic analysis of *Lipsothrix*.

01. Terminal flagellomere: (0) subequal to penultimate, (1) greatly reduced to less than 1/2 the penultimate flagellomere

02. Prunosity of flagellomeres: (0) absent, (1) present

03. Flagellomere elongation: (0) absent, (1) present

04. Setation of Sc: (0) present, (1) absent

05. Macrotrichia in apical wing cells: (0) absent, (1) present

06. Elongation of basal wing vein $R_5$: (0) absent, (1) present

07. Placement of wing crossvein $R_2$: (0), near split of $R_{2+3+4}$, (1) removed by more than 3 times its length from $R_{2+3+4}$

08. Wing vein $R_4$: (0) $R_{2+3}$ and $R_4$ subequal, (1) $R_4$ angled from $R_{2+3}$

09. Wing cell $dm$: (0) width subequal or less than twice the height, (1) elongate, width greater than 3x height

10. Radial veins: (0) strongly divergent at wing margin, (1) parallel or convergent at wing margin

11. Wing vein $R_{1+2}$: (0) straight to wing margin and captured by $R_2$, (1) decurved dorsally and partially captured by $R_2$

12. Tarsal claws: (0) tarsal claw teeth present, (1) tarsal claw teeth absent

13. Tarsomeres: (0) coloration similar to that of femur and tibia, and not white, (1) coloration abrupt white

14. Separation of aedeagal sheath: (0) absent, (1) present

15. Ventral lobe of aedeagus: (0) absent, (1) present
16. Form of ventral lobe: (0) inapplicable, lobe absent, (1) narrow lobe, (2) broad lobe, (3) narrow lobes attached to each of the separated aedeagal branches

17. Dorsal expansion of aedeagal sheath: (0) absent, (1) present

18. Form of dorsal expansion: (0) inapplicable, (1) broad lobe, (2) weakly raised dorsal element, expanded to show separation from aedeagus (3) separation of aedeagal sheath present, but not dorsally expanded

19. Dorsal lobe of aedeagus medially divided into two prominent lobes: (0) absent, (1) present

20. Dorsal ridge of aedeagal sheath: (0) absent, (1) present

21. Split posterior face of aedeagus: (0) absent, (1) present

22. Split anterior of aedeagal sheath: (0) absent, (1) present

23. Apex of aedeagus directed anteriorly: (0) absent, (1) present

24. Aedeagus sinuous: (0) absent, (1) present

25. Terminal branches of aedeagus: (0) one, (1) two

26. Basal branches of aedeagus: (0) two, (1) one

27. Projected ventral parameres: (0) absent, (1) present

28. Elongate terminal branches of aedeagus: (0) absent, (1) present

29. Apex of aedeagus: (0) sclerotized, (1) degenerate, weakly produced

30. Ejaculatory apodeme: (0) present as single branch or absent, (1) medially divided into two lobes

31. Interbase I: (0) length of interbase beyond based not enlarged, (1) interbase enlarged at ¾ the length before narrow acute apex

32. Base of interbase: (0) not enlarged, (1) enlarged
33. Scalloping of basal interbase: (0) absent, (1) present
34. Rotation of basal interbase: (0) absent, (1) present
35. Compression of basal interbase: (0) absent, (1) present
36. Interbase II: (0) inapplicable, (1) interbase beyond base with parallel margins, (2) basal arm of interbase with dorsal and ventral edges to give rectangular appearance
37. Acute apex of dorsal gonostylus: (0) present, (1) absent
38. Dorsal gonostylus apex blunt beyond tooth: (0) absent, (1) present
39. Posterior directed aedeagus: (0) absent, (1) present
40. Wing vein R2: (0) present, (1) absent
41. Tibial spurs: (0) present, (1) absent
42. Interbase: (0) present, (1) absent
43. Expanded interior interbase apodeme: (0) absent, (1) present
44. Medial connection of interbase: (0) present, (1) absent
45. Medial tooth of dorsal gonostylus: (0) absent, (1) present
46. Ventral gonostylus: (0) present, (1) absent
47. Branches of Rs to margin: (0) three, (1) one
CHAPTER 6: GENERAL CONCLUSIONS

Through systematic research we seek to understand the scope and nature of Earth’s diversity and describe the processes by which it was formed. The science of taxonomy is the framework of this research, providing the network by which we describe, name, and organize this observed diversity. This science is not a static endeavor, instead, the hypotheses proposed must be rigorously tested in order to provide support for their taxonomic and phylogenetic ideas. As the toolkit of the taxonomist increases, new tools are made available that create novel and easily transmitted taxonomic tools for specimen identification, test long-standing hypotheses of relatedness, and examine species and assemblage distributions. The initiation of new taxonomic projects are, however, often impacted by aspects of the taxonomic impediment.

