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# Resolving the Systematics of Acronictinae (Lepidoptera, Noctuidae), the Evolution of Larval Defenses, and Tracking the Gain/Loss of Complex Courtship Structures in Noctuidae

Brigette Zacharczenko

University of Connecticut, [brigette.zacharczenko@gmail.com](mailto:brigette.zacharczenko@gmail.com)

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Resolving the Systematics of Acronictinae (Lepidoptera, Noctuidae), the Evolution of Larval  
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Brigette Valencia Zacharczenko, PhD

University of Connecticut, 2017

Moths and caterpillars of the noctuid genus *Acronicta* Oschenheimer, 1816, widely known as dagger moths, have captured the imagination of taxonomists for centuries. Morphologically enigmatic adults and highly variable larvae prompted A. R. Grote to proclaim, "There would seem to be no genus which offers a more interesting field to the biologist for exploration," (1895). Without known synapomorphies for *Acronicta*, or the subfamily Acronictinae, their circumscriptions have changed over time. This dissertation delves into the taxonomic history of these taxa, setting the stage for a worldwide phylogenetic analysis of Acronictinae. The diversity of larval forms is considered in a tri-trophic framework, quantifying bottom up (host plant) and top down (predator) effects through measures of diet breadth, morphology, and behavior, all in a phylogenetic context. Adult courtship structures, present in some acronictine species, are scored across the family Noctuidae, to aid in the study of the evolution of complex morphological traits.

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Brigette Valencia Zacharczenko

B.S., McGill University, 2010

A Dissertation

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2017

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2017



APPROVAL PAGE

Doctor of Philosophy Dissertation

Resolving the Systematics of Acronictinae (Lepidoptera, Noctuidae), the Evolution of Larval  
Defenses, and Tracking the Gain/Loss of Complex Courtship Structures in Noctuidae

Presented by  
Brigette Valencia Zacharczenko, B.S.

Major Advisor

---

David L. Wagner

Associate Advisor

---

Elizabeth Jockusch

Associate Advisor

---

Chris Simon

Associate Advisor

---

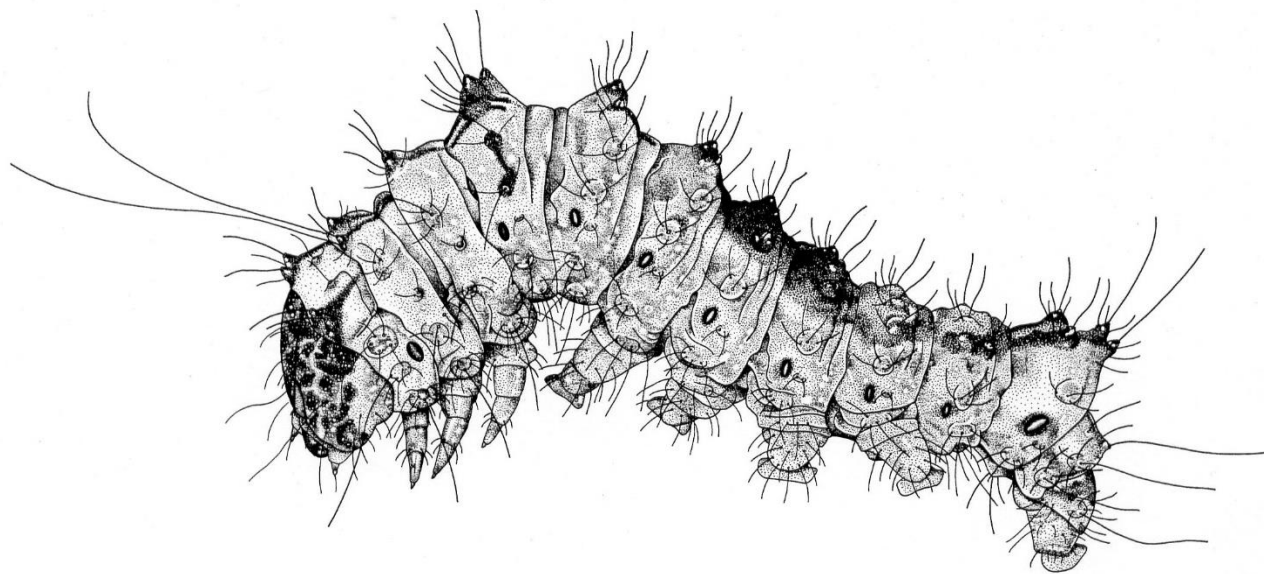
Michael Singer

University of Connecticut  
2017

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I blame most of this on my father, Nicholas, who always says “use your head”. He told me at an early age that catching bugs could be a career, and I believed him. Also culpable is my mother, Sherelyn, who only weakly protested to me bringing insects and other creatures into the house. The remainder of my family has also supported this crazed adventure of mine wholeheartedly. I could not have survived graduate school without my wonderful friends, my patient committee members, and my soon-to-be husband Dillon. And of course, my advisor, Dave Wagner, who has always believed in me and supported me.

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*Acronicta falcula* (Grote, 1877)

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# Chapter 1: Taxonomic History of Acronictinae and *Acronicta*

## Introduction

Moths and caterpillars of the noctuid genus *Acronicta* Oschenheimer, 1816, widely known as dagger moths, have captured the imagination of taxonomists for centuries. The genus is recognized from Africa, Asia, Australia, Europe, and North America with greatest species diversity in China and the eastern United States. Morphologically enigmatic adults and highly variable larvae prompted A. R. Grote to proclaim "There would seem to be no genus which offers a more interesting field to the biologist for exploration," (1895). Along with related genera in the subfamily Acronictinae Harris, 1841, *Acronicta* underwent a whirlwind of taxonomic revision in its infancy, rife with synonyms and rivalries between lepidopterists, which continue to this day. Different definitions of Acronictinae have yielded anywhere from one to >20 genera, and afforded *Acronicta* <10 to over 200 species. Currently the North American Acronictinae are undergoing a thorough revision of their alpha taxonomy, and acronictines of the world are the subject of their first phylogenetic studies. With many taxonomists and systematists currently collaborating on this group, we are sure to learn a great deal about these moths and their evolutionary history. This dissertation, incorporating adult morphology, larval morphology, larval behavior, and both mitochondrial and nuclear DNA, brings together phylogenetic, morphological, and behavioral information about acronictines to facilitate study of their evolutionary history. This first chapter is an overview of the taxonomic history of *Acronicta* and Acronictinae, setting the stage for the rest of my work.

## Methods

An extensive literature search was performed for this chapter. Seventy publications were consulted and referenced in a relational database in Microsoft Access. For each publication the following attributes were recorded: number of genera the authors listed in Acronictinae, the number of subgenera listed in *Acronicta*, and the number of subgeneric names the authors treated as full genera. The names of all genera and their current taxonomic standings were also listed. The relational database format allows for each taxon to be associated with multiple literature sources. By including the year and geographical region of each publication, the concept of the subfamily and genus over time and space can be examined.

References were primarily sourced from library holdings (at the University of Connecticut, and borrowed from other institutions), and the Biodiversity Heritage Library website (<http://www.biodiversitylibrary.org/>). Foreign language publications were translated via Google Translate (<https://translate.google.com/>) and with the help of colleagues.

### Section 1: Acronictinae

Often incorrectly attributed to Heinemann, 1859, the subfamily Acronictinae was first proposed by Harris in 1841 as Acronyctadae (Harris 1841; Schmidt and Lafontaine 2013), though other groupings of various ranks had been proposed earlier (Hübner 1820). Harris's Acronyctadae was based on the genus *Acronycta* Treitschke, 1825, without any mention of other group members. Since then, membership in the subfamily has been dynamic. Because there are no universally accepted synapomorphies for the subfamily (Wagner 2007 b, Rota et al. 2016), there are no clear criteria by which to include or exclude taxa. Consequently, inclusion has been granted to unrelated taxa and denied to true members with differing morphologies.

Acronictinae has incorporated species now believed to be members of 13 other subfamilies (some in different families), and upwards of 100 genera. See Table 1 for review of genera placed, at one time or another, within Acronictinae, vs. their current placement. There has been considerable overlap with the subfamilies Amphipyridae Guenée, 1837, Bryophilinae Guenée, 1852, Cuculliinae Herrich-Schäffer, 1850, Dilobinae Aurivillius, 1889, Dyopsinae Guenée, 1852, Hadeninae Guenée, 1837, Pantheinae Smith, 1898, and Raphiinae Beck, 1996. At times Acronictinae have been divided into tribes; the typical circumscription of the tribe Acronictini may more accurately reflect our current understanding of Acronictinae.

The generic composition of Acronictinae has experienced temporal and geographic patterns of change, influenced by the study of larval vs. adult characters of regional faunas. Figure 1 illustrates the composition of Acronictinae over time, giving the number of genera included in regional publications. Eleven genera have been confirmed as belonging to the subfamily in a recent molecular phylogenetic analysis (Rota et al., 2016), however an additional 18 genera remain to be evaluated with molecular data. Species estimates are over 200 for the subfamily, and depend largely on the number of genera included.

Both the genus *Acronicta* and the subfamily Acronictinae have gone through multiple name changes due to priority, synonymy, suppression, unjustified emendations, misspellings, and rivalries. Common spellings include the following (in order of their appearance in the literature): *Apatele* Hübner, 1806; *Acronicta* Ochsenheimer, 1816; *Acronycta* Treitschke, 1825; and *Apatela* Stephens, 1829. These names have served as the basis for subfamily names, i.e. Apatelae,

Apatelidae, Acronictinae, Acronyctinae, etc. The valid accepted name for the genus is *Acronicta*, and the subfamily name is Acronictinae.

### **19<sup>th</sup> century: getting started**

Jacob Hübner was a German entomologist working in the early to mid-1800s who named a considerable number of acronictine taxa. His first genus name for an acronictine group in 1806, *Apatele*, was later suppressed – however that name was used as the basis for a subfamilial name and taxa of other ranks by himself and other taxonomists. In 1820 he published on the Stirps, or “stock” Apatelae, in which he listed three “families”: Mirae, Perconformes, and Consimiles. Each family had one or more coiti (singular, coitus), which are equivalent to our genera. These were all coined by Hübner for this publication, unless otherwise noted: Mirae: *Exaereta*; Perconformes: *Hyboma*, *Triaena* Hübner, 1818, *Jocheaera*, and *Acronicta*; Consimiles: *Colocasia* Ochsenheimer, 1816, *Pharetra*, and *Arctomyscis*. Interestingly in this publication he used Apatelae for the stock name, yet used *Acronicta* instead of *Apatele* as a genus name. Of the species listed in his coiti, Hübner included only two which are no longer considered acronictines: a notodontid (*Exaereta*) and a pantheine (*Colocasia*); the other coitus names have become synonyms of *Acronicta*. This early attempt at organizing lepidopteran taxa was insightful, yet confusion as to the ranks of his published names caused a fracas among taxonomists. Stirps had no defined rank, perhaps at the subfamily or tribal level, but would sometimes be used as generic-level names, credited to Hübner. Some lepidopterists would consider themselves “Hübnerian or anti-Hübnerian,” depending on whether they accepted his classification schemes (Smith 1884). Hübner’s Apatelae appeared to be a good start for the grouping of acronictines,



but without the ICZN (founded in 1895), there was no code for assessing the validity of Hübner's names.

The next worker to attempt a classification of European noctuids was Guenée (1841). In his index *Noctuarum Europaeorum* he had the following hierarchy for acronictines: Family Nocturni, Division Noctuae, Tribe Bombycoidi, and then a list of genera: *Semaphora*, *Apatela*, *Acronycta*, *Colocasia*, and *Diphthera* Hübner, 1806 (Guenée 1841). Bombycoidi, or variations of that name, appeared in several lists by other authors but did not become the subfamily name, due to its given tribal rank. The credit for the accepted subfamily name goes to Harris (1841), who crafted the name Acronyctadae for the genus *Acronycta*, and colloquially referred to the species as Acronyctians. Ignoring Harris or perhaps because he was unaware of the work, Guenée used the subfamily name Bombycoidae to refer to acronictines in a later list (Boisduval and Guenée 1852).

As taxonomists worked their way to into the faunas of Russia and Asia, more genera were named; some of these have kept their generic status, while others have since been synonymized. One European worker, Lederer, offered his contribution to acronictine systematics with the new genus *Arsilonche* in his list of taxa from Europe, Russia, and Asia (Lederer 1857). While he did not subdivide what he called Noctuinen into smaller taxa such as subfamilies, he listed *Diloba* Boisduval, 1837, *Simyra*, *Arsilonche*, *Eogena* Guenée, 1852, *Clidia*, *Demas* Stephens, 1829, and *Acronycta* as the first several genera in his list of Noctuinen (Lederer 1857). *Arsilonche* was later used for both Eurasian and North American taxa, as either a synonym of *Simyra* or its own genus. A Eurasian acronictine genus, *Craniophora*, was described soon after by Snellen (1867).

<sup>1</sup>This genus often had its species pulled into *Acronicta*, including its type *C. ligustri*, and so was relegated into synonymy in many works.

Another early acronictine worker, and one of the first to attempt a worldwide classification of the group, was Augustus Radcliffe Grote. He was a prolific 19<sup>th</sup> century German lepidopterist who worked tirelessly in North America. Grote had a particular fondness for acronictines, and even had an *Acronicta* species named after him (e.g., *Acronicta radcliffei* Harvey, 1875). In addition to multiple species and generic descriptions of his own (e.g., Grote 1864, 1874, 1895), he frequently discussed the taxonomic assemblage of what he called Apatelidae (after the genus *Apatela*, a synonym of *Acronicta*, following a Hübnerian classification scheme). With knowledge of both the European and North American noctuid faunas, Grote was in a unique position to comment on the evolution and classification of acronictine taxa. But in addition to core acronictines, his definition of Apatelidae included seven genera now known to belong to Pantheinae, Raphiinae, Diphtherinae Fibiger and Lafontaine, 2005, and Amphipyrynae. Despite this overreach, he amalgamated genera from both continents into mostly cohesive groupings – recognizing the relatedness between *Apatela*, *Arsilonche* Lederer, 1857, *Simyra* Ochsenheimer, 1816, *Harrisimemna* Grote, 1873, and *Oxicesta* Hübner, 1819 (Grote 1896). He also created several subgeneric names, which would later be elevated to full generic status (by some workers). In a later publication he remarked that *Panthea* and *Apatela* are united by characters which are likely convergent (Grote 1899), a position often ignored by later taxonomists who continued to group acronictines and pantheines.

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<sup>1</sup> Its name means “skull-bearer” in Dutch, due to the “white drawing on the back, according to the shape of a skull” (translated into English) (Snellen 1867).

Ignoring this early attempt at reconciling the works of European and North American lepidopterists, most subsequent workers focused on the genera of a particular region. As noted above, the subfamily name Acronictinae was established in North America, where it has typically featured a small assemblage of seemingly allied genera (with a few notable exceptions). Despite not using subfamilies, Smith (1983) grouped an assemblage of pantheines, raphiines, and acronictines as basal genera in Noctuidae: *Panthea* Hübner, 1829, *Demas*, *Raphia* Hübner, 1821, *Charadra* Walker, 1865, *Feralia* Grote, 1874, *Momaphana* Grote, 1874, *Moma* Hübner, 1820, *Arsilonche*, *Merolonche* Grote, 1882, *Acronycta*, *Harrisimemna*, *Cerma* Hübner, 1818, and *Polygrammate* Hübner, 1809 (Smith 1893). The inclusion of *Cerma* foreshadowed its recent rehoming to the subfamily – *Cerma* would not be formally recognized as an acronictine genus until 2007 (Wagner 2007a). Smith's (1893) concept of *Cerma* included one current-day species (*cora*), and one moth now in *Cryphia* Hübner, 1818. The remaining *Cerma* species, *C. cerintha*, was placed amongst acontiines in the genus *Chamyris* Guenée, 1852.

The first (and only) monographic treatment of North American Acronictinae was done by Smith and Dyar (1898), advancing the lifelong studies of C.V. Riley on the nominate genus. Following Grote's framework, they went a step further and defined two tribes based on wing venation, genitalic structures, and larval characters: Pantheini and Acronyctini (while admitting that Pantheini was likely deserving of subfamilial ranking). They removed some taxa, such as *Raphia* and *Moma*, due to larval characters. Their Pantheini featured three North American genera: *Panthea*, *Demas*, and *Charadra*. Acronyctini featured four genera: *Acronycta*, *Arsilonche*, *Merolonche*, and *Harrisimemna*. *Polygrammate* was added to Acronyctini post-hoc, based

primarily upon its shared pupation habit with *Harrisimemna* – burrowing into wood and removing the frass in neatly rolled balls (Smith and Dyar 1898). Their remarkable foresight has been borne out with further examination of morphological and molecular data (Rota et al. 2016); pre-pupal ball-rolling was the basis for adding both *Comachara* and *Cerma* to the subfamily in recent years (Wagner et al. 2006; Wagner 2007b). *Cerma*, previously placed with *Polygrammate* in Smith’s catalogue, was not included by Smith and Dyar because its larvae were unknown – thus their unique cocooning behavior had not yet been observed. The tribe Acronyctini of Smith and Dyar represents the core of what we believe to be Acronictinae today.

### **Early 20<sup>th</sup> century: catalogues**

The early 20<sup>th</sup> century seemed to represent a lull in systematic work of Acronictinae – instead the subfamily was mentioned primarily within broad checklists, catalogs, and books. One of the earliest was a tome of North American Lepidoptera by Dyar (1902). Despite his expertise, the acronictines were listed without designation, and intermixed with unrelated genera, within the subfamily Noctuinae. *Acronicta* was listed as a synonym of *Apatela*, a reversal from his previous work with Smith (1898).

Two of these early lists had a profound impact on the circumscription of Acronictinae in subsequent publications: a palaearctic catalog put together by Seitz (1909)<sup>2</sup>, and a world catalog

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<sup>2</sup> There is debate over the true publication date of this work (Volume 3), and of the names credited to Warren. Most cite the reference as appearing in 1909, which is also used for Warren’s names. However citations vary depending on the English or German version, and the page number. New names from page 11 are said to be published in 1907, and those on pages 16 and 18 in 1909. Copies of several pages were said to be received by the BMNH in 1907, without a printed date on the materials, so that stamped date was accepted for the names, and later listed in Hampson’s checklist (Hampson 1909). Scanned copies of both the German and English versions,

by Hampson (1908, 1909). The section of Seitz's catalog on Noctuidae was written by Warren, who included 18 genera in the Acronictinae. He circumscribed the subfamily based on wing coloration and patterning, "having larvae more or less hairy," and varied wing venation. Acronictinae were split into five subgroups by forewing characters. Warren's (1909) Group A included *Panthea* and *Moma*, now in Pantheinae and Dyopsinae, respectively. Group B included *Canna* Walker, 1865 (= *Nacna* Fletcher, 1865), *Daseochaeta* Warren, 1907, *Diphtherocome* Warren, 1907, and *Diphthera* Hübner, 1806 (= *Moma*), now in Amphipyridae, Cuculliinae, Acronictinae (questionable), and Dyopsinae, respectively. Group C included *Colocasia* Ochsenheimer, 1816, *Oxicesta*, *Eogena*, and *Euromoia* Staudinger, 1892, now in Pantheinae, Acronictinae, and Hadeninae, respectively. Group D included *Simyra*, *Arsilonche*, and *Leiometopon* Staudinger, 1888, now in Acronictinae and Hadeninae. Group E included *Acronicta*, *Chamaepora* Warren, 1909, *Anacronicta* Warren, 1909, *Panthauma* Staudinger, 1892, and *Xanthomantis* Warren, 1909, now in Acronictinae and Pantheinae. Many of these generic names were new, created by Warren for this publication. While subgroup A (and potentially B) did not include any modern members of Acronictinae, subgroups C, D, and E all contained at least one acronictine genus. Genera of Pantheinae were likewise scattered amongst the groups. It is clear the characters used by Warren to make assignments were convergent, yet his publication remains a laudable early attempt to reconcile the genera from the expansive palaearctic region.

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available online, show 1914 as the publication date for the entire work, while the forward by Seitz, in which he references Hampson's classification scheme, is signed 1913. However for Hampson to have included some of Warren's genera in his 1909 checklist (only those listed with the 1907 date), parts of Seitz's work must have been published prior to 1909. Warren's names credited to 1909 were not listed by Hampson.

Hampson's (1908) worldwide catalog treated Acronyctinae as a large "catch-all" taxon, encompassing three volumes of his checklist (7, 8, and 9). Volume 7 contained his key to genera, in which he listed his new North American genus *Agriopodes*. *Agriopodes* encompassed North American species previously assigned to *Moma*, returning *Moma* to its status as a purely European genus. Volume 8 contained the true acronictines, and nearly one hundred other non-acronictine genera. *Agriopodes* was listed with *Leuconycta*, *Daseochaeta*, and *Canna*, close to *Acronycta* and allies (*Craniophora*, *Eulonche* Grote, 1873, and *Merolonche*) (Hampson 1909). Several (but not all) presently known acronictine genera are in his work. The remainder of the genera in Hampson's Acronyctinae include taxa now assigned to Amphipyrinae, Condicinae Poole, 1995, Cuculliinae, Hadeninae, Heliethinae Boisduval, 1828, and Oncocnemidinae Forbes and Franclemont, 1954 (Hampson 1909; Rota et al. 2016). Hampson's use of Acronictinae as a broad category, lacking any known synapomorphies, continues to this day in some faunal (regional) works.

One way around the subfamily issue was to not bother with subfamilies at all, and list *Acronicta* and related genera within Noctuidae as was done by Dyar (1902). This approach was used in North America by Holland in his seminal work, *The Moth Book* (Holland 1917). A contemporaneous book, *The Insects of Florida*, also sidestepped the recognition of noctuid subfamilies (Grossbeck 1917).

A Hampsonian approach, perhaps to an extreme, was championed in Africa, in Janse's *The Moths of South Africa* (Janse 1921). Janse in fact considered Noctuinae as a subfamily, with the tribe Trifini and subtribe Acronictae. With the warning that it "...is perhaps the least well-defined group of all the Noctuinae..." he proceeded to reject Warren's decision to split

Amphipyridae and Acronictidae, deciding the morphological characters used were “hardly convincing.” In this way Janse’s subtribe became decidedly mixed, with 72 genera in Acronictidae, which derive from multiple modern subfamilies. In contrast, Gaede’s (1934) subsequent treatment on Afrotropical noctuids listed only *Daseiochaeta*, *Thalatha*, *Craniophora*, and *Acronicta* in Acronictidae.

A few years later, McDunnough published his now-classic checklist of North American Lepidoptera (1938). His catalog reflected the findings of Smith and Dyar (1898), but elevated the tribes Acronictini and Pantheini to the subfamilies Acronictidae and Pantheinae. McDunnough’s Acronictidae included only *Acronicta*, *Merolonche*, *Simyra*, and *Harrisimemna*. Other North American acronictine genera not yet treated to a great extent by other authors—for example *Agriopodes*, *Cerma*, and *Polygrammate*—remained relegated to Amphipyridae. *Cerma cerintha*, assigned to the genus *Chamyris*, was listed in Acontiinae (McDunnough 1938). It is unclear why Smith and Dyar’s insight into *Polygrammate*’s status as an acronictine was ignored.

One year after McDunnough’s checklist was published, a new North American acronictine was described by Franclemont, but in the subfamily Sarrothripinae Hampson, 1894 (Franclemont 1939). He created the genus *Comachara* Franclemont, 1939 for one species, based on adult characters. It took 67 years for *Comachara*’s true membership in Acronictidae to be recognized, based on its larval behavior and morphology (Wagner et al. 2006).

In Eurasia another acronictine genus, *Cranionycta* Lattin, 1949, was described as a unique genus separate from *Craniophora*. *Cranionycta* was described for the new species *oda*, which Lattin

(1949) considered to have genitalia different enough from *Craniophora* and *Acronicta* to justify recognition of a new genus.

### **Mid to late 20<sup>th</sup> century: renewed interest**

As the 20<sup>th</sup> century marched on, there was a crescendo of interest in acronictines, due to an interest in Noctuidae more broadly. Much more work was done in Asia, and the focus on larval characters was renewed in all regions of the world. No consensus on the definition for Acronictinae was yet developed, so the subfamily continued to experience conflicting circumscriptions.

A problematic set of taxonomic decisions, including the description of several new genera, was put forth by Kozhanchikov (1950) in a book dedicated to a worldwide analysis of acronictines and their kin. In addition to traditional study of adult morphology and genitalia, he also described larval chaetotaxy, host plants, pupal morphology and behavior, thermal tolerances, growth rates, and geographic distributions. He recognized that with their wide distributions and rampant polymorphisms, more study would be required to fully understand these taxa (Kozhanchikov 1950). Despite his attention to detail, Kozhanchikov mistakenly combined two disparate groups, Acronictinae and Orgyinae, as well as scattered genera from a half dozen other noctuid subfamilies, into the family he named Orgyidae. Orgyinae approximates what is currently known as Lymantriinae (family Erebidae) (*Orgyia* Ochsenheimer, 1810 was chosen for the basis of his subfamily and family names due to priority; *Lymantria* was described in 1819 by Hübner). Acronictinae was said to have little in common with Noctuidae; purported similarities with Orgyinae included wing venation, genitalia, mouthparts, larval setae, pupal morphology, and



cocoon structure (Kozhanchikov 1950). The book included two proposed phylogenies: one showing the placement of Orgyidae (Figure 2A), and one with the distribution of genera within the family (Figure 2B). Acronictinae was split into two tribes: Momini and Acronictini. Momini held 22 genera, including four newly described by Kozhanchikov: *Acronictoides*, *Belciades*, *Subleuconycta*, and *Thyatirides*. This tribe encompassed taxa now known from a wide range of subfamilies including Pantheinae, Raphiinae, Dyopsinae, Calpinae, Hadeninae, and Cuculliinae. The tribe Acronictini included 9 genera split into two unnamed groups. The first included *Eogena*, *Acronicta*, and *Craniophora* and the second included *Arsilonche* and *Oxycesta*; the other four genera remained unplaced in the phylogeny. Two new genera were described within Acronictini: *Subacronicta* and *Hampsonia* (Kozhanchikov 1950). Only one of his acronictine genera, *Leiometopon*, is no longer considered to be a member of the subfamily; otherwise his Acronictini was a good, but not complete, circumscription of Acronictinae. While many of Kozhanchikov's generic names have persisted, his proposal for the family Orgyidae was highly problematic and has been soundly rejected by other taxonomists (as well as all molecular evidence for Noctuoidea).

In North America, Forbes (1954) broke ranks with McDunnough's (1938) checklist (with a restrictive definition of Acronictinae) and broadened the subfamily to encompass 73 genera in North America – reminiscent of Janse's approach of combining Acronictinae and Amphipyrynae. Forbes split the genera into two series; the second series encompassed true acronictines and a host of genera now assigned to Agaristinae Boisduval, 1833, Amphipyrynae, Condicinae, Hadeninae, and other subfamilies. However, Forbes did group acronictines together in the list, into the tribe Acronictini. He brought *Agriopodes* and *Polygrammate* back into Acronictinae,

listed in Acronictini with *Apatela* (= *Acronicta*), *Simyra*, *Merolonche*, and *Harrisimemna*. *Cerma*, however, remained separated from this assemblage, listed as an isolated genus. Another unusual acronictine genus, *Comachara*, he placed in the Sarrothripinae, while acknowledging that it was not a good fit (Forbes 1954).

Despite a new focus on the larval stage, workers in both North America and Europe continued to have difficulty determining the limits of Acronictinae. According to S. E. Crumb (1956), “No characters have been found which would completely separate the Pantheinae from the Acronyctinae.” Consequently, his North American treatment included *Raphia*, *Panthea*, *Charadra*, *Colocasia*, and *Lichnoptera* Herrich-Schäffer, 1856, in addition to his six genera of “Acronyctinae proper”: *Acronycta*, *Merolonche*, *Simyra*, *Agriopodes*, *Polygrammate*, and *Harrisimemna*. His treatment resembled the arrangement proposed by Forbes (1954)—not unsurprisingly given that Forbes, a brilliant scholar, was considered to be the premier New World lepidopterist and had only just recently completed his opus on the eastern Noctuidae s. lat. The bird-dropping mimic *Cerma* was transferred into Crumb’s (1956) newly described subfamily, Lithacodiinae. Meanwhile in Europe, Herbert Beck began his assessment of Acronictinae (and other Noctuidae), which would become a lifelong effort. He included *Colocasia*, *Moma*, *Panthea*, *Episema* Ochsenheimer, 1816, and *Apatele* in what he called *Apatelinae* (Beck 1960). The arrangement proposed by Beck included pantheines, as well as one genus of Cuculliinae.

Emblematic of the challenges of the taxon’s taxonomy, lepidopterists still could not agree on the name of the genus (*Acronicta*, *Acronycta*, *Apatele* or *Apatela*) or the subfamily (Acronictinae,

Acronyctinae, Apatelinae, etc.) well into the 20<sup>th</sup> century, let alone its content. Both matters are more thoroughly addressed in Section 2.

Books and field guides of the time followed an assortment of major works, though these by necessity focused on taxa from their own region. Regional guides are important to consider, as they are the publications sought by amateurs and a spectrum of non-specialist researchers alike for making taxonomic determinations. In North America, Kimball's (1965) guide to insects of Florida (useful throughout much of the Eastern United States) had a familiar pantheine/acronictine grouping, with *Raphia*, *Panthea*, *Colocasia*, *Charadra*, *Lichnoptera*, *Acronicta*, *Simyra*, and *Harrisimemna*. Later, an attempt at a definitive checklist (following McDunnough in 1938) was assembled by Franclemont and Todd (1983) for the Noctuidae of North America. This checklist, which is still the definitive North American checklist today for many lepidopteran families, took a more restrictive view of the subfamily by splitting Acronictinae and Pantheinae. Acronictinae included *Acronicta*, *Merolonche*, *Simyra*, *Agriopodes*, *Polygrammate*, *Harrisimemna*, and *Cryphia*. Only one of these, *Cryphia*, is no longer considered an acronictine, but belongs in Bryophilinae. Two remaining North American acronictines, *Comachara* and *Cerma*, were moved to other subfamilies distant to Acronictinae. *Comachara* was moved from Sarrothripinae to Lithosiinae (an arctiine group), and *Cerma* was placed in Acontiinae. A few years after the Franclemont and Todd checklist, *Cryphia* remained in Acronictinae but was moved into a separate tribe (Bryophilini) by Ferguson (1988) who split the subfamily into two tribes.

One of the most influential worldwide checklists was the *Lepidopterorum Catalogus Noctuidae* (new series), Poole's (1989) Herculean effort at cataloging not only species, genera, and subfamilies, but type species, original descriptions, and synonyms for noctuids worldwide. He included 17 genera in Acronictinae, which are predominately still considered acronictines today; two clearly aberrant genera have subsequently been reassigned to Dyopsinae (*Belciades*) and Amphipyryinae (*Nacna*). Several other included genera, mostly from Africa and Australia, have not yet been confirmed (see Table 1). Three acronictine genera were erroneously included in Amphipyryinae by Poole: *Cerma*, *Eogena*, and *Oxicesta*. The puzzling *Comachara* was not addressed (because it had been moved to the Arctiidae). Going a step further than Ferguson, *Cryphia* was pulled out into its own subfamily, Bryophilinae. The European *Moma*, typically treated as an acronictine, was listed in Pantheinae – a position ignored by many other taxonomists (Poole 1989). Many acronictine synonyms were dealt with, including several of Kozhanchikov's generic names (e.g., *Hampsonia*, originally described with *H. albonigra* and *H. jankowskii*, was regarded to be a subjective homonym and replaced with *Hampsonidia* by Inoue (1958). Ultimately both names were synonymized with *Craniophora* by Poole). Phylogenetic relationships between subfamilies were not proposed, but this catalog became (and remains) a benchmark taxonomic reference for noctuid workers. Poole's catalogue is the most complete modern check-point for noctuid taxonomy, and was frequently referenced for the decisions listed in Table 1.

Regional identification guides by Rings et al. (1991) (Ohio), Handfield (1999) (Quebec), and Covell (1984) (Eastern North America) continued the trend of a restricted concept of

Acronictinae in North America, going a step farther by excluding genera of both Pantheinae and Bryophilinae.

In a later Moths of North America (MONA) fascicle, Poole considered Acronictinae, Pantheinae, and Bryophilinae to be separate subfamilies, yet united as a clade (Poole 1995). While he based their unity on secondary larval hairs, he remarked he had “an unsupported feeling that the Pantheinae and Acronictinae are not closely related despite the similarity of their larvae” (Poole 1995). Another oft-cited work by Poole, *Nomina Insecta Nearctica*, included the following list for the Nearctic fauna: *Acronicta*, *Agriopodes*, *Anterastria*, *Harrisimemna*, *Merolonche*, *Polygrammate*, and *Simyra*. This is the first and only mention of *Anterastria* as an acronictine in any published work, though it has had an affinity with *Agriopodes* (Schmidt et al. 2014). At the family level, *Comachara* remained assigned to Arctiidae, following Franclemont and Todd (1983).

Across the ocean, the trend toward splitting pantheines and bryophilines (and other taxa) from Acronictinae was more scattered and contentious, with frequent reversals. An Irish guide to Lepidoptera split Acronictinae and Pantheinae, yet included the bryophiline *Cryphia* in Acronictinae (Baynes 1964). A Swedish book on moths, *Nordens Nattflyn*, was a step ahead by splitting Acronictinae, Bryophilinae, and Pantheinae – the only members of Acronictinae were *Moma*, *Simyra*, *Acronicta*, and *Craniophora* (Gullander 1971). Despite these arrangements, other European guides, such as the *Noctuidos Espanoles*, continued to take a broad view. This Spanish treatment listed 14 genera in Acronictinae, including genera now placed in Pantheinae, Dyopsinae, and Bryophilinae (Calle 1982). This book was one of the few to include *Oxicesta*

since its inclusion by Grote in the late 19<sup>th</sup> century (1896) (perhaps prompted by its treatment in Kozhanchikov's Acronictini). A year later an influential series authored by Lorimer (1983), covering Europe and Asia, listed only *Cryphia*, *Acronicta*, *Moma*, and *Craniophora* in Acronictinae. This work evidently had an impact on future guides and checklists, which tended to follow this arrangement. A Polish lepidopteran guide listed only *Acronicta*, *Simyra*, and *Moma* amongst its acronictines (Heintze 1990), while a British caterpillar guide followed the Lorimer arrangement with the addition of *Simyra* (Porter 1997). However a Eurasian work, focusing primarily on Russian taxa, included a different assortment: *Acronicta*, *Moma*, *Colocasia*, *Episema*, and *Daseochaeta* – pulling some cuculliines from earlier publications (such as *Daseochaeta* from Hampson and Warren, and *Episema* from Beck) (Merzheevskaya 1988). While throughout these works there was disagreement on whether to include pantheines, bryophilines, and cuculliines, either whole or in part.

By the late 20<sup>th</sup> century, Beck had spent a considerable amount of time studying acronictines (and other noctuids *sensu lato*), and had refined his definition of the subfamily. He adopted the name Acronictinae instead of Apatelinae, and used three tribes within it: Pantheini, Acronictini, and Craniophorini (he created a fourth tribe, Bryonyctini, in 1996 which was not included in his work a few years later) (Beck 1996, 1999). Notable genera included in Acronictini were *Oxicesta* and *Eogena*, which had only been placed in Acronictinae by a handful of previous workers (Grote 1896; Hampson 1909; Warren 1909; Kozhanchikov 1950; Calle 1982), but were typically ignored in most other works. Beck's decisions were weighted heavily with larval evidence: the larvae of *Oxicesta*, *Eogena*, *Simyra*, and some *Acronicta* species are remarkably similar in setal types, setal arrangements, color, diet breadth, and general habitus – made clear when their

images are arranged side-by-side in Beck's (1999) work. He also revived the status of several genera and subgenera which had been synonymized by various workers (Poole 1989), such as *Arsilonche*, a synonym of *Simyra* (Beck 1996). The inclusion of pantheines as a tribe, instead of their own subfamily, speaks to the confused taxonomic concepts for many noctuoid taxa above the genus level that still plague noctuoid classifications to this day. Outside of Acronictinae, Beck (1996) created a new subfamily name for a genus often classified as an acronictine or pantheine: Raphiinae, for the genus *Raphia*.

Until the mid-20<sup>th</sup> century, North America, Europe, and Russia were the major hubs for work on acronictines. This changed with several Japanese publications which had a major influence not only on the generic composition of Acronictinae, but the ranking of various genera/subgenera of *Acronicta* (to be addressed in Section 2). The acronictine fauna is rich throughout Asia, with species, subgenera, and genera yet to be discovered or studied. In many cases, especially in China and Southeast Asia, the larvae are unknown. The year 1982 saw the introduction of two major works: the Moths of Japan (Inoue et al. 1982) and An Introduction to the Moths of South East Asia (Barlow 1982). While lepidopterists in North America and Europe were pruning taxa from Acronictinae, Inoue et al. and Barlow were bringing more into the fold. The Moths of Japan included taxa from Calpinae Boisduval, 1840 (Erebidae), Dyopsinae, Hadeninae, Amphipyrrinae, and Pantheinae; additionally, there were multiple synonyms of *Acronicta*, subgenera elevated to generic status, and several strictly Asian genera not yet treated in other works. Despite the inclusion of unrelated taxa, the Moths of Japan did include nearly all acronictine taxa of the area. Most notable was the inclusion of *Lophonycta* Sugi, 1970, an unusual genus described by one of the co-authors several years prior (originally described in Cryphiinae) (Sugi 1970; Inoue et al.

