ABSTRACT


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A molecular phylogenetic analysis of the hawkmoths was conducted using five protein-coding nuclear genes for 131 sphingid ingroups and eleven bombycoid outgroups. The study utilizes 6,793 bp of cDNA from CAD, DDC, EF-1α, period, and wingless. Genes were analyzed separately and in combination. Results from the combined simultaneous analysis corroborated many previously postulated sets of relationships based on larval, pupal, and adult morphological characters, but also uncovered many novel relationships. Application of parsimony and maximum likelihood optimality criteria led to the recovery of monophyletic Macroglossinae, Sphinginae, Acherontiini, Ambulycini, Philampelini, and Choerocampina. The most likely tree and the most parsimonious trees recovered the following relationships among subfamilies: Macroglossinae + (Sphinginae + Smerinthinae). Monophyly of the Sphinginae was corroborated with strong support in all analyses, as well as for the sister-group relationship of the paraphyletic Sphingulini + Sphinginae. A reconstruction of ancestral
states reveals that the short, non-feeding proboscis was the ancestral condition in the family. The nectar-feeding proboscis independently arose multiple times, but was subsequently lost at least three times. This thesis also includes a supplementary section in which the five gene dataset was combined with the barcoding region of the mitochondrial COI gene. The purpose of the supplementary section was to tentatively explore the effect of combining the COI barcoding region for available sphingid taxa to a larger dataset with greater character sampling.
MOLECULAR PHYLOGENETIC ANALYSIS OF THE HAWKMOTHS
(LEPIDOPTERA: BOMBYCOIDEA: SPHINGIDAE)
AND THE EVOLUTION OF THE SPHINGID PROBOSCIS

By

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Thesis submitted to the Faculty of the Graduate School of the University of Maryland in partial fulfillment of the requirements for the degree of Master of Science 2007

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“The ‘saturniid’ [non-feeding] strategy exhibited by many Smerinthini would appear to be the plesiomorphic biology for Sphingidae, while the ‘typical’ [nectar feeding] strategy ... would be apomorphic within the family. The interesting problem now is to resolve phylogenetic relationships of the family in order to determine the possible evolutionary pathways by which this latter strategy could have developed”

(Kitching and Cadiou, 2000: 9)
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## TABLE OF CONTENTS

Acknowledgments ............................................................................................................. ii

Table of Contents ................................................................................................................ v

List of Tables ........................................................................................................................ vii

List of Figures ........................................................................................................................ ix

### CHAPTER ONE- Phylogenetic analysis of the hawkmoths: Evidence from five protein coding nuclear genes (Lepidoptera: Sphingidae) ................................................................ 1

1.1. Introduction .................................................................................................................. 2

1.2. Materials and Methods ............................................................................................. 8

  1.2.1. Taxon Sampling .................................................................................................. 8

  1.2.2. Gene Sampling ................................................................................................ 9

  1.2.3. Nucleic acid extraction and RT-PCR ............................................................. 10

  1.2.4. Data matrix construction ............................................................................... 11

  1.2.5. Phylogenetic analyses ..................................................................................... 12

1.3. Results ....................................................................................................................... 15

  1.3.1. Sequence amplification success and base composition .............................. 15

  1.3.2. Phylogenetic analyses ..................................................................................... 15

1.4. Discussion ................................................................................................................. 19

  1.4.1. Monophyly of Sphingidae and basal divergences within the family ............ 19

  1.4.2. Relationships within Smerinthinae and Sphinginae ..................................... 21
1.4.3. Relationships within Macroglossinae .............................................. 26

1.5. Conclusion .............................................................................................. 31

CHAPTER TWO- Evolution of the sphingid proboscis ........................................ 33

2.1. Introduction .......................................................................................... 34

2.2. Materials and Methods ........................................................................ 37

2.3. Results ................................................................................................... 39

2.3.1. Proboscis length and nectar feeding ............................................... 39

2.3.2. Ancestral state reconstruction ......................................................... 40

2.4. Discussion .............................................................................................. 41

2.4.1. Evolution of nectar feeding in Sphingidae .................................... 41

2.4.2. Nectar feeding and correlations with other life-history traits 45

2.5. Conclusion .............................................................................................. 47

SUPPLEMENTARY MATERIAL- Single gene analyses and six gene simultaneous
analysis with COI ............................................................................................. 97

Supplement 1- Single gene analyses of nuclear protein-coding genes........ 98

Supplement 2- Six gene simultaneous analysis with COI ....................... 111

Literature Cited ............................................................................................. 124
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 1</td>
<td>Number of genes and sphingid taxa in Regier et al. (2001), Mignault (2003), and the current study</td>
<td>48</td>
</tr>
<tr>
<td>Table 2</td>
<td>Sphingid species and outgroups included in this study</td>
<td>49</td>
</tr>
<tr>
<td>Table 3</td>
<td>List of genes and primers used in this study</td>
<td>57</td>
</tr>
<tr>
<td>Table 4</td>
<td>Empirical base frequencies and GTR+$\Gamma$+I model parameters of the five genes in the ML analyses</td>
<td>58</td>
</tr>
<tr>
<td>Table 5</td>
<td>Summary of characters by gene and codon position</td>
<td>59</td>
</tr>
<tr>
<td>Table 6</td>
<td>Bootstrap, Bremer support (BS), and Partitioned Bremer Support (PBS) values for the MP all-taxon, five-gene simultaneous analysis</td>
<td>60</td>
</tr>
<tr>
<td>Table 7</td>
<td>Bootstrap, Bremer support (BS), and Partitioned Bremer Support (PBS) values for the MP 99-taxon analysis without missing data</td>
<td>65</td>
</tr>
<tr>
<td>Table 8</td>
<td>Calculation of the relative contribution index (RCI) for the 99-taxon dataset</td>
<td>69</td>
</tr>
<tr>
<td>Table 9</td>
<td>Node recovery and bootstrap support values with 5-gene, all combinations of 4-gene subdatasets</td>
<td>70</td>
</tr>
<tr>
<td>Table 10</td>
<td>List of sphingid species, nectar feeding records, and their average proboscis and forewing lengths</td>
<td>75</td>
</tr>
<tr>
<td>Table 11</td>
<td>Preliminary list of larval hostplant families for Sphingidae included in the present study</td>
<td>80</td>
</tr>
</tbody>
</table>
SUPPLEMENTARY TABLES

Table S1. Sphingid species and outgroups which were included in the six gene analysis with COI.

115
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Relationships of Sphingidae according to Rothschild and Jordan (1903)</td>
<td>89</td>
</tr>
<tr>
<td>2</td>
<td>Relationships of Sphingidae according to Nakamura (1976)</td>
<td>89</td>
</tr>
<tr>
<td>3</td>
<td>Relationships of Sphingidae according to Kitching and Cadiou (2000)</td>
<td>89</td>
</tr>
<tr>
<td>4</td>
<td>Parsimony cladogram of Regier et al. (2001)</td>
<td>90</td>
</tr>
<tr>
<td>5</td>
<td>Parsimony cladogram of Mignault (2003)</td>
<td>90</td>
</tr>
<tr>
<td>6</td>
<td>Likelihood tree of Mignault (2003)</td>
<td>90</td>
</tr>
<tr>
<td>7</td>
<td>Parsimony strict consensus of 12 MPCs of the all-taxon, 5-gene analysis</td>
<td>91</td>
</tr>
<tr>
<td>8</td>
<td>Most parsimonious cladogram of the 99-taxon, 5-gene analysis</td>
<td>92</td>
</tr>
<tr>
<td>9</td>
<td>Most-likely tree of the all-taxon, 5-gene analysis</td>
<td>93</td>
</tr>
<tr>
<td>10</td>
<td>Histogram showing the number of sphingid species relative to the average proboscis length for taxa included in the five gene analysis</td>
<td>94</td>
</tr>
<tr>
<td>11</td>
<td>Average proboscis length relative to average forewing length for each sphingid species</td>
<td>95</td>
</tr>
<tr>
<td>12</td>
<td>Proboscis length mapped onto the ML five gene tree</td>
<td>96</td>
</tr>
</tbody>
</table>
SUPPLEMENTARY FIGURES

Figure S1. MP strict consensus based on the CAD gene .................................................. 99
Figure S2. MP strict consensus based on the DDC gene .................................................. 100
Figure S3. MP strict consensus based on the EF-1α gene ............................................... 101
Figure S4. MP strict consensus based on the Period gene .............................................. 102
Figure S5. MP strict consensus based on the Wingless gene ........................................... 103
Figure S6. ML tree based on the CAD gene ................................................................. 104
Figure S7. ML tree based on the DDC gene ................................................................. 105
Figure S8. ML tree based on the EF-1α gene ............................................................... 106
Figure S9. ML tree based on the Period gene ............................................................... 107
Figure S10. ML tree based on the Wingless gene ......................................................... 108
Figure S11. MP strict consensus generated from the five gene dataset with third nucleotide positions removed ................................................................................. 109
Figure S12. MP strict consensus with nt3 of the EF-1α gene removed ......................... 110
Figure S13. ML tree of the six-gene simultaneous analysis with COI ............................. 114
CHAPTER 1

PHYLOGENETIC ANALYSIS OF THE HAWKMOTHS: EVIDENCE FROM FIVE PROTEIN CODING NUCLEAR GENES
(LEPIDOPTERA: SPHINGIDAE)
1.1. INTRODUCTION

Hawkmoths are one of the most conspicuous groups of moths, and they are found on every continent except Antarctica (Rothschild and Jordan, 1903; Kitching and Cadiou, 2000). Sphingids are models for studies on biochemistry (Willis et al., 1995; Wink and Theile, 2002; Bowers, 2003), functional morphology (Eaton, 1971; 1988), nutritional ecology (Slansky, 1993), physiology (e.g., Liu et al., 1998; Göpfert et al., 2002; Kelber et al., 2003; Wannenmacher and Wasserthal, 2003; Davidowitz and Nijhout, 2004; Davis and Hildebrand, 2006), plant-insect interactions (e.g., Jackson, 1990; Osier et al., 1996; Kessler and Baldwin, 2002; Agosta and Janzen, 2005), pollination biology (e.g., Gregory, 1963-1964; Nilsson et al., 1985; 1987; Haber and Frankie, 1989; 1992; Wasserthal, 1997; Nilsson, 1998; Raguso and Willis, 2002), biogeography (Beck et al., 2006c), population genetics (Hundsdoerfer and Wink, 2006) and developmental genetics (Song and Gilbert, 1994; Jindra et al., 1997; Jochova et al., 1997). Due to their large size, sphingids have also been the focal group in faunistic studies to assess habitat quality for conservation (Beck et al., 2006a). Some species are agricultural pests (Winder, 1976; Coffelt and Schultz, 1990; Bellotti et al., 1992; 1993), and some are biological control agents (Batra, 1984). Recently, sphingids have become a model group to study taxonomic species boundaries with the onset of DNA barcoding (Janzen et al., 2005; Hajibabaie et al., 2006). Despite their conspicuous nature and their role in a wide range of biological systems, a robust phylogenetic analysis of hawkmoth genera has not been conducted.

Phylogenetic analyses of hawkmoths have generally focused within a tribe or lower (e.g., Acherontiini (Kitching, 2002; 2003), Ambulycini [Kitching, unpublished data, 1993], Hyles (Derzhavets, 1993; Hundsdoerfer et al., 2005a; 2005b)), and relationships of
many sphingid taxa still remain largely unknown. The only published modern phylogenetic analysis on higher relationships within the family was the preliminary molecular analysis of Regier et al. (2001) which included two genes and fourteen species.

Sphingidae include 201 genera and almost 1400 species classified into three subfamilies: Macroglossinae, Smerinthinae, and Sphinginae (Kitching and Cadiou, 2000). Morphological studies on Bombycoidea strongly support the monophyly of the Sphingidae (Minet, 1994; Lemaire and Minet, 1999). Although several putative apomorphies have been proposed for each subfamily (Minet, 1994), monophyly remains speculative for nearly all tribes and subtribes, particularly that of the Smerinthinae. Smerinthines have been noted for sharing life history strategies such as non-feeding mouthparts with another macrolepidopteran family, the Saturniidae (Janzen, 1984), and was predicted to be the basal subfamily of Sphingidae (Kitching and Cadiou, 2000).