The formulation of this research program was deterred by taxonomic barriers that disrupted the originally proposed research, but rerouted the emphasis into new avenues of study. One of the original goals of this work was a descriptive survey of the crane flies of Thailand that would provide diagnoses for each encountered species, with original descriptions produced for any species or genera found to represent new entities to science. The reality of the situation proved that neither specific nor generic identifications could be determined due to a lack of taxonomic resources, and existing species and generic diagnosis that proved inadequate in delineating either group. The research presented within this dissertation revised the original objectives by incorporating new taxonomic tools in order to address these encountered problems. The goal of this work was to then provide better taxonomic resolution for the Tipuloidea by conducting a systematic investigation at multiple taxonomic levels.
The phylogenetic hypothesis of the Tipuloidea offers better resolution and support for a classification system that describes the evolutionary diversification of the group. Although these analyses did not incorporate all Tipuloidea taxonomic diversity, the framework provided by this research illustrates that the simple explanation of four major crane fly lineages does not adequately describe the evolutionary history of the group. Instead, a more complicated explanation of ancient lineages and recent radiations is observed. The novel application of molecular sequence data to the analysis of the Tipuloidea utilized new evidence that largely agreed with the phylogenetic signal provided by the morphological data. The incorporation of morphological data in the analysis did, however, provided a strong set of evidence and should be incorporated in any future study. The support and evidence provided by this phylogenetic hypothesis serves as the basis for a new classification system, one that will better define this diverse group and provide greater stability to future workers.

The diagnosis of the subfamily Limoniinae expands on the phylogenetic classification of the Tipuloidea and better defines the synapomorphies by which the genera can be grouped. The succinct diagnoses provided for included genera adequately defines the current understanding of each taxonomic unit, but strongly indicates that many of these groups are based on either weak or highly subjective characters that are in need of additional investigation. The production of the key to the Oriental Limoniinae developed a taxonomic resource for a region that previously had no available taxonomic tools. In providing this taxonomic resource it is hoped that future research of the Limoniinae of the Oriental Region is facilitated.
By utilizing the taxonomic key developed in the diagnosis of the Limoniinae, the crane fly fauna of Thailand was addressed. The fauna of this region was seen to be much more diverse than in any previous survey, and predicted even higher levels of species diversity with additional collection. The elevated diversity of this region is seen to be a result of the placement of Thailand in an intersection of regions that incorporates biotic elements from the surrounding faunal pool. The diverse topology of the region acts as a biotic bridge that brings temperate elements into a more tropical fauna, resulting in the elevated total observed diversity.

The incorporation of the revision of Lipsothrix provides a species level investigation by which the diversification and distribution of a monophyletic group of species was observed. Though widely distributed across the Northern Hemisphere, the taxonomic knowledge of this group is maintained largely within the Nearctic and Western Palearctic Regions. This result may be indicative of the total faunal knowledge for the Tipuloidea. Outside of the areas of greatest taxonomic expertise (Nearctic and Palearctic), both species distributions and natural histories are poorly understood. As was shown in the phylogenetic analysis of the Lipsothrix, the understanding of any regional clade is likely to be affected by species found outside the region of interest. It is therefore imperative that future revision work of crane fly groups be focused on all inclusive species, and not focus on any particular subset of taxa. The new methodologies for species delineation and distributional range estimation provide new insight into how species are defined.

Within the Tipuloidea, the high level of knowledge pertaining to the abundant species diversity acts to mask the underlying deficiencies in classification, phylogeny, and natural history. The lack of readily available taxonomic tools further reduces the knowledge of this
group to little more than historic records within catalogs. This dissertation approached these systematic deficiencies at multiple taxonomic levels in order to address these issues and provide the groundwork for future studies.