1982). Sugi later went on to write a guide to lepidopteran larvae of Japan, adopting a more restrictive view of acronictines. This may be in part due to the unknown larvae of some taxa (such as *Lophonycta* and *Narcotica* Sugi, 1982), but also the special interest Sugi appears to have had in the group. Despite multiple synonyms of *Acronicta*, his only missteps were the inclusion of *Belciades* Kozhanchikov, 1950, *Moma*, and *Gerbathodes* Warren, 1911 in Acronictinae (Sugi 1987). Barlow's (1982) effort was much farther from the mark. Only one genus out of 11, *Acronicta*, truly belonged in Acronictinae; the rest are currently regarded to belong to Hadeninae. A later work by Holloway (1989), corrected most of these miss-assignments, but still included one hadenine (*Platyprosopa* Warren, 1913). In addition to *Acronicta*, Holloway also included *Craniophora*, *Thalatha* Walker, 1862, and *Thalathoides* in the subfamily. The latter genus was also described in this same work. *Thalatha* and *Thalathoides* appear to be good acronictines, but still await molecular characterization. In a description of the Acronictinae of Sumatra by Kobes (1995) a similar group of genera were listed: *Acronicta*, *Craniophora*, *Thalatha*, *Thalathoides*, *Platyprosopa*, and *Tycracona*; the latter is yet another hadenine genus.

Further south, in Australia, lepidopterists were relatively quiet about Acronictinae as so few species occur there. In a classic book, the Moths of Australia (Common 1990), the author noted that Acronictinae cannot be distinguished from Amphipyridae, though offered *Craniophora* as a likely Australian acronictine genus. As a consequence Amphipyridae and Acronictinae have been treated together in most Australian treatments, e.g., Edwards' (1996) Checklist of the Lepidoptera of Australia.



During this period there were several attempts made towards worldwide classifications within Noctuidae. A landmark paper by Speidel et al. (1996) used an extensive study of morphology to evaluate the systematics of the family. Based on characters of the tympanum, genitalia, and secondary sexual characters (particularly the abdominal triline brush organs, or TBOs) they separated Acronictinae from Pantheidae (raised to family level) and Bryophilinae. Based on the presence of TBOs a former acronictine genus, *Lophonycta* was removed and elevated to the status of a new subfamily, the Lophonyctinae Speidel et al., 1996 (though in this work, *Lophonycta* was previously considered a quadrifine in the subfamily Acontiinae). Likewise another Asian quadrifine acontiine genus (Poole 1989), *Sinocharis* Püngeler, 1912, was recognized as the sole genus of Sinocharinae Speidel et al., 1996, based on the presence of abdominal brush organs—see also discussion in Chapter 5.

Another phylogenetic treatment for worldwide Noctuidae was proposed by Kitching and Rawlins (1998) in a volume covering the evolution, systematics, and biogeography of Lepidoptera – this work is considered a milestone publication by lepidopterists, and is still widely consulted today. They contended that Acronictinae was a basal triline subfamily without TBOs; it was listed as a paraphyletic lineage alongside Bryophilinae and Raphiinae (Kitching and Rawlins 1998). They defined the subfamily as *Acronicta* and close relatives. A complete list of contained genera was not provided, but in addition to the nominate genus, the following genera were mentioned: *Craniophora*, *Thalatha*, *Thalathoides*, and *Simyra*. The subfamily's status as a monophyletic group was questioned due to the lack of unambiguous synapomorphies – acronictine species were recognized to have highly variable larval morphology, larval diet breadth, male genitalia, and pupal characters (Kitching and Rawlins 1999). They also made changes to other groups

which included genera not yet recognized as acronictines. In this same work, Kitching and Rawlins moved a few New World taxa into the subfamily Afridinae (Nolidae). Included were genera placed in the Lithosiinae by Franclemont and Todd (1983), including the enigmatic and mostly forgotten *Comachara*—the New World’s smallest acronictine.

As these phylogenetic hypotheses and classification schemes developed, the use of molecular markers for elucidating phylogenetic relationships of Lepidoptera was in its infancy. The first study on noctuids (Weller et al. 1994) used ND1 and the 28B region of the 28S rRNA subunit of 26 species, including one acronictine: *Acronicta tritona*. Acronictinae was listed as an “unplaced” subfamily, which appeared in different regions of the tree depending on the analysis. With only mitochondrial data, *Acronicta* grouped with either notodontids (a distantly related family, thus a clearly erroneous placement) or noctuines and other trifine noctuids. With combined mitochondrial and rRNA data, *Acronicta* grouped with the trifine noctuids (Weller et al. 1994). Due to low taxon sampling, subfamilial relationships of Acronictinae were left as yet undetermined. Meanwhile nuclear genes and other markers were being sampled and tested for their use in insect phylogenies (i.e. Friedlander et al. 1992, 1994, 1996), and in particular for Lepidoptera (i.e. Cho et al. 1995; Mitchell et al. 1997; Friedlander et al. 2000). None of these offered insight into acronictine relationships, but they set the stage for further studies.

## **21<sup>st</sup> century: DNA and larvae**

For the first ~150 years of taxonomic work on Acronictinae, the characters used for systematic placements were primarily morphological, based primarily on adult characters. However the turn of the century saw the increased availability and use of molecular data. These molecular data

have begun to inform our taxonomic and systematic decisions, resolving many nomenclatural disputes. Increased ubiquity and use of the internet, as well as the speed of international loans of books and specimens, has allowed a renaissance in acronictine systematics – workers are increasingly cognizant of the systems used in other regions of the world. As the boundaries of Acronictinae continue to be clarified, no doubt more species will be discovered or moved into (or out of) the subfamily based on our changing definition of the group and accumulating DNA data.

In 2005 Fibiger and Lafontaine, noctuid systematists from Europe and North America, respectively, combined forces to propose a revised classification of Holarctic Noctuidae. They focused on morphology, especially of the male genitalia. In their treatment, Sinocharinae and Lophonyctinae remained separate subfamilies, following Speidel (1996). Their phylogeny of noctuid subfamilies kept Acronictinae basal to the clade of taxa containing abdominal courtship brushes (TBOs), in a position near a clade of Diphtherinae and Raphiinae. Their only other change of note to Acronictinae was to add the genus *Miracavira* Franclemont, 1937, without explanation, except that it was previously considered an amphipyrene. Published in the same series, Fibiger and Hacker crafted a list of European noctuids, including *Acronicta*, *Simyra*, *Craniophora*, *Oxicesta*, *Eogena*, and *Moma*, in Acronictinae (Fibiger and Hacker 2005).

In North America, the early 21<sup>st</sup> century saw the resolution of some questionable generic placements, primarily due to the efforts of David Wagner, with special interest in larval systematics. His first field guide to caterpillars of eastern North America listed *Acronicta*, *Simyra*, *Polygrammate*, and *Harrisimemna* in Acronictinae, a conservative grouping (Wagner 2005). In the following years his interest in the subfamily was piqued, primarily due to the varied

morphology and behavior of the larvae. One investigation began with a misidentification – a supposed larva of *Polygrammate hebraeicum* Hübner, 1818 was identified by a colleague as *Comachara cadburyi* Franclemont, 1939. This misidentification highlighted an intriguing similarity, especially as *Comachara* was thus far assigned alternatively to Sarrothripinae, Lithosiinae, or Afridinae (Wagner et al. 2006). This led to an in-depth investigation of all life stages of *C. cadburyi*. Both *Polygrammate* and *Comachara* larvae have the same food plant (*Nyssa*), feeding habits (scraping windows into the leaves), coloration (green with white spots and stripes), final-instar color change (to a darker, mottled form), and pupation behavior (tunneling into wood and forming the chips into balls). This pupation behavior is shared with another acronictine genus, *Harrisimemna*. There are also similarities in the shape and chorionic ornamentation of the ova, and in genitalic features of the adults. These pieces of evidence led Wagner to move *Comachara* into Acronictinae (Wagner et al. 2006).

Wagner turned toward another tunneling-and-ball-rolling genus: *Cerma*. The two species in the genus, *C. cerintha* (Treitschke, 1826) and *C. cora* Hübner, 1818, have had tumultuous taxonomic histories. Due to the bird-dropping coloration of the adult forewings, they have been associated (either together or separately) with acontiines (McDunnough 1938; Franclemont and Todd 1983), amphipyrrines (McDunnough 1938), lithacodiines (Crumb 1956), eustrotiines (Fibiger and Lafontaine 2005), and with Forbes' broad concept of Acronictinae (Forbes 1954). Wagner (2007b) associated *Cerma* with Acronictinae based on preliminary COI (mitochondrial DNA) evidence, and a suite of larval morphological and behavioral characters. *Cerma* was excluded from Acontiinae and Eustrotiinae due to its prolegs, raised pinacula, long pigmented setae, and lack of thickened setae on the anal plate (Wagner 2007a). Similarities to Acronictinae include

fusion of thoracic dorsal pinacula, setal characters, A8 dorsal hump, defensive postures, and the tunneling-and-ball-rolling pupation habit, which places *Cerma* near *Harrisimemna* (Wagner 2007a). These data were expanded upon in a subsequent publication (Wagner 2007b) with the addition of further larval characters, adult morphology, genitalia, and COI sequences – which grouped *Cerma* with *Comachara* and *Polygrammate*. Most remarkably, *Cerma* males have abdominal brush organs (TBOs), not previously known from acronictines aside from the banished *Lophonycta*. The larvae also lack secondary setae and the extra seta on the L3 pinaculum, features previously considered synapomorphies for the subfamily (though the larval setae in general are reduced) (Crumb 1956; Kitching and Rawlins 1998; Wagner 2007b). With the addition of *Cerma*, the definition of the subfamily became further confused by providing additional exceptions to the shaky understanding of what defines an acronictine.

Wagner (2008) was also able to remove a non-acronictine from the subfamily due to larval study. The genus was *Miracavira*, recently added by Fibiger and Lafontaine (2005). Though there was originally no published explanation for its inclusion, the adults are green lichen-mimics, reminiscent of *Agriopodes* (and *Chloronycta*) species. The larvae were unknown or not considered. After Wagner had a chance to study larvae of *Miracavira brillians*, it became clear that the larvae do not comport with acronictine features; in all ways they resemble amphipyrids, especially those of the tribe Psaphidini. Thus the genus ended its brief stay with Acronictinae (Wagner et al. 2008).

Powell and Opler (2009), in their guide to the Moths of Western North America, their treatment of the subfamily featured the only *Acronicta*, *Merolonche*, *Simyra*, and *Agriopodes*. It wasn't

until a thorough checklist, put together in the following year that many synonyms were dealt with and Wagner's findings were embraced. Lafontaine and Schmidt (2010) authored an annotated checklist of Noctuoidea of North America: they assigned *Merolonche* as a synonym of *Acronicta* and listed the following Nearctic acronictine genera: *Acronicta*, *Simyra*, *Agriopodes*, *Polygrammate*, *Harrisimemna*, *Comachara*, and *Cerma*.

Meanwhile, the journey toward broad noctuid phylogenies based on nuclear genes was gaining momentum. Mitchell and Mitter used two nuclear genes (*elongation factor 1-alpha* and *dopa decarboxylase*) for their Noctuidae analysis, after a thorough review of “post-Hampsonian” era classification schemes (Mitchell et al. 2006). Only three North American acronictines (*Acronicta*, *Simyra*, and *Polygrammate*) were used in this early molecular study. *Simyra* had a rather long branch, offering what appeared to be support of its separation from *Acronicta* – but with only two *Acronicta* species, themselves with long branches, these trees were not definitive. Mitchell et al. (2006) concluded that Acronictinae belonged in a grade of amphipyrene tribes, which differed between the maximum parsimony and maximum likelihood analyses. In the maximum parsimony analysis the acronictines rested closest to Azeniini and Grotellini. In the maximum likelihood tree they were sister to a clade of Oncocnemidinae and Agaristinae; that clade was in turn sister to Psaphidinae, Amphipyryni, Stirinae, and Grotellini.

Following these advances, a sequencing campaign led by Niklas Wahlberg, Reza Zahiri, and colleagues began working on resolving the relationships within the Noctuoidea (Zahiri et al. 2011, 2012, 2013a). In 2013 they published their results on basal subfamily relationships within Noctuidae (Zahiri et al. 2013b) based on seven nuclear genes and one mitochondrial gene.

Among acronictines they included species of *Acronicta*, *Agriopodes*, *Comachara*, *Polygrammate*, *Craniophora*, *Cerma*, and *Harrisimemna*. Despite including taxa from across the Holarctic, the selected acronictine genera and species had a North American bias. All seven of the above genera formed a clade, with *Agriopodes* nesting within *Acronicta*. Their tree corroborated the decisions made by Wagner (2006; 2007b) to move *Comachara* and *Cerma* into Acronictinae. A weakly associated clade of Acronictinae, Metoponiinae, and Amphipyriinae began to dispel the notion of Acronictinae's relationship with Pantheinae, Raphiinae, Bryophilinae, and others, espoused by many early workers (Zahiri et al. 2013b) or that the subfamily might nest within the Amphipyriinae

Lafontaine and Schmidt's (2010) taxonomic decisions in their annotated checklist for Nearctic Noctuoidea included several species synonymies within *Acronicta* and signaled the start of their interest and involvement in acronictine systematics. Their attentions turned to *Agriopodes*, which was nested within a clade of *Acronicta* species in Zahiri et al.'s (2013b) molecular phylogeny. *Agriopodes* was a genus of lichen-mimic moths sporting beautiful green coloration, unusual for acronictines, which to be gray and rather undistinguished. Based on molecular data and both adult and larval morphology, *Agriopodes* was found to be polyphyletic and thus was entirely rearranged by Schmidt et al. (2014). The green adult coloration shared by all members of the genus, turned out to be convergent, revealed by the larval data collected by co-authors Wagner and Zacharczenko. Schmidt et al. synonymized *Agriopodes geminata* (Smith, 1903) with the type species *A. fallax* (Herrich-Schäffer, 1854). A COI phylogeny showed that *A. fallax* nested within *Acronicta*, and so *Agriopodes* was synonymized with *Acronicta*. The remaining member

of the genus, *Agriopodes tybo* (Barnes, 1904), was determined to lie outside of *Acronicta* (but within Acronictinae), and given a new genus name: *Chloronycta* Schmidt and Anweiler, 2014.

The works of Wagner, Schmidt, and their co-authors demonstrate the importance of utilizing all available lines of evidence when making taxonomic decisions. Even without COI data, larval morphology and behavior pointed toward the positions of *Chloronycta*, *Comachara*, *Cerma*, and *Agriopodes* within Acronictinae. These characters were only seldom used by past acronictine workers, who instead favored the classical (and in this case, confounding) adult characters, including genitalia. For these acronictine genera COI has been useful in confirming phylogenetic underpinnings, yet the phylogenetic results needed to be regarded with caution, because COI can be unreliable for the inference of accurate phylogenies, and especially for older divergences. In practice, COI should be used in conjunction with multiple nuclear genes, as was done by Zahiri et al. (2013b) and others.

Despite the primarily temperate range of Acronictinae, they do find their way into Central America. A guide to the Butterflies and Moths of Costa Rica (Chacon and Montero 2007) listed two *Acronicta* species, which phenotypically resemble their North American congeners, but have not yet been sampled for DNA. No other acronictine genera are known from Central or South America, and no taxonomic Neotropical treatments deal with the placement of *Acronicta*.

While this taxonomic activity took place in the New World, Europe was relatively quiet. There were, however, two major works which currently frame our understanding of European acronictines. The first was a larval tome, with extensive morphology and exhaustive (fully



referenced) host plant lists for each species: Larvae of Northern European Noctuidae (Ahola and Silvonen 2005). Ahola and Silvonen's treatment of Acronictinae included *Acronicta*, *Simyra*, *Craniophora*, *Eogena*, *Oxicesta*, and *Moma*. They diverged from Beck's arrangement of tribes, and used Acronictinae, Pantheinae, etc. as their own subfamilies (Ahola and Silvonen 2005). The most definitive work, Noctuidae Europaeae Volume 11 (Fibiger et al. 2009), came a few years later as part of an expansive series on Noctuidae. Fibiger *et al.* included the same genera as Ahola and Silvonen, supporting the inclusion of *Moma* and the exclusion of the commonly added bryophiline *Cryphia*. During this time, another genus/subfamily was moved near Acronictinae and Raphiinae, which would later be presented as a possible acronictine: *Balsa* Walker, 1860 (Balsinae) (Lafontaine and Fibiger 2006). Lafontaine and Fibiger also expressed support for Mitchell et al.'s ideas for acronictine relationships (near amphipyrrines).

Russian taxonomists were in a unique position to comment on acronictine species with both European and Asian affinities. In a set of keys for the identification of Russian insects in the Far East, Kononenko (2003) listed 11 genera in Acronictinae: *Cymatophoropsis*, *Belciades*, *Euromioia*, *Moma*, *Nacna*, *Gerbathodes*, *Acronicta*, *Simyra*, *Subleuconycta*, *Craniophora* and *Cranionycta*. A later book, focused on foodplants of Russian noctuid larvae, included a similar list; the Asian *Euromioia*, *Subleuconycta*, and *Cranionycta* were omitted, while the European *Oxicesta* and *Eogena* were added (Matov and Kononenko 2012). (More on these taxa appears below.)

Through the early 21<sup>st</sup> century in Asia, most treatments embraced a narrowing concept of Acronictinae. However, several workers continued to include taxa from other subfamilies –

especially Hadeninae. A few local guides of the time, such as *The Families of Malesian Moths and Butterflies* (Holloway et al. 2001) and the *Illustrated Guide for the Korean Insect Larvae* (Sohn 2006), listed *Acronicta* and *Craniophora*, with Sohn also adding *Moma*. Journal articles began referencing this narrow definition as well – Han and Kononenko (2010), in a paper describing several new species, listed only *Acronicta* and *Craniophora* as acronictine genera. However a new guide to Japanese moths, following the work of Inoue et al. (1982), embraced Inoue et al.'s concept of Acronictinae by including taxa from disparate subfamilies. The *Standard of Moths in Japan* (Volume II) included an almost identical list of taxa, with a few exceptions. The authors did not include many of *Acronicta* synonyms (or subgenera), *Lophonycta* was placed in Lophonyctinae, *Sinocharis* was placed in Sinocharinae, and some species of *Craniophora* were split off into *Cranionycta* (Kishida 2011). A guide to the Moths of Thailand (Kononenko and Pinratana 2013) listed only *Acronicta*, *Craniophora*, *Cranionycta*, *Thalathoides*, *Simyra*, and *Platyprosopa* (a hadenine, as listed by Holloway (1989)). The Australian section of the Lepidoptera Barcode of Life website listed *Acronicta*, *Craniophora*, *Thalatha*, and *Bathytricha* Turner, 1920 (a hadenine) as acronictines in its checklist; however, the list does not appear to be connected to actual COI barcode results (iBOL 2009). None of the Asian or Australian acronictines had yet been analyzed in a molecular phylogenetic study.

Since Janse (1921) and Gaede (1934), African acronictines were seldom addressed in checklists or other works. An overview of the history of Afrotropical acronictines was given by Krüger (2001) in his description of three new *Acronicta* species. He expressed doubt as to the monophyly of Acronictinae proposed by Kitching and Rawlins (1999), but did not propose any taxonomic decisions beyond his own species descriptions. The most recent checklist for African

moths is an online database, built and curated by de Prins and de Prins (2015). It references over 5,000 published sources and is continuously updated. For Acronictinae they list the following genera (accessed 1 January 2016): *Acosmetia* Stephens, 1829, *Acronicta*, *Amphia* Guenée, 1852, *Auchecranon* Berio, 1978, *Craniophora*, *Diphtherocome*, *Kuehneana*, *Madeuplexia*, *Simyra*, and *Thalatha* (de Prins and de Prins 2015). Of these, the subfamilial placements of *Acosmetia*, *Amphia*, *Auchecranon*, *Diphtherocome*, *Keuhneana*, and *Madeuplexia* are still unknown; they have not yet been sampled for DNA analysis nor studied for their morphology, but it seems likely that many of these are included because they are simply of the amphipyrene-acronictine grade, and ultimately will be classified outside of the Acronictinae as presently understood.

Despite the differing definitions of Acronictinae around the world, there has been a general consensus to limit membership in the group by removing pantheines, hadenines, bryophilines, and others. Acronictinae itself moved amongst clades of subfamilies, sometimes with Pantheinae, Raphiinae, and Bryophilinae, other times with Amphipyrinae. Further progress could not be made without molecular data – too many morphological features of the adults and larvae had proven to be convergent or confounding. The task of determining the phylogenetic placement of Acronictinae was taken up by collaborating laboratories in the United States (Wagner and Zacharczenko), and Finland (Rota, Wahlberg, and Zahiri). The goal was to gather DNA from a range of Holarctic genera in order to infer a more robust phylogeny for the subfamily. Two major analyses were done: 1) a Noctuidae analysis, with 14 outgroup and 81 ingroup taxa, which examined the placement of Acronictinae within Noctuidae; and 2) an Acronictinae analysis, with 8 outgroup and 80 ingroup taxa, which examined the placement of genera within Acronictinae and offered a preliminary look at the arrangement of species (and

subgenera) within *Acronicta* (Rota et al. 2016). Several works were used as taxonomic benchmarks for current names: Lafontaine and Schmidt (2010), Fibiger et al. (2009), Han and Kononenko (2010), and Kishida (2011), plus Schmidt's (2014) recent work on *Agriopodes* and *Chloronycta*. This study used the same 8 gene regions (7 nuclear and one mitochondrial) that had been used for several of Zahiri et al.'s noctuid phylogenies (Zahiri et al. 2012, 2013a, 2013b).

Rota et al.'s (2016) Noctuidae analysis showed several European and Asian “acronictine” taxa falling far from Acronictinae: *Belciades* and *Moma* in Dyopsinae, *Gerbathodes* as sister to several pantheines, *Naca* as sister to several amphipyrrines, *Balsa* as sister to *Raphia* in Raphiinae, and *Cryphia* in Bryophilinae – see Figure 3. Despite these subfamilies so often intermingling with acronictines in taxonomic works, none appears closely related to Acronictinae except Amphipyrrinae, which was the (weakly supported) sister clade in their analysis. However Amphipyrrinae did not have wide coverage (only two species); more thorough taxon sampling would be required in order to determine which noctuid clade(s) was truly sister to Acronictinae (Rota et al. 2016), and whether both families were monophyletic with respect to one another. Most importantly, Rota et.al. demonstrated which genera belong within Acronictinae. With such a robust outgroup (encompassing almost all noctuid subfamilies), this study confirmed that *Lophonycta* and *Sinocharis* are acronictines, along with the recently added *Comachara* and *Cerma*. One little studied Asian genus, *Narcotica*, was also shown to be an acronictine (Rota et al. 2016).

The Acronictinae analysis delved deeper into the subfamily, with at least the type (and typically other members) of each genus included among the 80 ingroup taxa. *Lophonycta* came out as the

sister to the rest. The remaining genera (aside from *Acronicta*) formed an unresolved polytomy with three clades: 1) *Narcotica*, *Polygrammate*, and *Comachara*, 2) *Sinocharis*, *Cerma* and *Harrisimemna*, and 3) *Chloronycta* and *Craniophora*. Interestingly, the known ball-rollers (*Polygrammate*, *Comachara*, *Cerma*, and *Harrisimemna*) did not form a monophyletic group, bringing into question how the ball-rolling behavior evolved and whether it was gained or lost multiple times. However it must be noted, of the life histories *Narcotica* and *Sinocharis* are still unknown, so the true distribution of ball-rolling behavior in lower acronictines is unknown. *Sinocharis*, a bird-dropping mimic as an adult, appears to fit in nicely with fellow bird-dropping mimic *Cerma* and black/white/brown *Harrisimemna*. They also share triline brush organs (TBOs) – *Sinocharis* and *Cerma* each have a full complement of brush morphology (see Chapter xx), while *Harrisimemna* has only the associated pheromone gland (no brushes or pocket). As noted above, The TBO is present in *Lophonycta* as well, solidifying the trait as characteristic of (at least a portion of) the subfamily. The remaining clade, with *Craniophora* and *Chloronycta* (which should also have *Cranionycta* as the genus for *C. jankowskii*<sup>3</sup>), poses a taxonomic conundrum. Depending on the analysis, *Chloronycta* came out as sister to the rest, or nested within the *Craniophora*-*Cranionycta* clade. It is unclear whether *Chloronycta* should be considered a single North American representative of either *Craniophora* or *Cranionycta*, or if it should remain as a sister taxon in its own genus. Further taxon sampling (and genetic data) will be required to determine its true phylogenetic position.

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<sup>3</sup> While *C. jankowskii* had been listed in *Craniophora*, along with *C. oda*, in the Moths of Japan (Inoue et al. 1982), the two species were listed in the genus *Cranionycta* in the most recent guide to Japanese moths (Kishida 2011). *Cranionycta* had previously been listed as a synonym of *Craniophora* (Poole 1989), but Poole's decisions were generally ignored in Japanese works. According to an acronictine taxonomist specializing in *Craniophora*, *Cranionycta* is deserving of genus status due to the genitalic differences originally described by Lattin (Adam Kiss, pers. comm.).

In the Rota et al. (2016) Acronictinae analysis, *Acronicta* was only monophyletic with the inclusion of *Simyra*, *Oxicesta*, and *Eogena*. These three genera were all subordinate within the *nervosa* clade, which itself is nested deeply within *Acronicta*. Additionally *Simyra* and *Oxicesta* were found to be polyphyletic; in the case of *Oxicesta* the position of Rota et al. was likely due to insufficient gene coverage as opposed to actual polyphyly (Alberto Zilli pers. comm.; Rota et al. 2016).

Rota et al. (2016) proposed the following taxonomic changes: *Gerbathodes* was assigned to Pantheinae, *Moma* was assigned to Diopsinae, *Nacna* was assigned to Amphipyrinae, *Lophonycta* was assigned to Acronictinae (rendering Lophonyctinae a synonym), *Sinocharis* was assigned to Acronictinae (rendering Sinocharinae a synonym), and the following were considered new synonyms of *Acronicta*: *Simyra*, *Eogena*, and *Oxicesta* (Rota et al. 2016).

As the Rota et al. paper was going into print, many of the names and ranks used in previous papers were still not in wide circulation, such as the 2014 change of *Agriopodes* to *Acronicta* and *Chloronycta* (Schmidt et al. 2014). This change appeared almost immediately on the crowd-sourced BugGuide.net (BugGuide 2015) and the carefully curated Moth Photographer's Group website (Moth Photographer's Group 2015). However commonly used checklists such as The Global Lepidoptera Names Index (Beccaloni et al. 2005) and the Butterflies and Moths of the World Generic Names and their Type-species (Pitkin and Jenkins 2004) (both run by the Natural History Museum, London) have not been updated since 2005 and 2004, respectively. Individual pages may have been updated more recently, but this must be checked on every individual page.

This lag in formal acceptance of new generic combinations becomes problematic when individuals reference these websites in their curation efforts, collections, and publications.

The arrangement of taxa in the current molecular phylogeny does not yet suggest (reveal) any good adult or larval synapomorphies for Acronictinae. Presently, there are no known morphological characters that can be used to assign membership to the subfamily. Perhaps the addition of more taxa will prompt new lines of inquiry. There are multiple Asian, African, Central American, and Australian taxa yet to be collected for DNA analysis (Table 2). The collecting effort is currently underway by Wagner, Zacharczenko, Rota, and collaborators and a follow-up publication with greater geographic sampling of *Acronicta* is in development. With a greater understanding of the history of Acronictinae, spanning over 100 years and a nearly worldwide distribution, we can target taxa most in need of phylogenetic clarification.

## **Section 2: *Acronicta***

### **Early 19<sup>th</sup> century: what's in a name?**

Most noctuid species were given the genus name *Noctua* or *Phalaena* when they were described in the 18<sup>th</sup> century; *Noctua* was elevated to the family name Noctuidae, and *Phalaena*—its taxonomic equivalent—was suppressed by the International Commission of Zoological Nomenclature (ICZN) for the purposes of the Law of Priority in 1957 (Nye 1975). Even before this decision, taxonomists recognized the futility of giving so many thousands of species the same genus name, and so other generic names were being proposed. In 1806 Hübner had included *Apatele* in a list for “... experts to inspect and pass judgement on.” He included a single acronictine, *Apatele aceris*, a widespread European species. Due to an ambiguous publication date, and whether the list was meant as a nomenclatural act vs. idea to share with colleagues, this

publication was later suppressed by two separate ICZN acts in 1926 (opinion 97) and 1954 (opinion 278). These officially rendered the name provided next by Ochsenheimer, *Acronicta*, the first available name (Nye 1975). Ochsenheimer published the name *Acronicta* in 1816, incorrectly listing *Apatelae* (Hübner's *Stirps*, genus-level name, not published until 1820) instead of *Apatele* as a synonym for his new genus (Ochsenheimer 1816). Until the suppression of *Apatele* (and later, despite the suppression), various taxonomic works of acronictines referred to either *Acronicta* and *Apatele* – depending on whether or not the author subscribed to a Hübnerian classification (despite the fact that Hübner himself used *Acronicta* in his 1820 paper).

In addition to the issue of which is the accepted name, the history of *Acronicta* has been rife with debates as to which species should be included. Like its subfamily Acronictinae, there are no clear morphological synapomorphies for *Acronicta*. Many diagnostic characters have been proposed, such as larval setae and adult wing venation, but all suffer from exceptions. This had led to the naming of multiple taxa which have since alternated between generic and subgeneric status, and thus between valid names (when treated as genera) and synonyms of *Acronicta*. Wing patterns, male genitalia, and larval characters give general clues, and speak to the similarity of species-group arrangements across continents. However exceptions abound, and the regional specificity of most classification schemes render them incomplete; there has been much temporal and geographical differences of opinion in the use of the many generic-level names. When *Acronicta* is studied in more detail, the genus tends to be split into finer components. Currently, most of the previously proposed subgenera/genera for Palearctic acronictines are considered synonyms of *Acronicta*, largely because the genus requires greater taxon sampling for a more



comprehensive (molecular) phylogeny before the genus can be appropriately divided in natural groups (Rota et al. 2016).

Ochsenheimer's 1816 publication was a list of European moths; several of the generic names were his own creation. In addition to introducing the name *Acronicta*, he listed *Simyra* in the same work (Ochsenheimer 1816). As their relatedness was not yet known, they were not listed together. An appeal to stability was made by the first revisors in 2016, so the more familiar *Acronicta* was kept and *Simyra* was subsumed as its synonym (Rota et al. 2016). Until that time, *Simyra* remained a separate genus with a holarctic distribution, with nomenclatural issues of its own.

Hübner spent the early 19<sup>th</sup> century attempting to classify European Lepidoptera. His works created five genus-level names which are currently considered synonyms of *Acronicta*, but in the past enjoyed use as both full genera and subgenera: *Triaena*, *Hyboma*, *Jocheaera*, *Pharetra*, and *Arctomyscis* (Hübner 1818, 1820). These taxa were grouped primarily by wing markings and coloration. While they were all in Apatelae, only *Hyboma*, *Triaena*, and *Jocheaera* were grouped with *Acronicta* in his "second family." *Pharetra* and *Arctomyscis* joined *Colocasia* in his "third family." He named another acronictine taxon, *Oxicesta* (Hübner 1820), though it was originally listed in a distant grouping of noctuoids. *Oxicesta* held as a valid genus until 2016, when it was synonymized with *Acronicta* based on molecular and larval evidence. As these names are among the earliest, in addition to Ochsenheimer's *Simyra*, they may yet have utility as subgeneric taxa, or even raised back to generic-level status, once the phylogenetic relationships within *Acronicta* are better resolved.

Misspellings added further confusion. A colleague and collaborator of Ochsenheimer's, Treitschke, made an unjustified emendation of the genus *Acronicta* by spelling it *Acronycta* in 1825. This spelling caught on, even with Ochsenheimer himself, and competed with the Hübnerian *Apatele*. A few years later *Apatele* experienced its own misspelling, when Stephens (1829) published the name as *Apatela*. This spelling became the most common, though attributed to Hübner instead of Stephens. Due to Treitschke's spelling of *Acronycta* the "nycta" ending became quite popular, and continued to be used for naming related taxa. *Acronyctia* was introduced by Meigan in 1831, but has been seldom seen since. Sodoffsky considered *Acronycta* to be an inappropriate name, and proposed *Cometa* instead (Sodoffsky 1837). This objective synonym was wholly rejected, considered an unnecessary replacement name. Sodoffsky (1837) also offered *Asema* as a replacement for *Simyra*. Neither name gained the attentions of other taxonomists.

Guenée had an unusual way of resolving acronictine nomenclatural issues; he included both *Apatela* and *Acronycta* in his index of European noctuids. He also created the genus name *Semaphora*, a synonym of Hübner's *Triaena* (Guenée 1841). This name was later misspelled by Agassiz (1847) as *Sematophora*. *Eogena* was listed several hundred pages deeper into the list, and so was not yet recognized as an acronictine. Like *Oxicesta*, it was synonymized with *Acronicta* in 2016 (Rota et al. 2016). Two acronictine taxa were next named by Guenée (1852): *Microcoelia* and *Eogena*. *Microcoelia* listed with *Diphthera*, *Colocasia*, *Acronycta*, and others, suggesting its affinity to Acronictinae (Boisduval and Guenée 1852). It was created for the species *fragilis* Guenée, a definite *Acronicta*, but with at least one exceptional feature: the

presence of secondary setae on the larval head. This character kept *Microcoelia* separate from *Acronicta* until other features of the larvae and adult led to its synonymy.

### **Late 19<sup>th</sup> century: from genera to subgenera**

The late 19<sup>th</sup> century was a tumultuous period of attempted organization and naming of acronictines throughout Europe and North America, building on the efforts begun by Hübner, Ochsenheimer, and Guenée. In Europe, Butler had some unusual ideas for classification, which inspired rebuttal publications. Chapman focused heavily on rearing observations, providing detailed accounts of ova, larvae, and pupae. Meanwhile in North America, Grote took on the task of grouping taxa into subgenera, creating a scheme combining North American and European taxa.

Butler's work in Acronictinae began, unwittingly, with his description of *Plataplecta* in a publication on Japanese moths, which he originally recognized as a subgenus and grouped in what he called Hadenidae (Butler 1878). It was not brought into Acronictinae as a genus until later Japanese publications (Inoue et al. 1982). *Plataplecta* was eventually brought back to subgenus status (Han and Kononenko 2010; Volynkin et al. 2015), despite having been earlier synonymized with *Acronicta* by Poole (Poole 1989, 1996). While the adult morphology appears to be acronictine, it has not yet been sampled for DNA analysis. Similarly Butler later (1890) described the Indian genus *Pseudepunda* in the group he called Noctuities, which was soon afterwards considered a synonym of *Acronycta* by Hampson and later authors (Hampson 1894; Poole 1989, 1996).

Butler's most infamous work came in 1879, when upon observing a drawer of adult and larvae identified as acronictines, he noted their varied affinities to other lepidopteran families. While these resemblances were previously known, they were considered mimics or otherwise not addressed in favor of other characters of the ova, adults, and pupae which tie them together. Despite the history of work on acronictines thus far, he went about documenting differences between acronictine species, both as larvae and adults, and reclassified European taxa into three other families: Arctiidae, Liparidae, and Notodontidae (Butler 1879).

Butler's taxonomic decisions were taken to task by Chapman (1890), who claimed Butler's paper "...propounded such extraordinary ideas that I felt it was necessary that further research should confirm or refute them." Chapman focused on ova, larval, and pupal characters, which afforded him insights not fully borne out until modern day. He was ultimately dismissive of Butler's ideas, and promoted his own views of acronictine relationships, using the subfamily name Acronyctadae (after Harris's original use) and the genus name *Acronycta*. Chapman (1890) predicted the relatedness of *Simyra* and *A. rumicis* – only recently revealed in Rota et al.'s (2016) molecular phylogeny, where several *Simyra* species were shown to fall into the clade with *A. rumicis*, characterized by bristly larvae. Chapman recognized that resolving the limits of the subfamily is difficult and therefore concluded the group should be limited to those with obvious affinities. He listed several characters of the genus and related genera: [somewhat] flattened, ribbed ova; first instar with 11<sup>th</sup> segment paler and smaller (this numbering includes the head as segment 1); as well as pupal characters. Chapman proposed three groups within *Acronycta*: 1: *auricoma*, *myricae*, *menthanthidis*, *venosa*, *rumicis*; 2: *psi*, *tridens*, *strigosa*, *alni*, *megacephala*, *leporina*, *aceris*; and 3: *ligustri*. He "very unwillingly" provided names for these groups, which

did not exactly align with previously proposed names. For group 1, he gave the genus name *Viminia*, after a hoop-like structure of the pupa (vimen = barrel hoop). He noted similarities of egg structure and laying (laid in groups), larval hairiness, and pupal coloration and morphology. For group 2, he gave the name *Cuspidia*, after the terminal spines of the pupae. The dome-shaped ova, laid singly, set them apart, as did additional pupal characters. Group 3 only held one species, *ligustri*, pulled from the genus *Craniophora* Snellen, 1867. At the time Chapman (1890) gave it the name *Bisulcia* Chapman, 1890.

In North America, one of the first lepidopterists to tackle acronictine classification was Grote. He split his time between Europe and North America, and frequently collaborated with Chapman. In addition to many species names, Grote named the following subgenera of *Apatela*: *Eulonche*, *Lepitoreuma*, *Megacronycta*, *Mastiphanes*, *Merolonche*, *Philorgyia*, and *Tricholonche* (Grote 1873, 1882, 1896). He primarily focused on North American species, but did attempt a worldwide classification scheme in 1896.

In 1893, Butler conceded and recognized the errors of his 1879 work, confessing his ignorance of wing venation and larval characters: “I am therefore obliged to renounce my former opinion and admit that *Acronycta* is in truth a genus of Noctuae, probably nearest to *Polia*” (Butler 1893). He went on to propose “sections” of *Acronycta*, corresponding to subgenera, for species of Europe, North America, and Asia. He included a “typical section” in addition to sections named *Megacronycta*, *Arctomyscis*, *Apatela*, *Lepitoreuma*, *Pharetra*, *Triaena*, *Hyboma*, *Jocheaera*, *Mastiphanes*, and *Merolonche* (Butler 1893). None of these names were his own, but they did point to a greater understanding of the history of the group. However his turn-around

did not deter others from referencing his original, misguided publication. Dyar, a larval specialist, remarked that Butler's views "illustrate the difference between a classification based on superficial resemblance versus one on phylogenetic characters" (Smith and Dyar 1898). Grote (1899) was particularly harsh in a work describing the specializations of adult vs. larval lepidopterans. "Mr. Butler's paper on *Apatela* remains, at least, an exquisite satire on a generic classification from larval characters alone." I must add however, that had Butler or Grote carefully examined larval features, an entirely satisfactory classification could have been constructed/proposed that would have been superior to those (based on adult characters) that were in force until Rota et al. (2016).