There have been several efforts to reconstruct relationships of Sphingidae using morphology (e.g., Rothschild and Jordan, 1903; Nakamura, 1976; Kitching, 2000; Figs. 1-3), but delimiting and coding adult and immature characters in a modern cladistic context has been challenging (Kitching, pers. com.). In their monumental revision on Sphingidae, Rothschild and Jordan (1903) classified hawkmoths into two groups, the “Sphingidae Semanophorae” and the “Sphingidae Asemanophorae”, which roughly corresponds to Kitching and Cadiou’s (2000) Macroglossinae and (Smerinthinae + Sphinginae), respectively (Fig. 1). Although Rothschild and Jordan’s study came decades before the development of modern cladistic methodology (Hennig, 1950; 1965; 1966), Rothschild and Jordan presented a “tree” of all sphingid genera known at the time, and these genera were grouped according to shared morphological structures. Rothschild and
Jordan separated sphingids into Semanophorae and Asemanophorae based on one morphological feature: presence or absence of a patch of short sensory hairs (microtrichia) on the inner surface of the first segment of the labial palp (Rothschild and Jordan, 1903). It was later discovered that spiracular furrows on the pupa also supports the division of the family into these two groups (Mosher, 1918). Rothschild and Jordan assigned five subfamilies to the Sphingidae: Acherotiinae, Ambulycinae, Choerocampinae, Philampelinae, and Sesiinae. Their revision formed the foundation for sphingid classification, and for the following several decades, studies on sphingid classification mainly revised particular aspects of their work.

Janse (1932) lowered the taxonomic rank of Rothschild and Jordan’s subfamilies to tribes, and treated Semanophorae and Asemanophorae as subfamilies (Semanophorinae and Asemanophorinae). Carcasson (1968) replaced Rothschild and Jordan’s “Sesiinae” with Dilophonotini, and “Sesiicae” with Aellopodes. Hodges (1971) formally changed Semanophorinae and Asemanophorinae to Macroglossinae and Sphinginae after the type genus of each subfamily. Hodges also rejected many of Carcasson’s names because they were not based on any available generic name.

In a series of papers based on larval, pupal, and adult morphology, Nakamura (1976; 1977; 1978) reclassified particular sphingid tribes, and presented relationships of Japanese sphingid genera based on characteristics of the larva and pupa (Fig. 2). The tree he presented was not based on a modern cladistic analysis, but Smerinthini and Sphingini were thought to be sister-groups, and the remaining tribes forming a group which roughly corresponds to Macroglossinae sensu Kitching and Cadiou (2000).
Grouping Sphingidae into two subfamilies was generally accepted until the work of Minet (1994). Minet separated Sphinginae *sensu lato* into Smerinthinae and Sphinginae *sensu stricto* in part because it was believed that Sphinginae *s. l.* may be paraphyletic. Specifically, the labial palp character which Rothschild and Jordan first described cannot be used to describe a group because it was based on the *absence* of the microtrichial patch. Furthermore, this patch is also known in other bombycoid families, and was therefore thought to render Sphinginae *s. l.* paraphyletic (Lemaire and Minet, 1999).

The most recent major contribution to sphingid classification was the revision of (Kitching and Cadiou, 2000). In addition to stabilizing sphingid taxonomy and classification, Kitching and Cadiou also proposed provisional relationships of sphingids based on some unpublished morphological analyses. Unlike Rothschild and Jordan (1903) and Nakamura (1976), Kitching and Cadiou tentatively placed the Smerinthinae at the base of the family, and Sphinginae and Macroglossinae as more derived (Fig. 3). Within the Smerinthinae, Smerinthini was thought to be paraphyletic. However, their interpretation was “provisional and subject to change” (Kitching and Cadiou, 2000: 16), and I therefore consider their proposed phylogenetic relationships tentative.

Recent molecular phylogenetic analyses of Sphingidae (Regier *et al.*, 2001; Mignault, 2003) based on elongation factor-1α (EF-1α, Cho *et al.*, 1995), and dopa-decarboxylase (DDC, Fang *et al.*, 1997), preliminarily tested Kitching and Cadiou’s classification. Regier *et al.* (2001) found comparable information content and no significant conflict in signal between 1,240 bp of *EF-1α* and 709 bp of *DDC* across fourteen sphingids, and conducted combined analyses of the two genes under parsimony
(MP) and likelihood (ML) optimality criteria. The phylogeny which they presented (Fig. 4) was similar to the morphological interpretation of Rothschild and Jordan (1903) and Nakamura (1976), as relationships among subfamilies were: Macroglossinae + (Smerinthinae + Sphinginae). However, less than 15% of all recognized sphingid genera were included in their analysis, and three key tribes, Acherontiini, Ambulycini, and Sphingulini, were not included.

Mignault (2003) increased taxon sampling to 45 sphingid genera (Table 1), and also conducted a combined analysis of the two genes with MP and ML. The MP analysis resulted in a monophyletic Sphinginae, a strongly supported Sphingulini + Sphinginae, and a weakly supported monophyletic Macroglossinae (Fig. 5). Smerinthines were basal and paraphyletic with respect to the rest of the Sphingidae. The ML analysis (Fig. 6) resulted in subfamily relationships identical to Regier et al. (2001), excluding one sample which was labeled an acherontiine, but had part of its sequence switched with a macroglossine (see Figs 5, 6, figure legend). Ambulycini, Philampelini, and two tribes in the Dilophonotini (Dilophonotina and Hemarina), were monophyletic. Monophyly of Sphingulini was not tested, as Mignault’s study only included Hopliocnema brachycera (Lower) from this tribe. Due to computational limitations, Mignault (2003) did not calculate bootstrap support values for his ML analysis.

The current study builds upon the works of Regier et al. (2001) and Mignault (2003) increasing both taxon and gene sampling to test the monophyly of the Sphingidae, phylogenetic placement of subfamilies, tribes and subtribes, as classified in the revision of Kitching and Cadiou (2000). Although inclusion of morphological characters often has a significant and positive effect on phylogenetic signal in combined analyses (Baker et al.,
1998; Wahlberg et al., 2005; Wortley and Scotland, 2006), the current study does not include morphological characters as a coded morphological character set for the Sphingidae is as yet unavailable, and combined, simultaneous analysis of morphology and molecules must therefore be the focus of a future study.

Taxon sampling was increased because inclusion of additional sphingid genera is necessary to understand further the relationships of subtribes and genera. Taxa were also added because increasing taxon sampling has been shown to break long branches (Hillis, 1996; Graybeal, 1998); but see also Mitchell, 2000), and reduce phylogenetic error for both MP and ML optimality criteria (Zwickl and Hillis, 2002). Biases such as long-branch attraction (LBA, originally termed long-edge attraction (Hendy and Penny, 1989)) have been argued to be a drawback of parsimony in particular (Felsenstein, 1978), but it has been shown that ML can also suffer from long branch effects if the model is misspecified (Gaut and Lewis, 1995; Chang, 1996; Zhang et al., 2006), or prone to long-branch repulsion in particular situations (Siddall, 1998; Siddall and Whiting, 1999). The current study explores the effect of LBA as it pertains to the sphingid dataset presented here.

Additional genes were sequenced because increasing taxa while keeping gene number constant may lead to a decrease in accuracy due to introducing new long branches (Poe and Swofford, 1999), or reducing the relative amount of characters to resolve the newly added taxa (Kim, 1998; Bininda-Emonds et al., 2001). Multiple evolutionarily independent genes were chosen to reduce inherent biases which may be confined to a particular gene, and because combining characters from different genes tends to improve phylogenetic accuracy and support (e.g., Cummings et al., 1995; Otto et
al., 1996; Zardoya and Meyer, 1996; Cummings et al.; Yoder and Irwin, 1999; Mitchell et al., 2000; Rokas et al., 2003; Rokas and Carroll, 2005).

Specifically, this study utilizes 6,793 bp combined from five protein coding nuclear genes: EF-1α (EF-1a, Cho et al., 1995), DDC (DDC, Fang et al., 1997), CAD (Moulton and Wiegmann, 2003), period (Regier et al., 1998), and wingless (Brower and DeSalle, 1998). The five nuclear gene dataset was also supplemented with a 658 bp region of the mitochondrial Cytochrome-Oxidase-1 (COI) gene for 69 ingroup taxa for which this gene was available (Supplementary Table S1). The main purpose for adding COI was to include additional taxa which were not represented in the nuclear gene dataset, and to test the effect of adding a small mitochondrial gene to a much larger nuclear gene dataset.

1.2. MATERIALS AND METHODS

1.2.1. Taxon Sampling

The current study includes 106 sphingid genera (131 ingroup species), from all subfamilies, tribes and subtribes recognized in Kitching and Cadiou (Table 2). I included as many genera as possible, given the availability and quality of samples. Several genera were represented by more than one species. Specimens were collected on all continents, with help from many international collectors (see Acknowledgments).

Outgroup choice was based on the classification of Bombycoidea proposed by Minet (1991; 1994; Lemaire and Minet, 1999), in which nine families, including the Sphingidae, were arranged into putative monophyletic groups. According to Minet, the Sphingidae is the sister group to Brahmaeidae + Leponiidae, with Cartheidae being the
closest relative of the clade consisting of the Brahmaeidae, Lemoniidae, and Sphingidae (see Fig. 71 of Minet, 1994). A recent molecular analysis indicates very different relationships of Bombycoidea (Regier, in prep.). For this reason, eleven outgroups from eight different bombycoid families were included in the current study (Table 2). The primary purpose of this study was to test the monophyly of Sphingidae, and resolve relationships between sphingid genera. Due to limited space available on each page, outgroup relationships are excluded from all figures except figure 12.

1.2.2. Gene Sampling

Many recent studies on the molecular systematics of Lepidoptera have focused on a few selected genes (e.g., COI, EF-1α, wingless). Protein-coding nuclear genes have been successfully utilized in the Bombycoidea (Regier et al., 2000; 2001; 2002; 2005), and it is unfortunate that protein-coding nuclear genes are not further utilized in molecular phylogenetic studies of Lepidoptera. Such genes are minimally exploited, due mainly to the difficulty in developing primers and the ease of using genes that easily amplify (Cummings and Meyer, 2005). It is hoped that this study will help facilitate the use of some of these protein-coding nuclear genes to the larger community of lepidopteran molecular systematists.

This study included 2929 bp of CAD (46F-1028R), 1282 bp of DDC (1.2F-7.5sR), 1228 bp of EF-1α (30F-41.2R), 951 bp of period (197sF-532sR), and 403 bp of wingless (wg1-wg2a). Primer sequences of these five genes are listed in Table 3. Sequences will be assigned accession numbers and submitted to GenBank prior to publication of this manuscript. See Supplementary information for sequence information of COI.
1.2.3. Nucleic acid extraction and RT-PCR

Nucleic acid extractions were performed using the head or prothorax of each specimen to reduce the possibility of contamination, and to retrieve high concentrations of nuclear genes. In particular cases, a leg of a specimen was used because the rest of the body was unavailable (e.g., *Aleuron chloroptera*, *Deidamia inscriptum*). Nucleic acid extractions were conducted with the Promega SV Total RNA Isolation System (Promega, 2004), with slight protocol modifications (exclusion of part IV, E. steps 4, 5) to permit extraction of both genomic DNA and RNA. All specimens and extractions are stored at -85°C in the University of Maryland Lepidoptera molecular collection.

Selective amplification of gene coding regions (e.g., mRNA) on the genomic whole nucleic acid extraction was conducted using the reverse transcription polymerase chain reaction (RT-PCR) to avoid introns, and because RT-PCR has yielded better results than DNA-PCR in experiments conducted previously in the Regier Lab (Regier, 2006). The RT reaction solution (10 μL) was made with the following ingredients: 2 μL 25 mM MgCl₂, 1 μL GeneAmp 10X PCR Buffer II, 0.5 μL Reverse Transcriptase (50 units/μL), 0.5 μL RNase Inhibitor (20 units/μL; all obtained from Applied Biosystems), 2 μL 10 mM dNTPs, 1.25 μL primer, 1.75 μL deionized DEPC-treated H₂O, and 1.0 μL purified extract. Reactions were conducted on a MJ Research DNA Engine Peltier Thermal Cycler (PTC-200) pre-cooled to 4°C and incubated at 42°C for 35 minutes, followed by 99°C for 5 minutes.