Grote (1896) proposed his own acronictine classification scheme a few years after Butler's. Grote was a proponent of using subgenera to divide *Apatela*, and used many of the names proposed by Hübner, Guenée, Chapman, and others. These groups were based on both adult and larval characters, spanning a worldwide selection of taxa. In his seminal work, *Die Apateliden* (Grote 1896), he recognized the following subgenera for *Apatela*: *Acronicta*, *Apatela*, *Arctomyscis*, *Cuspidia*, *Eulonche*, *Hyboma*, *Jocheaera*, *Lepitoreuma*, *Megacronycta*, *Philorgyia*, *Triaena*, *Tricholonche*, and *Viminia*. Despite proposing the names himself a few years earlier, he did not include his own *Mastiphanes* or *Merolonche* as subgeneric names. Most of Grote's subgenera included one to three species; some had as many as seven. He considered Chapman's *Cuspidia* a synonym of *Craniophora*; he also co-opted *Cuspidia* as a subgenus within *Apatela* for the species *A. megacephala* (Grote 1896).

**Late 19<sup>th</sup> and early 20<sup>th</sup> century: avoiding subgenera**

Smith and Dyar (1898) did not include any subgenus designations in their monographic treatment of *Acronycta*. Instead they split the species into four groups based on Dyar's study of larval morphology. They believed that while hair modifications could have evolved quickly due to selective forces, hair placement likely evolved more slowly, and therefore should be more indicative of phylogenetic relatedness. Their four assemblages were Group *americana* (abundant secondary hairs and dorsal tufts), Group *lobelia* (weak secondary hairs and common mimicry), closely related Groups *hamamelis* and *persuasa* (secondary hairs absent, some primary hairs spatulate), and Group *auricoma* (tufts of hair on warts). They recognized that their Group *auricoma* was equivalent to Chapmans' *Viminia* (Smith and Dyar 1898). Their assemblages very closely align to the species groups found in Rota et al.'s (2016) molecular phylogeny, though Groups *hamamelis* and *lobeliae* are split in the phylogeny.

The trend of avoiding *Acronicta* subgenera was shared by other lepidopterists. While Warren (1909) created several new acronictine genera, he did not use any subgenera in his checklist; neither did he list any subgenera as synonyms. Hampson (1909) also avoided subgenera of *Acronycta* species, and included the following generic/subgeneric names as synonyms for *Acronycta*: *Acronicta*, *Apatela*, *Arctomyscis*, *Cuspidia*, *Hyboma*, *Jocheaera*, *Lepitoreuma*, *Mastiphanes*, *Megacronycta*, *Microcoelia*, *Pharetra*, *Philorgyia*, *Plataplecta*, *Pseudepunda*, *Triaena*, *Tricholonche*, and *Viminia*. After dismissing these names, he split the species into two large sections based on the type of hairs on the adult thorax. Hampson recognized several genera, such as *Eulonche* and *Merolonche* that are regarded to be synonyms of *Acronicta* today (Rota et al. 2016). As Warren's 1909 names were not yet available to him, Warren's *Chamaepora* was

not synonymized by Hampson. In a later checklist to the North American lepidopteran fauna, McDunnough (1938) did not list subgenera or any generic synonyms.

The Russian lepidopterist Kozhanchikov (1950) included a long list of synonyms for *Acronicta*: exactly copying Hampson's list, with the addition of *Chamaepora*. However, despite including these names as synonyms, several were used as subgenera. In addition to *Acronicta* (s. str.), he recognized *Triaena*, *Hyboma*, and *Pharetra*. He described one genus, *Subacronicta*, which would later float between generic and subgeneric status.

### **Late 20<sup>th</sup> century: bringing the genera back**

Despite the history of the genus, Forbes (1954) deemed *Apatela* to be the valid genus name instead of *Acronicta*. In fact, in a footnote he opined "I consider "*Acronicta*" a mere misprint, corrected in a later volume of the same work." That correction, however, was made by Treitschke (1825), and does not supersede the original description by Ochsenheimer. Forbes listed several subgenera, but with a caveat. "With the present confusion of names I cannot tell what are the proper subgeneric names for the sections of *Apatela*; probably Hübnerian names are available for most or all." Within Forbes' description of *Apatela* he listed five groups, separated by adult wing morphology, male genitalia, and larval characters. These groups were listed with subgeneric names; they corresponded most directly to Smith and Dyar's (1898) groups. In addition, some groups were broken down into subgroups, some in turn with their own subgeneric designations:



Forbes's Group 1 included larvae with dense secondary hair, matching Smith and Dyar's *americana* group. Group 1 was split into subgroups equivalent to what Forbes considered *Apatela* and *Acronycta*, based on adult hairs and the presence/absence of a basal dash on the forewing.

Group 2 had a mixture of disparate adult and larval morphologies; larvae were noted to have a moderate development of warts and setae. This group was considered equivalent to Chapman's *Cuspidia*, and matched Smith and Dyar's *lobeliae* group. Group 2 was split into three subgroups: one with no subgeneric equivalent, one with affinity to *Triaena*, and one with *Microcoelia*.

Group 3, with its spatulate hairs, matched Smith and Dyar's *persuasa* group.

Group 4, very similar in adult and larval appearance to Group 3, was aligned with Grote's *Lepitoreuma*, and corresponded to Smith and Dyar's *hamamelis* group.

Group 5, a mixture of *Pharetra* and *Viminia*, contained larvae with bristly tufts, like Smith and Dyar's *auricoma* group. Group 5 was split into two subgroups based adult characters, corresponding to *Pharetra* and *Eulonche*.

See Figure 4 for a comparison of these groups to Smith and Dyar (1898) and Rota et al. (2016). Forbes's intent was to focus on the species-level determinations in his work; he provided known groupings without making formal taxonomic decisions for generic-level names. In his description of a related genus, *Simyra*, he remarked on its similarity to the *Eulonche* group of

*Apatela*. Similarly he considered *Merolonche* to be “closely similar to *Apatela*, and perhaps not distinct”; *Agriopodes* was “hardly distinguishable from *Apatela*” (Forbes 1954). As so frequently turns out to be the case with Forbes’s taxonomic assessments, his observations were prescient, as *Simyra*, *Merolonche*, and *Agriopodes* were all later synonymized with *Acronicta* (Lafontaine and Schmidt 2010; Schmidt et al. 2014; Rota et al. 2016).

Despite, or perhaps because of, the complicated affair of *Acronicta* groups and subgenera, they were wholly avoided by Crumb (1956) in his larval opus. The species were, however, listed in the same general order as the groups of Smith and Dyar (1898) and Forbes (1954).

As new workers entered the acronictine arena, the delimitation of the genus continued to change. Subgenera of *Acronicta* experienced a resurgence in Japan, beginning with the work of Sugi. He described two new subgenera based on male genitalia: *Molybdonycta* and *Hylonycta* (Sugi 1979). These subgenera, among others, were raised to the genus level in the Moths of Japan, with Sugi as a co-author. In addition to genera now known from other subfamilies, the Japanese *Acronicta* sensu lato fauna was divided into nine genera: *Acronicta*, *Hyboma*, *Molybdonycta*, *Plataplecta*, *Triaena*, *Jocheaera*, *Hylonycta*, *Subacronicta*, and *Viminia* (Inoue et al. 1982).

One of the first European works to go back to using subgenera was a Spanish book of noctuids (Calle 1982), which delved deep into the literature for its taxonomic decisions. While it did not follow the Japanese example of elevating the taxa to full genera, it did recognize *Acronicta*, *Subacronicta*, *Triaena*, *Hyboma*, and *Viminia* as subgenera.

In North America, the checklist put together by Franclemont and Todd (1983) did not deal with subgenera, but offered an extensive list of synonyms for both genera and species. *Acronicta* was listed with 28 synonyms, encompassing all the names proposed by Hübner, Guenee, Butler, Grote, Chapman, Warren, and others (but not including Sugi's recent names). As in Crumb's work, *Acronicta* species were grouped so as to reflect presumed relatedness. This order generally matched earlier lists, but moved some of the groups around. Species were assigned numbers, which are still used by taxonomists and collection curators today.

Back in Japan, Sugi (1987) was undeterred by the synonymization of acronictine names in North American publications. He continued to follow Inoue et al. (1982), and included the generous complement of taxa (given above) as full genera in his larval work.

Poole proposed a similar arrangement as Franclemont and Todd in his series of publications: Poole's 1989 work on Noctuidae listed 23 synonyms of *Acronicta* (Poole 1989); his 1996 checklist added Sugi's *Hylonycta* and *Molybdonycta* as synonyms (Poole 1996). Poole's lists featured fewer names than Franclemont and Todd list because several misspellings were not included.

Concurrent with Poole's (1996) checklist, Beck (1996) published his interpretation of acronictine taxonomy – with a very different result. In addition to confirming the status of several oft-neglected genera (i.e. *Oxicesta*), he reinstated several synonyms/subgenera as full genera (status revived): *Triaena*, *Jocheaera*, *Subacronicta*, *Arctomyscis*, *Hyboma*, and *Viminia*. He also created the following genera: *Parasimyra*, with subgenera *Parasimyra* and *Transsimyra*; *Aneuviminia*;

and *Paraviminia*. The subgenus *Euviminia* was created for the revived genus *Viminia* (Beck 1996). As this was a work focused on European species, he did not include Inoue et al.'s (1982) names that had been applied to Asian taxa. Beck (1999) focused primarily on larval characters, in some cases basing new subgenera primarily on larval coloration. The same taxa were listed in his later work on European noctuid larvae.

As is commonly the case, different geographical areas were experiencing divergent opinions as to the circumscription of the genus *Acronicta*. In North America subgenera were set aside, and the genus was broadened to include a multitude of species. Asian taxonomists led the way in bringing back many names as full genera. In Europe the subgenera regained popularity, with Beck splitting the genus the mostly finely, proposing many new generic and subgeneric names, although most of his European workers all but ignored Beck's work because he was perceived as a splitter and to heavily influenced by larval characters.

### **21<sup>st</sup> century: reining in the subgenera**

As the century turned, the use of generic and subgeneric names for acronictines slowly dwindled – though they were harder to shake in Europe and Asia. A Russian key to insect genera included nine subgenera: *Acronicta*, *Triaena*, *Hyboma*, *Jocheaera*, *Viminia*, *Molybdonycta*, *Hylonicta*, *Plataplecta*, and *Subacronicta* (Kononenko 2003). Several of Beck's subgenera were listed as synonyms of *Acronicta* (*Euviminia*, *Aneuviminia*, and *Paraviminia*). In an account of European noctuid species, Fibiger and Hacker (2005) included *Acronicta*, *Subacronicta*, *Hyboma*, and *Viminia* as subgenera of *Acronicta* – a short list, ignoring the other various subgeneric names available for European species, including those crafted by Beck. Ahola and Silvonen's (2005)

European larval work avoided subgenera, instead listing them as synonyms of *Acronicta* – also ignoring Beck’s genera and subgenera. Faunal treatments in North America and Korea also avoided mention of subgeneric names (Covell 2005; Wagner 2005; Sohn 2006), as did as a work on acronictines of Israel (Kravchenko et al. 2006). It should be noted that subgenera may still be deemed useful by workers who do not include them in their publications. Field guides, for example, seldom employ subgenera. There does, however, appear to be a general consensus amongst lepidopterists worldwide to synonymize the various genera and subgenera of *Acronicta*. A few years later, another back-and-forth began. In the 11<sup>th</sup> volume of Noctuidae Europaeae, *Acronicta* was listed with 6 subgenera: *Acronicta*, *Hyboma*, *Jocleaera*, *Subacronicta*, *Triaena*, and *Viminia*. This work formally synonymized the remainder of Beck’s generic and subgeneric names, and was one of the few to address them at all (Fibiger et al. 2009).

A work on Chinese acronictines embraced a similar list of 8 subgenera – without *Hyboma* but with three Asian subgenera: *Hylonycta*, *Molybdonycta*, and *Plataplecta* (Han and Kononenko 2010). Meanwhile in North America, subgenera, as historically has been the case, were entirely avoided (Powell and Opler 2009; Lafontaine and Schmidt 2010). Kishida’s (2011) guide to the moths of Japan went with the trend of avoiding subgenera, and included many species in the large genus *Acronicta*. Focusing on Russian noctuid larvae, Matov and Kononenko (2012) chose not to list any subgeneric names for *Acronicta*, deviating from Kononenko’s previous publishing efforts where subgeneric designations were adopted. Wagner’s et al.’s (2011) latest guide, *Owlet Caterpillars of Eastern North America*, likewise had an inclusive *Acronicta*, though his choice to not include subgeneric names in his field guides is not indicative of their validity. The *Moths of Thailand* (Kononenko and Pinratana 2013) included two subgenera for their *Acronicta* species,

*Hyboma* and *Viminia*. A worldwide list of *Acronicta* subgenera was offered by Volynkin et al. (2015) in their assessment of the genus; they recognized 9 European and Asian subgenera – the effort appeared to be primarily based on Kononenko’s 2003 key to Russian insects.

Throughout this period subgeneric names were not elevated to full generic status, but wavered as to whether they belonged as subgenera or best ignored and treated as synonyms of *Acronicta* – a debate that will be prolonged by Rota et al.’s (2016) molecular phylogeny of Acronictinae. The analysis comprised species from North America, Europe, and Asia. The type species of 7 subgenera were included, only missing two Asian taxa: *Molybdonycta* and *Plataplecta*. In the resulting phylogeny, most subgenera were scattered throughout the tree of *Acronicta* species; a few subgenera were found to be polyphyletic. Three genera were synonymized with *Acronicta*: *Simyra*, *Eogena*, and *Oxicesta*; the authors treated the following subgenera as synonyms of *Acronicta*: *Hyboma*, *Hylonycta*, *Jocheaera*, *Subacronicta*, *Triaena*, and *Viminia* (Rota et al. 2016). It became clear that formal subgeneric names could not be assigned without an even more thoroughly sampled acronictine phylogeny. *Acronicta* species (and closely related taxa) from Australia, Africa, Central America, and additional species from Asia, Europe, and North America would need to be included sequenced and placed for the genus to be subdivided in a way that reflected presumed phylogenetic underpinnings. Once the relationships amongst *Acronicta* species are better known, it is possible, even likely, that subgeneric names will come back into common use, but with worldwide (as opposed to regionally-specific) meaning. Quite possibly some taxa will even be elevated to the level of full genera.

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## **Tables and Figures**

**Table 1.** Table of genera currently or formerly included in Acronictinae. Does not include complete list of genera from Hampson (1909), Forbes (1954), or the LepIndex (2005). \* = current membership in Acronictinae is unconfirmed.

Genus	Author, Year	Valid?	Synonym of	Region	Current subfamily	Reference consulted
<i>Acosmetia</i>	Stephens, 1829	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Acronicta</i>	Ochsenheimer, 1816	YES		World	Acronictinae	Harris, 1841
<i>Acronictoides</i>	Kozhanchikov, 1950	NO	<i>Gerbathodes</i>	Asia	n/a	Poole, 1989
<i>Acronycta</i>	Treitschke, 1825	NO	<i>Acronicta</i>	World	n/a	Poole, 1989
<i>Agriopodes</i>	Hampson, 1908	NO	<i>Acronicta</i>	North America	n/a	Schmidt <i>et al.</i> , 2014
<i>Amphia</i>	Guenée, 1852	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Anacronicta</i>	Warren, 1909	YES		Asia	Pantheinae	Kitching and Rawlins, 1999
<i>Aneuviminia</i>	Beck, 1996	NO	<i>Acronicta</i>	Europe	n/a	Fibiger <i>et al.</i> , 2009
<i>Anterastria</i>	Sugi, 1982	YES		World	Noctuinae	Lafontaine and Schmidt, 2010
<i>Apatela</i>	Stephens, 1829	NO	<i>Acronicta</i>	World	n/a	Fibiger <i>et al.</i> , 2009
<i>Apatela</i>	Hübner, 1806	NO	<i>Acronicta</i>	World	n/a	Poole, 1989
<i>Apsarasa</i>	Moore, 1867	YES		Asia	Hadeninae	Holloway, 1989
<i>Arctomyscis</i>	Hübner, 1820	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Arsilonche</i>	Lederer, 1857	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Auchecranon</i>	Berio, 1978	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Bathya</i>	Walker, 1865	YES		South America	Pantheinae	Poole, 1989
<i>Bathytricha</i>	Turner, 1920	YES		Australia	Hadeninae	Zilli <i>et al.</i> , 2005
<i>Belciades</i>	Kozhanchikov, 1950	YES		Asia	Dyopsinae	Rota <i>et al.</i> , 2016
<i>Belciana</i>	Walker, 1862	YES		Eurasia	Calpinae	Goater <i>et al.</i> , 2003
<i>Borbotana</i>	Walker, 1858	YES		Asia	Amphipyrrinae	Poole, 1989
<i>Bryopolia</i>	Boursin, 1954	YES		Asia	Cuculliinae	Poole, 1989
<i>Callopietria</i>	Hübner, 1821	YES		World	Eriopinae	Lafontaine and Schmidt, 2010
<i>Canna</i>	Walker, 1865	NO	<i>Nacna</i>	Asia	n/a	Poole, 1989
<i>Cerma</i>	Hübner, 1818	YES		North America	Acronictinae	Wagner, 2007
<i>Chamaepora</i>	Warren, 1910	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Charadra</i>	Walker, 1865	YES		Holarctic	Pantheinae	Ahola and Silvonen, 2005
<i>Chasmina</i>	Walker, 1856	YES		World	Bagisarinae	Kitching and Rawlins, 1999
<i>Chloronycta</i>	Schmidt and Anweiler, 2014	YES		North America	Acronictinae	Rota <i>et al.</i> , 2016
<i>Colocasia</i>	Ochsenheimer, 1816	YES		World	Pantheinae	Fibiger <i>et al.</i> , 2009
<i>Comachara</i>	Franclemont, 1939	YES		North America	Acronictinae	Wagner <i>et al.</i> , 2006
<i>Cometa</i>	Sodoffsky, 1837	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Cosmodes</i>	Guenée, 1852	YES		Australia	Hadeninae	Kitching and Rawlins, 1999
<i>Cranionycta</i>	Lattin, 1949	YES		Asia	Acronictinae	Kishida, 2011
<i>Craniophora</i>	Snellen, 1867	YES		World	Acronictinae	Rota <i>et al.</i> , 2016
<i>Cryphia</i>	Hübner, 1818	YES		World	Bryophilinae	Zahiri <i>et al.</i> , 2013
<i>Cuspidia</i>	Chapman, 1893	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Cymatophoropsis</i>	Hampson, 1894	YES		World	Acronictinae*	Kishida, 2011
<i>Daseochaeta</i>	Warren, 1907	YES		World	Cuculliinae	Ronkay and Ronkay, 1995
<i>Demas</i>	Stephens, 1829	NO	<i>Colocasia</i>	North America	n/a	Poole, 1989
<i>Diloba</i>	Boisduval, 1837	YES		Europe	Dilobinae	Zahiri <i>et al.</i> , 2013
<i>Diphthera</i>	Hübner, 1806	YES		North America	Nolidae (no subfamily)	Zahiri <i>et al.</i> , 2013
<i>Diphtherocome</i>	Warren, 1907	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Dypterygia</i>	Stephens, 1829	YES		World	Noctuinae	Lafontaine and Schmidt, 2010
<i>Dyzela</i>	Walker, 1858	YES		Asia	Bagisarinae	Zahiri <i>et al.</i> , 2013
<i>Eogena</i>	Guenée, 1852	NO	<i>Acronicta</i>	Europe	n/a	Rota <i>et al.</i> , 2016
<i>Episema</i>	Ochsenheimer, 1816	YES		Europe	Cuculliinae	Poole, 1989
<i>Eulonche</i>	Grote, 1873	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Euromioia</i>	Staudinger, 1892	YES		Asia	Acronictinae*	Kishida, 2011
<i>Euviminia</i>	Beck, 1996	NO	<i>Acronicta</i>	Europe	n/a	Fibiger <i>et al.</i> , 2009
<i>Feralia</i>	Grote, 1874	YES		North America	Amphipyrrinae	Lafontaine and Schmidt, 2010
<i>Gaujonia</i>	Dognin, 1891	YES		South America	Pantheinae	Kitching and Rawlins, 1999
<i>Gerbathodes</i>	Warren, 1911	YES		Asia	Pantheinae	Rota <i>et al.</i> , 2016
<i>Goenycta</i>	Hampson, 1909	YES		Asia	Acronictinae*	Kononenko and Pinratana, 2013
<i>Hampsonia</i>	Kozhanchikov, 1950	NO	<i>Craniophora</i>	Eurasia	n/a	Poole, 1989
<i>Harrisimemma</i>	Grote, 1873	YES		World	Acronictinae	Rota <i>et al.</i> , 2016

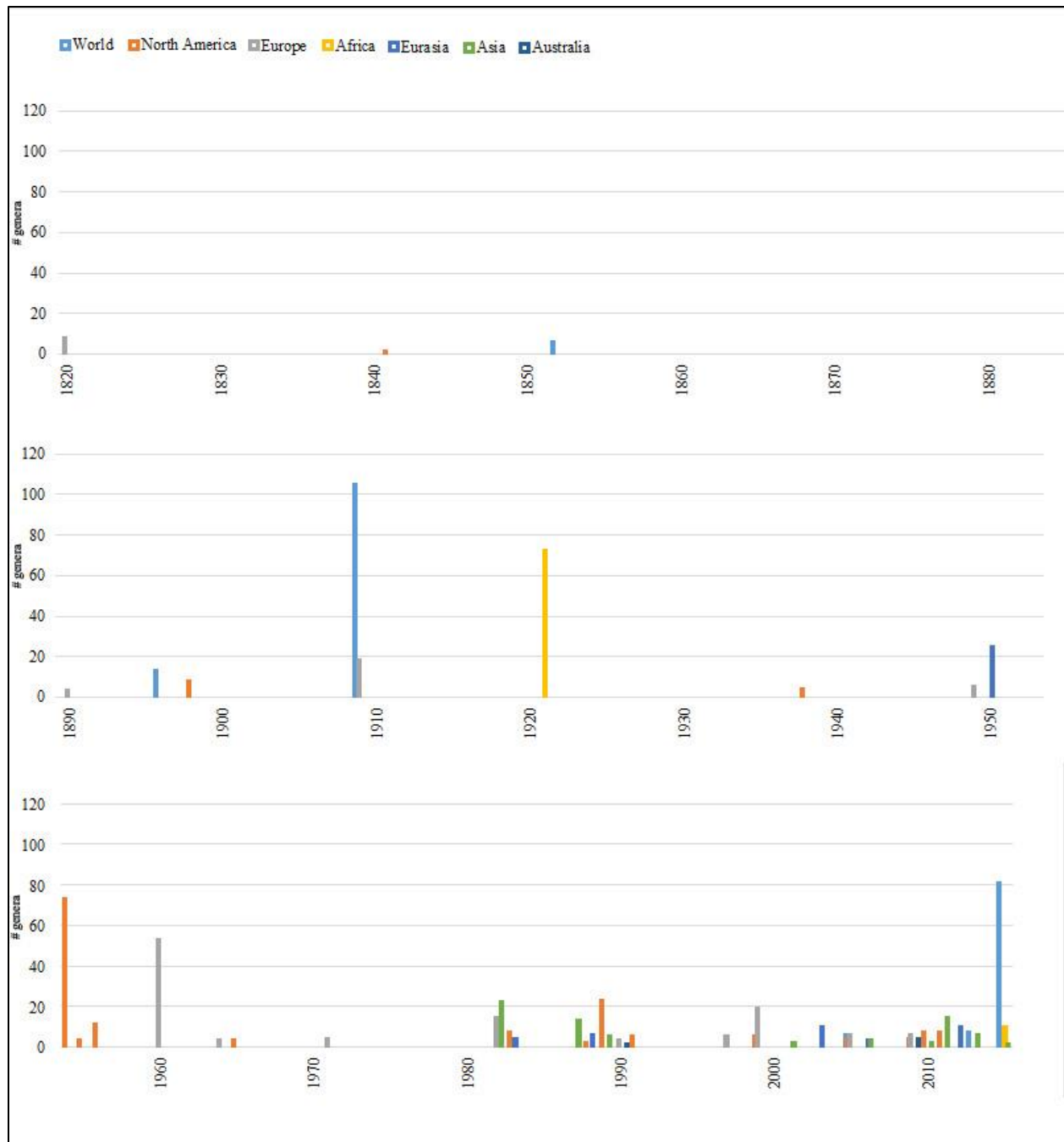


Table 1. continued

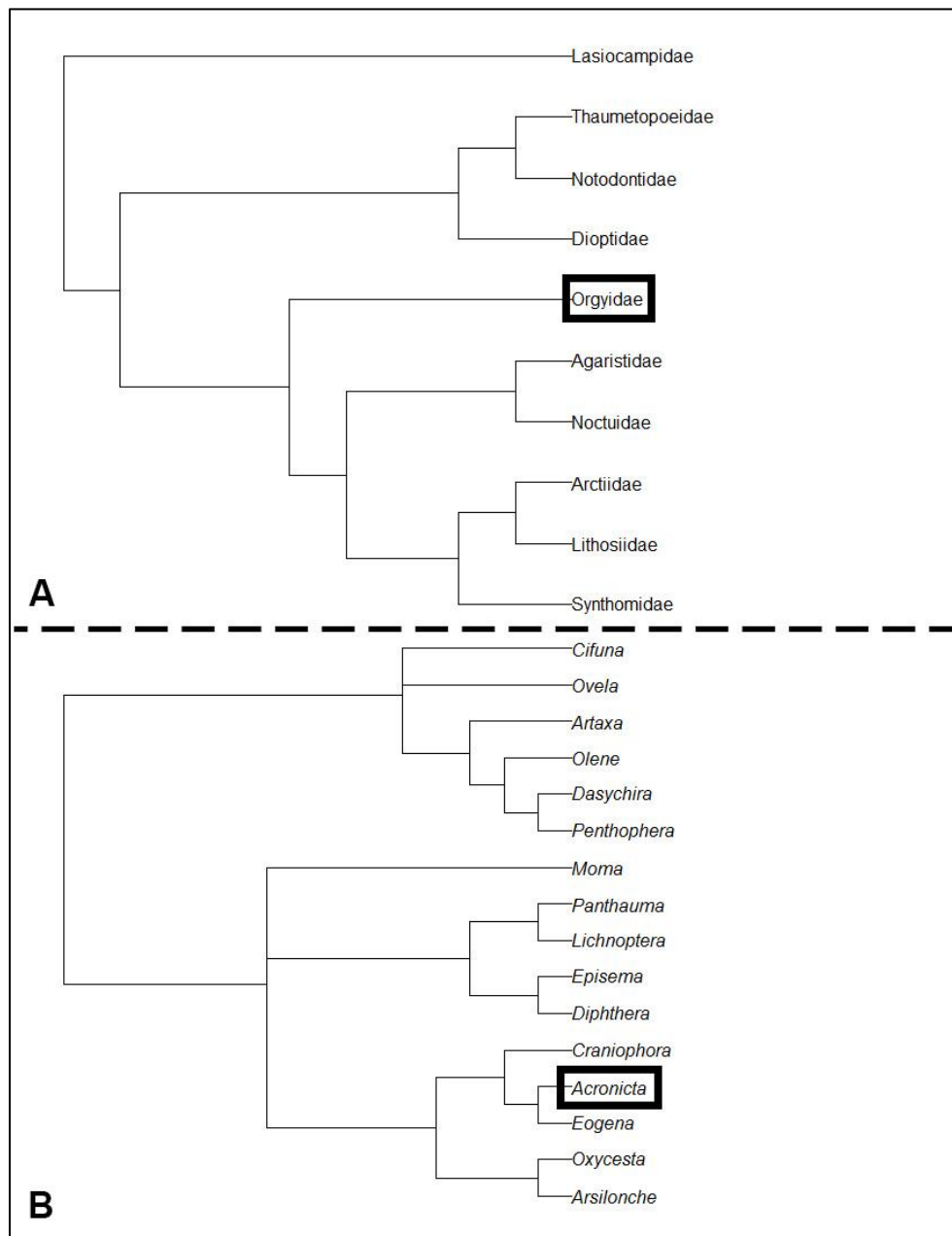
Genus	Author, Year	Valid?	Synonym of	Region	Current subfamily	Reference consulted
<i>Hyboma</i>	Hübner, 1820	NO	<i>Acronicta</i>	Eurasia	n/a	Poole, 1989
<i>Hylonycta</i>	Sugi, 1979	NO	<i>Acronicta</i>	Asia	n/a	Poole, 1996
<i>Jocheaera</i>	Hübner, 1820	NO	<i>Acronicta</i>	Eurasia	n/a	Poole, 1989
<i>Kuehneana</i>	Hacker and Saldaitis, 2011	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Leiometopon</i>	Staudinger, 1888	YES		Eurasia	Hadeninae	Kitching and Rawlins, 1999
<i>Lepitoreuma</i>	Grote, 1873	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Leuconycta</i>	Hampson, 1909	YES		North America	Condicinae	Lafontaine and Schmidt, 2010
<i>Libyphaenis</i>	Hampson, 1918	YES		Africa	Acronictinae*	Poole, 1989
<i>Lichnoptera</i>	Herrich-Schäffer, 1856	YES		Central+South America	Pantheinae	Hodges <i>et al.</i> , 1983
<i>Lophonycta</i>	Sugi, 1970	YES		Asia	Acronictinae	Rota <i>et al.</i> , 2016
<i>Madeuplexia</i>	Viette, 1960	YES		Africa	Acronictinae*	De Prins and De Prins, 2015
<i>Mastiphanes</i>	Grote, 1882	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Megacronycta</i>	Grote, 1873	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Meleneta</i>	J.B. Smith, 1908	YES		North America	Pantheinae	Lafontaine and Schmidt, 2010
<i>Merolonche</i>	Grote, 1882	NO	<i>Acronicta</i>	North America	n/a	Lafontaine and Schmidt, 2010
<i>Microcoelia</i>	Guenée, 1852	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Molyena</i>	Walker, [1866]	NO	<i>Thalatha</i>	Australia	n/a	Holloway, 1989
<i>Molybdonycta</i>	Sugi, 1979	NO	<i>Acronicta</i>	Asia	n/a	Poole, 1996
<i>Moma</i>	Hübner, 1820	YES		World	Dyopsinae	Rota <i>et al.</i> , 2016
<i>Momophana</i>	Grote, 1874	NO	<i>Feralia</i>	North America	n/a	Poole, 1989
<i>Mourea</i>	Orfila and Rossi, 1957	NO	<i>Victrix</i>	Europe	n/a	Poole, 1989
<i>Nacna</i>	Fletcher, 1865	YES		Asia	Amphipyriinae	Rota <i>et al.</i> , 2016
<i>Narcotica</i>	Sugi, 1982	YES		Asia	Acronictinae	Rota <i>et al.</i> , 2016
<i>Nyctobrya</i>	Boursin, 1957	NO	<i>Cryphia</i>	Europe	n/a	Poole, 1989
<i>Oxicesta</i>	Hübner, 1819	NO	<i>Acronicta</i>	Europe	n/a	Rota <i>et al.</i> , 2016
<i>Pachylepis</i>	Felder, 1874	NO	<i>Yepcalphis</i>	Asia	n/a	Poole, 1989
<i>Panthauma</i>	Staudinger, 1892	YES		Eurasia	Pantheinae	Kitching and Rawlins, 1999
<i>Panthea</i>	Hübner, 1820	YES		World	Pantheinae	Zahiri <i>et al.</i> , 2013
<i>Parasimyra</i>	Beck, 1996	NO	<i>Acronicta</i>	Europe	n/a	Fibiger <i>et al.</i> , 2009
<i>Paraviminia</i>	Beck, 1996	NO	<i>Acronicta</i>	Europe	n/a	Fibiger <i>et al.</i> , 2009
<i>Pharetra</i>	Hübner, 1818	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Philorgyia</i>	Grote, 1896	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Plagideicta</i>	Warren, 1914	NO	<i>Mudaria</i>	Asia	n/a	Holloway, 1989
<i>Plataplecta</i>	Butler, 1878	NO	<i>Acronicta</i>	Asia	n/a	Poole, 1989
<i>Platyprosopa</i>	Warren, 1913	YES		Asia	Acronictinae*	Kononenko and Pinratana, 2013
<i>Polionycta</i>	Hampson, 1909	YES		Central America	Hadeninae	Kitching and Rawlins, 1999
<i>Polygrammate</i>	Hübner, 1809	YES		North America	Acronictinae	Rota <i>et al.</i> , 2016
<i>Prometopus</i>	Guenée, 1852	YES		Europe	Eriopinae	Fibiger and Hacker, 2007
<i>Pseudepunda</i>	Butler, 1890	NO	<i>Acronicta</i>	Asia	n/a	Poole, 1989
<i>Raphia</i>	Hübner, 1821	YES		World	Raphiinae	Lafontaine and Schmidt, 2010
<i>Sasunaga</i>	Moore, 1881	YES		Asia	Amphipyriinae	Poole, 1989
<i>Semaphora</i>	Guenée, 1841	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Sematophora</i>	Agassiz, 1847	NO	<i>Acronicta</i>	Europe	n/a	Poole, 1989
<i>Simyra</i>	Ochsenheimer, 1816	NO	<i>Acronicta</i>	World	n/a	Rota <i>et al.</i> , 2016
<i>Sinocharis</i>	Püngeler, 1912	YES		Asia	Acronictinae	Rota <i>et al.</i> , 2016
<i>Spodoptera</i>	Guenée, 1852	YES		North America	Noctuinae	Lafontaine and Schmidt, 2010
<i>Subacronicta</i>	Kozhanchikov, 1950	NO	<i>Acronicta</i>	Eurasia	n/a	Poole, 1989
<i>Subleuconycta</i>	Kozhanchikov, 1950	YES		Asia	Acronictinae*	Kishida, 2011
<i>Thalatha</i>	Walker, 1862	YES		Asia	Acronictinae*	Kishida, 2011
<i>Thalathoides</i>	Holloway, 1989	YES		Asia	Acronictinae*	Kononenko and Pinratana, 2013
<i>Thyatirides</i>	Kozhanchikov, 1950	NO	<i>Cymatophoropsis</i>	Eurasia	n/a	Poole, 1989
<i>Transsimyra</i>	Beck, 1996	NO	<i>Acronicta</i>	Europe	n/a	Fibiger <i>et al.</i> , 2009
<i>Triaena</i>	Hübner, 1818	NO	<i>Acronicta</i>	Eurasia	n/a	Poole, 1989
<i>Tricholonche</i>	Grote, 1896	NO	<i>Acronicta</i>	North America	n/a	Poole, 1989
<i>Trichosea</i>	Grote, 1875	YES		Europe	Pantheinae	Fibiger <i>et al.</i> , 2009
<i>Trisuloides</i>	Butler, 1881	YES		Asia	Pantheinae	Behounek <i>et al.</i> , 2011
<i>Tycracona</i>	Moore, 1882	YES		Asia	Hadeninae	Kitching and Rawlins, 1999
<i>Uniramodes</i>	Berio, 1976	YES		Africa	Acronictinae*	Schmidt, pers. comm.
<i>Victrix</i>	Staudinger, 1879	YES		Europe	Bryophilinae	Fibiger <i>et al.</i> , 2009
<i>Viminia</i>	Chapman, 1890	NO	<i>Acronicta</i>	World	n/a	Poole, 1989
<i>Xanthomantis</i>	Warren, 1909	NO	<i>Trisuloides</i>	Eurasia	n/a	Poole, 1989

**Table 2.** Genera currently in Acronictinae. The final column indicates whether the genus has been sampled in the molecular phylogeny by Rota *et al.* (2016). All taxa with “no” in this column are considered unconfirmed acronictines, and should be sampled for future phylogenetic analyses.

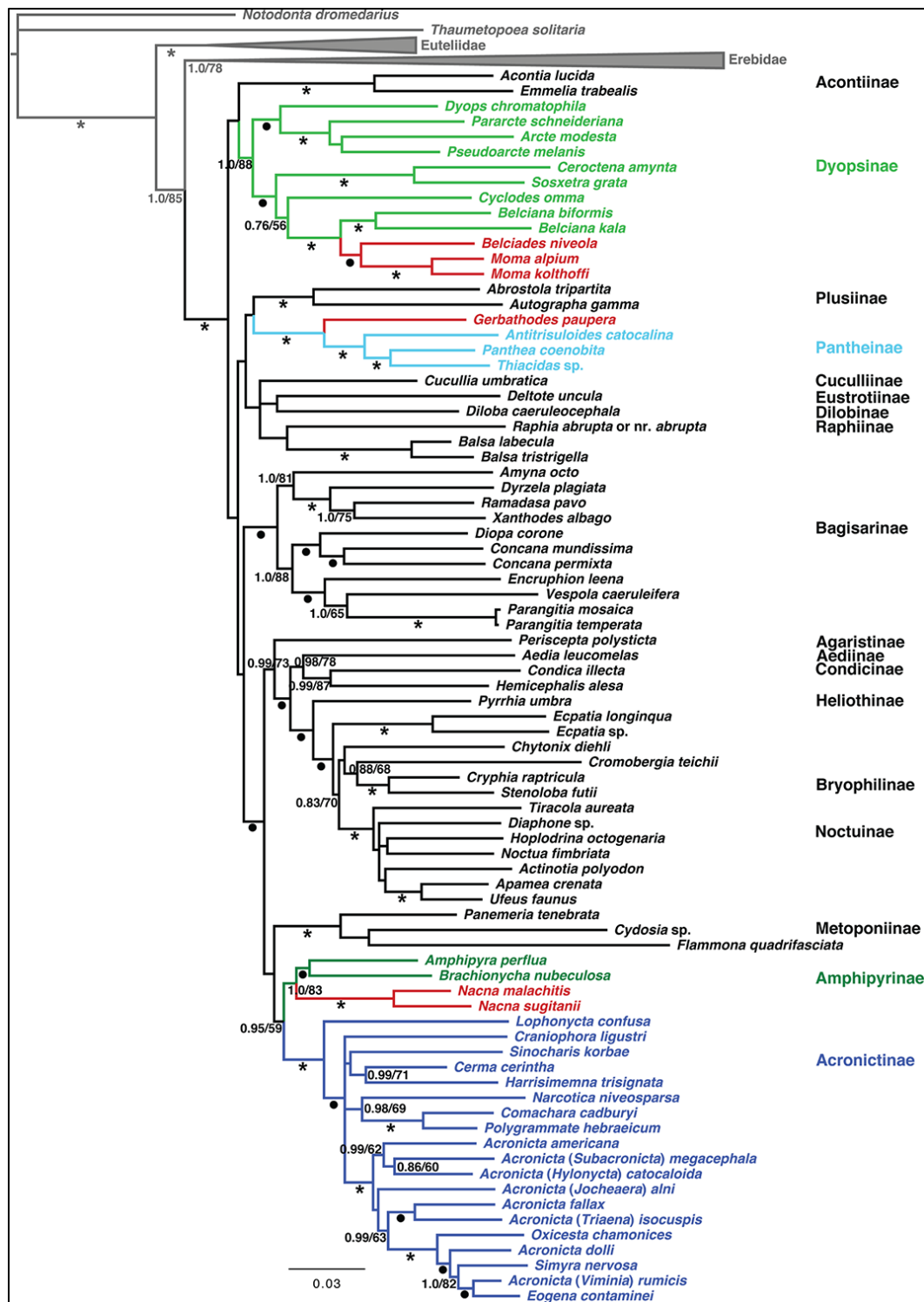
Genus	Author, Year	Region	Sampled in molecular phylogeny
<i>Acosmetia</i>	Stephens, 1829	Africa	No
<i>Acronicta</i>	Ochsenheimer, 1816	World	Yes
<i>Amefrontia</i>	Hampson, 1899	Asia	No
<i>Amphia</i>	Guenée, 1852	Africa	No
<i>Andobana</i>	Viette, 1965	Africa	No
<i>Apocalymnia</i>	Hampson, 1908	Asia	No
<i>Apsaranycta</i>	Hampson, 1914	Asia	No
<i>Auchecranon</i>	Berio, 1978	Africa	No
<i>Cerma</i>	Hübner, 1818	North America	Yes
<i>Chloronycta</i>	Schmidt and Anweiler, 2014	North America	Yes
<i>Comachara</i>	Franclemont, 1939	North America	Yes
<i>Cranionycta</i>	Lattin, 1949	Asia	Yes
<i>Craniophora</i>	Snellen, 1867	World	Yes
<i>Cymatophoropsis</i>	Hampson, 1894	World	No
<i>Diphtherocome</i>	Warren, 1907	Africa	No
<i>Euromioia</i>	Staudinger, 1892	Asia	No
<i>Goenycta</i>	Hampson, 1909	Asia	No
<i>Harrisimemna</i>	Grote, 1873	World	Yes
<i>Kuehneana</i>	Hacker and Saldaitis, 2011	Africa	No
<i>Libyphaenis</i>	Hampson, 1918	Africa	No
<i>Lophonycta</i>	Sugi, 1970	Asia	Yes
<i>Madeuplexia</i>	Viette, 1960	Africa	No
<i>Narcotica</i>	Sugi, 1982	Asia	Yes
<i>Platyprosopa</i>	Warren, 1913	Asia	No
<i>Polygrammate</i>	Hübner, 1809	North America	Yes
<i>Sinocharis</i>	Püngeler, 1912	Asia	Yes
<i>Subleuconycta</i>	Kozhanchikov, 1950	Asia	No
<i>Thalatha</i>	Walker, 1862	Asia	No
<i>Thalathoides</i>	Holloway, 1989	Asia	No



**Figure 1.** Trends in the generic composition of Acronictinae from 1820 to 2016, from 70 publications. Bar height is the number of genera included in Acronictinae in one publication. Bars are color coded by geographic region of publication.

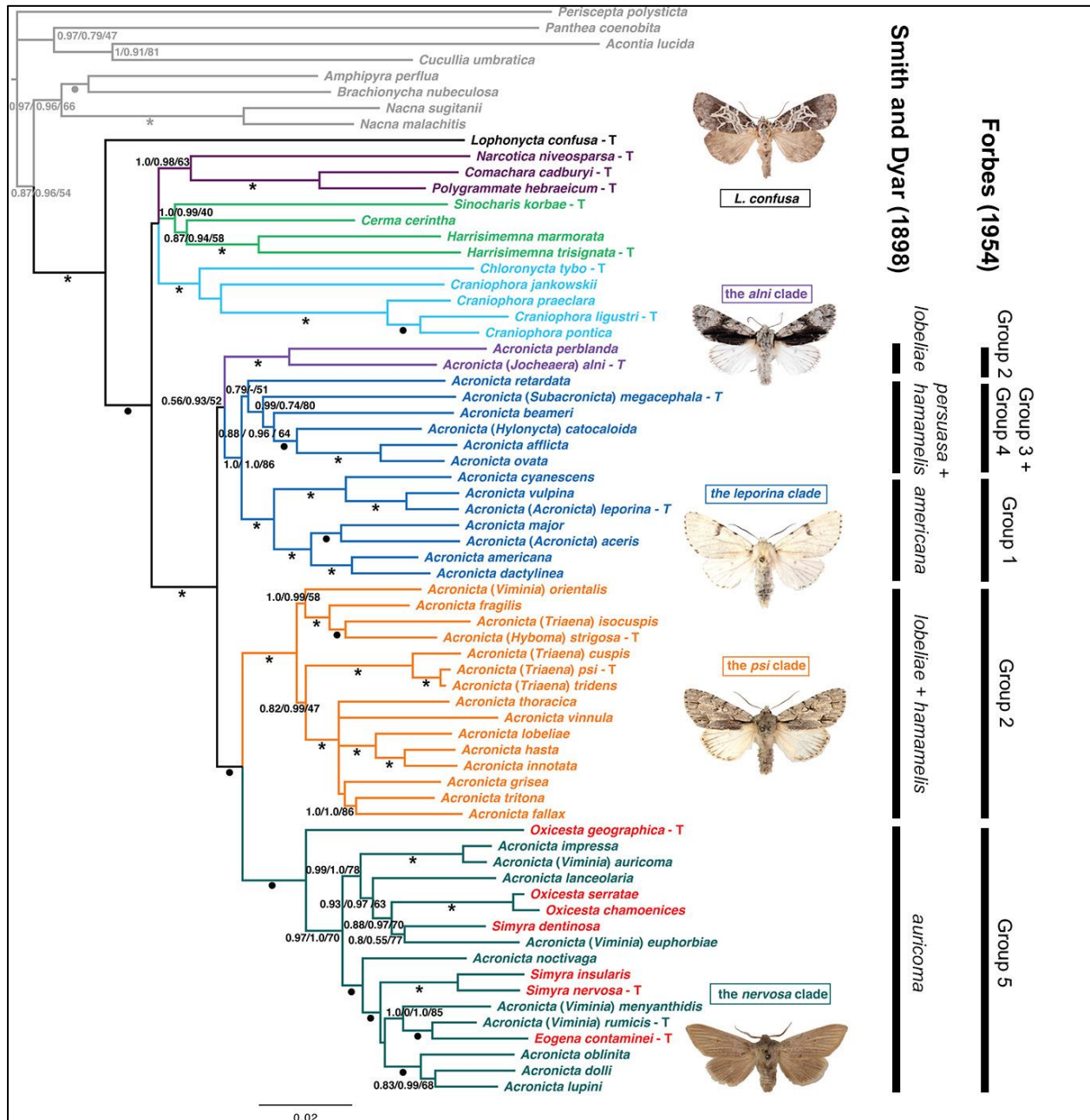


**Figure 2.** Tree adaptations from Kozhanchikov, 1950. A: placement of subfamily Orgyidae among lepidopteran subfamilies. B: placement of genera within Orgyidae, highlighting the position of *Acronicta*.



**Figure 3.** Figure from Rota et al. (2016), illustrating placement of Acronictinae (in blue) among noctuid subfamilies. Outgroups are shown in gray. Branch support notation: PP – Bayesian posterior probability; ML BS – maximum likelihood bootstrap; \* PP=1.0, ML BS=100; • PP=0.99–1.0, ML BS=90–100; no support listed when PP<0.95 or ML BS<50; otherwise

support listed with first number representing the PP from the four-partitioned Bayesian analysis and the second the ML BS.



**Figure 4.** Comparison of species group concepts within *Acronicta*. Tree figure by Rota et al. (2016), with species groups represented by colored branches. T = type species. Outgroups are shown in gray. Branch support notation same as in Figure 3. Species groups for Smith and Dyar (1898) and Forbes (1954) represented by labeled black bars.

## Chapter 2: Systematics and Phylogeny of Acronictinae

### Introduction

The noctuid moth subfamily Acronictinae has had a tumultuous taxonomic past. Without any universal morphological synapomorphies in either the adults or larvae, membership in the taxon has vacillated between highly restricted (1 genus) and catch-all (>20 genera) concepts. Likewise, this pattern holds true for the nominal genus *Acronicta*, which has ranged from narrow (<10 species) to broad (>200 species). These discrepancies follow both temporal and geographic trends; typically, workers focus on taxa from their own region (Kozhanchikov 1950; Forbes 1954; Inoue et al. 1982; Holloway 1989; Fibiger et al. 2009; and many others). Worldwide treatments have suffered from grouping unrelated taxa (Hampson 1909), ignoring taxa outside of Europe and North America (Boisduval and Guenée 1852; Grote 1896; Fibiger and Hacker 2005), or only touching upon a few taxa (Speidel et al. 1996). While acronictine species have been used in some modern molecular phylogenies (Weller et al. 1994; Zahiri et al. 2013b), the sampling has been too sparse to address any questions concerning relationships within the group. A worldwide synthesis of acronictine relationships is needed before evolutionary questions can be addressed with rigor.

This task is now under study by a group of noctuid workers from North America and Europe. The findings of Rota et al. (2016) represent the first molecular phylogenetic analysis of Acronictinae. The study had three overarching goals: to find the placement of Acronictinae within Noctuidae, to determine the membership of taxa within Acronictinae and *Acronicta*, and to provide a framework for further evolutionary inquiry. Species derived from North America, Europe, and Japan. While this still leaves major regions unsampled (Africa, Australia, mainland

Asia), the chosen taxa represent nearly all known genera and species groups. One mitochondrial and seven nuclear genes were sequenced, which have been used successfully in other lepidopteran phylogenetic studies (Zahiri et al. 2011, 2012, 2013a, 2013b; Regier et al. 2017). Maximum likelihood and Bayesian analyses were performed on partitioned sequence data in order to generate trees. Acronictinae were found to be sister to Amphipyrinae at a mid-level position within Noctuidae, but with very weak support. Genera that grouped into a clade with *Acronicta* (*Lophonycta*, *Narcotica*, *Comachara*, *Polygrammate*, *Sinocharis*, *Cerma*, *Harrisimemna*, *Chloronycta*, and *Craniophora*) encompass the current understanding of Acronictinae. Two genera which formerly anchored their own subfamilies, *Sinocharis* (Sinocharinae) and *Lophonycta* (Lophonyctinae), had their subfamilial names formally synonymized. Several recent taxonomic decisions were upheld, such as the inclusion of *Comachara* (Wagner et al. 2006) and *Cerma* (Wagner 2007a, 2007b) within Acronictinae. Four genera formerly included in Acronictinae, *Belciades*, *Gerbathodes*, *Moma*, and *Nacna*, were re-assigned to Pantheinae, Dyopsinae, and Amphipyrinae respectively. Perhaps more controversially, three genera were found to be subordinate within the nominate genus, and were synonymized with *Acronicta*: *Eogena*, *Oxicesta*, and *Simyra*. Within the nominate genus, four species groups were identified/circumscribed, but no formal species group or subgeneric names were proposed.

This chapter builds upon the framework provided by Rota et al. (2016) in order to further explore the relationships among genera of Acronictinae. The three major goals of this study are to see how increased taxon sampling affects hypothesized relationships, to assess the robustness of the topology through different phylogenetic analyses, and to provide trees that can be used to



address evolutionary questions about *Acronicta* and the subfamily more generally. It will also be possible to further investigate the arrangement of species groups, and whether they align with past attempts at assigning species group or subgeneric names. An additional 35 *Acronicta* species were sampled for the same eight genes, bringing the total of *Acronicta* species to 82.

## Methods

### *Specimen collection*

Adult moths, either dry (< 10 years old) or preserved in 95-100% ethanol, were procured for DNA extraction of all species except three, for which larvae in 95% ethanol were used. One specimen was sampled for each species. One or more legs were removed from each specimen for DNA extraction. Voucher specimens for Nearctic and Asian taxa are deposited at the University of Connecticut, USA and the University of Guelph, Canada. Vouchers for Palearctic taxa are deposited at the University of Turku, Finland and Lund University, Sweden.

Specimens were collected by, or with the help of, the following individuals (in order of the number of species added to the study): *North America*: David Wagner, Reza Zahiri, Brigitte Zacharczenko, Steve Johnson, Evan Rand, Jen Bundy, Darryl Willis, Benedict Gagliardi, Moria Robinson, Michael Singer, Chuck Harp, David Bettman, Loran Gibson, Delmar Cain, John Palting, Barb Bartell, Ron Wielgus, Eric Quinter, Vernon Brou, Peter Haggard, and Erin Haugh; *Europe*: Jadranka Rota and Niklas Wahlberg; *Asia*: Markku Pellinen and Keitaro Eda. Specimen details (locality, collection date, and collectors) are given in Supplementary Table S1.

### *Taxonomic benchmarks*

The taxonomic decisions of Rota et al. (2016) were followed. These include the synonymy of *Eogena*, *Oxicesta*, and *Simyra* with the genus *Acronicta*, the synonymy of all *Acronicta* subgeneric names, and the placement of four former acronictine genera into other subfamilies. One alteration was made; *Craniophora jankowskii* was moved to *Cranionycta*, as per Kishida (2011) and Kiss (pers. comm.).

#### *Taxon sampling and species groups*

A total of 101 taxa were selected for this study: 82 species of *Acronicta*, 13 other species (representing 10 other genera) of Acronictinae, and 6 outgroup taxa. All ingroup taxa and two outgroup taxa from the Acronictinae analysis of Rota et al. (2016) were used (n=62), and four taxa from the Noctuidae analysis in the same work. Species groups for *Acronicta* species were provisionally assigned based on the Rota et al. tree and previous literature, and confirmed after tree building. Two outgroup taxa from Rota et al. (2016) were used, plus 4 other outgroup taxa. The following acronictine genera were included: *Acronicta*, *Cerma*, *Chloronycta*, *Comachara*, *Cranionycta*, *Craniophora*, *Harrisimemna*, *Lophonycta*, *Narcotica*, *Polygrammate*, and *Sinocharis*. The type species was sequenced for all genera except *Cerma* and *Cranionycta*. Outgroup taxa include noctuid species formerly included in Acronictinae, but now relegated to other subfamilies; the genera include: *Belciades* (Dyopsinae), *Gerbathodes* (Pantheinae), *Moma* (Dyopsinae), and *Nacna* (Amphipyridae). *Nacna* is considered the closest outgroup taxon due to its position in Amphipyridae (Figure 14, Rota et al. 2016; Kevin Keegan unpublished data), so trees were rooted using the remaining outgroup taxa. All species and species groups used in this study are listed in Table 1.

### *DNA extraction, amplification, and sequencing*

Sequence data were used from eight molecular markers: one mitochondrial gene region, and seven nuclear gene regions. The mitochondrial gene region was the beginning and end sequences of *cytochrome oxidase subunit I* (COI). The seven nuclear single-copy protein coding genes were *elongation factor-1alpha* (EF-1 $\alpha$ ), *ribosomal protein S5* (RpS5), *carbamoylphosphate synthase domain protein* (CAD), *cytosolic malate dehydrogenase* (MDH), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), *isocitrate dehydrogenase* (IDH), and *wingless*. These gene regions have yielded credible phylogenies in multiple molecular studies of Noctuidae, and Acronictinae specifically (Zahiri et al. 2013b; Schmidt et al. 2014; Regier et al. 2017; Rota et al. 2016; Zenker et al. 2016). Sequences for 62 taxa appeared in Rota et al. (2016), while the remainder were newly generated. GenBank accession numbers (for some but not all taxa) are listed in Supplementary Table S2. DNA extraction, PCR amplification, and sequencing followed the Lepidoptera-specific protocols of Wahlberg and Wheat (2008). Not all gene regions were successfully sequenced for all specimens; the number of bases and overall percentage of nucleotides recovered are given in Supplementary Table S2.

### *Datasets*

Due to the varied success of sequencing for different samples (especially older specimens), a subset of taxa was created with a 50% coverage cut-off point. This reduced the 101-taxon dataset to 91 taxa, removing 10 specimens with low-sequence coverage. These will hereafter be referred to as the *complete* dataset and the *50% coverage* dataset respectively. The taxa removed from the *50% coverage* dataset are noted in bold in Supplementary Table S2. Having these two datasets

for comparison serves to determine whether the addition of low-coverage specimens impacts the topology of the phylogeny.

### *Sequence statistics*

Each gene was examined separately in PAUP\* (version 4.0) (Swofford 2003) to determine the percentage of varied and parsimony informative sites, alpha shape parameter, transition/transversion (TS/TV) ratio, and AT bias (via base composition) (Table 2). Sequence statistics for each gene and the combined dataset were calculated for all taxa and for all the ingroup taxa (Acronictinae). The TS/TV ratios and  $\alpha$  shape parameters were estimated under the HKY85+ $\Gamma$  model of sequence evolution.

### *Partitioning and model selection*

Before phylogenetic analyses were conducted, the sequences were partitioned to account for variable rates of evolution among different gene regions and codon positions. Underpartitioning can have significant impacts on a tree, and may result in highly supported but incorrect topologies (Kainer and Lanfear 2015). For this study, different partitioning schemes were compared in order to reveal problematic clades (Rota 2011). The concatenated sequence data (for both the *complete* and *50% coverage* datasets) were partitioned in two ways using the program PartitionFinder (Lanfear et al. 2012): by codon position (for each gene) and with kmeans partitioning (Frandsen et al. 2015). Codon-position partitioning was run with 24 possible parts, and resulted in 12 partitions for both the *complete* and *50% coverage* datasets. Kmeans partitioning, which treats each nucleotide position as potentially having its own evolutionary rate

and groups sites accordingly, resulted in 11 partitions for the *complete* dataset and 9 partitions for the *50% coverage* dataset.

Each gene was then evaluated separately and partitioned by codon position. The individual gene analyses only included taxa for which the respective genes were represented with at least 50% coverage, resulting in the following datasets: CAD = 90 taxa, COI = 93, EF1 $\alpha$  = 78, GADPH = 82, IDH = 38, MDH = 82, RpS5 = 98, and wingless = 93. PartitionFinder provided support for partitioning each gene into three partitions (first, second, and third codon positions) except wingless, which had two (grouping the first and second codon position). Individual genes were not partitioned using kmeans. Models for all partitions were chosen by PartitionFinder.

#### *Removal of COI*

For the *complete* and *50% coverage* datasets, a separate analysis was done without COI to determine the impact of COI on the topology and support of the phylogeny. Since one taxon (*Oxicesta geographica*) had only COI available, it was dropped from all COI-removal analyses.

#### *Removal of Outgroups*

To test for the sensitivity of each analysis to outgroup selection, some analyses were run with outgroup taxa removed. The acronictine *Lophonycta confusa*, recovered as sister to the remainder of the subfamily in Rota et al. (2016) and in all analyses here including outgroups, was used as the outgroup for rooting.

#### *Maximum Likelihood*

Maximum likelihood analyses were conducted with GARLI v. 2.01 (Zwickl 2006) using the Computational Biology Core Facility of the University of Connecticut. Analyses were run for the *complete* and *50% coverage* datasets with partitioning by codon position, and kmeans partitioning. Analyses without COI were done for the *complete* and *50% coverage* datasets with partitioning by codon position. A maximum likelihood analysis was run for each gene, partitioned by codon position. All GARLI analyses were run with 1000 bootstrap replicates, from which the best tree was chosen.

### *Bayesian Inference*

Bayesian analyses were conducted with MrBayes (Ronquist et al. 2012) using the Computational Biology Core Facility of the University of Connecticut. Analyses were run for the *complete* and *50% coverage* datasets with partitioning by codon position. Analyses without COI were done for the *complete* and *50% coverage* datasets with partitioning by codon position. Models were chosen by PartitionFinder. All Bayesian analyses were run for 10 million generations with four heated chains, sampling trees every 1000 generations; 30% of trees were discarded as burn-in. Priors were left at defaults. Results were evaluated using log-likelihood plots in Tracer v.1.6 (Rambaut and Drummond 2007).

### *SVD Quartets*

SVD quartet analyses were conducted with PAUP\* (version 4.0) (Swofford 2003). SVD Quartets were used to estimate species trees under the coalescent model in order to take into account incomplete lineage sorting (Chifman and Kubatko 2014). Analyses were run for the *complete*

and 50% coverage datasets without partitioning. Each analysis was run with 20,000 quartets and 100 bootstraps replicates. Each analysis generated a 50% majority rule consensus tree.

### *Tree Figures and Comparisons*

Trees were visualized using the packages APE (Paradis et al. 2004), distory (Chakerian and Holmes 2013), phangorn (Schliep 2011), and phytools (Revell 2012), implemented in R (R Development Core Team 2008). Trees were compared side by side using the *phylo.diff* command in distory, which highlights branch differences between trees. Trees were also compared by their topology, bootstrap support values, and posterior probability values.

### *Summary Trees*

Summary trees were created to represent the *complete* datasets. Each summary tree utilized the topology of the Bayesian and ML codon partitioned phylogenies, and the ML kmeans partitioned phylogeny. Branches with less than 70% bootstrap support or 95% posterior probability were collapsed.

### *Support Values*

Support values were grouped into categories of high, moderate, and low support. For Bayesian analyses, posterior probability values are high = 1, moderate = 0.95 to 0.99, low <0.95. For maximum likelihood and SVD quartet analyses, bootstrap support values are: high = 90 to 100, moderate = 70 to 89, low < 70. A bootstrap value over 70 is usually considered reliable, and has a history of use in phylogenetic analyses. Using simulation, Hillis and Bull (1993) showed that

for their analyses, bootstrap values < 70% generally overestimated accuracy, while bootstrap values > 90% usually underestimated accuracy.

All analysis types and partitioning schemes are listed in Table 3.

## Results

### *Summary Trees*

By collapsing branches with low support, it is easier to visualize trends. The maximum likelihood summary tree (Figure 1) and Bayesian summary tree (Figure 2) are similar in their topologies. These phylogenies, along with results from all the other trees, help to demonstrate which taxa and nodes are poorly supported, and which clades are well-supported. For example, the variable arrangement of the acronictine sister genera illustrate the uncertainties in their relatedness. The maximum likelihood kmeans summary tree (Figure 3) illustrates the unusual yet uncertain placement of the *alni* clade.

### *Monophyly of Acronicta*

*Acronicta* was recovered as monophyletic in all but two treatments: the gene trees for COI and IDH. In the COI gene tree *Cranionycta jankowskii* came out as sister to *A. retardata* with low support (BS = 51), a clade in turn sister to the remaining *Acronicta* with negligible support (BS = 7). These two taxa hail from different continents, so ancient hybridization is unlikely. The IDH gene tree had few taxa (38) and some unusual arrangements. Rooting on the one remaining outgroup taxon (*Gerbathodes paupera*) caused a clade of multiple acronictine genera to split *Acronicta*, separating the *increta* clade and *leporina* clade from the rest. This tree also yielded an



unusual position for *A. retardata*, which formed a basal polytomy with the outgroup and the rest of the tree. Removal of *Gerbathodes* and rooting with *Lophonycta* solved this issue. While issues remain in the deeper nodes, support values increase closer to the tips, and the species group relationships are mostly intact. For the remaining gene trees, support for *Acronicta* monophyly ranged from BS = 8 to 71. Bayesian trees all gave high support (PP = 1), except for the *complete* analysis without COI (polytomy, PP = 0.53). Maximum likelihood trees gave low to high support (BS = 43 to 100) for *Acronicta* monophyly; trees from the *complete* dataset generally had the highest support at this node and for species groups.

#### *Position of Lophonycta*

The genus *Lophonycta* was consistently recovered as sister to the remainder of the subfamily Acronictinae. Support for this position was high in all Bayesian analyses (PP = 1), except for the *complete* no-COI analyses (PP = 0.85). Maximum likelihood analyses ranged from low (BS = 62) to high support (BS = 100). Two gene trees, CAD and EF1a, gave low to high support (BS = 63, 92). The remainder of the gene trees had *Lophonycta* intermixed with other acronictine genera in a variety of clades. Support values for these positions were low (BS < 68), but *Lophonycta* was never associated with outgroup taxa. An argument was made by Rota et al. (2016) for *Lophonycta* to remain within Acronictinae, instead of constituting its own subfamily (with a few species).

#### *The Backbone*

Within the genus *Acronicta*, there is much interest (and differences of opinion) over the arrangement of species groups/subgenera. Five clades are recognized in this work: *alni*, *leporina*,

*increta*, *nervosa*, and *psi*. The phylogenetic position of the smaller *alni* clade has implications for the evolution of larval morphology, especially the paddle-shaped setae shared with several species of the *increta* clade. The most common relationship found, with a varying degree of support, places the *alni* clade sister to (*increta*, *leporina*), which in turn are sister to (*psi*, *nervosa*)), see Figure 4 and Table 4. This matches the results found by Rota et al. (2016), though they had not distinguished the *increta* clade from the *leporina* clade.

All Bayesian analyses resulted in PP = 1 for the most basal *Acronicta* node (node 1 in Figure 4), except for the *complete* analysis with the removal of COI (PP = 0.65). Maximum likelihood BS values for *complete* and *50% coverage* datasets ranged from low (BS = 43) to high (BS = 100). Within the *complete* dataset, both codon partitioning and kmeans partitioning gave strong support (BS = 100), and the removal of COI gave moderate support (BS = 79). Within the *50% coverage* dataset, the removal of COI gave the best support (BS = 87), followed by kmeans partitioning (BS = 51) and codon partitioning (BS = 43). SVD quartets had low support for both *complete* and *50%* (BS = 30, 44). Two gene trees resulted in this arrangement but with low support, CAD (BS = 54) and MDH (BS = 14). Four alternative arrangements of these clades were found for the 6 remaining genes, with BS support ranging from 8 to 71.

At the node connecting the *alni* clade to *increta* and *leporina*, Bayesian analyses resulted in low to high support (PP = 0.66 to 1). Maximum likelihood trees, including two gene trees (CAD and wingless) had low to high support (BS = 20 to 97); the *50%* codon partitioning analysis had the highest support. The *50%* SVD tree also had this arrangement (BS = 45). Five other topologies for the placement of the *alni* clade were recovered. Kmeans partitioning for both the *complete*

and 50% datasets placed *alni* sister to (*psi*, *nervosa*) (BS = 49, 90) as did COI and EF1a (BS = 4, 37). The remaining gene trees resulted in polytomies or had *alni* sister to the rest of *Acronicta*, all with low support. The *complete* SVD tree caused the *alni* clade to render the *increta* clade polyphyletic (BS = 26).

Within the *alni* clade, two of the members are clearly related by their nearly identical adult and (exceptionally unique) larval morphology: European *A. alni* and North American *A. funeralis*. The North American *A. perblanda*—a small, rare species—bears no obvious wing marking affinities to the other two species, and is less than half the wingspan of most *Acronicta*. In the original description, it is hypothesized to be affiliated with members here grouped within the *psi* clade (Ferguson 1988). The larva is unknown, but unlikely to be as showy as *alni* and *funeralis*. *A. perblanda* is recovered as sister to (*alni*, *funeralis*) in every tree besides the gene tree for RpS5. Support for this clade in Bayesian trees was high (PP = 0.98 to 1), and low to high in ML trees (BS = 56 to 100).

More distally, the relationship between the *increta* clade and the *leporina* clade (node 3 in Figure 4) has variable support, likely due to the presence of rogue taxa (discussed later). Support in Bayesian analyses ranged from PP = 0.51 to 1, while support in maximum likelihood analyses ranges from BS = 11 to 96. The grouping of the *nervosa* clade and the *psi* clade is more robust and well supported. Bayesian analyses range from PP = 0.82 to 1, while maximum likelihood analyses range from BS = 45 to 100.

### *The Tips*

Relationships among species within *Acronicta* clades with shorter branch lengths were generally conserved, with moderate to high support, across the different analyses. Species groupings varied, but many sister taxon relationships remained unperturbed by partitioning, inference method, or the removal of COI. The pairs *A. vinnula* and *A. lepetita*, *A. hastulifera* and *A. dactylina*, *A. alni* and *A. funeralis*, and *A. psi* and *A. tridens* were recovered as sister taxa in every treatment. *A. barnesi* and *A. perditia* were recovered as sister taxa in every treatment except one gene tree. Other strongly supported species-pairs include *A. fallax* and *A. tritona*, *A. fragilis* and *A. heitzmani*, and *A. falcula* and *A. grisea*.

### *The Acronictine Genera*

Within the acronictine genera, three main clades are apparent (Figure 5 and Table 5). The “P” clade consists of *Polygrammate* and *Comachara*. The “C” clade consists of *Chloronycta*, *Cranionycta*, and *Craniophora*. The “S” clade consists of *Sinocharis*, *Cerma*, and *Harrisimemna*. The genus *Narcotica*, when present in the *complete* analyses or gene trees, is found in either the “P” or “S” clade. The arrangement of these genera, including which genera were sister to *Acronicta*, varied considerably among analyses. The sister clade to *Acronicta* in most analyses was either the “P” clade, or an arrangement of all of these main basal clades (Figure 5 and Table 5), however in no case was there high support on all nodes. Low support was found for two gene trees (*Ef1 $\alpha$* , *CAD*), while the remaining gene trees had either extremely low support (*BS* < 10) or non-monophyletic arrangements of the genera within these clades.

Within the “C” clade, three possible arrangements were recovered (Figure 6 and Table 6). The arrangement of this clade has implications for the taxonomy of each genus. If either *Chloronycta* or *Cranionycta* were found to emerge from within *Craniophora* there could be justification for synonymy. This did not occur in any trees for this study. However, that is only because *Cranionycta jankowskii* was pulled from *Craniophora*. If this species were left within *Craniophora*, the genus would be rendered polyphyletic by *Chloronycta* in most trees.

### *Rogue Taxa*

The species *A. retardata* has no clear phylogenetic placement based on adult or larval morphology. It has been listed with other members of the *increta* clade due to wing pattern similarities and its small size (Hodges et al. 1983). The larva, however, is markedly divergent in morphology and host plant use from those of other *Acrionicta*. In these analyses, it most often came out as sister to (*increta* group, *leporina* group) (Figure 7 and Table 7). This relationship is plausible, considering the species shares host plant affinities with the *leporina* clade (i.e., some members feed on *Acer* species). Strong support was found for *complete* and 50% Bayesian analyses and ML analyses (PP = 1, 1; BS = 100, 93). The removal of COI resulted in the same relationship, but with lower support (PP = 0.86, 0.97; BS = 24, 97). SVD quartets for the 50% dataset had low support (BS = 64). Eight other placements of *A. retardata* were found for the kmeans partitioned analyses, individual gene trees, and SVD quartets for the *complete* dataset. These all had low support (BS = 26 to 60). Both kmeans analyses placed *A. retardata* sister to the *increta* clade, but with low support (BS = 27, 60). These discrepancies are not due to low sequence coverage: *A. retardata* had 87% coverage.

Within the *increta* clade, one species has doubtful membership: *A. megacephala*. In every *complete* MB and ML analysis it is sister to the remainder of the *increta* clade, typically with low support. Within gene trees it is either sister to the *increta* clade or sister to both *increta* and *leporina*. Its most unusual position is found in the *complete* SVD quartet tree, where it forms a clade with *A. retardata*, in turn sister to the *alni* clade (Supplementary Figure S23). The support values are quite low (BS = 26 for both nodes). Whether this uncertainty is biologically meaningful or due to low sequence coverage (34%) is unclear. The larva shares morphological characters and host plant affinities with both the *increta* and *leporina* clades. Its hairiness, head color, and feeding on *Populus* and *Alnus* species lends it more to the *leporina* clade than the *increta* clade, which are primarily *Quercus* feeders. The resting posture and dorsal coloration of the larvae, and wing patterns of the adult (in particular the distinctly ringed orbicular spot) align it with the *increta* clade. It is possible *A. megacephala* is deserving of its own species group assignment; it has previously been assigned to the genus *Subacronicta* due to its unique features (Kozhanchikov 1950).

Another species difficult to place was *A. geographica*, which had low sequence coverage (21%); the only gene region recovered was COI. It was formerly in the genus *Oxicesta*, along with *A. serratae* and *A. chamoenices* (Rota et al. 2016). Due to strong similarities in adult and larval morphology (Beck 1999), including adult genitalia (Kiss, pers. comm.), it stands to reason the three species would form a clade within *Acronicta*. While *A. serratae* and *A. chamoenices* were sister taxa in every tree (for which they were included) with moderate to high support, *A. geographica* was typically recovered as sister to the entire *nervosa* clade. This result is highly suspicious, and is likely due to the low sequence coverage of all three species. It is unlikely that

the sequence for *A. geographica* was contaminated, as a BOLD (Barcode of Life Database) search using the COI sequence yielded a 100% match to previously published sequences for *A. geographica*.

### *Removal of Outgroups*

For the *complete* and 50% ML and MB analyses, removal of outgroups had little to no impact on the topology within the genus *Acronicta*. Differences were noticed in the arrangement of the sister genera. In each case, removal of outgroups pulled the acronictine sister taxa into a clade (excluding *Acronicta* and *Lophonycta*). Within the clade, these trees had a different arrangement from all the others (Figure 5, Table 5), but with low support.

## **Discussion**

### *Comparison of Phylogenetic Analyses*

Maximum likelihood (ML) and Bayesian (MB) methods are currently among the most widely used and trusted means for generating molecular phylogenies. While maximum likelihood uses bootstrapping to generate nodal support, Bayesian methods result in posterior probability values; these two types of support cannot be easily compared (Huelsenbeck et al. 2002; Douady et al. 2003). Maximum likelihood is determined to be more conservative, and thus less likely to give false positives (= false but highly supported nodes) (Douady et al. 2003). It is beneficial to use both (and other) methods in order to judge the robustness of a phylogenetic hypothesis, and determine which clades are sensitive to analysis type. Within lepidopteran studies, both reliability measures have a long history of use for phylogenetic analysis of nuclear and mitochondrial sequences; they are typically used in conjunction with each other (Zahiri et al.

2011, 2012, 2013a, 2013b; Schmidt et al. 2014; Rota et al. 2016; Zenker et al. 2016). For this study, ML and MB trees were compared across multiple treatments. In all of these the backbone of the tree and arrangement of clades within *Acronicta* were consistent (Supplementary Figures S1 – S14). This is clearest in the summary trees, in which poorly supported clades were collapsed (Figures 1, 2, and 3). Discrepancies were found in the arrangement of acronictine sister genera, and between some species in the species-group clades.

ML and MB trees were also compared to phylogenies generated via SVD Quartets, a coalescent-based method to estimate species trees. This method is most useful to deal with incomplete lineage sorting (ILS), which can cause gene trees to differ from the species tree (Chou et al. 2015). SVD Quartet trees for both the *complete* and *50% coverage* datasets had the same species-group backbone arrangements as the ML and MB trees, with variable bootstrap support. The greatest differences, again, involved relationships among acronictine genera, and the arrangement of some species within the *Acronicta* species-groups, i.e., in those areas of low bootstrap support regardless of analysis type. All three methods offer suggestions on which areas of the acronictine phylogeny are robust, and which require further scrutiny, although some arrangements suggested by SVD seem suspect and unsupported based on morphology and known life history data.

### ***Partitioning Schemes***

One of the variables used to test the robustness of the acronictine phylogeny was the choice of partitioning scheme. By accounting for variation in substitution rates among nucleotide positions with multiple models, partitioning has the potential to offer increased accuracy in phylogenetic



inference (Brown and Lemmon 2007). However, under- or overpartitioning can oversimplify or overfit the data (Kainer and Lanfear 2015). Experimenting with different partitioning schemes has demonstrated the impact it can have on a phylogeny (McGuire et al. 2007; Rota 2011). Two methods were used here: partitioning by codon position, and kmeans partitioning. Both methods used PartitionFinder (Lanfear et al. 2012) on the concatenated sequence data. One method used the traditional PartitionFinder algorithm to partition by the codon position of each gene. Each dataset (*complete*, *50% coverage*, and the taxa for each individual gene) was partitioned separately. Kmeans partitioning was done on a subset of datasets. Unlike partitioning by codon position, kmeans does not use any input categories; each nucleotide position is considered separately and positions are grouped in an iterative fashion (Frandsen et al. 2015). The largest effect of partitioning scheme on relationships was in the placement of the *alni* clade in *Acronicta*. While nearly every other tree placed the *alni* clade as sister to *increta* and *leporina*, trees partitioned by kmeans placed the *alni* clade as sister *nervosa* and *psi* (Figure 3). Support varied depending on the number of taxa (see Supplementary Figures S11 and S12). Kmeans partitioning also resulted in a unique placement of *A. retardata*, not shared by other treatments. Another study comparing partitioning schemes found kmeans performs poorly in part due to the grouping of invariant sites into potentially large partitions (Baca et al. 2017). Based on my assessment of the morphological traits of larvae, it seems unlikely that the *alni* clade could be sister to *nervosa* and *psi* – questioning the utility of kmeans partitioning for this dataset.

### ***Effect of COI***

The gene COI, the first portion of which is commonly used for identification (barcoding) of animals, has limitations in phylogenetic analyses. While it may perform well for taxa that have

diverged < 20 million years ago (Marshall et al. 2016), it can be inaccurate for determining deeper splits (Hajibabaei et al. 2006). COI also tends to exhibit incomplete lineage sorting, making them potentially susceptible to introgression (Phillips et al. 2013). The Barcode of Life project (Hajibabaei et al. 2007) and a wealth of other papers (e.g., Ballard and Whitlock 2004) warn against inferring phylogenetic trees made solely from COI (or other mitochondrial sequences). Others make strong arguments for their utility, especially when combined with nuclear DNA (Fisher-Reid and Wiens 2011). Overall the inclusion of mitochondrial markers with nuclear genes—with a range of evolutionary rates—is encouraged (Moore 1995; Rubinoff and Holland 2005). COI was removed from some analyses to determine the impact this gene region has on the acronictine topology. While there was no disruption to the *Acronicta* species-group backbone, some support values were lowered (Table 4). The arrangements of acronictine genera were unique in the no-COI trees, forming two arrangements that differed from all the rest (Figure 5). The COI gene tree (Supplementary Figure S15), when considered on its own, provided very low support for acronictine genera and the *Acronicta* backbone; the nodes with highest support were near the tips of the tree. In this case COI is not considered to have a drastic effect on the acronictine topology, though some support is gained through its addition.