An individual PCR reaction consisted of a 10 μL RT reaction, and 40 μL of the following ingredients: 3 μL 25mM MgCl₂, 4 μL GeneAmp 10X PCR Buffer II, 31.25 μL
deionized DEPC-treated H₂O, 0.5 μL AmpliTaq (50 units/μL, Clontech), 1.25 μL primer. Touchdown thermal cycling (Don et al., 1991) was employed in the amplification of in vitro synthesized cDNA. For the first 25X cycles, annealing temperature was iteratively decreased by 0.4°C per cycle, while extension time was iteratively increased by 2 seconds per cycle. After 25X touchdown cycles, traditional 3-step PCR at a standard annealing temperature was conducted for an additional 13 cycles, increasing the extension time by 3 seconds each cycle. Thermal cycling was completed with a final extension at 72°C for 10 minutes.

PCR products were visualized using agarose gel electrophoresis and ethidium bromide staining. Double stranded amplification products were isolated from agarose gels, and isolated bands were melted at 70°C for 8 minutes, before 1 mL of Promega, Wizard PCR Preps DNA Purification Resin was added to each sample and cooled at 25°C for 2 minutes. Samples were placed on 20-channel Vac-Man Laboratory vacuum manifolds and washed with 80% isopropanol to purify products. For all genes except wingless, products were reamplified using PCR and nested primers to improve yield and ensure clean results. For fragments with weak amplification, products were gel isolated and purified a third time and both strands were directly sequenced from M13 sites at the 5’ end of all primers.

1.2.4. Data matrix construction

Sequence chromatograms were checked for accuracy and contigs were edited and assembled with the Staden GAP4 software package (Staden et al., 2000). Sequence alignments were conducted manually using the Genetic Data Environment (GDE)
software (Smith et al., 1994). Manual alignments were employed as RT-PCR yields few introns and alignment has been proven straightforward (Regier, 2006). For each gene, a data matrix was constructed in GDE and saved as a Nexus-formatted text file.

Single gene matrices were sequentially combined to create a matrix of five genes using the “New Matrix Merge” command in Winclada (Nixon, 2002). Simultaneous analyses were conducted because novel relationships may be uncovered through the combination of multiple partitions (Chippindale and Wiens, 1994), and because they provide the greatest possible explanatory power over other consensus methods (Farris, 1983; Nixon and Carpenter, 1996). However, parsimony analyses with lots of missing data can lead to a plethora of most-parsimonious trees (Nixon and Wheeler, 1992; Wilkinson, 1995; 2003), and support values can be sensitive to missing data (Makovicky, 2000; Wilkinson, 2003; Brower, 2006). Simply for the purpose of testing for the relative contribution of each gene towards the MP topology, a smaller 99-taxon dataset was constructed by removing all taxa that had missing data for over half of any partition. A dataset without third codon positions (nt3) was also created. Third positions were deleted in Winclada (Nixon, 2002) with following the commands: “Analyze/Moleculoid/Select third positions FROM CURSOR; delete selected chars”.

1.2.5. Phylogenetic analyses

Phylogenetic analyses were conducted under MP and ML optimality criteria. MP analyses were conducted using Winclada (Nixon, 2002) and NONA (Goloboff, 1999). Heuristic searches were computed with the following commands: “hold 1000” (sets the maximum number of trees to be stored in memory as 1000), “hold/100” (sets 100 trees to
be retained during each replication), “mult*100” (generates a Wagner tree based on a randomized taxon order and conducts SPR, where branches are clipped and reattached to the tree in all possible positions), “max*” (conducts TBR, where each clipped branch is reattached in all possible positions and re-rooted at each possible attachment point).

Congruence between multiple most-parsimonious cladograms (MPCs) was assessed using a strict consensus tree (Sokal and Rohlf, 1981). Branch support was evaluated using the bootstrap (Felsenstein, 1985), Bremer Support (BS; Bremer, 1988; 1994), and Partitioned Bremer Support (PBS; Baker and DeSalle, 1997; Baker et al., 1998).

MP bootstrap values were computed in NONA (Goloboff, 1999) with 500 replications, 100 search replications (mult*100), and holding 10 starting trees (hold/10). BS and PBS values were calculated in TreeRot (Sorenson, 1999) and the subsequent command files executed in PAUP* (Swofford, 2002) for both all-taxon and 99-taxon datasets, and each analysis was repeated. PBS values were calculated to estimate congruence between data partitions and to test the relative contribution of each gene to each node. A metric for measuring congruence between partitioned datasets, here called the relative congruence index (RCI) was calculated by dividing the total PBS value by the number of parsimony informative characters.

Models for maximum likelihood (ML) were chosen using the Akaike Information Criterion (AIC, Akaike, 1973) implemented in Modeltest (Posada and Crandall, 1998). MrMTgui (Nuin, 2007) was used as an interface program to calculate the best model for each gene. In all cases (including COI), the best model was determined to be the general-time-reversible substitution model (Lanave et al., 1984; Rodriguez et al., 1990), with a gamma distribution and invariant sites (GTR+I+Γ).
All ML analyses were conducted in Garli ver. 0.951 (Zwickl, 2006). Garli uses a genetic algorithm as described by Lewis (1998) which involves the evolution of a population of solutions, each which encodes a tree topology, branch lengths, and model parameters to search for the optimal solution (Zwickl, 2006). Fitness is assigned to each individual based on its log likelihood score, and fitness is recalculated after random mutations are applied to individuals. Individuals with the highest log likelihood (-lnL) values are kept as parents for the next generation, and this process is repeated until a higher log likelihood score cannot be obtained.

A random starting tree was chosen in Garli, and none of the Garli default settings were changed except for the number of generations to termination, which was doubled to improve the search for the most optimal solution (genthreshfortopoterm = 20,000). To further assure the search for best tree, the search process was repeated eight times for each ML analysis. To assess the relative contribution of each gene toward the five-gene simultaneous ML analysis, I conducted single gene ML analyses and analyses that included four genes in all combinations. For each ML bootstrap analysis, 500 bootstrap replications were conducted (bootstrapreps = 500), and the bootstrap value for each clade was examined in PAUP*4b10 (Swofford, 2002). All analyses presented in this study were rooted with Macrothylacia rubi (L.), and computed on a Windows PC platform with 3.0 GHz, Opteron 175 dual processors.
1.3. Results

1.3.1 Sequence amplification success and base composition

Sequencing reactions were successful for over 80% of taxa for each gene. *Wingless* was the most successful, with 132 successful sequencing reactions, while *period* was the least successful (Table 2). Base frequencies were approximately equal in all genes except *CAD* and *wingless*. *CAD* showed a slight A-T bias, while *wingless* showed a G-C bias (Table 4). Similar biases were documented in studies that have utilized *CAD* or *wingless* (e.g., Brower and DeSalle, 1998; Moulton and Wiegmann, 2003; Nazari et al., 2007). The percentage of parsimony-informative characters per gene (within Sphingidae) was highest for *period* (55.9%), and lowest for *EF-1a* (25.4%; Table 5). For each gene, third codon positions had the greatest number of parsimony-informative characters, and nt3 was close to saturation for all genes except *EF-1a*.

1.3.2. Phylogenetic analyses

The MP simultaneous analysis included 3044 parsimony-informative characters, and the analysis yielded 12 MPCs (L = 43023, CI = 0.15, RI = 0.53; Fig. 7). The MP analysis recovered a monophyletic Sphingidae (bootstrap = 100%; from hereon bootstrap values indicated by percentages only), monophyletic Sphinginae (99%) and a poorly supported monophyletic Macroglossinae (51%). Monophyletic tribes and subtribes recovered include: Acherontiini, Ambulycini, Choerocampina, Hemarina, and Philampelini (all with ≥ 94%; summarized in Table 6). The clade comprising Sphinginae + paraphyletic Smerinthinae was recovered (87%, node 2), and Sphinginae and
paraphyletic Sphingulini was well supported (98%, node 7). Results from individual analyses are presented as supplementary material (Figs. S1-S10).

Bremer support values were calculated to estimate support for each node in the MP five gene simultaneous analysis. PBS was calculated to determine the relative contribution of each gene to each node in the overall topology, which may not be obvious from separate analyses of each dataset. Within a combined-gene analysis framework, a positive PBS value for a particular node and a particular gene indicates support from that particular partition, while negative values indicate negative contribution from that gene for that particular node. A PBS score of zero indicate the indifference of that partition to that particular node (Baker and DeSalle, 1997; Baker et al., 1998; Gatsey et al., 1999; Gatsey and Arctander, 2000). Interestingly, PBS values calculated from the combined-gene analysis suggest that the largest gene, CAD, contributed the least when PBS values were summed over all nodes. The total summed PBS value of CAD was -1046.55, while the total PBS for DDC was 1880.08 (Table 6). This was unexpected, as the MP single gene analysis of CAD was overall fairly similar in topology to the tree resulting from the simultaneous analysis. When examined carefully, it was discovered that TreeRot was often assigning negative PBS values to clades all the members of which were not present in a particular partition. For instance, *Amplypterus mansoni* + *A. panopus* is well supported in the simultaneous analysis (bootstrap = 100%, Bremer Support = 37, node 66), but while the entire CAD sequence was available for *Amplypterus panopus* it was missing for *A. mansoni*. The PBS value for this node was positive for all genes except CAD, which received a PBS value of -28.85. It remains unclear if there is a calculation or implementation error in TreeRot, but the current results suggest that when TreeRot
calculates PBS values, negative PBS values are assigned to a clade that includes a taxon with considerable missing data and a taxon without missing data. Theoretically, however, the net contribution to the particular branch should be zero.

CAD is also the largest of all five genes analyzed (more than double the size of any of the other genes), and it is therefore possible that a greater negative contribution is being assigned to this partition because of its size. Strange values were also obtained when the analysis was repeated. Further investigation of the effect of missing data to PBS clearly is necessary.

The MP 99-taxon analysis (which excluded taxa with missing data > 50% for any partition) resulted in one MPC (Fig. 8). Overall, this tree was similar in topology to the strict consensus from the all-taxon analysis, but differed slightly in the position of several taxa. PBS values from the 99-taxon analysis demonstrate that all gene partitions contribute positively to the tree generated from the simultaneous analysis (Table 7). This analysis was repeated multiple times and similar results were obtained. A measure of the relative contribution of each gene was calculated by dividing the total PBS value by the number of parsimony informative characters. This index, here termed the Relative Contribution Index (RCI), was highest for EF-1a, and lowest for wingless (Table 8, for further details on this method see: Wahlberg et al., 2005).

The ML simultaneous analysis resulted in a tree similar to the all-taxon MP strict consensus but support for many relationships was stronger (Fig. 9). Within the well supported Sphingidae (100%) monophyletic subfamilies included Sphinginae (100%) and Macroglossinae (97%), the latter which was poorly supported in the MP analysis. Monophyletic tribes and subtribes recovered include the Acherontiini (100%),
Ambulycini (100%), Choerocampina (88%), Hemarina (100%), and Philampelini (100%). As with the MP analysis, a monophyletic Sphinginae + paraphyletic Smerinthinae (88%, node 2) was recovered, and Sphingulini + Sphinginae was well supported (100%, node 7).

For all genes, nt3 provided the greatest amount of parsimony informative characters. Greater than 90% of the characters at the third codon position (nt3) were parsimony informative for all genes except EF-1α (Table 5). This suggests that nt3 may be saturated and causing unwanted “noise” which may affect the resulting tree (e.g., Mindell et al., 1996; Naylor, 1997 #366, but see also Wenzel and Siddall, 1999). Exclusion of nt3 resulted in an MP tree that was considerably less resolved, with many uncertain deep relationships (Supplementary Fig. S11). The number of MPCs rose from twelve to over ten thousand when third positions were excluded. Support values after excluding nt3 were much lower than when all nucleotide positions were included (Table 6). When nt3 was excluded, high support (> 90%) was recovered for only 21 nodes, while the nt-all dataset recovered 76 nodes of high support. Similar results were recovered for the ML nt-12 analysis, which also resulted in lower bootstrap support compared to the ML simultaneous analysis (Table 9). Although exclusion of nt3 may be necessary at deeper levels (Mindell et al., 1996; Naylor and Brown, 1997), inclusion of nt3 is essential for resolving some relationships within Sphingidae.