### ***Outgroup Selection***

Outgroup selection can have myriad effects on the topology of phylogenies (Lecointre et al. 1993). For example, dissimilarity of sequences, such as % G+C content or substitution rate, between outgroup and ingroup taxa, will confound molecular models. This typically results from choosing outgroup taxa which are too distantly related to the ingroup. Therefore different in group arrangements can be returned depending on the outgroup choice (Rota-Stabelli and

Telford 2008; Ware et al. 2008; Puslednik and Serb 2008). This study compared the usage of multiple outgroup taxa vs. the removal of outgroup taxa (which used the acronictine *Lophonycta confusa* for rooting). The removal of outgroups had no effect on the topology of the genus *Acronicta*, and mild effects on support values. Larger changes were noted in the arrangement of the remaining acronictine genera, and which taxa were considered sister to *Acronicta*. For both the ML and MB analyses, removal of outgroups resulted in the clustering of acronictine genera into one clade, sister to *Acronicta* (with *Lophonycta* as the outgroup). Since most trees have low support for these sister-genus arrangements, including the trees with outgroups removed, the validity of any particular arrangement remains equivocal.

### ***Gene Trees vs Species Trees***

In addition to the treatments using concatenated sequence data, separate trees were developed for each gene region. Individual gene trees were analyzed to look for the sources of low support values or anomalous phylogenetic placements. The discordance among gene trees and species trees due to lineage sorting is a pervasive issue in systematics, and is to be expected (Degnan and Rosenberg 2006). Adding more sequences may not be a solution, studies with 100s of loci still do not typically find a match between individual gene trees and the resulting species tree (Degnan and Rosenberg 2009; Ruane et al. 2015). This was true of this study; none of the gene trees matched the concatenated ML, MB, or SVD trees. Some gene trees appeared to perform better than others due to taxon sampling; although it may be safer to say that genes successfully sequenced from fewer taxa had more aberrant topologies (see Supplementary Figures 15 – 22). As expected, individual gene trees typically yielded different *Acronicta* backbone topologies with low support, and highest support for some of the tip pairings and a few small clades.

### ***Effects of Missing Data (DNA and taxa)***

When taxa are observed to behave errantly in a topology (readily apparent in the individual gene trees, Supplementary Figures 15 – 22), the original sequences can be examined for issues. Typically these “rogue taxa” have poor sequence coverage for that gene, or in the case of concatenated analyses, for all genes. Without much sequence to work with, analyses will group these taxa based on fragments which may not reflect their true relatedness. For this study, sequence coverage ranged from 11% to 96%. One solution, utilized in this paper, is to remove poorly performing taxa by choosing an arbitrary cut-off point for sequence coverage (in this case, 50%). Another solution would be to re-sequence species with low coverage so that the genes are better represented. However, the source of failure may not be easily addressed. Age and moisture can degrade the DNA of pinned specimens, making it difficult to extract intact genetic material. The rarity of a species or locality may make it difficult to procure a fresher specimens for many taxa. This reveals a dilemma: to exclude taxa with low sequence coverage at the expense of poorer taxon sampling, or include those taxa with the knowledge that their phylogenetic placement may not be accurate. Some argue that missing data may not necessarily have deleterious effects on a phylogeny, and that it is better to include more information (even if it is incomplete) (Wiens 2003; Wiens and Morrill 2011; Streicher et al. 2016). Others have demonstrated that missing data can significantly skew both ML and MB analyses, urging caution (Lemmon et al. 2009). This study approached this dilemma by removing taxa with large amounts of missing data. The *complete* dataset included all sampled taxa regardless of missing sequence data. The *50% coverage* dataset included only those taxa with 50% or more of the sequence data, removing 10 taxa from the analyses. Comparing these datasets across all treatments, no general

patterns emerged. The *Acronicta* backbone topology remained consistent, and variability at the other nodes is intermixed with the other phylogenetic variables (partitioning, outgroups, etc.). While some taxa with poor sequence coverage end up in unusual places (see *A. geographica*, Supplementary Figures S1, S5, S7, S11, and S13), their presence does not significantly alter the topology of the tree.

There is another aspect to the missing data argument: incomplete taxon sampling at a global level. While *Acronicta* was well sampled for this study, the remaining acronictine genera were sparsely sampled. Notably, the genus *Craniophora* is known to have up to 26 species (Poole 1989), with the majority of diversity in Asia; 10 species are known from China (Han and Kononenko 2010). This study sampled only four species, with two present in the 50% dataset. There are many other acronictine genera not sampled at all for this study, primarily from Russia, Southeast Asia, Africa, and Australia. And as noted above, the closest outgroup taxa for the Acronictinae are not yet known with certainty. Thus until we can acquire, sequence and include additional taxa weakly supported aspects of our analyses should be considered preliminary. Conversely, many of relationships with *Acronicta* appear to be robust, and I doubt that the addition of additional taxa or sequence data will perturb the stronger nodes reported here.

Regardless of the proportions of missing data, for either DNA or taxa, these phylogenies would benefit from additional nuclear gene sequences. Advances in Next Generation Sequencing stand to offer hundreds to thousands of additional nuclear genes from which to infer phylogenies (Breinholt et al. [accepted]; Lemmon and Lemmon 2013). While adding more genes doesn't always improve the accuracy of a species tree (Philippe et al. 2011; Ruane et al. 2015), it may be

an avenue worth exploring to see if we can bring resolution to poorly supported clades, especially for genus-level relationships in Acronictinae.

### ***Fast Radiation***

While it will be possible to increase nodal support with increased taxon sampling and by adding to existing sequence data, some parts of a phylogenetic tree may remain difficult to fully resolve due to the speed of cladogenesis. Rapid radiations manifest as a series of short internal branches on a tree, though this pattern can also reflect inappropriate gene selection, modeling, or other analytical issues (Whitfield and Kjer 2008; Giarla and Esselstyn 2015). Insects are known to have many ancient, difficult-to-resolve radiations (Whitfield and Kjer 2008; Misof et al. 2014).

On the acronictine tree there are two areas that appear to represent rapid radiations: the relationship between *Acronicta* and the other acronictine genera, and the (deep) relationships among the five *Acronicta* species groups identified in this study (Figure 8). These regions are always represented by short internal branches, with support values that vary among analyses. It is possible that the selected genes have either been evolving too quickly or too slowly, leaving these middle areas unresolved.

It would be interesting to explore the underlying causes for both radiations. Mapping of hostplant usage and larval morphologies around these two areas of diversification would be worthy of investigation, but as of yet, life histories are not known for several of the key genera. Perhaps the addition of molecular clock data would reveal geographical, geological, or climatological events that could have promoted speciation rates.

### *Implications for Taxonomy*

These results support the major findings of Rota et al. (2016). Species in the three genera synonymized with *Acronicta* (*Eogena*, *Oxicesta*, and *Simyra*) all remain nested within the genus. *Sinocharis* remained solidly amongst the acronictine genera, and *Lophonycta* was well supported as the sister taxon to the rest of the subfamily. One deviation was the movement of *Craniophora jankowskii* into *Cranionycta*. Evidently the male genitalia of *jankowskii* are a better fit for *Cranionycta* (Adam Kiss unpublished data). If *C. jankowskii* were to remain in *Craniophora*, it would render the genus paraphyletic, due to the placement of *Chloronycta* (Figure 6). Further taxon sampling of both *Craniophora* and *Cranionycta* are needed to determine (and refine) the monophyly of each genus. The relationships among the remaining genera of Acronictinae also suffer from undersampling, which is evident in their variant topologies and low support values in the phylogenetic treatments presented here. While the membership of each genus within the subfamily is confirmed, their relationships to each other will require additional data. There are several Old World genera that have at some point been treated as acronictines that remain to be investigated. The addition of these taxa in future studies should bring clarity to the acronictine phylogeny.

This study supports the grouping of *Acronicta* into species groups, and the potential value of recognizing subgenera in the future. *Acronicta* has a long history of splitting and subdivision, i.e., where taxa that are demonstrably subordinate (based on this phylogenetic study within the nominate genus) are recognized as full genera (Grote 1896; Inoue et al. 1982; Beck 1996; Fibiger et al. 2009, this thesis Chapter 1). All previous attempts suffered from geographical (parochial) biases, and relied on morphological characters. This study, a preliminary but global examination

of phylogenetic relationships with Acronictinae, provides a much stronger basis for the circumscription of monophyletic genera and the identification of subgenera/genera within the cosmopolitan nominate genus.

However, even with molecular phylogenies and the distinct *leporina*, *increta*, *alni*, *psi*, and *nervosa* clades, there are still problematic taxa. *Acronicta retardata* and *A. megacephala* require further genetic sampling or further taxon sampling to be confidently placed in a clade (or shown to represent a unique entity of equal standing). The addition of taxa from Asia, South Africa, Australia, and other undersampled regions will very likely add support and robustness to the acronictine phylogeny and classifications based on it. It is recommend that until a more thorough, worldwide sampling is achieved, no formal names should be assigned to *Acronicta* species groups. Application of names for *Acronicta* species groups (e.g., subgenera) will only serve to increase confusion until they can be applied consistently across the genus. Almost assuredly, other groupings will reveal themselves, once the acronictine faunas of Africa, Australia, and Southeast Asia are better known.

### ***Implications for Morphological Evolution***

A well-supported phylogeny is an essential tool in the study of character evolution. By mapping morphological, behavioral, and other life history traits, patterns and trends can be tested in a phylogenetic framework. For *Acronicta*, this will be especially powerful for the study of their fascinating and varied larval traits. *Acronicta* caterpillars sport an array of setal types, coloration, resting postures, defensive behaviors, and diet breadths; not to mention their penchant for



mimicry and hypermetamorphosis. A phylogeny will help elucidate the ancestral conditions for the many of the associated traits, and clarify synapomorphies for genera and species groups.

### ***Moving Forward***

Presently, I and my collaborators are gathering acronictine genera and species from around the world for phylogenetic analysis. Our goal is to have a representative from every genus currently proposed to be in the subfamily, in order to support their inclusion or exclusion from Acronictinae. In all cases our goal will be to acquire the type species or a species that is demonstrably allied to it. A list of all candidate genera has been compiled by Zacharczenko. Within acronictine genera, and especially the cosmopolitan nominate genus and *Craniophora* + *Cranionyctya*, more extensive species sampling will help to clear up uncertainties about monophyly. By including *Acronicta* species from across the entire range of the genera, species groups can be more certainly circumscribed and, where necessary, formally named. By defining the generic members of Acronictinae we can build support for a globally recognized definition for the subfamily. With more complete taxon sampling we can answer many more questions about taxonomy, morphology, and evolutionary history in this subfamily with greater confidence.

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## Tables and Figures

**Table 1.** List of species and their species group affiliations per this study. Taxa are arranged alphabetically by species group, then species. Taxa newly sequenced for this study are marked with an asterisk (\*).

Species	Group	Species	Group	Species	Group
<i>Acronicta alni</i>	alni	<i>Acronicta euphorbiae</i>	nervosa	<i>Acronicta mansueta</i> *	psi
<i>Acronicta funeralis</i> *	alni	<i>Acronicta geographica</i>	nervosa	<i>Acronicta morula</i> *	psi
<i>Acronicta perblanda</i>	alni	<i>Acronicta impleta</i> *	nervosa	<i>Acronicta orientalis</i>	psi
<i>Acronicta afflicta</i>	increta	<i>Acronicta impressa</i>	nervosa	<i>Acronicta psi</i>	psi
<i>Acronicta atristrigata</i> *	increta	<i>Acronicta insularis</i>	nervosa	<i>Acronicta radcliffei</i> *	psi
<i>Acronicta beameri</i>	increta	<i>Acronicta lanceolaria</i>	nervosa	<i>Acronicta strigosa</i>	psi
<i>Acronicta brumosa</i> *	increta	<i>Acronicta longa</i> *	nervosa	<i>Acronicta strigulata</i> *	psi
<i>Acronicta catocaloida</i>	increta	<i>Acronicta lupini</i>	nervosa	<i>Acronicta superans</i> *	psi
<i>Acronicta exempta</i> *	increta	<i>Acronicta menyanthidis</i>	nervosa	<i>Acronicta thoracica</i>	psi
<i>Acronicta exilis</i> *	increta	<i>Acronicta nervosa</i>	nervosa	<i>Acronicta tridens</i>	psi
<i>Acronicta haesitata</i> *	increta	<i>Acronicta noctivaga</i> *	nervosa	<i>Acronicta tritona</i>	psi
<i>Acronicta increta</i> *	increta	<i>Acronicta obliterata</i>	nervosa	<i>Acronicta valliscola</i> *	psi
<i>Acronicta liturata</i> *	increta	<i>Acronicta perdita</i> *	nervosa	<i>Acronicta vinnula</i>	psi
<i>Acronicta marmorata</i> *	increta	<i>Acronicta rumicis</i>	nervosa	<i>Acronicta retardata</i>	"rogue"
<i>Acronicta megacephala</i>	increta	<i>Acronicta serratae</i>	nervosa	<i>Cerma cerintha</i>	sisters
<i>Acronicta modica</i> *	increta	<i>Acronicta sperata</i> *	nervosa	<i>Chloronycta tybo</i>	sisters
<i>Acronicta ovata</i>	increta	<i>Acronicta betulae</i> *	psi	<i>Comachara cadburyi</i>	sisters
<i>Acronicta theodora</i> *	increta	<i>Acronicta browni</i> *	psi	<i>Cranionycta jankowskii</i>	sisters
<i>Acronicta aceris</i>	leporina	<i>Acronicta clarescens</i> *	psi	<i>Craniophora ligustri</i>	sisters
<i>Acronicta americana</i>	leporina	<i>Acronicta connecta</i> *	psi	<i>Craniophora pontica</i>	sisters
<i>Acronicta auricoma</i> *	leporina	<i>Acronicta cuspidis</i>	psi	<i>Craniophora praeclara</i>	sisters
<i>Acronicta cyanescens</i>	leporina	<i>Acronicta falcula</i> *	psi	<i>Harrisimemna marmorata</i>	sisters
<i>Acronicta dactylina</i>	leporina	<i>Acronicta fallax</i>	psi	<i>Harrisimemna trisignata</i>	sisters
<i>Acronicta hastulifera</i> *	leporina	<i>Acronicta fragilis</i>	psi	<i>Lophonycta confusa</i>	sisters
<i>Acronicta leporina</i>	leporina	<i>Acronicta grisea</i>	psi	<i>Narcotica niveosparsa</i>	sisters
<i>Acronicta lepusculina</i> *	leporina	<i>Acronicta hamamelis</i> *	psi	<i>Polygrammate hebraeicum</i>	sisters
<i>Acronicta major</i>	leporina	<i>Acronicta hasta</i> *	psi	<i>Sinocharis korbae</i>	sisters
<i>Acronicta rubricoma</i> *	leporina	<i>Acronicta heitzmani</i> *	psi	<i>Belciades niveola</i>	outgroup
<i>Acronicta barnesi</i> *	nervosa	<i>Acronicta innotata</i>	psi	<i>Gerbathodes paupera</i>	outgroup
<i>Acronicta chamoenices</i>	nervosa	<i>Acronicta interrupta</i> *	psi	<i>Moma alpium</i>	outgroup
<i>Acronicta contaminata</i>	nervosa	<i>Acronicta isocuspis</i>	psi	<i>Moma kolthoffi</i>	outgroup
<i>Acronicta dentinosa</i>	nervosa	<i>Acronicta lepetita</i> *	psi	<i>Nacna malachitis</i>	outgroup
<i>Acronicta dolli</i>	nervosa	<i>Acronicta lithospila</i> *	psi	<i>Nacna sugitanii</i>	outgroup
<i>Acronicta edolata</i> *	nervosa	<i>Acronicta lobeliae</i>	psi		

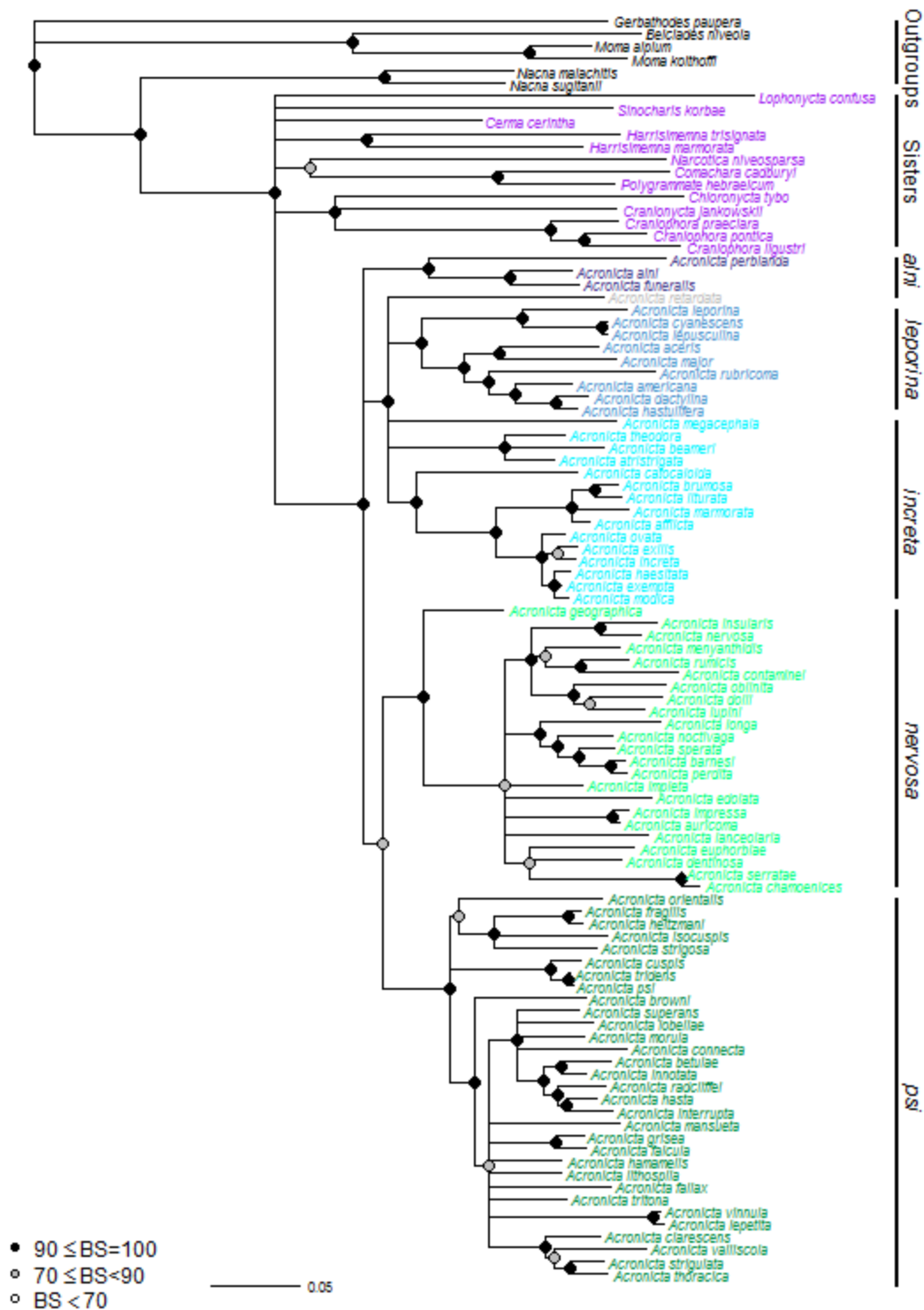


**Table 2.** Sequence statistics from each of the 8 gene regions, comparing total sequences and ingroup (Acronictinae) sequences. The value next to each name is the number of nucleotides in the targeted region.

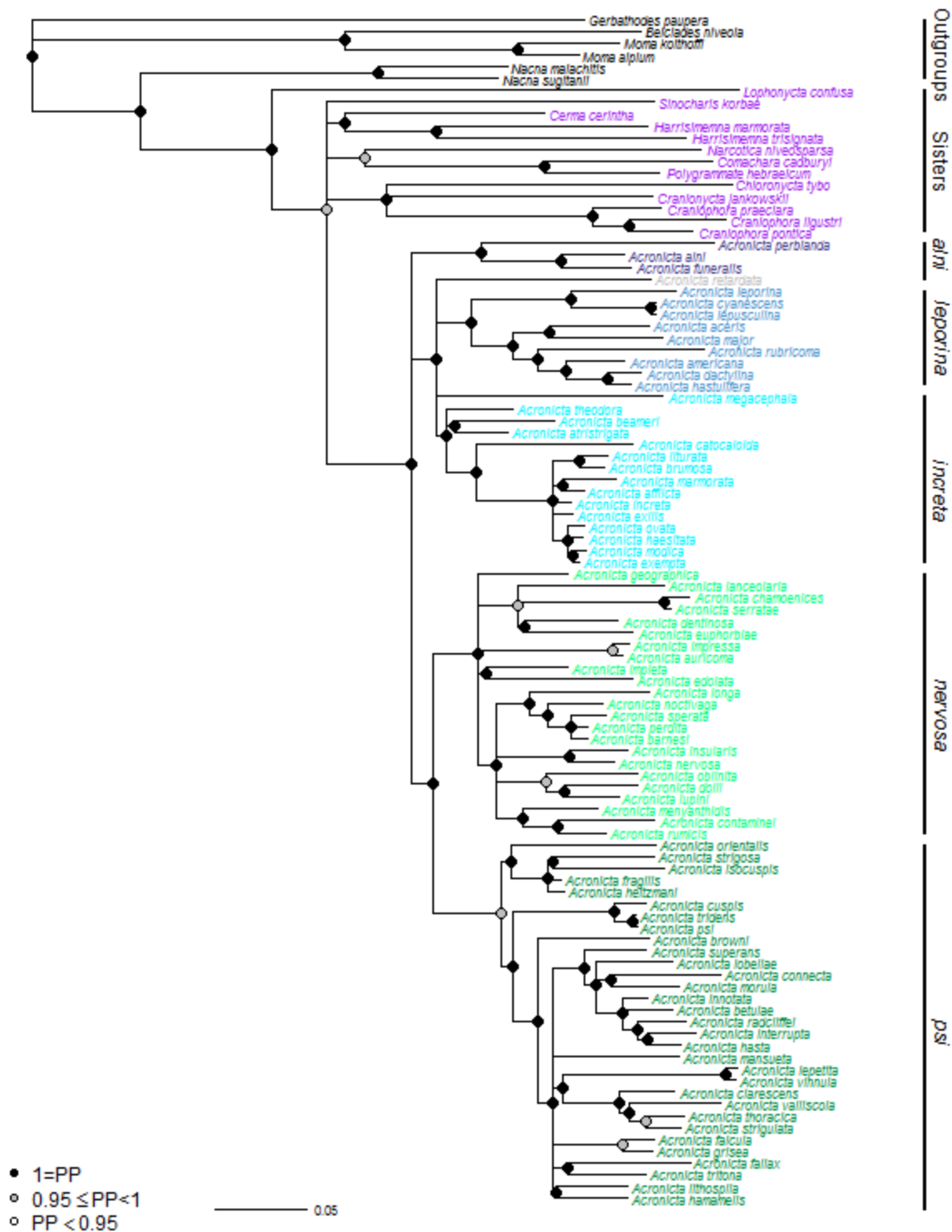
	<b>CAD (826)</b>		<b>COI (1476)</b>		<b>EF1<math>\alpha</math> (1240)</b>	
	Total	Ingroup	Total	Ingroup	Total	Ingroup
Number of varied sites	292 (35%)	258 (31%)	575 (39%)	555 (38%)	309 (25%)	290 (23%)
Number of parsimony sites	227 (28%)	188 (23%)	492 (33%)	473 (32%)	232 (19%)	209 (17%)
% AT	65%	65%	71%	71%	47%	47%
TS/TV	3.230	3.287	2.745	2.898	3.988	3.771
$\alpha$ shape parameter	0.193	0.199	0.238	0.230	0.145	0.147
	<b>GADPH (691)</b>		<b>IDH (722)</b>		<b>MDH (407)</b>	
	Total	Ingroup	Total	Ingroup	Total	Ingroup
Number of varied sites	240 (35%)	233 (34%)	266 (37%)	234 (32%)	146 (36%)	139 (34%)
Number of parsimony sites	189 (27%)	175 (25%)	180 (25%)	172 (24%)	120 (29%)	113 (28%)
% AT	46%	46%	58%	58%	53%	53%
TS/TV	2.917	2.982	2.368	2.369	2.764	2.824
$\alpha$ shape parameter	0.199	0.192	0.252	0.209	0.209	0.215
	<b>RpS5 (603)</b>		<b>Wingless (400)</b>		<b>Combined (6365)</b>	
	Total	Ingroup	Total	Ingroup	Total	Ingroup
Number of varied sites	199 (33%)	189 (31%)	143 (36%)	137 (34%)	2170 (34%)	2048 (32%)
Number of parsimony sites	181 (30%)	165 (27%)	116 (29%)	107 (27%)	1737 (27%)	1616 (25%)
% AT	50%	50%	41%	41%	56%	56%
TS/TV	2.642	2.568	3.499	3.268	2.458	2.513
$\alpha$ shape parameter	0.150	0.142	0.192	0.179	0.228	0.215

**Table 3.** All analysis types and partitioning schemes used in this study, and their associated figures. ML = Maximum likelihood, MB = MrBayes, SVDQ = SVD quartets, PF = PartitionFinder using codon positions, kmeans = PartitionFinder using kmeans, one = data treated as a single partition, RO = remove outgroups.

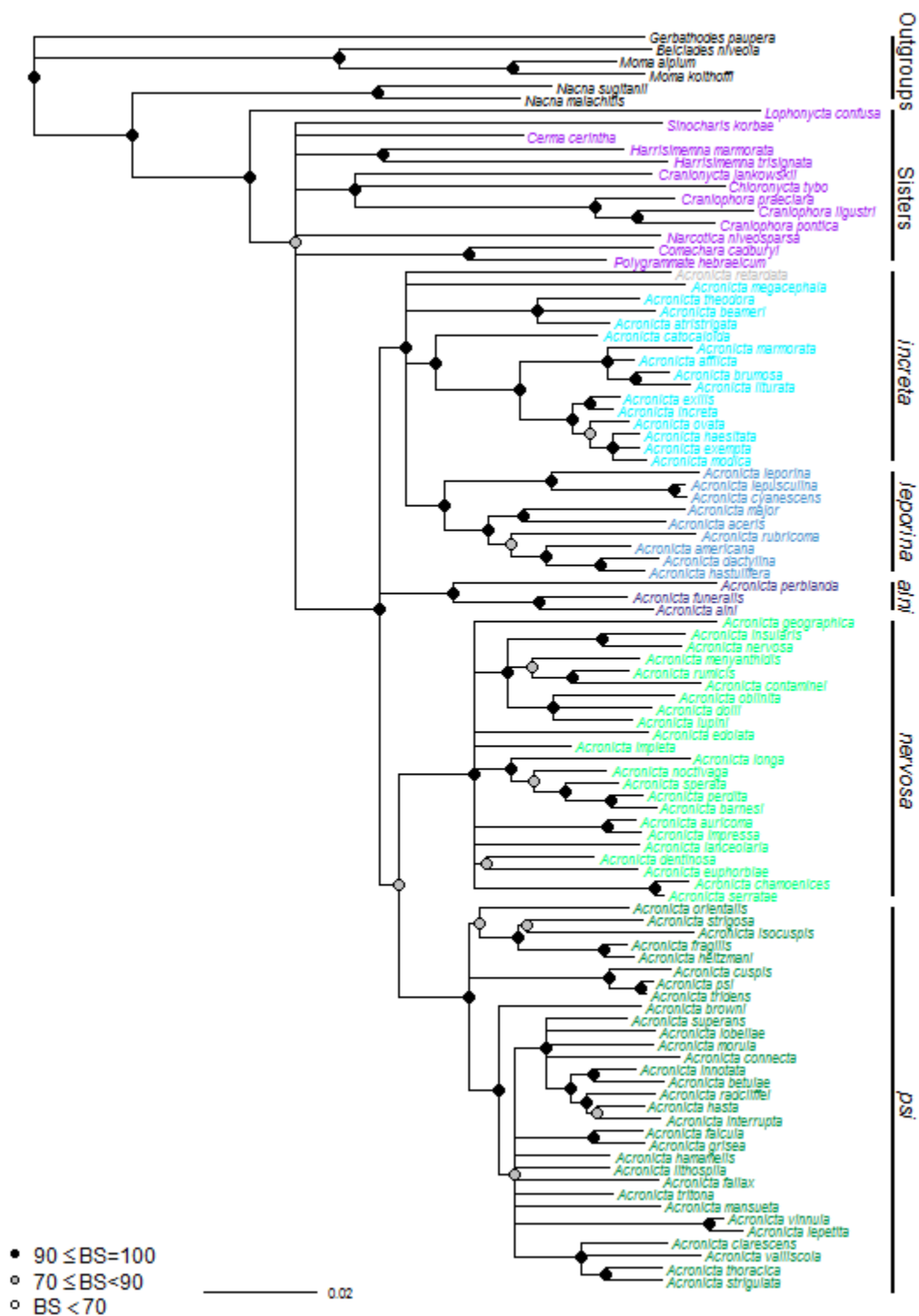
Analysis	Gene(s)	# taxa	Partitioning	Figure
ML summary	all	101	PF	1
MB summary	all	101	PF	2
ML summary	all	101	kmeans	3
MB	all	101	PF	S1
MB	all	91	PF	S2
MB	all (no COI)	100	PF	S3
MB	all (no COI)	91	PF	S4
MB	all	95 (RO)	PF	S5
MB	all	86 (RO)	PF	S6
ML	all	101	PF	S7
ML	all	91	PF	S8
ML	all (no COI)	100	PF	S9
ML	all (no COI)	91	PF	S10
ML	all	101	kmeans	S11
ML	all	91	kmeans	S12
ML	all	95 (RO)	PF	S13
ML	all	86 (RO)	PF	S14
ML	COI	93	PF	S15
ML	CAD	90	PF	S16
ML	EF1 $\alpha$	78	PF	S17
ML	GADPH	82	PF	S18
ML	IDH	38	PF	S19
ML	MDH	82	PF	S20
ML	RpS5	98	PF	S21
ML	wingless	93	PF	S22
SVDQ	all	101	one	S23
SVDQ	all	91	one	S24



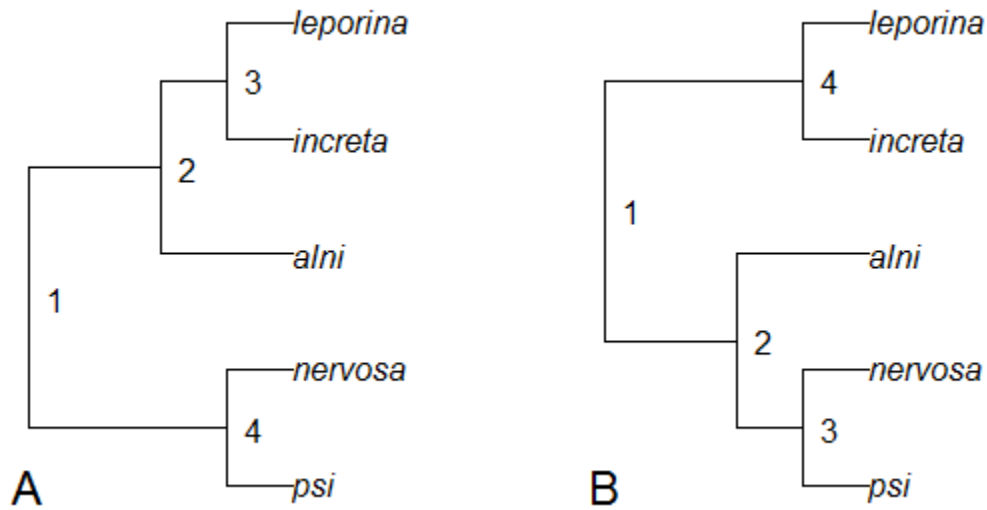
**Figure 1.** Maximum likelihood tree for *complete* dataset (101 taxa) with all genes analyzed using 12 partitions. Nodes are colored according to bootstrap support values. Nodes with <70% support are collapsed.



**Figure 2.** Bayesian tree for *complete* dataset (101 taxa) with all genes analyzed using 12 partitions. Nodes are colored according to posterior probability values. Nodes with <95% support are collapsed.



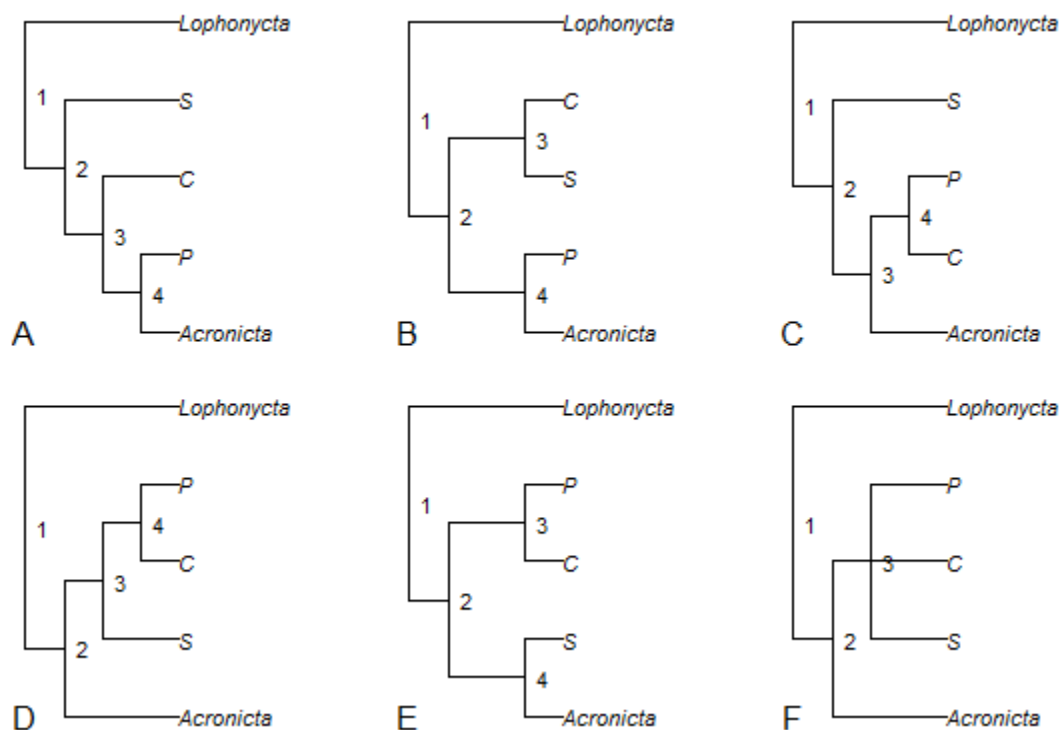
**Figure 3.** Maximum likelihood tree for *complete* dataset (101 taxa) with all genes analyzed using kmeans partitioning. Nodes are colored according to bootstrap support values. Nodes with <70% support are collapsed.



**Figure 4.** Two most common backbone topologies showing the relationship of the *alni* group to the other species groups. Associated nodal support for phylogenetic analyses are given in Table 4.

**Table 4.** Accompanying data for Figure 4. Support values are listed as bootstrap (0-100) or posterior probability (0-1). ML = Maximum likelihood; MB = MrBayes; SVDQ = SVD quartets; RO = remove outgroups; PF = PartitionFinder. Any analyses not in the table were left out due to lack of monophyly of the species groups, or for having alternate relationships not shared with other analyses.

	Support				Phylogeny			
	1	2	3	4	Analysis	Gene(s)	# taxa	Partitioning
A	100	66	54	100	ML	all	86 (RO)	PF
	100	54	27	85	ML	all (no COI)	100	PF
	100	40	28	80	ML	all	101	PF
	87	60	15	98	ML	all	95 (RO)	PF
	87	42	36	100	ML	all (no COI)	91	PF
	44	45	96	46	SVDQ	all	91	one
	43	97	49	91	ML	all	91	PF
	1	1	1	1	MB	all	86 (RO)	PF
	1	1	0.9	1	MB	all (no COI)	100	PF
	1	0.9	0.7	1	MB	all	95 (RO)	PF
	1	0.9	1	1	MB	all (no COI)	91	PF
	1	0.8	0.7	1	MB	all	91	PF
B	100	49	85	91	ML	all	101	kmeans
	51	90	100	95	ML	all	91	kmeans

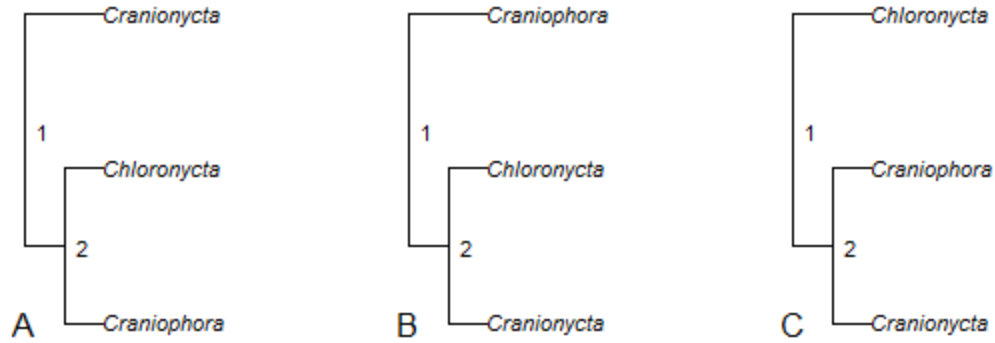


**Figure 5.** Six most common topologies showing the relationships of acronictine genera. Aside from *Lophonycta* and *Acronicta*, genera are split into clades: S = *Sinocharis*, *Cerma*, and *Harrisimemna*; C = *Craniophora*, *Cranionycta*, and *Chloronycta*; P = *Polygrammate*, and *Comachara*. Associated nodal support for phylogenetic analyses listed in Table 5.

**Table 5.** Accompanying data for Figure 5. Support values are listed as bootstrap (0-100) or posterior probability (0-1). ML = Maximum likelihood; MB = MrBayes; SVDQ = SVD quartets; RO = remove outgroups; PF = PartitionFinder. Any analyses not in the table were left out due to lack of monophyly of the species groups, or for having alternate relationships not shared with other analyses.

	Support				Phylogeny			
	1	2	3	4	Analysis	Gene(s)	# taxa	Partitioning
<b>A</b>	100	73	25	17	ML	all	101	kmeans
	85	17	28	100	ML	all	91	kmeans
	70	33	42	100	ML	all	91	PF
	1	1	1	1	MB	all	91	PF
<b>B</b>	100	63	12	30	ML	all (no COI)	100	PF
	62	34	16	100	ML	all (no COI)	91	PF
	1	0.9	0.4	0.5	MB	all (no COI)	100	PF
	1	1	0.5	1	MB	all (no COI)	91	PF
<b>C</b>	100	69	32	30	ML	all	101	PF
	1	1	0.7	0.8	MB	all	101	PF
<b>D</b>	100	100	41	26	ML	all	86 (RO)	PF
	100	100	35	18	ML	all	95 (RO)	PF
	1	1	0.7	0.9	MB	all	95 (RO)	PF
	1	1	0.5	0.4	MB	all	86 (RO)	PF
<b>E</b>	92	46	11	7	ML	EF1a	71	PF
<b>F</b>	63	10	6		ML	CAD	90	PF

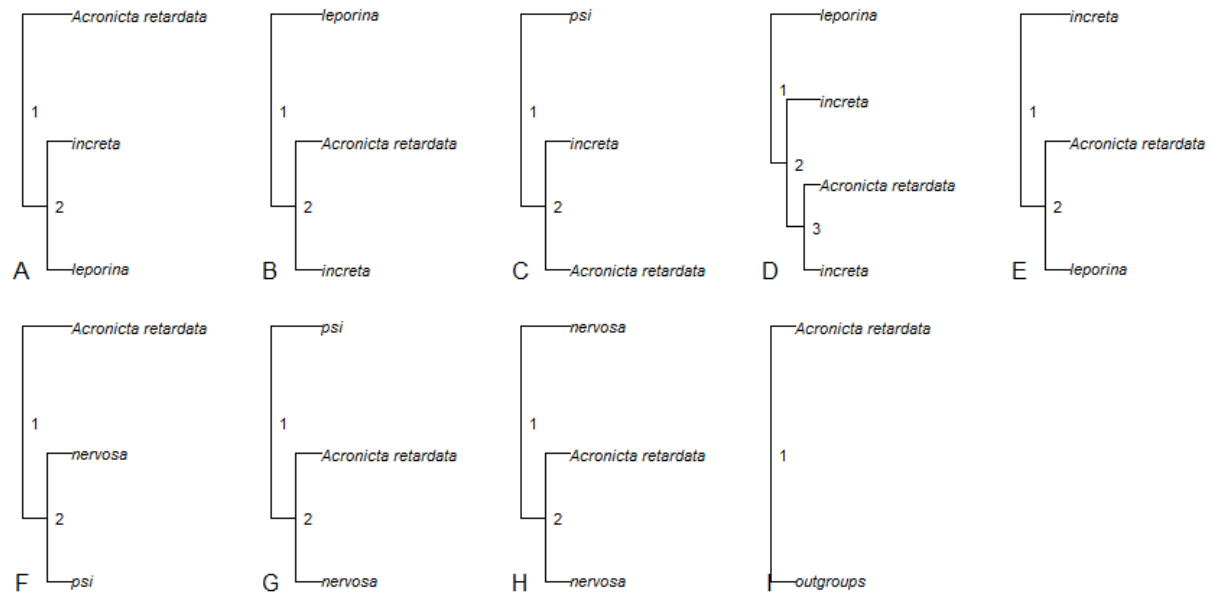




**Figure 6.** Three most common topologies showing the relationships among *Craniophora*, *Cranionycta*, and *Chloronycta*. Associated nodal support for phylogenetic analyses listed in Table 6.

**Table 6.** Accompanying data for Figure 6. Support values are listed as bootstrap (0-100) or posterior probability (0-1). ML = Maximum likelihood; MB = MrBayes; SVDQ = SVD quartets; RO = remove outgroups; PF = PartitionFinder. Any analyses not in the table were left out due to lack of monophyly of the species groups, or for having alternate relationships not shared with other analyses.

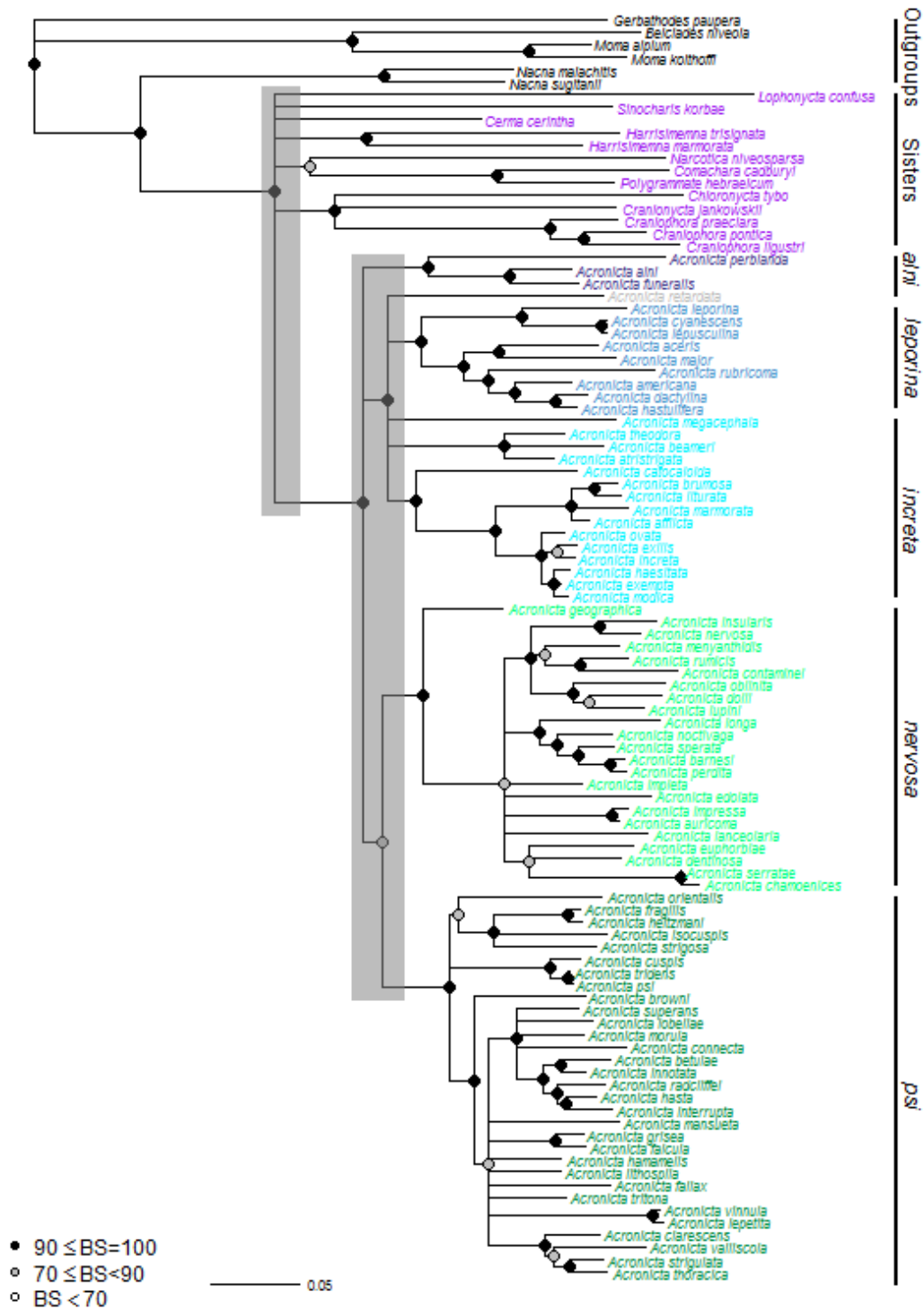
	Support		Phylogeny			
	1	2	Analysis	Gene(s)	# taxa	Partitioning
A	99	47	ML	all	91	kmeans
	99	42	ML	all	86 (RO)	PF
	95	42	ML	all (no COI)	91	PF
	94	52	ML	all	91	PF
	53	40	ML	EF1a	71	PF
	29	40	SVDQ	all	91	one
	13	21	SVDQ	all	101	one
	1	0.6	MB	all (no COI)	91	PF
	1	0.3	MB	all (no COI)	100	PF
	0.7	1	MB	all	91	PF
B	1	0.4	MB	all	101	PF
	98	39	ML	all	101	PF
	98	30	ML	all (no COI)	100	PF
	49	37	ML	CAD	90	PF
	100	26	ML	all	95 (RO)	PF
C	98	49	ML	all	101	kmeans
	21	40	ML	wingless	93	PF



**Figure 7.** Nine most common topologies showing the placement of *Acronicta retardata* within *Acronicta* in relation to species group clades. Associated nodal support for phylogenetic analyses listed in Table 7.

**Table 7.** Accompanying data for Figure 7. Support values are listed as bootstrap (0-100) or posterior probability (0-1). ML = Maximum likelihood; MB = MrBayes; SVDQ = SVD quartets; RO = remove outgroups; PF = PartitionFinder. Any analyses not in the table were left out due to lack of monophyly of the species groups, or for having alternate relationships not shared with other analyses.

	Support			Phylogeny			
	1	2	3	Analysis	Gene(s)	# taxa	Partitioning
<b>A</b>	100	49		ML	all	91	PF
	99	54		ML	all	86 (RO)	PF
	97	36		ML	all (no COI)	91	PF
	95	27		ML	all (no COI)	100	PF
	94	15		ML	all	95 (RO)	PF
	93	28		ML	all	101	PF
	64	96		SVDQ	all	91	one
	1	1		MB	all	86 (RO)	PF
	1	1		MB	all (no COI)	91	PF
	1	0.9		MB	all	101	PF
	1	0.9		MB	all (no COI)	100	PF
	1	0.7		MB	all	95 (RO)	PF
	1	0.7		MB	all	91	PF
<b>B</b>	95	60		ML	all	91	kmeans
	91	27		ML	all	101	kmeans
<b>C</b>	6	18		ML	EF1a	71	PF
<b>D</b>	31	38	32	ML	CAD	90	PF
<b>E</b>	9	37		ML	GADPH	82	PF
<b>F</b>	25	40		ML	MDH	82	PF
<b>G</b>	28	48		ML	RpS5	98	PF
<b>H</b>	8	29		ML	wingless	93	PF
<b>I</b>	26	26		SVDQ	all	101	one



**Figure 8.** Maximum likelihood tree for complete dataset (101 taxa) with partitioning by codon position. Nodes are colored according to bootstrap support values. Gray bars illustrate periods of short internal nodes, potentially relating to fast radiations.

## Supplementary Figures

### Color guide for all figures:

Black = Outgroup taxa

Purple = Acronictinae genera (excluding *Acronicta*)

Dark blue = *alni* clade

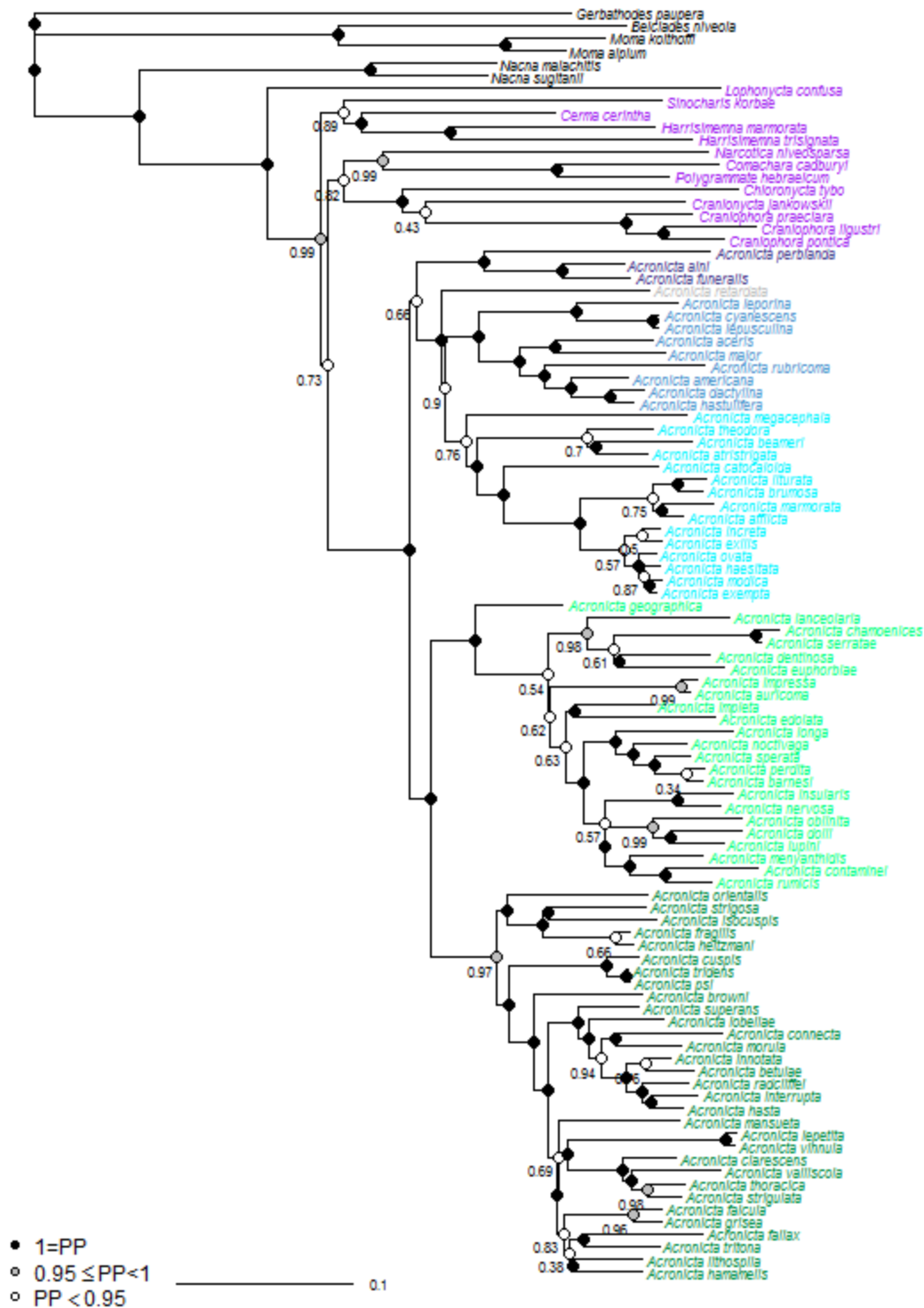
Medium blue = *leporina* clade

Light blue = *increta* clade

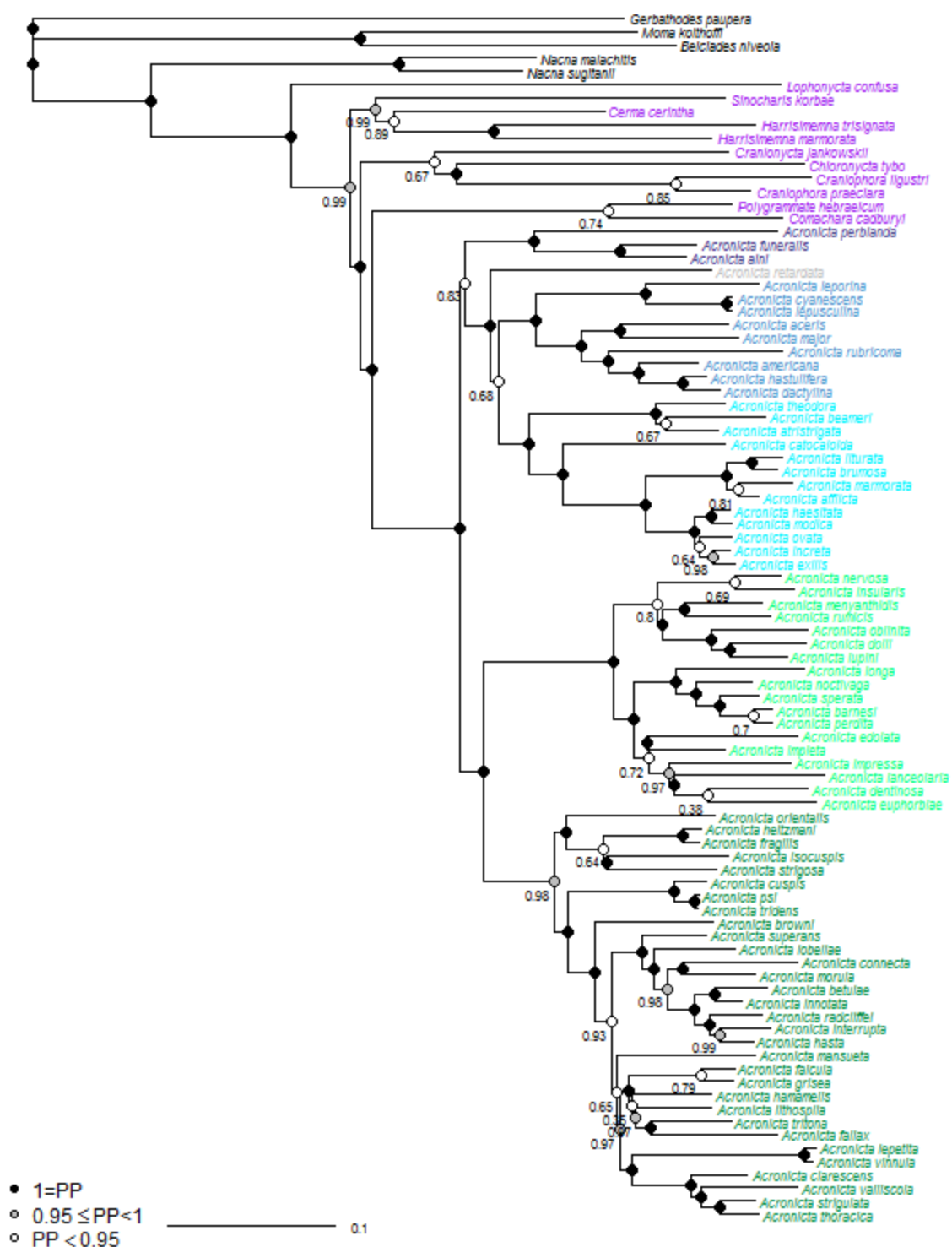
Light green = *nervosa* clade

Dark green = *psi* clade

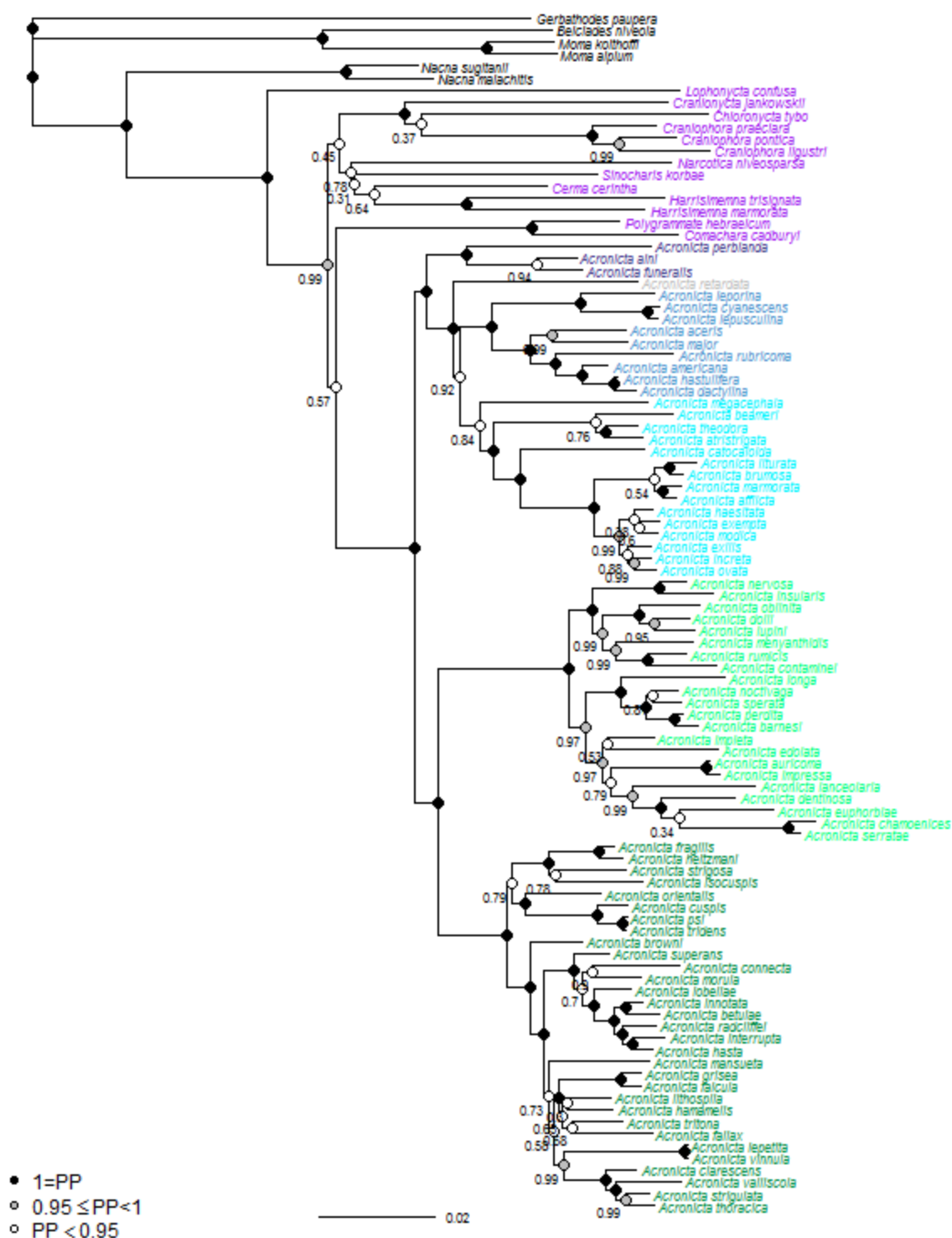
Gray = Unplaced



**Figure S1.** Bayesian phylogeny for *complete* dataset (101 taxa), with all genes analyzed using 12 partitions. Nodes are colored according to posterior probability values.



**Figure S2.** Bayesian phylogeny for 50% coverage dataset (91 taxa), with all genes analyzed using 12 partitions. Nodes are colored according to posterior probability values.

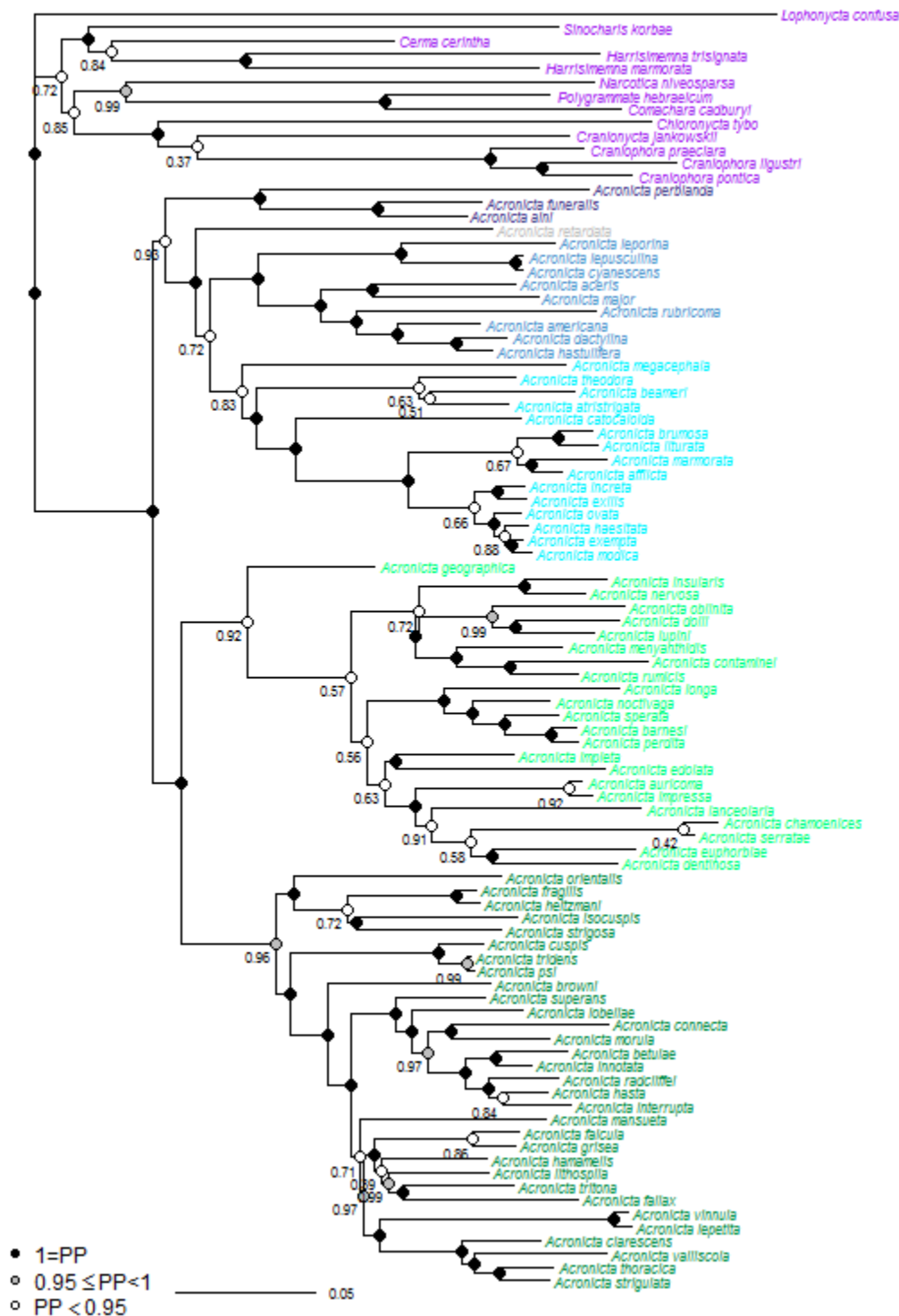


**Figure S3.** Bayesian phylogeny for *complete* dataset (100 taxa), with nuclear genes analyzed using 12 partitions (COI excluded). *A. geographica* was removed because no nuclear sequences were available. Nodes are colored according to posterior probability values.

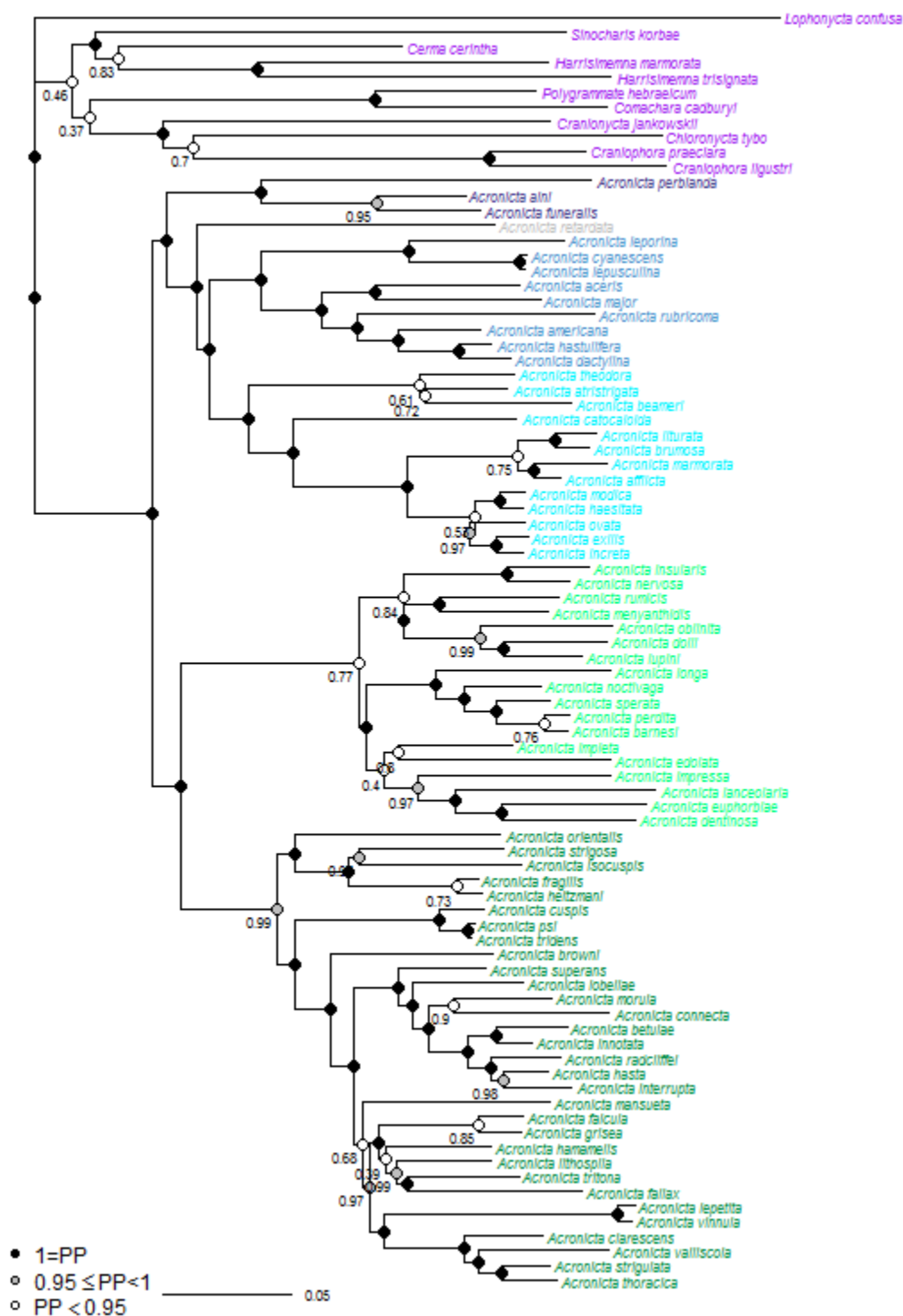




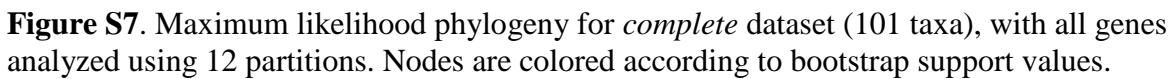
**Figure S4.** Bayesian phylogeny for 50% coverage dataset (91 taxa), with nuclear genes analyzed using 12 partitions (COI excluded). Nodes are colored according to posterior probability values.



**Figure S5.** Bayesian phylogeny for *complete* dataset with outgroups removed (95 taxa), with all genes analyzed using 12 partitions. Nodes are colored according to posterior probability values.

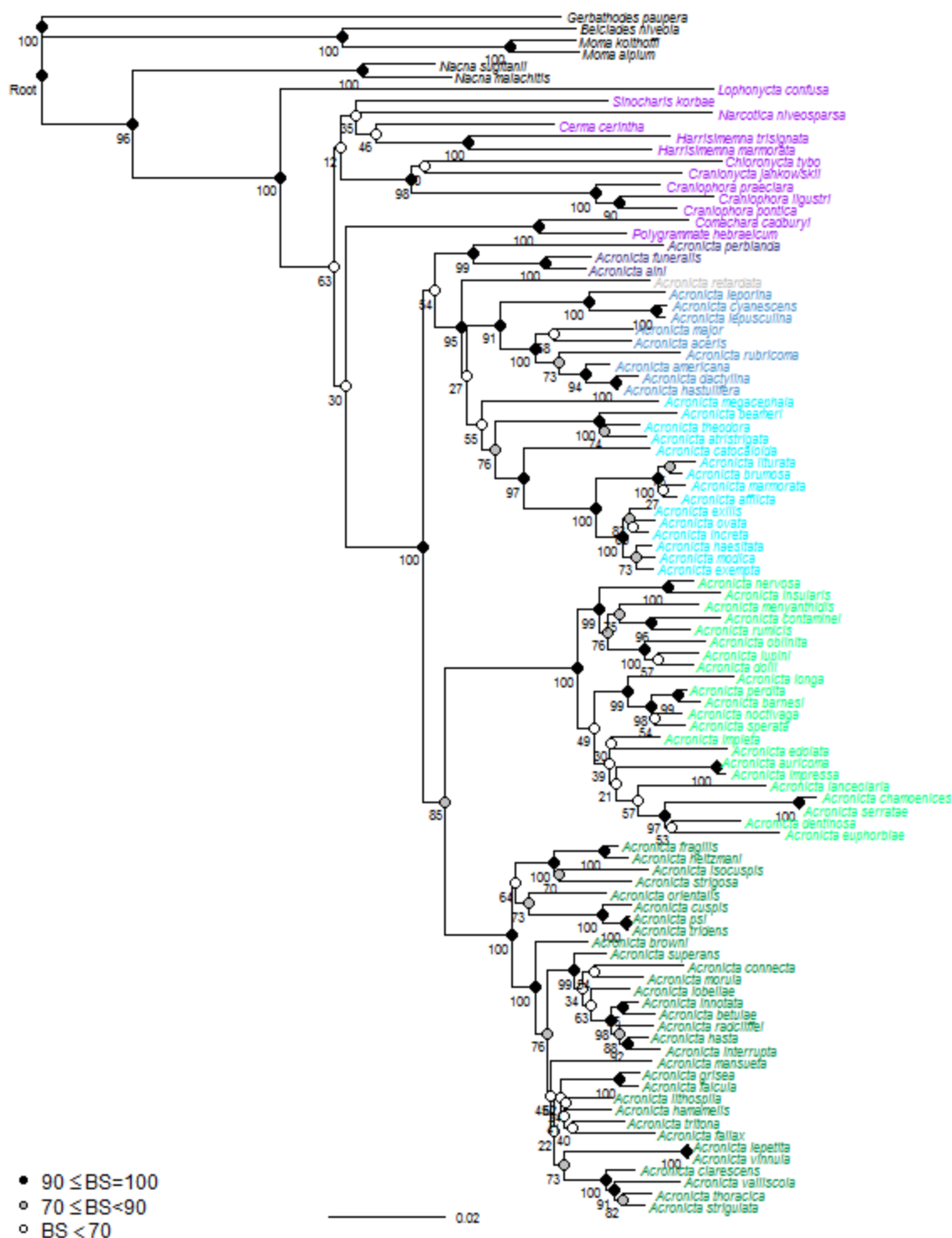


**Figure S6.** Bayesian phylogeny for 50% coverage dataset with outgroups removed (86 taxa), with all genes analyzed using 12 partitions. Nodes are colored according to posterior probability values.