Since EF-1α was demonstrated as the most informative gene with the highest RCI value (Table 8), and because EF-1α was the slowest evolving gene among all five genes (based on the highest percentage of parsimony informative characters at the third codon position of EF-1α, Table 5), I examined whether third codon position characters of EF-1α
were contributing significantly to overall tree structure. I removed all third codon positions of \textit{EF-1\alpha} and reran the MP analysis. The result (Supplementary Fig. S12) shows that much of the phylogenetic information for deep nodes within the Sphingidae comes from the third position of \textit{EF-1\alpha}, indicating that its slower rate of molecular evolution is critical for the present study.

The contribution of each gene partition to the ML tree was assessed by excluding one of the five genes and comparing bootstrap support values for each node. Support for many deep divergences within the Sphingidae decreased when CAD was excluded (Table 9), but exclusion of each of the other four genes did not affect support values of deep nodes. Interestingly, exclusion of DDC revealed higher support for several nodes (e.g., nodes 12, 30, 37) that were not obtained when any other single gene was excluded. These results suggest that CAD is contributing substantially to deep divergences within Sphingidae, while DDC may contain strong conflicting signal for particular nodes. However, further analyses are required to examine the effect of gene size, as CAD is more than twice the size of any other gene included in this study.

1.4. DISCUSSION

1.4.1 Monophyly of Sphingidae and basal divergences within the family

The present study reveals a novel hypothesis for sphingid relationships, which contain elements of prior studies. Results were most congruent with the molecular analyses of Regier \textit{et al.} (2001) and Mignault (2003), although increased taxon sampling uncovered many well supported relationships among taxa that were not included in their studies. Simultaneous analysis under both optimality criteria yielded a monophyletic
Sphingidae (100% MPML) and the monophyly of the family is also corroborated by at least nine larval, pupal, and adult synapomorphies (Minet, 1994). Both MP and ML analyses recovered a monophyletic Macroglossinae (51% MP, 96% ML, node 3), and a clade comprising of a paraphyletic Smerinthinae + Sphinginae (87% MP; 97% ML, node 2). *Langia zenzeroides* was the most basal taxon within this clade (node 2), but the basal position of *L. zenzeroides* at node 2 was not recovered in any of the single gene analyses. This result indicates that the combination of multiple datasets can uncover relationships that are not present when partitions are analyzed independently, as previously demonstrated (Chippindale and Wiens, 1994).

Differences between MP and ML topologies lie mainly in the placement of several long-branched taxa (i.e., *Cypa decolor, Cautethia spuria, Neogurelca himachala,* and *Sphingonaepiopsis gorgoniades*). To explore the difference between the two topologies, different combinations of outgroups were initially excluded. In each MP exclusion analysis, one or more of the four sphingids with the longest terminal branches moved to the base of the Sphingidae. Instability in the position of particular ingroup taxa caused by exclusion of particular outgroups suggests that these long-branched ingroups may be attracted to certain outgroups via LBA when other outgroups are excluded. To determine whether LBA was a factor in the simultaneous analysis with all outgroups, the analysis was repeated without outgroups, and the ingroup topology was compared. Topologies were fundamentally very similar, the only difference was in the MP analysis, where *C. decolor* was recovered as the sister taxon to the clade consisting of the Smerinthinae + Sphinginae excluding *Langia*. These results suggest that LBA may be an
artifact in the MP analysis when particular outgroups are excluded, but inclusion of all outgroups simultaneously does not appear to affect ingroup relationships significantly.

1.4.2 Relationships within Smerinthinae and Sphinginae

Within Smerinthinae, the tribe Smerinthini was paraphyletic in all analyses conducted. Paraphyly of Smerinthini was predicted based on morphology (Kitching and Cadiou, 2000). Monophyletic Ambulycini + paraphyletic Smerinthini (excluding *Langia*) was recovered in the ML analysis (97%, node 6) but other deep divergences among the Smerinthinae remain speculative, as deep relationships of this group were typically characterized by short internal branch lengths and weak bootstrap support under both optimality criteria.

Several well-supported groups were recovered within Smerinthini. *Laothoe*, *Pachysphinx*, *Paonias*, and *Smerinthus* form a well supported monophyletic group (100% MPML, node 30 MP, 31 ML), and clades nested within this group are also relatively well supported (≥ 88% MP, ≥ 98% ML). Following Rothschild and Jordan (1903), Kitching and Cadiou (2000) predicted the monophyly of *Pachysphinx, Paonias*, and *Smerinthus*. *Laothoe* is widely distributed from Ireland across to China and its larva feeds on leaves of *Populus* and *Salix* (Pittaway, 1997-2006), the same larval hosts of the temperate New World *Pachysphinx* (Hodges, 1971). Unlike *Laothoe* and *Pachysphinx*, whose larval hosts are restricted to the Salicaceae, *Paonias* and *Smerinthus* are polyphagous, and feed on a variety of different hostplant families (Hodges, 1971). The current study suggests a larval host shift from monophagy to polyphagy in this particular clade, and the secondary development of the adult hindwing eyespot in *Paonias* and *Smerinthus*. 
The clade containing *Amorpha*, *Mimas*, and *Phyllosphingia* was well supported (100% MPML, node 49 MP, 71 ML). Recovery of *Amorpha* + *Phyllosphingia* as sister genera corroborates evidence from larval and pupal morphology and larval hostplants being Juglandaceae (Pittaway and Kitching, 2006). Pupal morphology may also support the affinity of these two genera with *Mimas* (Kitching, pers. com.). Monophyly of the *Clanis*-group, including *Clanis*, *Afroclanis*, *Neoclanis*, and *Viriclanis* was also well supported (100% MPML, node 36 MP, 29 ML). *Clanis* is distributed in Asia, and the latter three are restricted to mainland Africa.

Kitching and Cadiou (2000) predicted the monophyly of *Daphnusa*, *Gynoeryx*, *Likoma*, and *Marumba* based on similar forewing line patterns and tarsal morphology. Although *Gynoeryx* was unobtainable for inclusion in the current study, *Daphnusa*, *Likoma*, and *Marumba* form a well supported monophyletic group (100% MPML, node 71 MP, 73 ML). The sister-group relationship of this “Likoma-group” with the *Polyptychus*-group” is well supported (94% MP, 99% ML). The *Polyptychus* group was represented in the current analysis by *Neopolyptychus*, *Polyptychus*, *Polyptychoides*, and *Pseudoclanis*, and its monophyly was also well supported (100% MPML). Although the pupal stage of *Chloroclanis* is unknown, all other genera in this clade (*Andriasa*, *Neopolyptychus*, *Polyptychoides*, *Polyptychus s.s.*, and *Pseudoclanis*) have a row of punctures near the anterior edge of some lateral segments of the pupa. However, this feature is not found in *Polyptychus andosa* or many other *Polyptychus*, suggesting that further division of *Polyptychus* is required (Ian J. Kitching, pers. com.).

Monophyly of Ambulycini was well supported (100% MPML). Within the tribe, two clades follow their geographic distribution: the Neotropical *Adhemarius* +
Protambulyx and the Old World Ambulyx + Amplypterus. A morphological analysis (Kitching unpublished data, 1993), places Ambulyx and Amplypterus as basal within the Ambulycini. It has been hypothesized, however, that some Old World Ambulycini (e.g., Akbesia, Batocnema, Compsulyx) may be more closely allied to the Neotropical species than Ambulyx + Amplypterus based similarities of the hindwing eyespot marking and a spinose gnathos in the male genitalia (Kitching and Cadiou, 2000). A future study incorporating more taxa and characters will test this hypothesis.

The current study strongly supports a sister-group relationship of the paraphyletic Sphingulini + monophyletic Sphinginae (98% ≥ MPML, node 7). Rothschild and Jordan (1903) placed seven genera in the Sphingulini as the sister group to the Sphinginae, but none of the other studies predicted the placement. Nakamura (1977) noted that both groups share a unique character: “[the] caudal end of [the] pupal eye piece [is] attached to the structure restricting the proximal margin of the maxilla” (Nakamura, 1977: 6). However, Nakamura did not place the Sphingulini as sister to the Sphinginae in any of his figures (Nakamura, 1976; 1977; 1978).

Monophyly of Sphingulini has remained uncertain, but morphology suggests that Dolbina and Kentrochrysalis are closely related (Rothschild and Jordan, 1903; Eitschberger and Zolotuhin, 1997; Kitching and Cadiou, 2000). The current analysis renders the tribe paraphyletic, as the Australian Hopliocnema is sister to the reciprocally monophyletic Sphinginae and Dolbina + Kentrochrysalis. This paraphyly is not unexpected as Sphingulini was diagnosed by Rothschild and Jordan (1903) solely on character reductions and absences.
Monophyly of Sphinginae was strongly supported (≥ 99% MPML), and relationships among taxa in the subfamily are nearly identical under both optimality criteria (difference being the polytomy of Sphinx in the MP strict consensus). Within the Sphinginae, Acherontiini is monophyletic (100% MPML). Acherontiini include five genera, four of which are included in the present study. A feature of the labial palp and three characters of the genitalia support the monophyly of the tribe (Kitching, 2002; 2003). Although Callosphingia could not be obtained for inclusion into the current study, relationships among Acherontia, Agrius, Coelonia, and Megacorma are congruent with Kitching’s (2002; 2003) morphological analyses under equal weighting (see Fig. 22 in Kitching 2002).

Acherontiini and Xanthopan are known to share a unique hearing organ which is used to detect ultrasonic wavelengths of bats (1999a; Göpfert and Wasserthal, 1999b; 2002). These hearing organs differ slightly from ears found in the Choerocampina, although all sphingid hearing organs are composed of a specialized sound-receiving structure on the labral pilifer and labial palp (Göpfert et al., 2002). Specifically, the pilifer of particular Acherontiini and Xanthopan lack a distinct distal lobe, the second palpal segment is deeply depressed without being swollen or lacking in hairs, and a scale plate that interacts with the pilifer is also present on the labial palpus (Göpfert et al., 2002).

Kitching (2002) noted that Acherontiini also share similar pupal morphology with Xanthopan and the Cocytius-group (Cocytius + Neococytius). He therefore tested whether these long-tongued sphingines form a monophyletic group, but was unable to determine the exact placement of Xanthopan (Kitching, 2002), as different weighting schemes
placed the genus in different positions of the tree. The current study reveals that
*Xanthopan* and the *Cocytius*-group are closely related (100% MPML, nodes 52 MP, 97 ML), and suggests two independent origins of the hearing organ in Sphinginae.

The monotypic *Dolba hyloeus* (Drury) was recovered within the speciose genus *Manduca* with very strong support (100% MPML). Rothschild and Jordan (1903) recognized *Dolba* as a genus separate from *Manduca* based mainly on the presence of “lashed eyes”. However, where this character has been used in other groups, it has been found wanting as a synapomorphy (e.g., in Noctuidae 1984; Kitching, 1987) and it is certainly insufficient to form the basis of a genus. Although changing the classification of Sphingidae is not the immediate goal of this study, the molecular results indicate that the monotypic *Dolba* should be synonymized with *Manduca*.

The clade containing *Sphinx* is strongly supported (100% MPML, node 53 MP, 33 ML). Tuttle (in press) proposed to include 21 species of *Sphinx* in a newly resurrected genus, *Lintneria* Butler, based on larval and adult characters. Butler (1876) believed that the more rounded forewings of particular *Sphinx* species were substantially different, and therefore erected this genus over a century ago. Forbes (1911) noted the close similarity in the larva of *Lintneria* and *Sphinx*, but described the unique mesothoracic dorsal hump of *Lintneria* as the distinguishing feature. Despite these distinctive characters of *Lintneria*, subsequent studies generally placed these species in *Sphinx*. Recent larval rearing experiments and a closer examination of adults corroborate the previous findings, and it has been shown that that the first four instars of all members of *Lintneria* for which the larval stages are known have a large, fleshy, dorsal protuberance that angles anteriorly, and adults have unique wing markings that are typically not found in *Sphinx*.
sensu stricto (Tuttle, in press). The present molecular analysis included two species, *S. istar* (Rothschild and Jordan) and *S. merops* Boisduval, which are proposed to be transferred to *Lintneria*. These two species have a more southerly distribution compared to the other *Sphinx* species in the present study, and together form and separate, well supported clade (100% MPML, node 77 MP, 125 ML).

The second strongly supported clade within *Sphinx* includes *S. caligineus*, *S. chersis* and *S. dollii*, together with *Isoparce cupressi*, and *Lapara coniferarum* (100% MPML). *Sphinx caligineus*, *S. dollii*, *I. cupressi* and *L. coniferarum* form a monophyletic group, and larvae of these species are unique in that they feed on conifers (Hodges, 1971). Furthermore, the proboscis of these conifer-feeding species is substantially reduced (see Chapter 2). Strong support for these two clades corroborates resurrection of *Lintneria* based on larval and adult morphology, and suggests that *Isoparce* and *Lapara* should be synonymized with *Sphinx*.

1.4.3 Relationships within Macroglossinae

A monophyletic Choerocampina was recovered (94% MP; 88% ML) in the paraphyletic tribe, Macroglossini. Choerocampines have a swollen, air-filled second labial palp segment that is devoid of hair or scales (Roeder and Treat, 1970), and monophyly of this subtribe was predicted (Kitching and Cadiou, 2000). Like the Acherontiini and *Xanthopan*, the second labial palp segment of Choerocampina is used as an ‘ear’ in combination with the pilifer to detect ultrasonic sounds emitted by echolocating bats (Roeder et al., 1968). A recent study demonstrates that particular choerocampines produce ultrasound in response to bat calls, and these responses may be
used to startle the bat, jam biosonar, or warn the predator (Barber and Conner, submitted).

Choerocampines and hawkmoths in the Smerinthini, Sphingini, Sphingulini, and diurnal Macroglossina typically have genital stridulatory organs which are similar, but differ slightly in morphology (Kitching and Cadiou, 2000). The functional significance of these stridulatory organs remains unknown, but the organs are presumed to be used for courtship (Barber, submitted; Kitching and Cadiou, 2000; for an account of male hawkmoth using acoustic sounds in the vicinity of a female, see Mell [1922]). If stridulatory organs are used during courtship, members of the opposite sex must be able to recognize stridulatory stimuli. The primary function of the pilifer/labial palp ultrasonic hearing organ of Choerocampina may therefore be to detect these signals during mating, and its function to detect ultrasounds of bats may be a secondary gain which evolved thereafter (Kitching and Cadiou, 2000; Barber and Conner, submitted). The question of how and why stridulatory organs evolved in the Sphingidae will be the focus of a future study which includes additional physiological data and additional sampling of sphingid taxa.

Within Choerocampina, the Neotropical genus *Xylophanes* forms a monophyletic group, although this clade was not strongly supported (84% MP, 83% ML). In both MP and ML analyses, *Cechenena, Rhagastis* and *Theretra* together form a monophyletic group (80% MP, 90% ML). These three genera share similar eyespot patterns along the body of the larva, and were believed to be fairly closely related (Nakamura, 1976).

The Southeast Asian *Eupanacra* was recovered as the sister group of the Choerocampina, and *Eupanacra + Choerocampina* is well supported (96% MP, 99%
ML). Ancestral to this divergence is *Gnathothlibus*, and the relationship (*Gnathothlibus (Eupanacra (Choerocampina)) is also well supported (100% MPML). The general biogeographical pattern within this clade suggests a dispersal event from the Old World (e.g., *Eupanacra, Gnathothlibus*) to the New World by the ancestor of *Xylophanes* and another by the ancestor of *Hyles*. Subsequently, there was a dispersal event back into the Old World (for further discussion on the biogeography of *Hyles*, see: Hundsdoerfer *et al.*, 2005a).

Macroglossina was polyphyletic, and the subtribe was separated into several fairly well-supported monophyletic groups. The clade comprising of the temperate *Proserpinus-group (Arctonotus, Euproserpinus, Proserpinus)* was well supported (100%, MPML, nodes 87 MP, 91 ML). All three genera share larval hostplants of the Onagraceae (Hodges, 1971), and these genera were thought to be morphologically closely related to each other and to *Amphion* (Rothschild and Jordan, 1903; Kitching and Cadiou, 2000). Interestingly, both analyses recovered *Pachygonidia* (Dilophonotini, here represented by *P. subhamata*) as the sister group to the *Proserpinus* group, although this relationship was not strongly supported (69% MP, 68% ML). However, inclusion of *Pachygonidia* within Macroglossina is fairly unambiguous (96% MP, 100% ML).

Two species of *Ampelophaga* were included in this study, *A. dolichoides* (Felder) and *A. rubiginosa* (Bremer & Grey). Based on adult morphology, Rothschild and Jordan (1903) included *Ampelophaga dolichoides* in *Ampelophaga* but they noted a close affinity between this genus and *Elibia*, in which they included only a single species, *E. dolichus* (they also included the second current species of *Elibia, E. linigera*, in *Ampelophaga*). Recently, the immature stages of *dolichoides* were discovered and an
apparent similarity with *Elibia* was revealed. Although the pupa of *dolichoides* lacks a free, jug-handle tongue-case found in *E. dolichus*, the species was tentatively transferred to *Elibia* (Pittaway and Kitching, 2006). Results from the present study corroborate the inclusion of *dolichoides* in *Elibia*, as it was recovered as the sister taxon to *E. dolichus* (89% MP, 90% ML). *Ampelophaga rubiginosa, Clarina*, and *Darapsa* are essentially congeneric (their male genital structures are essentially identical; Kitching, pers. com.), and their relationship (*Darapsa (Ampelophaga rubiginosa + Clarina)*) is well supported by molecules (100% MP, 99% ML) and morphology (Kitching and Cadiou, 2000).

Philampelini was represented by three species of *Eumorpha*. All species were recovered together in the same clade with strong support (100% MPML). Surprisingly, the dilophonotine genus *Enyo* was recovered as the sister group to *Eumorpha*, although not strongly supported in either analysis (67% MP, 53% ML). Philampelini also includes one other genus, *Tinostoma*, which is an endemic of the Hawaiian island of Kauai (Kitching and Cadiou, 2000). Unfortunately, *Tinostoma* is known from only a few specimens, and could not be obtained for inclusion in the current study.

The subtribe Dilophonotina is restricted to the New World and is predominantly Neotropical, and the larvae of many species feed on Vitaceae (Tuttle, in press, see also Table 11). Dilophonotina was paraphyletic in all analyses, but a well-supported monophyletic group exists within the tribe (100% MPML; node 20 MP, 26 ML). Monophyly of this clade was previously predicted based on morphology (Kitching and Cadiou, 2000). Monophyly of *Aellopos, Eupyrhaglossum, Nyceryx*, and *Perigonia* is also well-supported (100% MPML), which is also corroborated by morphology (Kitching
and Cadiou, 2000). All subordinate relationships within this clade were well supported (≥ 96% MP, ≥ 99% ML).

Similarly, Erinnyis, Hemeroplanes, Isognathus, Madoryx, and Pseudosphinx form a well supported group (100% MPML). There is evidence that two dilophonotine genera, Erinnyis and Pseudosphinx, exhibit an acoustic response, although they are considerably less sensitive to acoustic signals than the choerocampines (Roeder, 1972). Unlike species with palp/pilifer acoustic hearing organs of the Choerocampina and Acherontiini, hearing organs of these two dilophonotine genera are not on the labial palp or pilifer, and their location remains unknown (Roeder, 1972).

The present study recovered a well supported Hemarina (100% MPML). This subtribe includes two diurnal clear-winged sphingid genera, Cephonodes and Hemaris, and monophyly of Hemarina was previously predicted based on morphology (Kitching and Cadiou, 2000), and there mounting evidence that these two genera may need to be sunk into one genus (Ian J. Kitching, pers. com.). Interestingly, the placement of Hemarina differs between MP and ML trees. In the MP tree, the clade composed of Neogurelca + Sphingonaepiopsis (75% MP, 99% ML) is the sister group of Hemarina, while this tribe is placed at the base of the Macroglossinae in the ML tree. Both Hemarina and the clade comprising of Neogurelca + Sphingonaepiopsis are long-branched taxa. In order to test whether MP resolution was caused by LBA between Hemarina and Neogurelca + Sphingonaepiopsis, the MP analysis was repeated without Neogurelca and Sphingonaepiopsis. When Hemarina were excluded, Neogurelca + Sphingonaepiopsis moved to the base of the Sphingidae. The shift in position of Neogurelca + Sphingonaepiopsis and Hemarina when either is removed provides
preliminary evidence for LBA between Hemarina and *Neogurelca + Sphingonaepiopsis* (see also Fig. 8 for position of Hemarina in the 99-taxon analysis which did not include *Neogurelca* and *Sphingonaepiopsis*).

1.5. CONCLUSION

The current molecular analysis corroborated many previously postulated sets of relationships based on larval, pupal, and adult morphological characters. However, it also uncovered many novel relationships. Molecular data strongly supports the monophyly of Sphinginae and its sister relationship to the paraphyletic Sphingulini, although many deep relationships within the paraphyletic Smerinthinae remain ambiguous. Additional genes and taxa may resolve the uncertainty within the Smerinthinae, as deep divergences within this subfamily are characterized by weak support and short internal branches. Monophyly of Macroglossinae was strongly supported in the ML analysis, although it was much lower in the MP analysis. MP was subject to LBA within Macroglossinae, and inclusion of additional closely-related sphingids, such as the yellow hindwinged species of *Temnora* which superficially resemble *Neogurelca* and may help break these long branches. The current study also demonstrated the utility of the five protein-coding genes for resolving relationships within a family of Lepidoptera, and the synergistic effects which are generated when independent genes are analyzed together in a simultaneous analysis.

The supplementary six gene analysis demonstrates that small amounts of data from the barcoding region of the COI gene can be useful in uncovering relationships when combined with a larger dataset with dense taxon and gene sampling. However,
considerable missing data can depress bootstrap and BS values, and the effect of missing data on PBS needs to be further explored. Understanding the effect of missing data on PBS is imperative, as many recent phylogenetic studies are implementing PBS with large taxon and gene sampling. Specifically, future studies should be conducted on a smaller dataset with fixed taxon and gene size, and missing data should be simulated to test the effect of missing data on PBS.
CHAPTER 2

EVOLUTION OF THE SPHINGID PROBOSCIS
2.1. INTRODUCTION

It has been well known that some hawkmoth adults have extremely long proboscises, while others have very short tongues and can be non-feeding (Rothschild and Jordan, 1903; Fleming, 1968; Miller, 1997b; Kitching and Cadiou, 2000). The evolution of the long tongue in particular sphingid species has been hypothesized as an example of coevolution between pollinating sphingids and flowers from which they extract nutrient-rich nectar (Darwin, 1862). Perhaps the most well-known example of this interaction is *Xanthopan morganii praedicta* Rothschild and Jordan and *Angraecum sesquipedale* Thouars in Madagascar (Kritsky, 1991). In *The origin of species*, Darwin (1859:202) stated, “As certain moths of Madagascar become larger through natural selection … as the proboscis alone was lengthened to obtain honey from … deep tubular flowers … the seedlings would generally inherit long nectaries; and so it would be in successive generations of the plant and of the moth.” This model has been a classic example of a “coevolutionary race” (Darwin, 1862) whereby the evolution of increasing flower depth leads to the subsequent increase in hawkmoth tongue length.