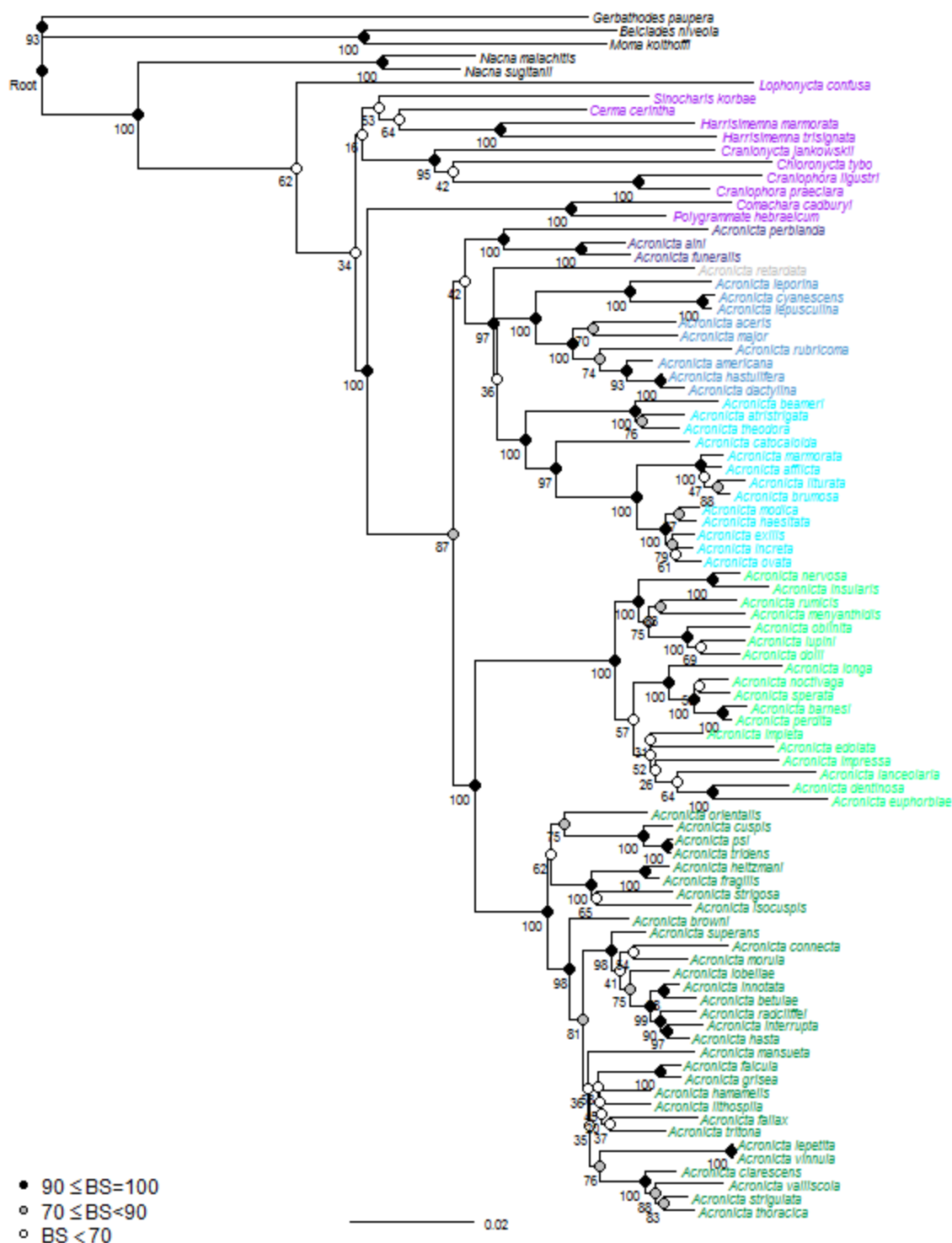




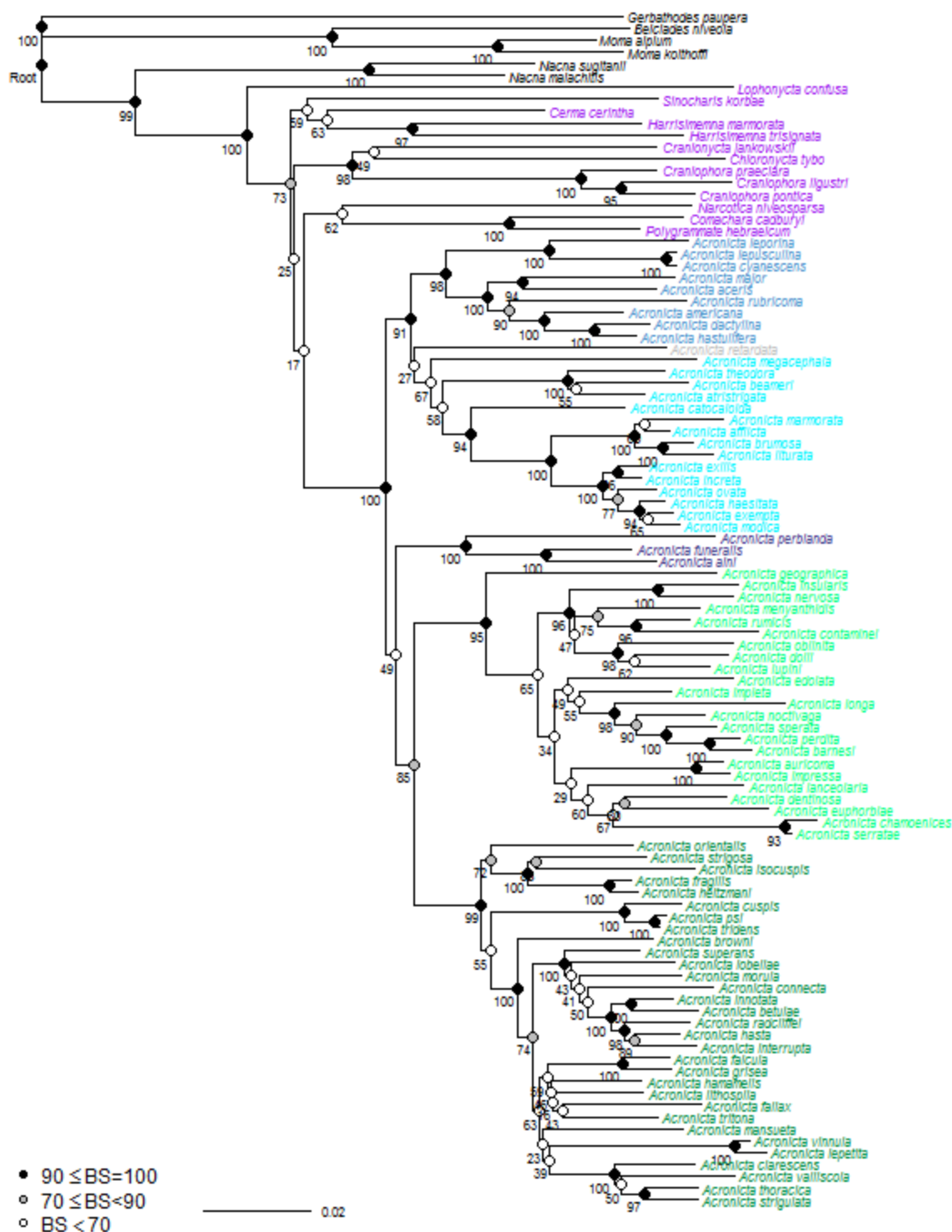
**Figure S8.** Maximum likelihood phylogeny for 50% coverage dataset (91 taxa), with all genes analyzed using 12 partitions. Nodes are colored according to bootstrap support values.



**Figure S9.** Maximum likelihood phylogeny for *complete* dataset (100 taxa), with nuclear genes analyzed using 12 partitions (COI excluded). *A. geographica* was removed because no nuclear sequences were available. *Nodes* are colored according to bootstrap support values.

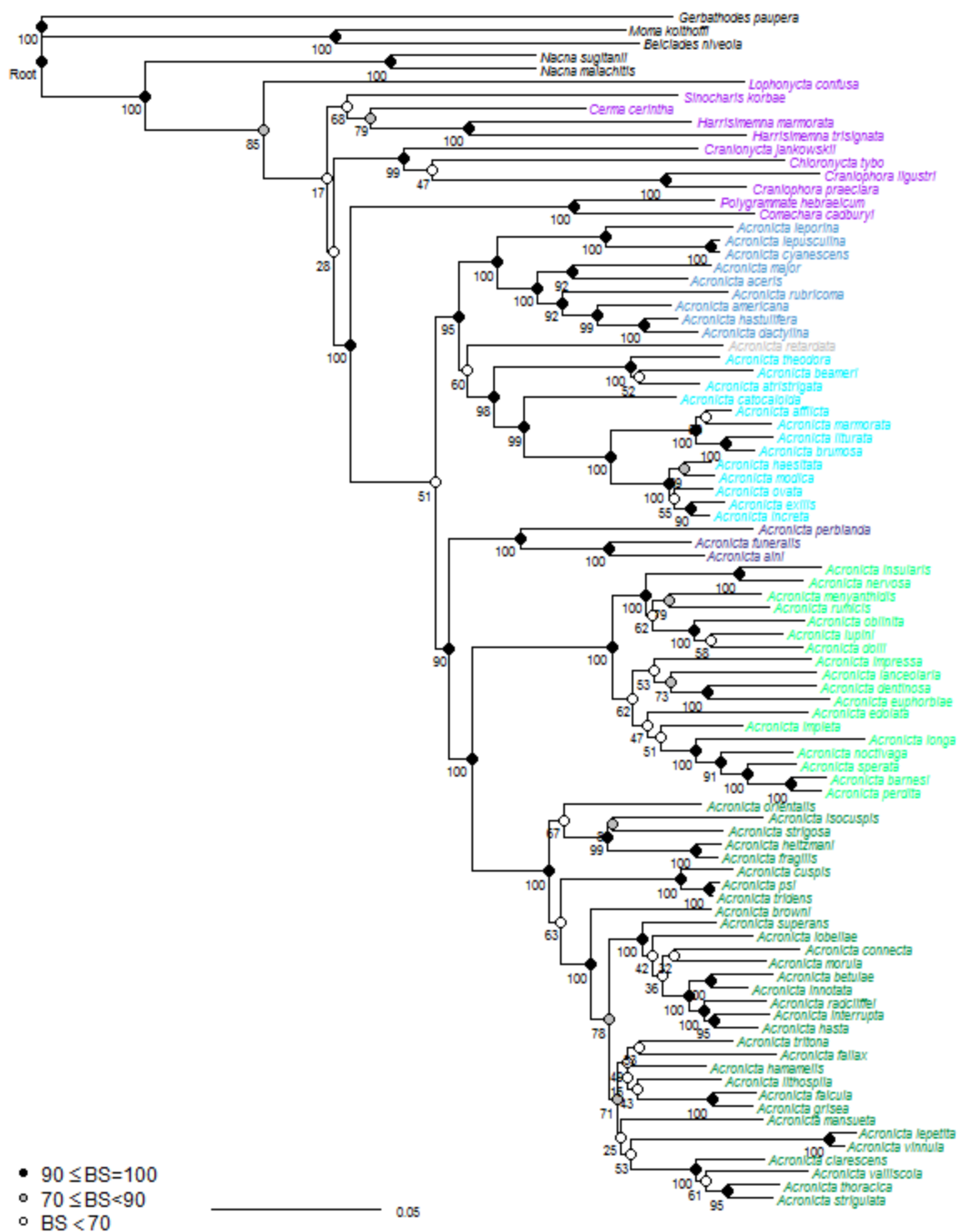


**Figure S10.** Maximum likelihood phylogeny for 50% coverage dataset (91 taxa), with nuclear genes analyzed using 12 partitions (COI excluded). Nodes are colored according to bootstrap support values.

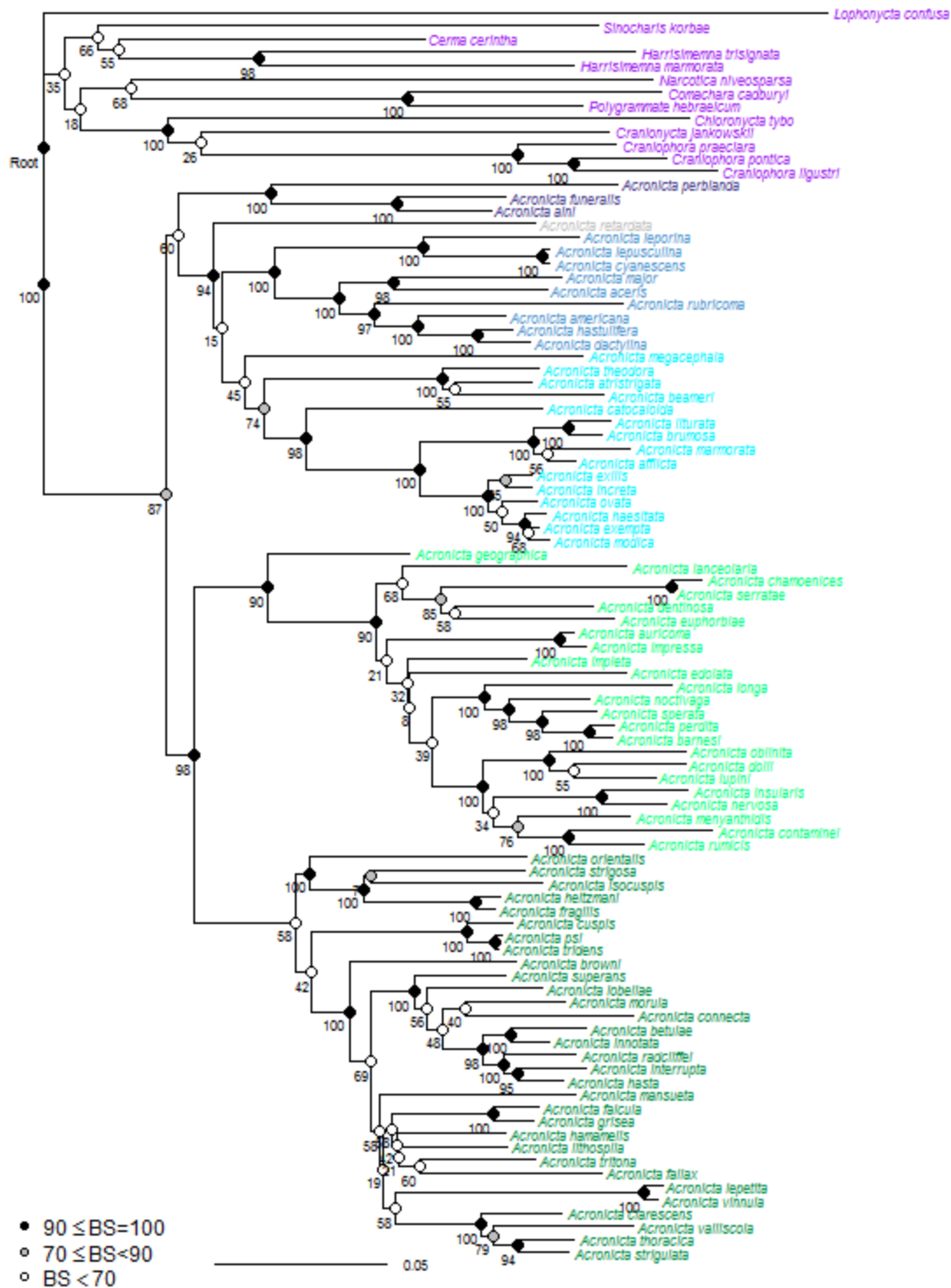


**Figure S11.** Maximum likelihood phylogeny for *complete* dataset (101 taxa), with nuclear genes analyzed using 11 partitions generated with kmeans. Nodes are colored according to bootstrap support values.

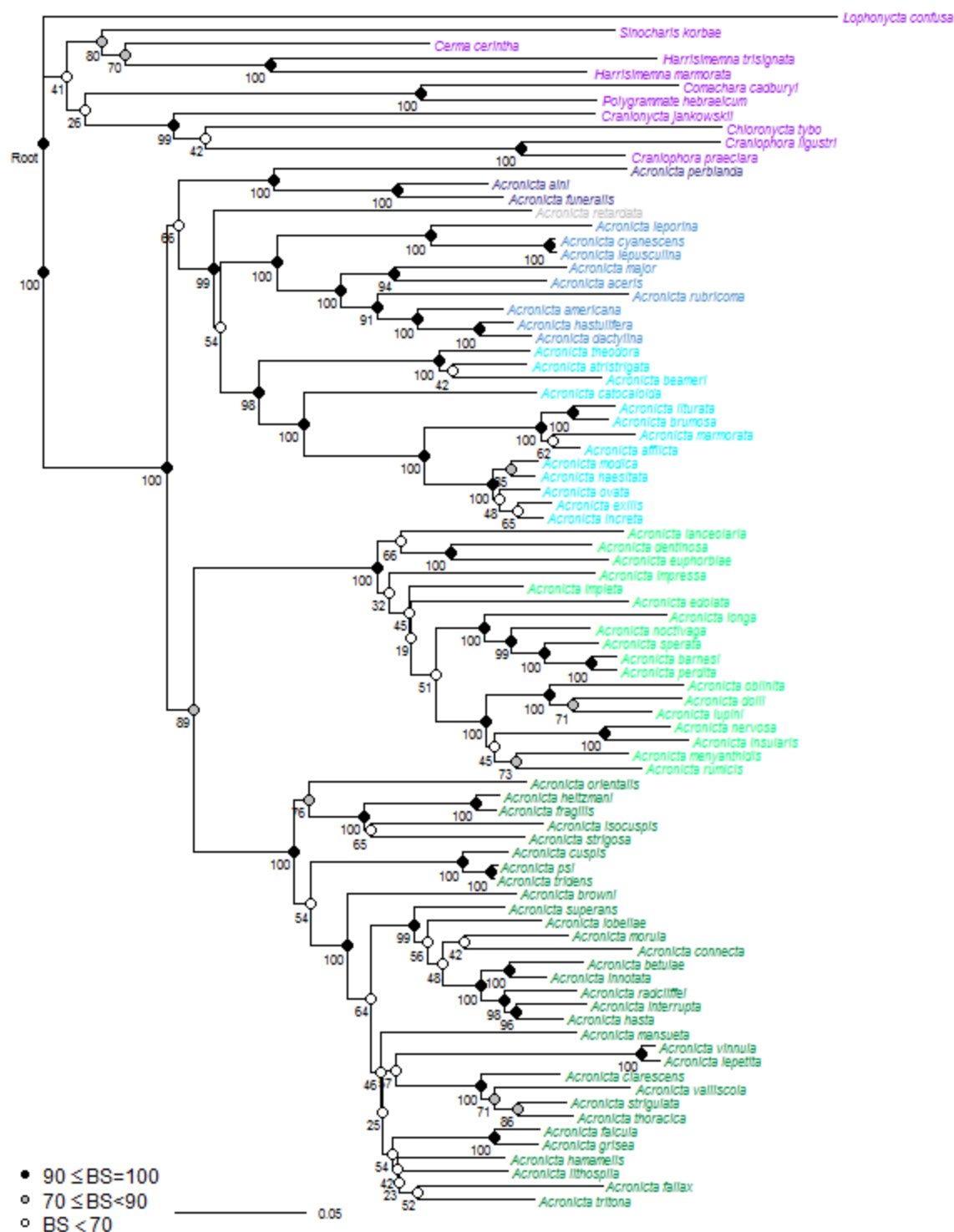




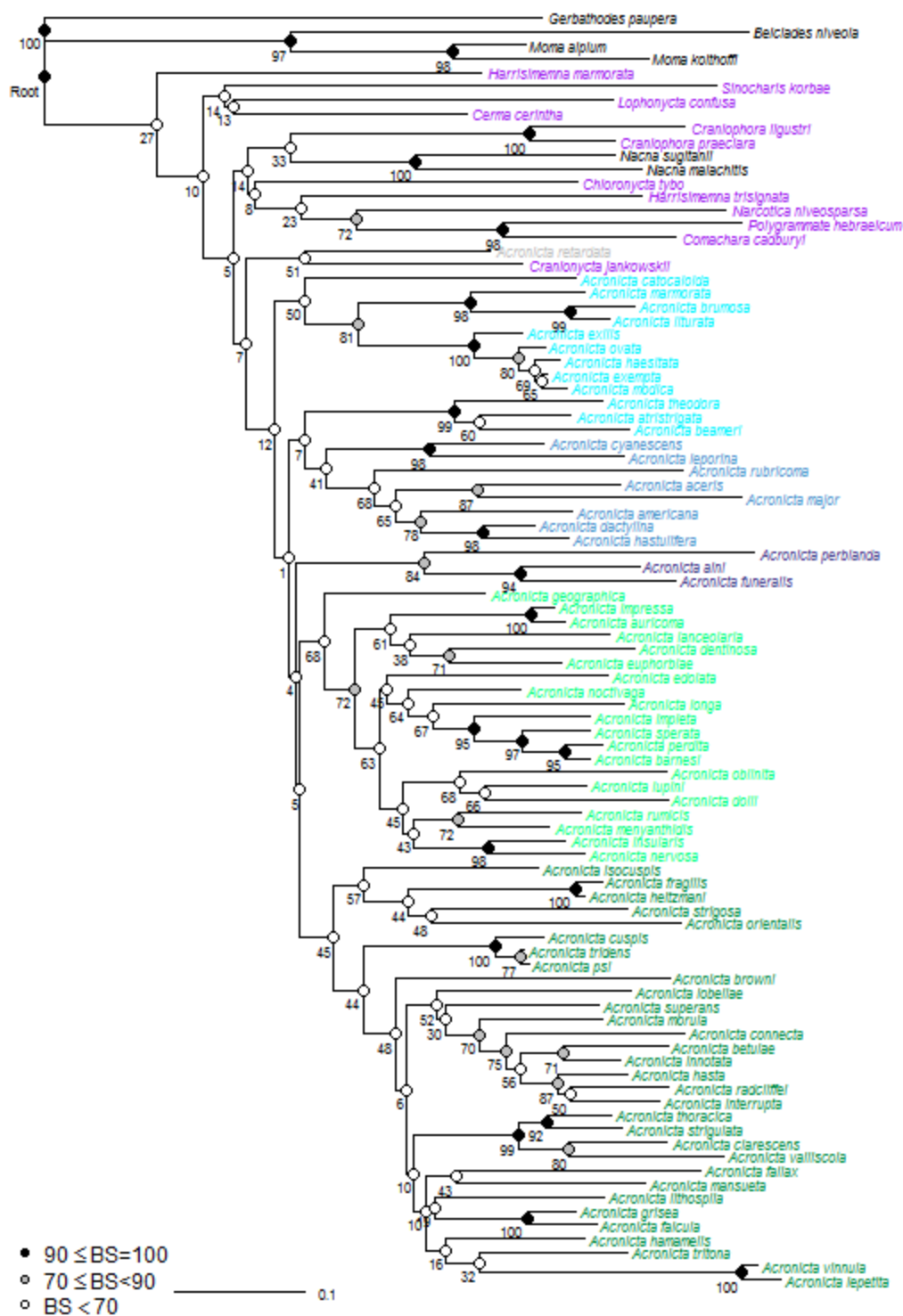
**Figure S12.** Maximum likelihood phylogeny for 50% coverage dataset (91 taxa), with nuclear genes analyzed using 11 partitions generated with kmeans. Nodes are colored according to bootstrap support values.



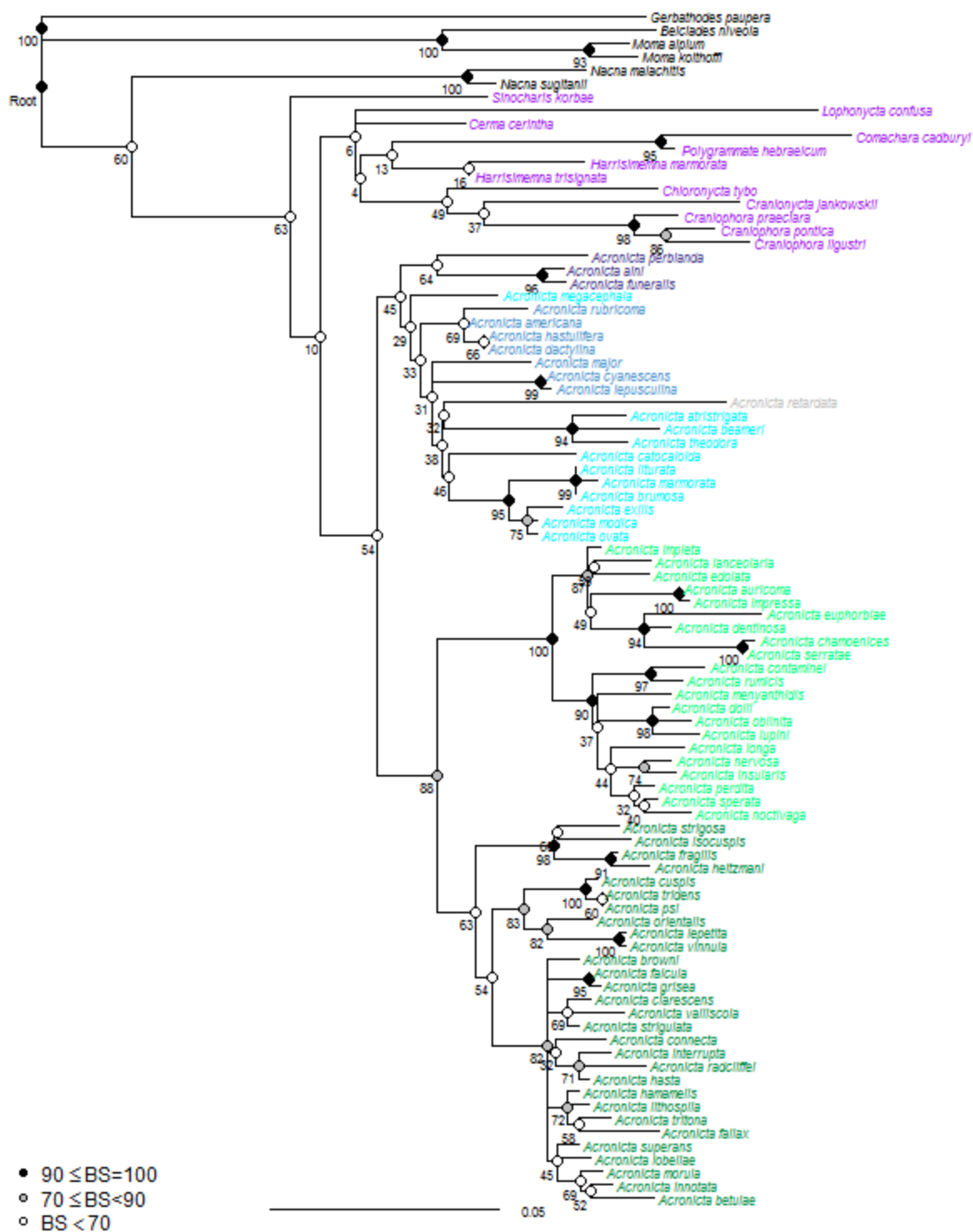
**Figure S13.** Maximum likelihood phylogeny for *complete* dataset with outgroups removed (95 taxa), with nuclear genes analyzed using 12 partitions. Nodes are colored according to bootstrap support values.



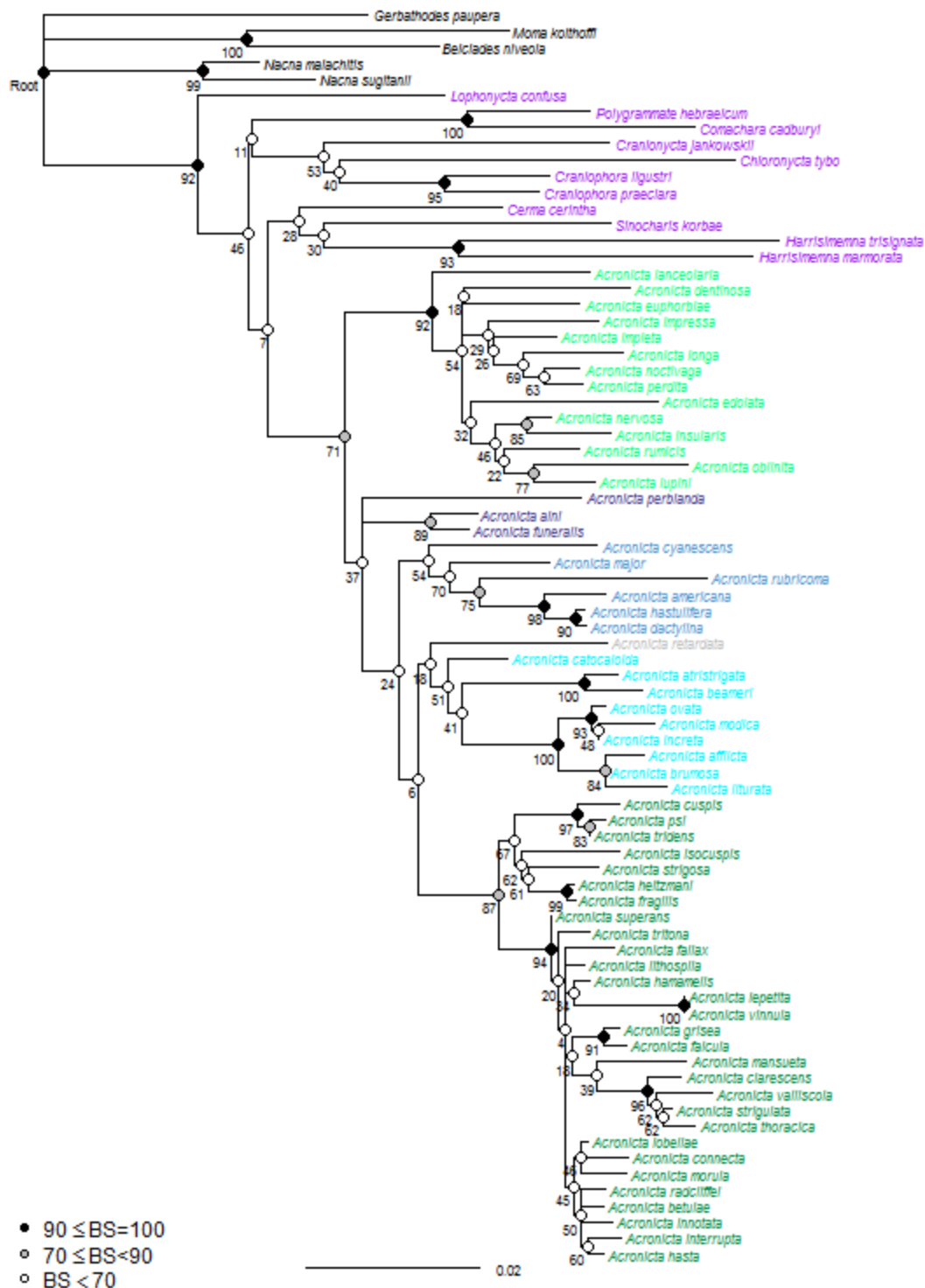
**Figure S14.** Maximum likelihood phylogeny for 50% coverage dataset with outgroups removed (86 taxa), with nuclear genes analyzed using 12 partitions. Nodes are colored according to bootstrap support values.



**Figure S15.** Maximum likelihood phylogeny for COI (93 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.

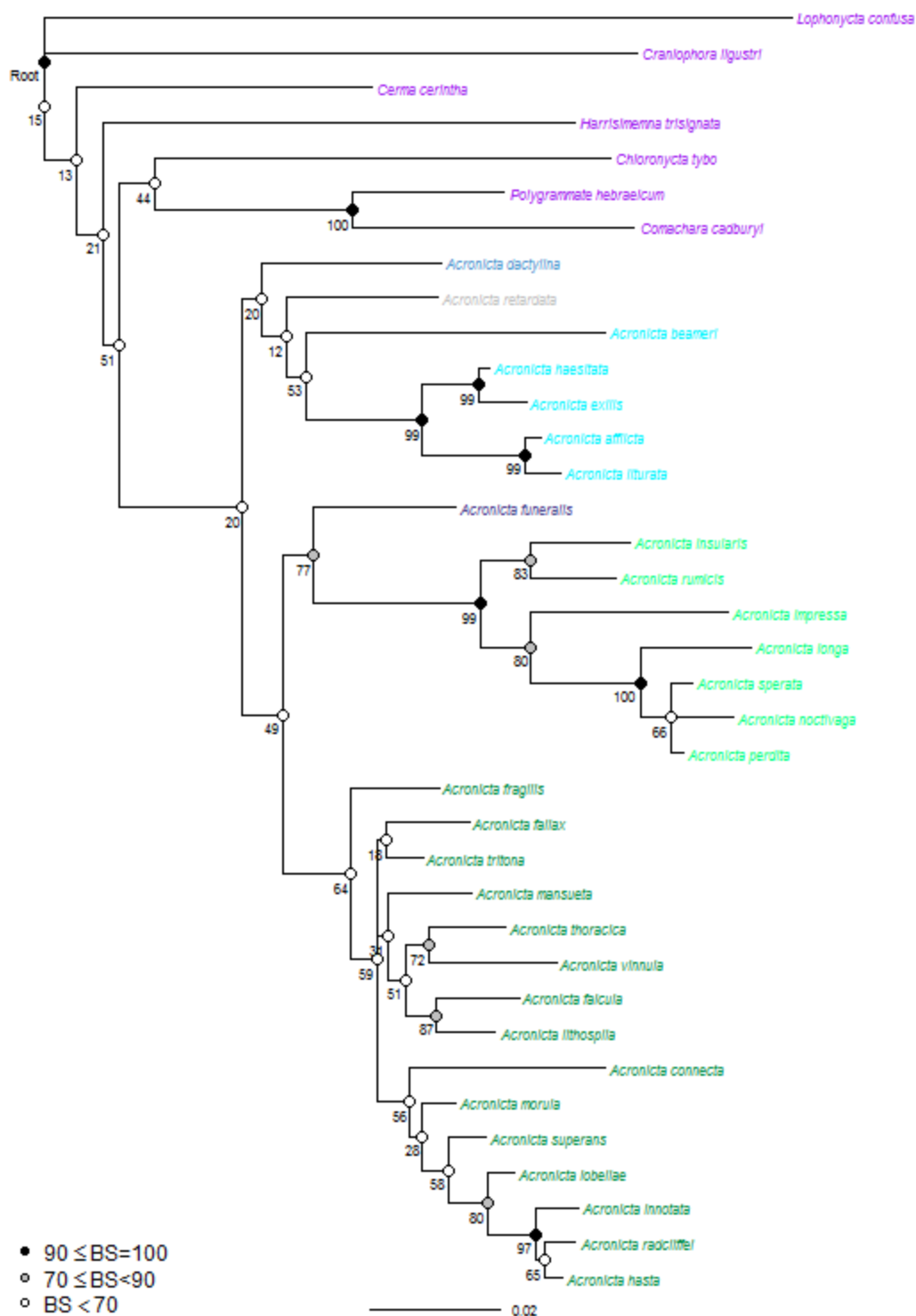


**Figure S16.** Maximum likelihood phylogeny for CAD (90 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.



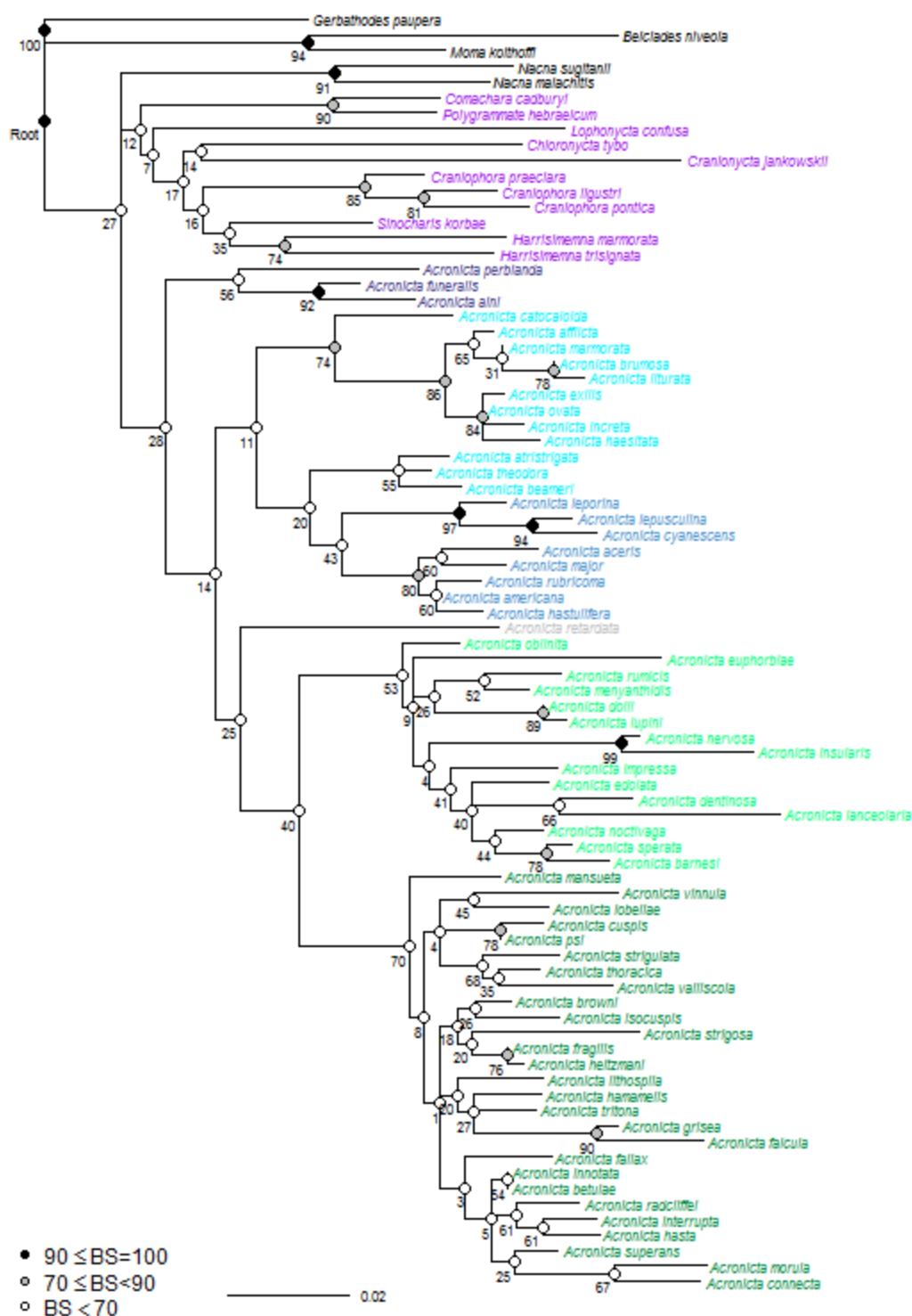
**Figure S17.** Maximum likelihood phylogeny for EF1α (78 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.