Nilsson (1985; 1988; 1998) experimentally tested various predictions of Darwin’s proposal and found support for this coevolutionary hypothesis. Wasserthal (1992; 1997; 1998) presented an alternative model in which the long-tongued sphingid has evolved to increase the distance from shallow flowers and allow for sideways hovering behavior in order to prevent being ambushed by predators which may be resting on the flower. Wasserthal’s hypothesis is based on the fact that many long-tongued hawkmoths also feed on nectar from flowers with very short tubes. This “pollinator shift” hypothesis is a modification of the coevolutionary race model. Preadapted long-tongued sphingids shift
from feeding on flowers with short corollas to flowers that have long tubes, and the occurrence of long-tongued species on long-tubed flowers exerts selective pressure towards floral tube elongation.

Despite numerous competing hypotheses on the evolutionary process by which the sphingid tongue may have lengthened (Wasserthal, 1997; Janzen, 1984; Nilsson et al., 1985; Miller, 1997b), very few studies report hawkmoth tongue length in a comprehensive manner, and even fewer studies examine nectar feeding records across the entire family. Miller (1997) compiled a list of tongue lengths for 152 sphingid species and stated, “Tongue shortening to 10 mm or less renders hawkmoths incapable of nectar foraging” (Miller, 1997: 11). Miller’s decision to categorize functionality on tongue length was based on an anatomical study by Fleming (1968), in which internal cranial muscles of short and long-tongued sphingids were examined. Fleming presented measurements of fifteen hawkmoth species, and concluded that the reduction or absence of particular muscles renders short-tongued species to have non-functional proboscises. Contrary to Miller’s statement, Fleming never explicitly stated that proboscis length shortening below 10 mm implies non-nectar feeding.

The discovery of muscle reduction in particular sphingids led Fleming (1968) to postulate that short-tongued sphingids, such as smerinthines, were derived from sphingids with longer tongues. The hypothesis that the long sphingid tongue is an ancestral condition dates back to Rothschild and Jordan’s (1903) classification and treatment of sphingid relationships. Rothschild (1903) believed that long tongues are found in basal sphingids, and shorter tongues became “reduced in each derivation from [the] ancestral type” (Rothschild and Jordan, 1903; xcix). Recent coevolutionary hypotheses on long
tongue evolution in Sphingidae (e.g., Nilsson, 1988; Wasserthal, 1992; 1998; 1998) were
based on Rothschild and Jordan’s classification, and assumed that hawkmoths with long
tongues were basal in the family. Nilsson (1998: 260) stated, “The world’s most long-
tongued species of hawkmoths, one of which is X. morganii are also among the largest
and/or heaviest and most primitive …” Similarly, Wasserthal (1998 :459) asserted, “…
extremely long tongues are old adaptations…” If Rothschild and Jordan’s “retrogressive”
hypothesis is correct, one would expect the ancestral condition of the sphingid tongue to
be long, and derived sphingids to have shorter tongues.

Alternatively, Kitching (2000) predicted that smerinthines, with their short
tongues, are basal in the family (see quotation on the second page of this thesis). In
general, long-tongued hawkmoth species are found in the other two subfamilies, the
Macroglossinae, and Sphinginae (Miller, 1997b; Lemaire and Minet, 1999; Kitching and
Cadiou, 2000). Therefore, under Kitching and Cadiou’s scenario, one would expect a
general trend from short ancestral tongues to longer tongues in derived lineages. After
examining tongue length across different taxonomic ranks in Sphingidae, Miller (1997a)
also predicted that tongue length was ancestrally short and became longer over time.

Despite the competing hypotheses on proboscis length evolution, none of the
aforementioned authors formally tested their hypothesis because a sphingid phylogeny
was not available at the time. The only study which used modern phylogenetic
methodology to understand tongue length evolution in Sphingidae was the study of
Kitching (2002) on Acherontiini and several long-tongued, non-acheronitine sphingines.
Kitching categorized tongue length according to the number of coils in the pupal tongue
case, and conducted a rigorous cladistic analysis. Multiple weighting schemes were
implemented, and in all cases, nectar feeding hawkmoths with extremely long proboscises were never recovered as a monophyletic group, and the placement of *Xanthopan morganii* remained ambiguous.

To date, a phylogenetic study that examines nectar feeding and tongue length evolution across all sphingid subfamilies has never been conducted. The purpose of the present study is fourfold: (1) to examine and measure proboscis length across a broad taxonomic range of sphingids, (2) to compile a list of valid field nectar feeding records for sphingids included in the current study, (3) to determine if nectar feeding is strongly correlated to tongue length, and (3) to determine how the nectar feeding behavior evolved in the family.

2.2. MATERIALS AND METHODS

Four hundred and seventeen sphingid specimens were examined in the course of this study. Specimens were studied at the Smithsonian Institution Maryland Support Center (MSC) in Suitland, Maryland. Species which were not represented at the MSC were examined from alcohol specimens preserved in the University of Maryland Lepidoptera frozen collection at College Park, Maryland. Eleven specimens were examined at the Natural History Museum in London. For each species, up to five specimens were examined and a combination of males and females were chosen whenever possible. Because proboscis length may vary within species (Miller, 1997b; Kitching, 2002), I chose specimens that were collected from different seasons and from a wide geographic range whenever possible.
For each species examined, the proboscis was removed by gently pulling the coil from underneath the head of the moth with a pair of fine forceps. Two forceps were used to assure that the tongue was being separated at its base. When proboscises were short, the labial palp was gently pushed aside, and the tongue removed. All proboscises were placed in a pre-labeled glassine envelope. Each tongue was then placed in a 1 mL solution of 10% KOH and heated on a hot plate for 10 minutes. After heating, the proboscis was uncoiled and its length measured with a millimeter ruler, washed with 70% ethanol, and placed into a gelatin capsule and pinned on the bottom of the specimen. Proboscises removed from specimens in the UMD alcohol collection were placed in gelatin capsules in glassine envelopes.

In order to standardize for body size, the length of the forewing (FWL) was measured from each specimen. The right forewing was arbitrarily chosen, but whenever the right forewing was missing or damaged, the left forewing was measured. FWL was calculated by measuring the distance from the wing base to the farthest point on the forewing tip. FWL was preferred over body length because body length can be subject to biases arising from body compression or extension. Furthermore, FWL was chosen because this measure has been used to standardize body size in Sphingidae and other Lepidoptera (e.g., Loder et al., 1998; Beck and Kitching, 2007), and because it is known to be strongly correlated with body weight in hawkmoths (Miller, 1997a).

Ancestral state conditions were determined using Mesquite Ver. 1.12 (Maddison and Maddison, 2006). A matrix of standard categorical data was created for one unordered character with three states: non-feeding (0), nectar feeding (1), nectar and beehive feeding (2). I define non-feeding species as species which do not feed on nectar from
flowers. Although there are occasional reports of sphingids feeding on water droplets (Kernbach, 1962; Pittaway, 1993), visiting mud puddles (Bänzinger, 1988; Büttiker et al., 1996), drinking tear from mammalian eyes (Bänzinger, 1988), and probing decaying animal remains (Sbordoni and Forestiero, 1985), these records were excluded because they are considered anomalies which do not constitute the regular diet of hawkmoths. Species with average tongue lengths less than 1 mm were coded as non-feeding, and those without any biological information regarding feeding behavior were left as missing data. All statistical analyses were conducted with the JMP Ver. 6 statistical software (JMP, 2006). Character states were mapped onto the five gene ML sphingid tree (Chapter 1, Fig. 9).

2.3. RESULTS

2.3.1. Proboscis length and nectar feeding

Average tongue length measurements per sphingid species ranged from less than 1 mm (Andriasa contraria, Hopliocnema brachycera, Marumba quercus) to 211.8 mm (Neococytius cluentius; Table 10). In general, shortest tongues were recorded from Smerinthinae, and longest tongues were found in particular species of Sphinginae. However, some smerinthines had much longer tongues than others in the subfamily (e.g., all Ambulycini examined had tongue lengths 22.8 mm – 35.8 mm), and some sphingines had very short tongues (e.g., Isoparce, Lapara; 6.9 mm and 4.6 mm respectively). Tongue length also varied within each species; Cocytius duponchel had the greatest intraspecific tongue length variation, which ranged from 73 mm to 150 mm. Results from the present study are comparable to previous reports on hawkmoth tongue length (e.g.,
Of the 131 sphingid species that were included in the present study, 61 had documented nectar-feeding records, 17 were reported in the literature to be non-feeding, and 32 remain unknown. A comparison of hawkmoth tongue length to known nectar feeding records shows that long-tongued species are generally nectar feeding, while short-tongued species are typically non-nectar feeding (Fig. 10). However, extrapolating functionality solely on the basis of length can be misleading, as there is an overlap in tongue length for nectar feeding and non-feeding species. Tongue lengths for nectar-feeding species were greater than 9.0 mm, while non-feeding species had tongue lengths less than 10 mm (Table 10; see also Fig. 10 for a comparison of average tongue lengths per species).

Comparison of tongue length to forewing length shows that the two variables are strongly correlated (Pearson’s Correlation Coefficient = 0.571, \( p < 0.0001 \); Fig. 11), corroborating results from previous studies which correlated hawkmoth tongue length and forewing length (e.g., Bullock and Pescador, 1983; Haber and Frankie, 1989; Miller, 1997b). These results illustrate the general trend for small sphingids to have short tongues, and large sphingids have longer tongues. Actual and relative proboscis lengths both show a similar pattern when compared (Fig. 12).
2.3.2. Ancestral state reconstruction

Reconstruction of ancestral states reveals that the short, non-feeding tongue is the ancestral condition in Sphingidae. The nectar-feeding long tongue independently evolved at least three times in the family, but was subsequently lost at least three times (Fig. 12).

2.4. DISCUSSION

2.4.1. Evolution of nectar feeding in Sphingidae

The plesiomorphic condition of the short, non-feeding proboscis supports the hypothesis of Kitching and Cadiou (2000). Within the typically short-tongued Smerinthinae, there was a transition from non-feeding (*Langia zenzeroides*) to nectar feeding in the Ambulycini (but see also Rothschild and Jordan [1903] for a discussion on *Trogolegnum*). Although nectar feeding has not been documented for any species in the Smerinthini, *Afroclanis calcareus* and *Clanis bilineata* may feed on flowers, as tongue length of these two species are substantially longer than other species in the tribe (24.0 mm and 26.0 mm respectively, Table 10; see also Carcasson [1968], Miller [1997]). Presence of long-tongued smerinthines in the sister-clade to Ambulycini suggests that long tongues may predate to the ancestor of the Ambulycini, but increased taxon sampling and additional field observations are necessary to verify this hypothesis.

Species in the Sphingulini also have very short, non-feeding proboscises, and the sister-group relationship of the paraphyletic Sphingulini and monophyletic Sphinginae is well supported (see Chapter 1). Sphingines are predominantly nectar-feeding, and present study reveals a behavioral shift from non-nectar feeding to nectar feeding in the ancestor of this subfamily (Fig. 12).
The basal clade in the Sphinginae includes three genera, *Cocytius*, *Neococytius*, and *Xanthopan*, all of which have extremely long tongues. *Xanthopan* is well known to feed on orchids in Africa (e.g., Darwin, 1862; Nilsson, 1988; Wasserthal, 1992; 1998), and the neotropical *Cocytius* has also been observed pollinating a long-tubed orchid, *Polyrrhiza lindenii* (Tuttle, in press) which has a corolla reaching 170 mm in length (Long and Lakela, 1971). Although we can only speculate the mechanism by which very long tongues evolved, strong support for the placement of *Xanthopan* in this clade suggests the possibility that the ancestor of *Cocytius*, *Neococytius* and *Xanthopan* may have coevolved with the flowers from which they feed. Preliminary morphological evidence supports the inclusion of the monotypic sphingid genus, *Amphimoea*, in this clade (Kitching and Cadiou, 2000). *Amphimoea walkeri* (Boisduval) also has a very long tongue which can reach 280 mm in length (Miller, 1997b). Unfortunately, too little is known about the biology of the species in these genera to assess whether they coevolved with long-tubed flowers.

Long tongues were also documented in the genus *Sphinx*. Average tongue length of *S. merops* and *S. istar* was 69.8 mm and 83.7 mm, respectively. However, proboscis length varied considerably in this genus, as the average tongue length of *Sphinx dolii* was only 9.0 mm. *Sphinx merops* and *S. istar* together form a well-supported clade (see Chapter 1) which is reciprocally monophyletic to the remaining *Sphinx* species. Correlation of tongue length to phylogeny reveals a geographic trend from long-tongued *Sphinx* species at low latitudes to shorter-tongued species which are distributed at higher latitudes. A similar latitudinal trend was documented across the Sphingidae (Miller, 1997b).
Reduction of tongue length also occurred within *Ceratomia*. Although the present analysis only included two species of *Ceratomia*, the two species sampled represent different feeding conditions within the genus. *Ceratomia catalpae* (7.6 mm) has lost its ability to feed on nectar (Fleming, 1968; Tuttle, in press), while *C. undulosa* (13.0 mm) still maintains the ability to feed (Fernald, 1884; Tuttle, in press). Observations on the natural history of these species are further supported by the fact that the proboscis extensor muscle is absent in *C. catalpae*, but present in *C. undulosa* (Fleming, 1968).

According to Schmitt (1938), fully functional mouthparts must have at least two pairs of proboscis extensor muscles.

Fleming (1968) also discovered that the dilator muscles of the sucking pump are weaker and divided into two parts in some individuals of *C. catalpae*, while these muscles are moderately developed in *C. undulosa* (but less so than very long-tongued sphingids). When describing the muscles of *C. catalpae*, Fleming (1968:22) stated, “the tendency to lose functional feeding apparatus is more advanced than in *C. undulosa* … Possibly [*C. catalpae*] is presently in a state of losing these muscles, since some individuals have fewer and/or smaller muscles than others.” Although not as prominent in *C. catalpae*, reduction of particular cranial muscles of *C. undulosa* compared to other sphingine species suggests that *C. undulosa* may also be in the process of losing its proboscis. Cranial muscle reduction may also be taking place in other taxa with tongues that are short but still functional (e.g., *Sphinx dollii*).

A secondary reduction of the proboscis also occurred within Acherontiini. *Acherontia* has a much shorter proboscis than any other taxon sampled within this tribe (Table 10). Like other species of *Acherontia*, *A. styx* feeds on honey from beehives
(Künckel d'Herculais, 1916; Pittaway, 1993), and an adult was observed to regurgitate honey when captured (Kitching, 2003). Based on a nearly perfect overlapping distribution, it is hypothesized that *A. styx* is a specialized cleptoparasite of *Apis cerana* (Kitching, 2003). Regardless of its host species, the tip of the proboscis of all *Acherontia* species is sharply pointed and modified to break capped honey cells in the hive (Kitching, 2003), but *Acherontia* still maintains its ability to feed on flowers (Tutt, 1904; Pittaway, 1993). The reduction in proboscis length and its unique morphological modifications were undoubtedly due to its close ecological association with *Apis*.

In Macroglossinae, tongue length varied from 4.3 mm to 85.3 mm (X-bar = 32.18). As the name suggests, all macroglossines were presumed to have long functional tongues (Lemaire and Minet, 1999), but a recent study on *Arctonotus lucidus* suggests otherwise (Rubinoff, 2001). The sister genus to the monotypic *Arctonotus* is *Proserpinus*, and the close affinity of these two genera is supported by molecules (Ch. 1, Fig. 9), morphology (Rothschild and Jordan, 1903), and larval hostplants on the Onagraceae (Hodges, 1971). *Proserpinus* includes six species (Pittaway, 1993), all of which are active as adults during the summer. *Arctonotus*, on the other hand, has a distribution that is restricted to localized habitats in Washington, Oregon and California, and is active mainly during cold months of the year (Hodges, 1971; Rubinoff, 2001) when flowers may not be readily available. Although there are certainly many alternative plausible hypotheses, I postulate that the fewer number of available flowers during adult activity times has led to a reduction in tongue length in this genus.
2.4.2. Nectar feeding and correlations with other life-history traits

Adult diet can influence various life-history traits, such as egg-production and longevity in Lepidoptera (e.g., Hill, 1989; Hainsworth et al., 1991; Karlsson, 1994; Fischer and Fielder, 2001). Lepidoptera that obtain resources during the adult stage for egg production and upkeep have been termed income breeders, while species with rudimentary non-feeding proboscises have been termed capital breeders because they must obtain all nutrients from larval hostplants (e.g., Sibly and Calow, 1984; Boggs, 1992; Tammaru and Haukioja, 1996; Bonnet et al., 1998), see also (Janzen, 1984; Beck et al., 2006c).

Janzen (1984) compared life history strategies of non-feeding saturniids and with nectar-feeding hawkmoths. He concluded that saturniids generally lay eggs in large batches, are typically polyphagous, and tend to feed on conspicuous plants with chemical toxins. Similarly, smerinthines generally have a rudimentary non-feeding proboscis, and develop a greater number of mature eggs at eclosion (Miller, 1997b), which suggests at least in part, a saturniid-like capital breeding life history strategy (Kitching and Cadiou, 2000). On the other hand, hawkmoths in the Macroglossinae and Sphinginae have an income breeding life history strategy as they generally possess a strong ability to fly, typically feed on nectar, have fast development before adulthood, and are believed to be specialized feeders of particular larval hostplants with higher food quality (Janzen, 1984).

Miller (1997b) further developed this idea after documenting a trend towards long hawkmoth tongues at low latitudes. He hypothesized that sphingids in tropical regions require long tongues, as they need more energy to disperse to look for inconspicuous, non-persistent larval food plants in structurally complex habitats. On the contrary,
hawkmoth species distributed at higher latitudes do not need to fly a much, as their food plants are more conspicuous, and easy to find. This food-searching hypothesis (here called the FS-hypothesis) has never been formally tested. A comparison of larval hostplants across sphingid subfamilies reveals that many smerinthines feed on trees, while Macroglossines are typically feeders of shrubs or vines (Table 10, see also Janzen [1984], Miller [1997]).

If the FS-hypothesis is correct, species with very long tongues would be predicted to be monophagous, while there would be a trend towards polyphagy in non-feeding sphingids. A preliminary comparison between tongue length and larval hostplants reveals a much more complex pattern. Species with very long tongues are often distributed at low latitudes and are monophagous (e.g., Cocytius, Xanthopan), but there are also species which have long tongues that have a cosmopolitan distribution (e.g., Agrius cingulata). There are also many non-feeding, monophagous smerinthines that are found in tropical habitats (e.g., Callambulyx tatarinovii, Cypa decolor; Table 10). The question of local versus global scale must be addressed as well, as there may be localized exceptions to the overall pattern.

Furthermore, one would expect nectar-feeding sphingids to have larger range sizes if they are searching for nectar and larval hostplants. Although range size is not a direct measure of how much a moth can fly during its lifespan, a recent study reveals that all three sphingid subfamilies all have similar range sizes (Beck et al., 2006b), and that adult feeding has little or no significant influence on range size (Beck and Kitching, 2007). Beck (2007) determined that polyphagy has the strongest influence on range size for sphingids, and their findings contradict the FS-hypothesis.
2.5. CONCLUSION

The present study was a preliminary step towards understanding proboscis length evolution in Sphingidae. Correlation of tongue length to phylogeny suggests that the ancestral condition of the sphingid tongue was short, and that nectar-feeding evolved independently at least three times within the family. Multiple independent losses from nectar-feeding to non-nectar feeding were also revealed in different subfamilies. Nectar feeding cannot be directly inferred from tongue length, nor can a value such as 10 mm be assigned to distinguish tongue functionality, as there is an overlap in length between nectar and non-nectar feeding tongues below 10 mm.

It is critical that future studies on sphingid phylogeny increase ingroup and outgroup sampling, as it is possible that “hidden signals” of life-history traits are present within particular clades for taxa not sampled. Future studies on hawkmoth tongue length evolution should also examine the amount of variation according to sex, geographic distribution, and seasonality. These additions, supplemented with further analysis of hostplant growth and secondary chemistry, may answer the question of whether sphingids developed long tongues to search for inconspicuous, non-persistent larval hostplants, and whether particular lineages subsequently gained very long proboscises due to tight ecological associations with particular flowers.
Table 1. Number of genes and sphingid taxa in Regier et al. (2001), Mignault (2003), and the current study. Classification is based on Kitching and Cadiou (2000). “Nuclear + COI” refers to the 6-gene simultaneous analysis in which available genbank COI sequences were combined with the five nuclear gene dataset generated from the current study (see supplementary materials for details on the 6-gene analysis).

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Table 2. Sphingid species and outgroups included in this study. In total, 131 ingroup and 11 outgroup species were included. Taxa are listed alphabetically by subfamily. Numbers indicate the sequenced fragment of the gene. A solid line “—” indicates that the sequence could not be obtained for that particular gene, “Locality” refers to the locality of the specimen from where it was collected, “Voucher #” refers to the University of Maryland Molecular Collection specimen voucher number. Genbank numbers are listed in square brackets where available. \( \text{PER} = \text{period} \), \( \text{WG} = \text{wingless} \). Refer to Table S1 for a list of species with COI data.

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<td><em>Marumba querzus</em> ([Denis &amp; Schiffermuller], 1775)</td>
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Sphingulini

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Sphinginae

Acherontini

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Sphinxini

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Table 3. List of genes and primers used in this study. “F” and “R” at the end of primer names refer to the forward and reverse primer. Primer names follow Regier (2006).

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Table 4. Empirical base frequencies and GTR+Γ+I model parameters of the five genes in the ML analyses. Base frequencies were fairly equal except for CAD and wingless. Γ = α estimated shape parameter, I = proportion of invariant sites.

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Table 5. Summary of characters by gene and codon position. Outgroups were excluded for these calculations.

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Table 6. Bootstrap, Bremer support (BS), and Partitioned Bremer Support (PBS) values for the MP five gene simultaneous analysis with 142 taxa. “nt-12” refers to an analysis which only included first and second codon positions. *, bootstrap values < 50%.

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Table 7. Bootstrap, Bremer support (BS) and Partitioned Bremer Support (PBS) values for the MP 99-taxon analysis without missing data. “nt-12” refers to an analysis which only included first and second codon positions.

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**TOTAL** | **2985** | **1439.1** | **526.3** | **206.6** | **598.9** | **214.5**
Table 8. Calculation of the relative contribution index (RCI) for the 99-taxon dataset.

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Table 9. Node recovery and bootstrap support values with 5-gene, all combinations of 4-gene sub datasets. ↓ = BP value at least 20% less than results from exclusion of any other single gene for this node; ↑ = BP value at least 20% greater than results from exclusion of any other single gene for this node. Clades of interest are in bold. * = bootstrap values < 50%, but in some cases bootstrap values < 50% are shown for comparison.

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*Three taxa (*Proserpinus clarkiae*, *Pachysphinx modesta*, *Paonias excaecata*) were removed from the four gene bootstrap analysis without *EF-1a* because these taxa included data for *EF-1a* only. Inclusion would result in missing data for all remaining gene partitions for the three taxa. Nodes 90, 91, and 112 were therefore collapsed.*
Table 10. List of sphingid species and their average proboscis and forewing lengths. “Nectar feeding” indicates whether nectar feeding has been reported for the particular species. An asterisk “*” indicates a behavior predicted from tongue length.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Proboscis Length</th>
<th>Forewing Length</th>
<th>Nectar Feeding</th>
<th>Reference</th>
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<td></td>
<td>( \bar{X} )</td>
<td>SD (N)</td>
<td>( \bar{X} )</td>
<td>SD (N)</td>
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<tr>
<td>Aellopos ceculus</td>
<td>18.0 ± 0.8</td>
<td>(4)</td>
<td>23.8 ± 3.1</td>
<td>(4)</td>
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<tr>
<td>Dilophonotini</td>
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<td>Aellopos tantalus</td>
<td>18.3 ± 1.0</td>
<td>(4)</td>
<td>27.0 ± 2.2</td>
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<td>Aeuron chloroptera</td>
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<td>37.3 ± 2.3</td>
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<td>Cautethia spuria</td>
<td>13.3 ± 1.8</td>
<td>(2)</td>
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<td>(2)</td>
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<td>Nyceryx magna</td>
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<td>63.5 ± 5.7 (4)</td>
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**Outgroups**

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<td><em>Lemonia dumi</em></td>
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<td><em>Macrothylacia rubi</em></td>
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<td><em>Oberthueria formosibia</em></td>
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1 Hodges (1971) originally stated that *Arctonotus lucidus* visits flowers during the day. However, Rubinoff (2001) experimentally tested whether adults can feed, and concluded that the mouthparts are too vestigial to feed on nectar from flowers.

2 Known to feed honey from beehives (Künckel d'Herculais, 1916), but also known to visit flowers (Pittaway, 1993).
Table 11. Preliminary list of larval hostplant families for Sphingidae included in the current study. Plant classification follows (APG II, 2003). Unfortunately, notable publications on sphingid larval hostplant records (e.g., Robinson et al., 2007) could not be included at the time when this table was constructed. Additional larval records will be subsequently added. For specific host plant species, refer to publications listed and the papers cited therein. “--” indicates that no hostplant record was found.

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<td>Chaerocina dohertyi</td>
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<td>(Pittaway and Kitching, 2006)</td>
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<td>Enyo ocypete</td>
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<td>Hippotion celerio</td>
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### Macroglossini: Macroglossina

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**SMERINTHINAE**

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**Sphingulini**

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Figs. 1-3. Relationships of Sphingidae based on morphology. 1. Adult morphology (Rothchild and Jordan, 1903). 2. Larval and pupal morphology (Nakamura, 1976). 3. Relationships inferred from Kitching and Cadiou (2000). Due to limited space, all terminals have been changed from species to Kitching and Cadiou’s (2000) tribes and subtribes. A double-line leading to a terminal indicates paraphyly, a dotted line indicates uncertain relationships, and a name in quotations indicates higher groupings recognized by the particular study.
Figs. 4-6. Relationships of Sphingidae based on molecules (EF-1α + DDC). 4. MP cladogram of Regier et al. (2001). 5. MP cladogram of Mignault (2003). 6. ML tree of Mignault (2003). Bootstrap values were not calculated in Mignault’s ML analysis due to computational constraints. Trees were based on all nucleotide positions, numbers above branches indicate bootstrap values > 50%, double-lines leading to terminals indicate paraphyly. Due to limited space, terminals have been changed from species to Kitching and Cadiou’s (2000) tribes and subtribes. *Mignault’s analyses included a species in the Acherontiini, Coelonia fulvinotata (Butler), which had part of its DDC sequence accidentally switched with a species in the Macroglossina, Macroglossum stellatarum (L.).
Fig. 7. Parsimony strict consensus of 12 MPTs (L=43023, CI=0.15, RI=0.53) based on the five gene simultaneous analysis. Bremer support indicated above branches, bootstrap (> 50%) indicated below. Nodes are labeled to the right of each internal branch. Colored dots indicate monophyletic subfamilies, colored clades indicate monophyletic tribes and subtribes recognized by Kitching and Cadiou (2000).
Fig. 8. The most parsimonius tree (L=36301, CI=0.17, RI=0.52) from the 99-taxon data matrix which excludes taxa with 50% missing data for any gene. Node numbers are indicated to the right of each node, Bremer Support above branches, Bootstrap support (> 50%) below.
Fig. 9. ML tree based on the five gene simultaneous analysis (-lnL = 194121.6532). Phylogram showing branch lengths on the right. Bootstrap (> 50%) indicated above each branch. Nodes are labeled to the right of each internal branch. Colored dots indicate monophyletic subfamilies, colored clades indicate monophyletic tribes and subtribes recognized by Kitching and Cadiou (2000).
Fig. 10. Histogram showing the number of sphingid species relative to the average proboscis length for taxa included in the five gene analysis. The histogram on the upper right shows the pattern at a finer scale up to 20 mm. Red bars indicate non-feeding species, green bars indicate nectar-feeding species, grey bars represent species in which feeding remains unknown. The blue line denotes Miller’s (1997) categorical division of nectar feeding and non-feeding sphingid taxa based solely on length.
Fig. 11. Average proboscis length relative to average forewing length for each species.
Fig. 12. Proboscis length mapped onto the ML five gene tree. Actual PL is the actual proboscis length averaged for each species; Relative PL is average proboscis length standardized for body size (proboscis length / forewing length).
SUPPLEMENTARY MATERIAL

SINGLE GENE ANALYSES

AND

SIX GENE SIMULTANEOUS ANALYSIS WITH COI
SUPPLEMENT 1

SINGLE GENE ANALYSES OF NUCLEAR PROTEIN CODING GENES

This section includes trees generated from single gene analyses for each of the five protein-coding nuclear genes. MP figures shown first (Figs. S1-S5), followed by ML figures (Figs. S6-S10).
Fig. S1. MP strict consensus of 3 MPTs based on the CAD gene (L=20202, CI=0.14, RI=0.53). Bootstrap values (> 50%) are indicated below branches.
Fig. S2. MP strict consensus of 128 MPTs based on the DDC gene (L=8569, CI=0.14, RI=0.59). Bootstrap values (> 50%) are indicated below branches.
Fig. S3. MP strict consensus of 6384 MPTs based on the EF-1α gene (L=3755, CI=0.17, RI=0.51). Bootstrap values (> 50%) are indicated below branches.
Fig. S4. MP strict consensus of 116 MPTs based on the period gene (L=9131, CI=0.15, RI=0.47). Bootstrap values (> 50%) are indicated below branches.
**Fig. S5.** MP strict consensus of 20000 MPTs based on the *wingless* gene (L=2346, CI=0.15, RI=0.48). Due to time constraints, the exact number of MPTs could not be calculated. Bootstrap values are therefore not shown.
Fig. S6. ML tree generated from the CAD gene (-lnL = 86356.14928). Bootstrap values (> 50%) are indicated below branches. The bar under “Sphingidae” indicates the branch length leading to the Sphingidae from the nearest outgroup (Bombyx mori L.).
Fig. S7. ML tree generated from the DDC gene ($-\ln L = 37127.65035$). Bootstrap values ($> 50\%$) are indicated below branches. The bar under “Sphingidae” indicates the branch length leading to the Sphingidae from the nearest outgroup (Bombyx mori L.).
Fig. S8. ML tree generated from the EF-1α gene (-lnL = 18452.54643). Bootstrap values (> 50%) are indicated below branches. The bar under “Sphingidae” indicates the branch length leading to the Sphingidae from the nearest outgroup (Bombyx mori L.).
Fig. S9. ML tree generated from the *period* gene (-lnL = 38040.1666). Bootstrap values (> 50%) are indicated below branches. The bar under “Sphingidae” indicates the branch length leading to the Sphingidae from the nearest outgroup (*Bombyx mori* L.).
Fig. S10. ML tree generated from the wingless gene (-lnL = 10577.89695). Bootstrap values (> 50%) are indicated below branches. The bar under “Sphingidae” indicates the branch length leading to the Sphingidae from the nearest outgroup (Bombyx mori L.).
Fig. S11. MP strict consensus generated from the five gene dataset with third nucleotide postions removed (L = 6942, CI = 0.27, RI = 0.58). Bootstrap values (> 50%) are indicated below branches.
Fig. S12. MP strict consensus of 125 MPCs with nt3 of EF-1α excluded (L = 39586, CI = 0.14, RI = 0.53).
Ideally, it is best to include as many taxa and as many data partitions as possible for any phylogenetic study. However, research funding and time are limiting factors. It is therefore essential to determine the best approach to tackle the particular phylogenetic question. Whether to choose more taxa or more genes has been an ongoing debate in phylogenetics (e.g., Mitchell et al., 2000; Pollock et al., 2002; Rokas and Carroll, 2005), but it has become evident that addition of both taxa and genes are imperative (Rokas, 2006). With the onset of the National Science Foundation’s Assembling the Tree of Life (AToL) program, the goal for many large-scale phylogenomic projects has been to construct a robust tree with as many taxa as possible without losing tree structure or getting strong support for incorrect relationships (Rokas, 2006).

One of the most commonly included genes in phylogenetic studies of arthropods is the COI gene, which has been shown to be useful for resolving recent divergences (e.g., Caterino et al., 2000; Sperling, 2003; Braby et al., 2006). A particular 648-bp region of the COI gene, known as the barcoding region (Hebert et al., 2003; Savolainen et al., 2005), has recently received attention as a tool to explore species boundaries between closely related taxa (e.g., Hebert et al., 2003; 2004a; 2004b; Kress et al., 2005). Numerous taxonomic projects have begun to compile COI barcodes for as many species as possible, which has resulted in the Consortium for the Barcoding of Life (CBOL), and online tools in aiding the acquisition, storage, analysis and publication of barcodes (Ratnasingham and Hebert, 2007). Despite the recent utility and availability of COI
barcodes, it remains unclear how much phylogenetic contribution the COI barcoding region can provide when combined with a much larger dataset.

This section was added as supplement to this thesis to explore the effect of combining the COI barcoding region for available sphingid taxa to a larger dataset which was sampled more thoroughly for five nuclear genes. A COI barcoding dataset was first constructed by downloading available sphingid COI sequences from Genbank in FASTA format. Each sequence was opened in BioEdit (Hall, 2001), and sequences were aligned with the COI sequence of *Bombyx mori* in ClustalW (Thompson *et al.*, 1994) and trimmed at both the 5’ and 3’ ends into a block which was 658 bp long. The COI matrix showed a strong A-T bias (31.8% A, 15.5% C, 14.5% G, 38.2% T). In total, 63 ingroup taxa included at least part of the COI sequence, 25 of which was represented solely by the COI sequence. A summary of the number of total characters for each taxon in the six gene matrix is listed in Table S1. Analyses were calculated for ML only, but will be subsequently explored under MP as well. The best model for COI was determined in Modeltest (Posada and Crandall, 1998) to be the GTR+$\Gamma$+$I$ model. The six gene simultaneous analysis was conducted in Garli ver. 0.951 (Zwickl, 2006), and the number of generations to termination was increased from 10,000 to 100,000.

The six gene ML tree was fundamentally very similar to the five gene ML tree. In particular cases, taxa which were represented solely by the COI gene were recovered close to other species in its genus (Fig. S13). For instance, *Erinnyis crameri* (Schaus) included only 583 bp of the COI gene, but was nested within a clade which included three other species of *Erinnyis* (the clade also included *Phryxus*). *Erinnyis* and *Phryxus* were previously predicted to be sister genera – the only morphological difference
between the two genera is the scalloping of the forewing margin (Rothschild and Jordan, 1903). The COI barcoding region for *Phryxus* was available for only 291 bp, and this result suggests that the COI may be accurately placing these taxa. Three additional species in the genus *Hyles* were also included in the analysis, and the relationship between species in the genus were (*H. lineata* (((*H. hippophaes* + *H. euphorbiae*) + (*H. gallii* + *H. nicaea*)))). This result is congruent with a previous study on *Hyles* which used three genes (Hundsdoerfer *et al.*, 2005a).

Without further in-depth analyses, it is difficult to assess whether these taxa are being correctly placed on the tree. It was also discovered that it is critical to have all taxa in the analysis sampled for COI, as placement of taxa can be influenced by whether the barcoding region was sampled for those particular taxa (e.g., taxa which are only represented by COI may be placed at the base of the tree because other closely related members do not include COI). Furthermore, results indicate that branch support values which were high in the five gene analysis can be depressed when considerable missing data are added (Fig. 12). As more sphingid barcoding sequences become available, I hope to incorporate additional data in order to explore the utility of the COI barcoding region in simultaneous analyses and test the effect of missing data on branch support values.
Fig. S13. ML tree (-lnL = -203427.4046) of the six gene simultaneous analysis with COI(GTR+Γ+I). Branch lengths shown on right side of figure. Bootstrap support (> 50%) below each branch. * = taxa which were sampled for COI only; ** = taxa which were sampled for both COI and at least one of the five nuclear genes.
Table S1. Sphingid species and outgroups which were included in the six gene analysis with COI. In total, 156 ingroup and 11 outgroup species were included (167 species total). Taxa are listed alphabetically by subfamily. “*” refers to taxa which are represented by the COI sequence only. “All Genes” refers to a combination of the five nuclear genes plus COI.

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Dilophonotina

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Hemarina

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