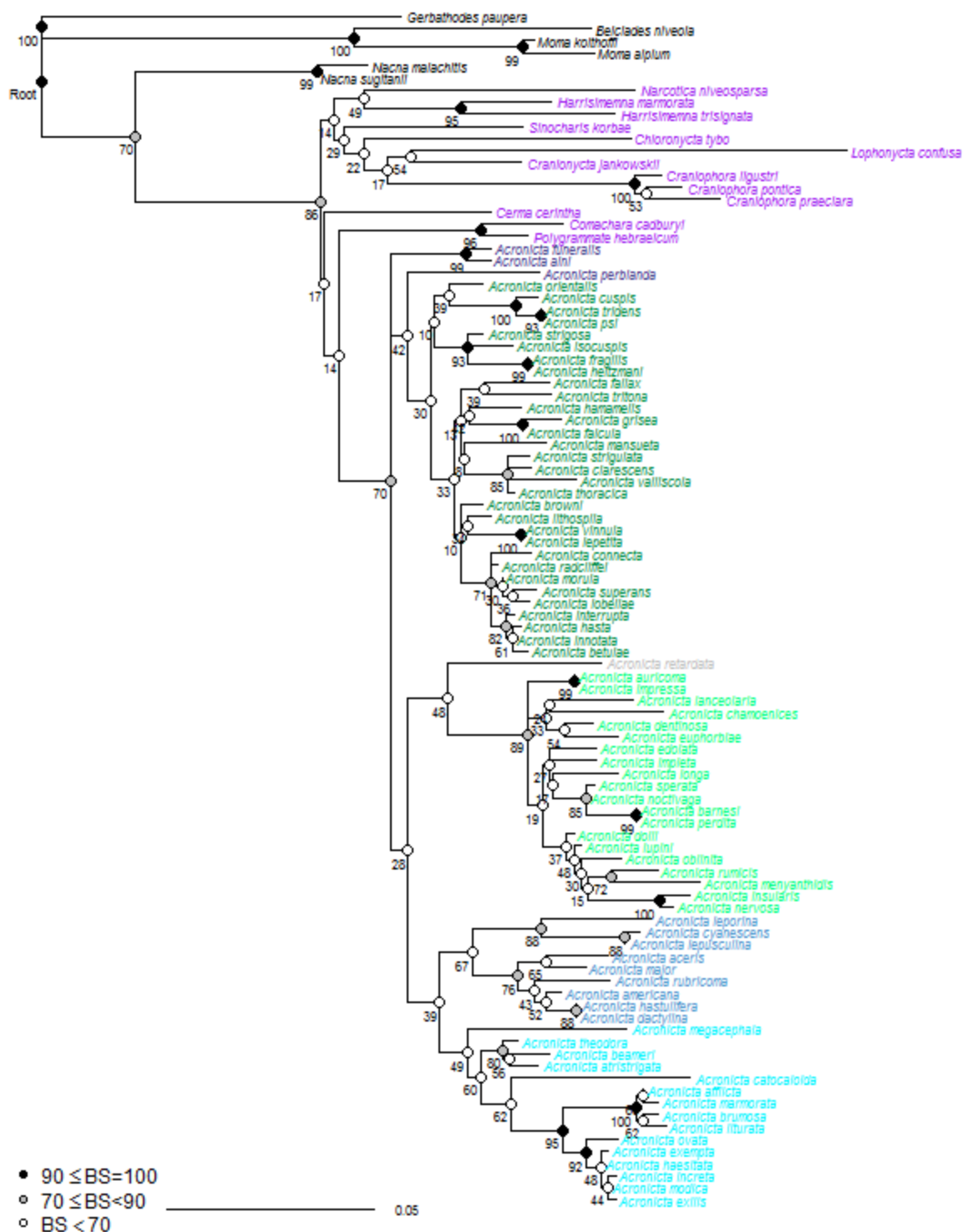


**Figure S19.** Maximum likelihood phylogeny for IDH (38 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.





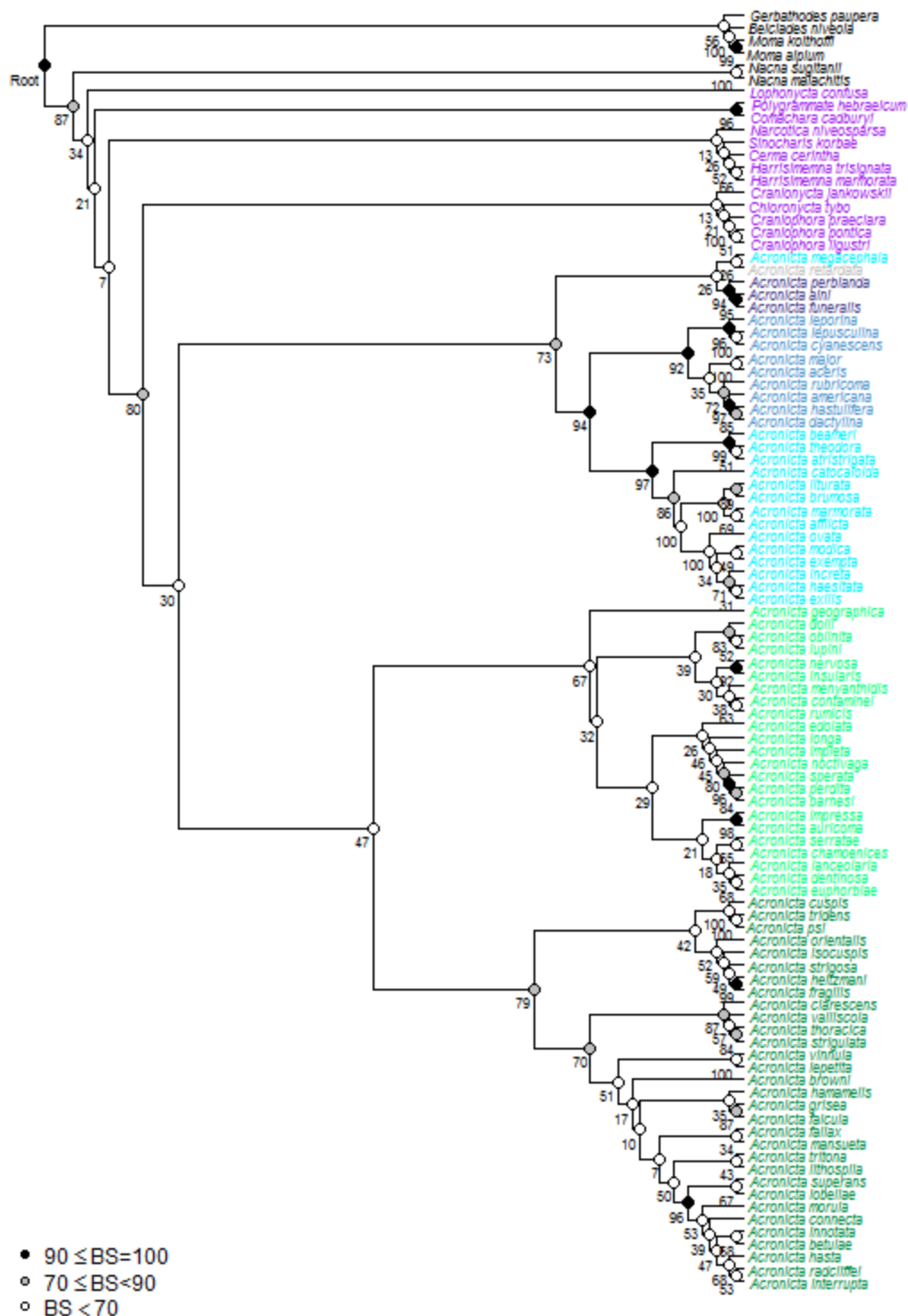
**Figure S20.** Maximum likelihood phylogeny for MDH (82 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.



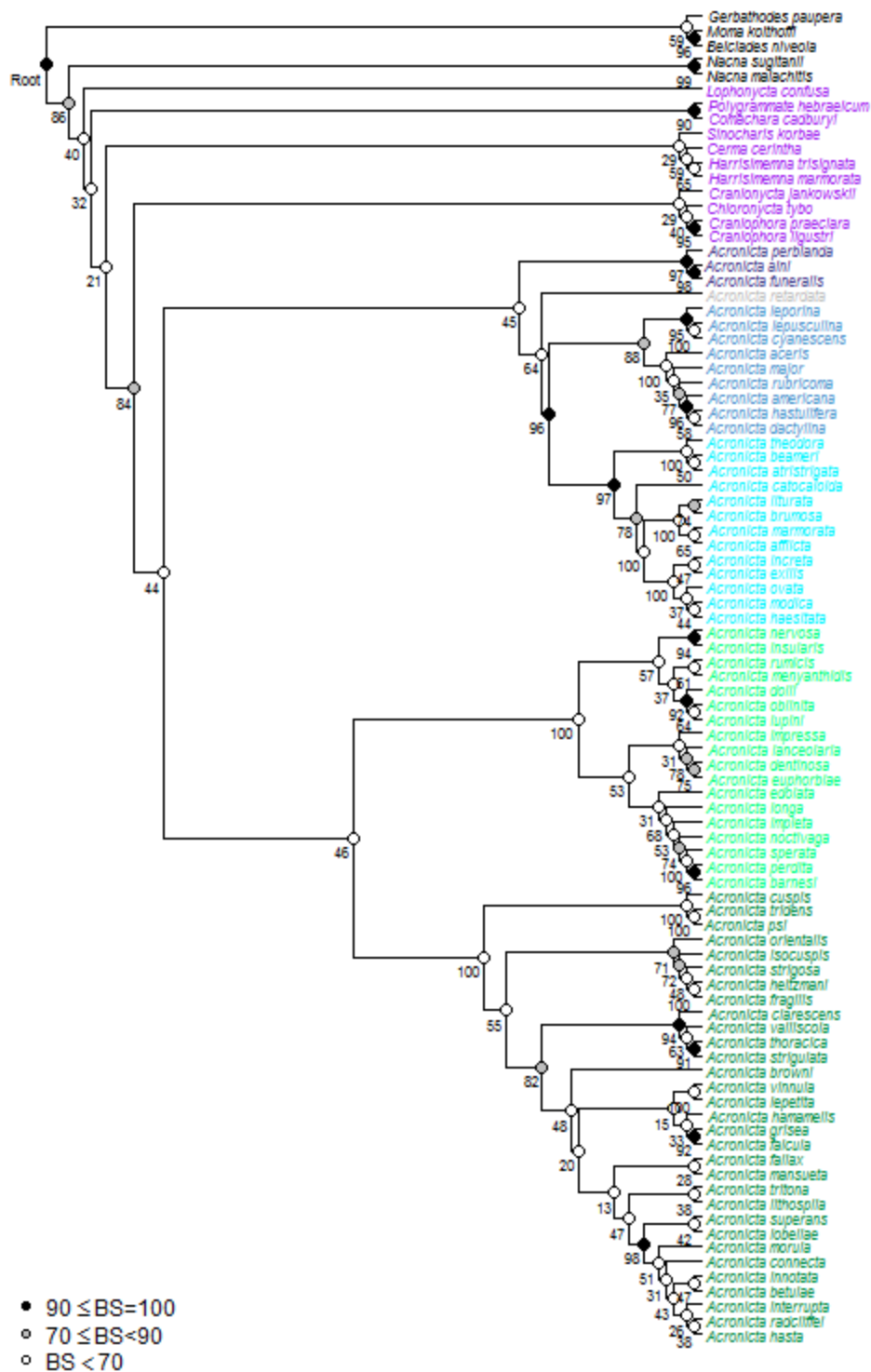
**Figure S21.** Maximum likelihood phylogeny for RpS5 (98 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.



**Figure S22.** Maximum likelihood phylogeny for wingless (93 taxa). Sequences were partitioned by codon position. Nodes are colored according to bootstrap support values.



**Figure S23.** SVD Quartet 50% majority rule consensus phylogeny for *complete* dataset (101 taxa), with all genes. Sequences were not partitioned. Nodes are colored according to Bootstrap Support values. Branch lengths are arbitrary.



**Figure S24.** SVD Quartet 50% majority rule consensus phylogeny for 50% coverage dataset (91 taxa), with all genes. Sequences were not partitioned. Nodes are colored according to Bootstrap Support values. Branch lengths are arbitrary.

## **Chapter 3: Defensive behaviors of *Acronicta* larvae in response to a potential predator (*Camponotus pennsylvanicus*) and forceps pinch tests**

### **Introduction**

Lepidopteran larvae face a deluge of threats in their daily life (Greeney et al. 2012). Both vertebrate and invertebrate predators abound, in addition to a horde of parasitoids looking for suitable hosts for their young. With soft, mostly unsclerotized bodies, caterpillars must rely on a suite of morphological, chemical, and behavioral traits in order to survive threats posed by this menagerie of enemies. Some defenses are physical barriers, such as hairs and spines, which may offer partial protection from parasitoids, and invertebrate predators such as ants and beetles (Weseloh 1976; Sheehan 1991; Montllor and Bernays 1993; Sugiura and Yamazaki 2014). Other morphological defenses include crypsis and aposematism, which enable caterpillars to either blend in with their surroundings, or give a warning signal about unpalatability; these traits can provide an advantage against larger visual predators such as birds (Strong et al. 1984; Bowers 1993; Stamp and Wilkins 1993; Ruxton et al. 2004). Of course, Batesian mimicry and startle coloration, by palatable species, also occur in many lineages (Janzen et al. 2010; Hossie and Sherratt 2012). Chemical defenses, which often relate to a caterpillar's diet (host plant derived metabolites may confer chemical advantages to the larvae), can be highly effective against some predators, such as ants (Dyer 1995). Behavioral defenses occur both before and after detection by a predator. Primary defenses, i.e., those in force before detection, can make a larva harder to detect or reach. Resting on the underside of a leaf, staying away from leaf edges, creating shelters, and minimizing obvious feeding damage are just four stratagems employed by caterpillars (Heinrich 1993; Montllor and Bernays 1993; Johnson 2014). Once a caterpillar has been detected and is approached, secondary defense behaviors are employed. Examples would

include turning away or hiding the head, jumping, or dropping from the plant (Gross 1993a). Counter-attacks, which are more aggressive behaviors, can include rearing up, twitching, waving, thrashing, regurgitating, biting, and even throwing the attacker (Gross 1993a; Dyer 1995; Greeney et al. 2012) (Figure 1). While twitching and thrashing can be considered evasive if they are done in order to avoid or escape (Gross 1993a), they can be considered aggressive if they are directed at the attacker. The type of defensive behavior utilized by a caterpillar may depend upon its species, size, age, degree of physical protection, diet breadth, the frequency and severity of attack, whether the predator is a vertebrate or invertebrate, and more (Gross 1993a; Dyer 1997). Defensive behaviors can require considerable energy, time, and risk.

This study utilizes larvae of the noctuid genus *Acronicta* (Acronictinae) to address several questions: **1) Are there lineage-specific responses to interactions with predators?** *Acronicta* species have a range of setal characters that provide them with different levels of protection. If setae provide effective defense, then a densely covered (hairy) caterpillar would not be expected to waste energy and time on lengthy or aggressive behaviors. This was observed to be true for larvae experiencing initial attacks by Johnson (2014). Species of *Acronicta* can be grouped into species groups, which share setal morphologies and other life history traits, such as diet breadth. Due to this array of life history traits, I hypothesize that *Acronicta* species will have a range of defensive responses. Species group patterns should arise, as well as patterns among larvae with similar levels of hairiness. **2) Do species react differently to different types of attack?**

Different predators present different risks to a caterpillar, which the larvae may be able to perceive and react to. A particular predator may also present different risks depending on how it approaches the caterpillar. I hypothesize that *Acronicta* larvae will respond more aggressively to

more risky interactions with a predator. Directed attacks would present a greater risk than incidental touching; a pinch to the integument would present a greater risk than touching and/or biting of setae. **3) How do defensive behaviors change through the development of a caterpillar?** If larvae are susceptible to different predation risks at different life stages (due to size, setal morphology, exposure, or other factors), then it follows that they could also react differently to an attack. Older, larger larvae may have enough bulk and morphological defenses to stay in place when faced with an invertebrate predator, and may even be able to inflict damage on their attacker. I hypothesize that earlier instars will exhibit more evasive behaviors (both in kind and frequency) to avoid predation risk, and later instars will exhibit more aggressive behaviors.

## **Methods**

Experimental trials using both an invertebrate predator (wild colony of carpenter ants) and a simulated biting predator (pinching with forceps) were conducted on 13 *Acronicta* species to record larval defensive behaviors. This builds upon the methods developed by others for conducting behavioral experimentation with noctuid larvae (Dyer 1995; Greeney et al. 2012; Johnson 2014). This chapter also provides quantified behavioral data that will be used in phylogenetic analyses of trait correlations in *Acronicta* larvae (see Chapter 4).

### *Taxon sampling*

Thirteen species (Table 1) were selected based on two criteria: their availability, and to represent the major *Acronicta* species groups. Availability depended on several factors: their availability, whether captive females routinely oviposited in captivity, the number of ova laid per clutch, and



the success I and others had in rearing sufficient numbers of larvae to the ultimate instar. Only two species were collected as wild middle instars. Selected taxa include at least two species for each major *Acronicta* species group, except for the *alni* clade which has only a single widespread species in North America (Figure 2). Related species (i.e., in same species group) typically share common setal characters, these are figured and described in Figure 2 and Table 3.

#### *Larval collection and rearing*

Caterpillars were primarily reared from eggs laid by captured females. Ova were collected from June to September in 2013, 2014, and 2015. Collection localities include Concord, NC; Storrs, CT; Haddam, CT; Hamden, CT; Athol, MA; Montague, MA; Keene, NH; and Santa Barbara, CA. Rearing larvae from eggs avoided the possibility of parasitoids which may affect caterpillar behavior (Adamo 1997; Karban and English-Loeb 1997) and assured that caterpillars of roughly equal fitness and age could be used in trials. Some individuals of two species (*A. ovata* and *A. increta*) were collected in the wild, and were continually monitored for parasitoids and relative health (frass production). None yielded parasitoids. Collection localities include Haddam and Hartford, CT. Larvae were reared in groups through early instars, and separated into individual vials in the penultimate and ultimate instar. Different larvae were used for the ant and pinch trials; not all species were used for both ant and pinch trials. Ant trials utilized only penultimate or ultimate instars. Premolt larvae were excluded. Pinch test trials used a range of middle and late instars. Each individual larva was tested for multiple interactions, either within the same day or over multiple trials.

Small branches of host plants for each caterpillar species were collected in Mansfield CT and brought into the lab. Host plants included *Acer saccharum*, *Alnus incana*, *Betula nigra*, *Prunus serotina*, *Quercus alba*, *Quercus rubra*, and *Ulmus americana*. Individual leaves were fed to larvae in vials. Larger branches were selected for experimental procedures between 3 and 24 hours before trials were to be conducted.

#### *Potential predator*

A colony of *Camponotus pennsylvanicus* De Geer, 1773 (black carpenter ant) was located in a disturbed area near a sidewalk on the University of Connecticut campus. The same colony was used for all trials. Minor and major workers were observed foraging for food and traveling back to their colony at the base of a sugar maple tree (*Acer saccharum*). This genus was chosen due to its known predation of large caterpillars, tendency to forage on trees, and its use in other predation studies (Fowler and Roberts 1980; Fuente et al. 1994; Johnson 2014). During the course of this study, one worker was observed bringing a large (1.5 cm long) noctuid larva to the nest.

#### *Ant trial procedure*

At least three hours prior to experimentation, between one and five caterpillars were placed on a branch of their host plant, and oriented in a natural position (Figure 3). This ensured that leaves hung in the same orientation as they would in the wild. Larvae were often restless when first placed on the plant – the 3+ hour settling period gave them time to feed normally and find an appropriate resting location as they would in the wild.

Each trial was conducted between 1700 and 1900 hours during the months of July, August, and September. *C. pennsylvanicus* workers primarily feed at night, beginning their foraging activities in the late afternoon (Fowler and Roberts 1980). For each trial, the host plant was placed in the foraging area of the ant colony, within 1 meter of the nest. One ant at a time was encouraged to crawl onto a small piece of bark, which was then placed near a leaf of the plant. This served to keep the ants' foraging instincts intact, and to reduce disruption of their natural behaviors. Each ant was allowed to explore the leaves and interact with larvae for 5-15 minutes. Trials were terminated when the ant dropped from the plant, had interacted with all the larvae, could not find the larvae within 15 minutes, or appeared overly agitated from handling. In some cases, one ant had several interactions with a single larva.

Salient interactions between the caterpillars and ants were documented. At least one interaction was recorded per larva. Interactions were video recorded (Canon PowerShot SX260) if the viewing angle, camera focus, and weather conditions were favorable. Ant data included class (major/minor), whether the ant's touches appeared incidental or directed, the ant's response to touching the larva, and the larva's response to being contacted by the ant. Incidental or directed touching was determined by the actions of the ant leading up to the touch. If the ant was making directed movements toward the larva, and then antennated or bit the larva, it was considered directed. If the ant was making random, exploratory movements not directed toward the larva but touched it with a leg or antenna during those travels, it was considered incidental. Caterpillar data included instar, location on the plant, and its response to being touched by the ant. Each trial was recorded as full descriptions of the behaviors observed, and later scored according to a scale.

### *Pinch test*

Forceps were used as a proxy for vertebrate attack, or grasping by a large invertebrate predator (such as a vespid wasp). This type of pinch test, a simulation of biting or grasping, has been used to elicit larval behaviors in multiple studies (Walters et al. 2001; Gentry and Dyer 2002; Johnson 2014). The same pair of fine-tip forceps was used for all trials.

### *Pinch trials procedure*

All pinch test trials were performed indoors. At least three hours prior to experimentation, larvae were provided small branches of their host plants. After this settling period, each branch was mounted with a clip for the leaves to hang in a natural position. Another five minutes were allotted for larvae to adjust to being moved. Video recording of every trial was done with a Dino-Lite Pro AM4113ZTS on a custom-built focusing rail. The pinch was administered once to the rear segments. The same person (BVZ) delivered every pinch to maintain consistency. Caterpillar data included instar, body length, and its reaction to being pinched.

### *Scoring method*

Past studies have characterized larval defensive behaviors with different systems or ad hoc classifications (Dyer 1995; Walters et al. 2001; Greeney et al. 2012; Johnson 2014) using broad categories of “evasive” and “aggressive” (Gross 1993a). In this study, behaviors were scored based on their level of evasiveness or aggressiveness. To subdivide these categories, a scale was created: evasive behaviors in the negative, no response at zero, and aggressive behaviors in the positive (Table 2). This scheme helped assess larval responses at a finer scale. Behaviors higher (or lower) on the scale indicate more severe responses. Biting is considered the most aggressive

response, which may also be coupled with throwing an ant off the leaf (or attempting to bite and throw the forceps in the vertebrate trials). Thrashing repeatedly may serve to thwart bird and parasitoid attacks (Walters et al. 2001), while a single thrash was sometimes observed to dislodge a small invertebrate predator, i.e., worker ant (personal observation). Waving the head side to side, rearing up, or twitching the head or rear end of the body were given the lowest positive score. Evasive behaviors begin with turning away from the stimulus, then partially curling the body. This is typically done by curling the head beneath the thoracic segments. Crawling away represents an evasion without risks of leaving the host plant, while curling and dropping is the most drastic evasive maneuver. Leaving the host plant is dangerous for a larva, especially for tree-feeders with specialized diets, which may have a distant, risky climb back up to suitable foliage. Dropping with a silk line (to return to the plant) is only observed through the second instar in *Acronicta* larvae (unpublished data). Because not all observed behaviors fit into these categories, unclassified behaviors were grouped into categories based on similar aggressiveness or evasiveness. If a larva exhibited multiple behaviors in succession, the final behavior was scored. Some examples of these behaviors are provided in Figure 4. The maximum, minimum, and average behavioral scores were calculated for each species for ant trials (Table 4) and pinch trials (Table 5), and plotted (Figures 5 – 10).

### **Species and species-group responses**

In addition to differences among species, larvae were compared for differences among species groups, and overall hairiness. To partially account for phylogenetic relatedness, under the assumption that closely related species are more likely to share traits, comparisons were made by combining data within species groups. To test the importance of general hairiness, species were

grouped by their hairiness score, a categorical trait. This left species groups 3 and 5 as-is, while combining groups 2 and 4. Though they have some different setal characters, their arrangement may effectively act as the same physical barrier to predators due to similar setal densities. Species groups were assigned numbers, and hairiness was scored as a combination of setal characters (Figure 2). One-way ANOVA (analysis of variance) tests were performed to find statistical differences between species, between species groups, and between hairiness categories for both ant trials and pinch trials (Tables 6 and 7). A phylogenetic assessment utilizing these data is performed in Chapter 4.

### **Responding to different types of attack**

To compare larval responses to different degrees of attack, comparisons were made between incidental and directed touching by ants in the ant trials. One-way ANOVA tests were performed to find statistical differences among caterpillar defensive responses between species (Tables 6 and 7). Two-sample t-tests assuming unequal variances were used to find differences between caterpillar defensive responses within species (Table 8). Comparisons were also made between ant trials and pinch trials with late instars (Table 9). Seven species were studied for both directed ant encounters and late instar pinch tests. These two were compared because all ant trials were conducted with late instars, and directed attacks would be most biologically similar to the pinch tests, both representing a threat from a potential predator.

### **Behavioral changes through development**

Only the pinch trials utilized both early and later instars. One-way ANOVA was performed to test for differences between caterpillar defensive responses at early and later instars between

species (Tables 10 and 11). Two-sample t-tests assuming unequal variances were performed to test for statistical differences between caterpillar defensive responses at early and later instars within species (Table 12).

## **Results**

### **Species and species-group responses**

Significant differences in average defensive behaviors were found between species in all analyses for ant trials and pinch trials. For the ant trials, no significant differences between species groups were found for the combined data across all trials. However, when the trials were split into incidental and directed encounters, species groups showed significant differences in defensive responses (Table 7, also see Figures 6 and 7). For the pinch trials, all analyses (combined, early instars, and late instars) gave significant differences between species groups and hairiness categories (Table 11).

### **Responding to different types of attack**

Of the 12 *Acronicta* species tested in the ant trials, four had a significant difference in defensive behavior between incidental and directed ant encounters (Table 8). Three of these are in species group 3 (*A. haesitata*, *A. increta*, and *A. ovata*), while one (*A. lobeliae*) is in species group 5. In all four cases, average defensive scores went from more evasive in incidental attacks to more aggressive in directed attacks. Some overall patterns are also revealed in the species group and hairiness category results. For both incidental and directed encounters, Species groups 2 and 4 had similar average scores which are marginally above zero, meaning their responses, regardless of ant encounter, were evasive or mildly aggressive. Group 5 species were more aggressive than

group 2 and 4 species in both types of encounters. Group 3 had the greatest variance in defensive behaviors. They were highly evasive in incidental encounters, and highly aggressive in directed encounters. The relationship of hairiness to aggressiveness changed depending on the type of interaction with a *Campanotus* worker. For incidental encounters, type 0 (modestly setose) larvae were the most evasive, while type 1 (moderately setose or hairy) and type 2 (densely setose or hairy) had similar scores. For directed encounters, type 0 were the most aggressive, followed by type 1, then type 2.

Of the seven species tested in both the ant and pinch trials, four had a significant difference between their responses to the two types of attack. The directions of these changes were not consistent across the species; three species (*A. americana*, *A. impleta*, and *A. lobeliae*) were more evasive to ants and more aggressive to pinch tests, while one species (*A. lupini*) was more aggressive to ants than to the pinch tests. It is difficult to generalize across species groups or hairiness categories, as so few representatives were able to be compared.

### **Behavioral changes through development**

All species had average behavioral scores in the negative (evasive) range for early instars. The behavioral repertoire of late instars was more variable between species, ranging from highly evasive to highly aggressive. Five species were studied for both early and late instars with the pinch test; of these, four had a significant difference in their responses (Table 12). In each case, the late instars responded more aggressively (or at least, less evasively) than the early instars. This pattern holds true across species groups, and across hairiness categories. Comparing species groups in early instars, groups 2 and 4 were more evasive than group 3 (group 5 was not



represented). In early instars, species which are hairier (type 2) were more evasive than those with the least number of setae (type 0). Comparing species groups in late instars, groups 3 and 5 had highly aggressive responses, followed by group 2, then group 4. This led to hairiness types 0 and 1 having the same high aggressive score, with type 2 slightly above zero.

## Discussion

These experimental trials offer interesting evidence for variation in larval defensive behavior between species, between instars, and between different types of attack. **1) Are there lineage-specific responses to interactions with predators?** Species groups within *Acronicta*, which have major differences in setal characters, have different behavioral defensive strategies. Better protected larvae are less likely to respond to ant attacks or pinching, while larvae with fewer setae tend to respond aggressively. Whether these patterns of morphology and behavior hold true for other species in the genus *Acronicta*, or for any other lepidopteran larvae, remains to be seen.

**2) Do species react differently to different types of attack?** Some species responded differently to incidental and directed encounters with ants. The degree of difference varied by the amount of morphological protection from setae; less hairy caterpillars have more extreme evasive responses to incidental touching by ants, and more aggressive responses to directed encounters. Hairier species displayed overall more evasive behaviors, and did not differentiate as much between incidental and directed encounters. Some larvae respond differently to directed ant encounters and pinch tests; in most cases, they respond more aggressively to pinching. Since pinches represent a direct attack by a relatively large enemy (as opposed to perturbation of the setae), it makes sense that a pinch would elicit more drastic behavioral responses. **3) Do defensive behaviors change through the development of a caterpillar?** The data collected

point to a shift in defensive behaviors as a larva ages. Earlier instars tend to perform evasive defenses, often dropping with the safety of a silk line (to return to their host). Older, heavier *Acronicta* larvae do not use a silk line, and tend to switch to other evasive behaviors, or aggressive behaviors, to deter a potential predator.

### **Species and species-group responses**

In this study, behavioral responses vary with species group; these species groups also show patterns in setal morphology. Splitting *Acronicta* larvae into hairiness categories served to assign group 3 to hairiness type 0, group 5 to type 1, and groups 2 and 4 to type 2. It should be noted that not every species from these species groups would fall into those categories. While hairiness is consistent among groups 1 through 4 (of known *Acronicta* larvae), species group 5 contains members with type 1 and type 0 levels of hairiness. Patterns of morphology and defensive behaviors in a phylogenetic context is addressed in Chapter 4.

Dyer (1997) demonstrated that spines and hairs provide differing amounts of protection to different invertebrate predators, but did not address how defensive behaviors differed among glabrous (smooth), spiny, and hairy larvae. If defensive behaviors are dependent on how well protected a larva is, then densely covered individuals should not waste energy on unnecessary behaviors such as thrashing. This result indeed emerged in both the ant trials and pinch trials (although in the ant trials, the data needed to be separated into incidental and directed ant encounters for the differences between species groups [or between hairiness categories] to be significant). Acronictine larvae which are more protected by setae (type 2: species groups 2 and 4) remained low (evasive) in their scored responses to ants. Several encounters were observed

where ants repeatedly chewed the setae of *A. impleta*, with little response from larvae for over a minute. Larvae with moderate to few setae (type 1: species group 5, and 0: species group 3) had very aggressive responses to directed ant encounters, likely due to the risk of an ant bite causing damage to their exposed cuticle. Individuals of all group 3 species (*A. haesitata*, *A. increta*, and *A. ovata*) were observed biting and throwing ants off the leaf they were perched upon. When turning toward an ant, rearing up, or thrashing, their mandibles were typically opened; it is likely more encounters would have ended with a tossed ant if the mandibles had made contact with an ant appendage. Species of these groups were also more likely to behave aggressively to incidental touching than the other groups. Due to their vulnerability, it may behoove them to react to slight stimuli, as there is a greater risk of potential injury. The defenses of early instars toward ants are unknown, though it is likely they are more susceptible to invertebrate attacks due to their smaller size. Interestingly, the early instars of species group 3 have sharp, barbed secondary setae, which are lost in later instars. Whether these offer some protection from predation is unknown.

From these experiments, it cannot be said for certain whether ants can successfully kill and carry off an *Acronicta* caterpillar; in no case was an ant observed to overcome an *Acronicta* caterpillar. Nor have I read of such of an occurrence in the literature. Perhaps the recruitment of multiple ants would be required to take on larvae of such size. Hence one of the advantages to biting and throwing an ant from a leaf (tree) is the ant would have no opportunity to recruit additional workers to the site of a perched caterpillar. Experiments with earlier instars would help determine whether an individual *Camponotus* worker poses a real threat to *Acronicta* larvae in any instar.

## **Responding to different types of attack**

When comparing the responses of larvae to incidental and directed touching by ants to the combined data, the importance of separating the data by the type of encounter is important. Larvae of some species had different behavioral responses to situations of different potential risk. The incidental touching of an ant tarsus or antenna may be akin to a wisp of silk, a leaf, or a raindrop: environmental actions which do not merit the energetic expense of an aggressive behavioral response. They may, however, warrant a mild evasive response, if it would protect the larval head or ensure a stronger grip. Conversely, the directed antennation, repeated touching, or biting by an ant may elicit an aggressive response which may deter the ant. Other studies have demonstrated that lepidopteran larvae react differently to the degree of perturbation, as simulated by the bending of larval setae. Whether the setae were bent quickly or slowly altered the behavior of the larvae, suggesting an adaptive and conditional response to different predation risks (Castellanos et al. 2011). This study demonstrates the degree to which larvae respond to a *Camponotus* attack also depends on their level of setal (mechanical) rotection. Of 12 species tested for both incidental and directed ant encounter trials, only four had significant behavioral differences. These were the least hairy larvae: i.e., those with the most exposed integument and vulnerable to injury from an ant bite. While they had the most evasive responses to incidental touching, they had the most aggressive responses to directed ant attacks. Though the remaining species did not differ significantly between types of encounters, mostly showed a trend toward increasing evasiveness when comparing incidental to directed attacks, the opposite pattern. Overall it appears that hairier larvae do not distinguish between incidental and directed encounters with ants, instead facing most perturbances with evasive actions, occasionally

thrashing to dislodge the irritation. Less hairy larvae are more apt to distinguish between encounters of low and high threat, and respond more aggressively to dangerous encounters.

Comparisons between ant trials and pinch trials reveal that these two attack types may represent different threat levels to *Acronicta* larvae. Two species showed no difference between the two methods, one species had too few data points to compare statistically, and the other four species showed significant differences. However, no patterns emerge for species groups or hairiness categories. Of the two that showed no difference, one was *A. dactylina* (group 2, type 2), and the other was *A. haesitata* (group 3, type 0). The species with differences between the trials belong to groups 2, 4, and 5 (types 1 and 2). Unfortunately, there was not more overlap between the data sets, and more species could not be compared. This offers some evidence that species may react to an ant antennation or bite differently from a bite directly on the body—a matter warranting further study to determine any directionality or dependence on morphology.

### **Behavioral changes through development**

Lepidopteran larvae are known to alter their defensive strategies as they grow; differences in size, morphology, and predation/parasitism risk go along with changes in behavior (Cornell et al. 1987; Gross 1993b; Montllor and Bernays 1993). This may be due to different predation pressures at different sizes; invertebrate predators may not be able to overcome large larvae, preferring smaller prey. Birds, however, may favor the larger, more nutritious larvae (Dempster 1967; Montllor and Bernays 1993). In this study, when faced with a pinch from a pair of forceps, the strategy for escape was observed to change as the larvae developed (for most species). Of the five species tested at both early (instars 1-3) and late (instars 4-5) stages, four species displayed

significantly different behaviors: in later instars, larvae responded more aggressively (or at least, less evasively). An early instar stands little chance against a biting predator the size of *Camponotus pennsylvanicus*. Of the five species for which early instars were available for pinch tests, curling and dropping from a silk line was commonly observed in three (*A. dactylina*, *A. haesitata*, and *A. oblinita*). The other two species dropped, but without a silk line. Some larvae were difficult to pinch, because they curled up as soon as the forceps touched their setae. This is one reason why trials were conducted after larvae assumed normal resting positions on their host plants, the dropping behavior would be lost on a flat surface. After the third instar, acronictine larvae no longer drop on a silk line (but may still drop from the plant). This change has been observed in multiple *Acronicta* species during rearing (personal observation). At later instars, *Acronicta* larvae may be too heavy to descend on silk (though many other species, primarily smaller geometrids, use belay lines throughout the larval stage (Wagner 2005)). It may also be risky for a caterpillar to leave its host plant, especially if dietarily specialized, and in later instars larvae switch strategies to primarily stay in place when attacked. Throughout all the late instar trials, there was a noted prevalence of thrashing and biting, with many larvae biting and trying to throw the forceps. Some generated enough force to be felt in my hand. These patterns suggest a general shift in defensive strategy as a larva matures: in earlier instars, when small and vulnerable, most caterpillars attempt to escape. In later instars, when leaving the host plant is riskier and without the safety of a belay line, larvae tend to exhibit more aggressive behaviors toward a potential predator. This is the opposite of what was found for buckmoth larvae (Saturniidae), which thrash as early instars and drop as later instars; however these defenses are modified due to their gregarious behavior with conspecifics (Cornell et al. 1987).

*Other interesting observations*

**Body size.** The ant trials used only penultimate or ultimate instars in order to maintain consistency, but body size was not measured. Different *Acronicta* species reach different sizes at their final instar—roughly a threefold difference is seen across the genus—therefore any factors related to size (such as instar) are in need of additional study. There are indications that body size may influence predation success and larval responses, and should be measured for all individuals (Gross 1993a; Dyer 1997).

**Multiple behaviors.** In some cases, larvae were observed to perform several behaviors in succession. These typically included aggressive behaviors, followed by evasive behaviors (like dropping off the plant). If the length of attack were recorded, the relationship between attack time and the succession of behaviors could be analyzed. This also relates to **severity of attack** and **repeated exposure**. Invertebrate attacks ranged from gentle antennation to multiple bites. Scoring attacks by severity could give insight into nuances in the larval responses. This study addressed severity by categorizing ant behaviors as directed or incidental. The directed category could be further divided into touching, biting, and repeated touching or biting. In some cases repeated exposure has been shown to lead to incremental sensitization, meaning repeated attacks resulted in more extreme responses (Walters et al. 2001). It has been noted that hairier species will typically not respond to the first attack, but do respond to subsequent attacks (Johnson 2014). This could explain why, in this study, the species covered by secondary setae had the most “no response” results, as they typically did not experience multiple attacks.

**Post-attack responses.** Some larvae were noted to have an extended post-attack response. After their initial responses in the pinch test trials, most individuals of *A. obliterata* (instars 4 and 5) returned to the original resting position, partially reared up with thoracic legs not touching the plant. They would then gently sway back and forth, held on by their prolegs. This rocking behavior continued for two to twenty minutes following an attack. This behavior was not observed for any other *Acronicta* species. The rocking behavior was not recorded for any invertebrate trials, but may have occurred. It is currently unknown what purpose this rocking may serve.

**Silk mats.** Some *Acronicta* routinely spin a silk mat upon which they perch when not feeding, especially for molting (pads are often used for molting, so the crochet hooks of their prolegs can remain firmly attached to the substrate and allow the larva to crawl out of its old integument). Interestingly, it was observed that ants would usually avoid silk mats, or retreat upon touching the silk threads, and therefore, did not contact larvae on silken mats. However, some larvae felt these vibrations and would defend their position by thrashing. Whether routine silk mat creation offers a defensive benefit, in addition to or aside from a molting benefit, is unknown. A behavioral study could be done comparing larvae on bare leaves to larvae on silk mats, and larvae which are undergoing the molting process.

### *Future Directions*

This study was originally conducted to provide behavioral data to examine the relationships between morphology, behavior, and diet breadth in *Acronicta* larvae (Chapter 4). In the process, several patterns of defensive behavior were elucidated. The type and degree of defensive



response is mediated by degree of physical protection, severity of attack, and instar. In the future, more experimental trials for both ant and pinch tests will be run with other *Acronicta* species to see whether these trends hold throughout the genus. Additionally, species from other genera, subfamilies, and families can be tested to see if these trends are common throughout Lepidoptera. Other factors such as body size and multiple behaviors will be taken into consideration. Ultimately, these data help us understand how lepidopteran larvae mediate predation risks through a range of behavioral responses.

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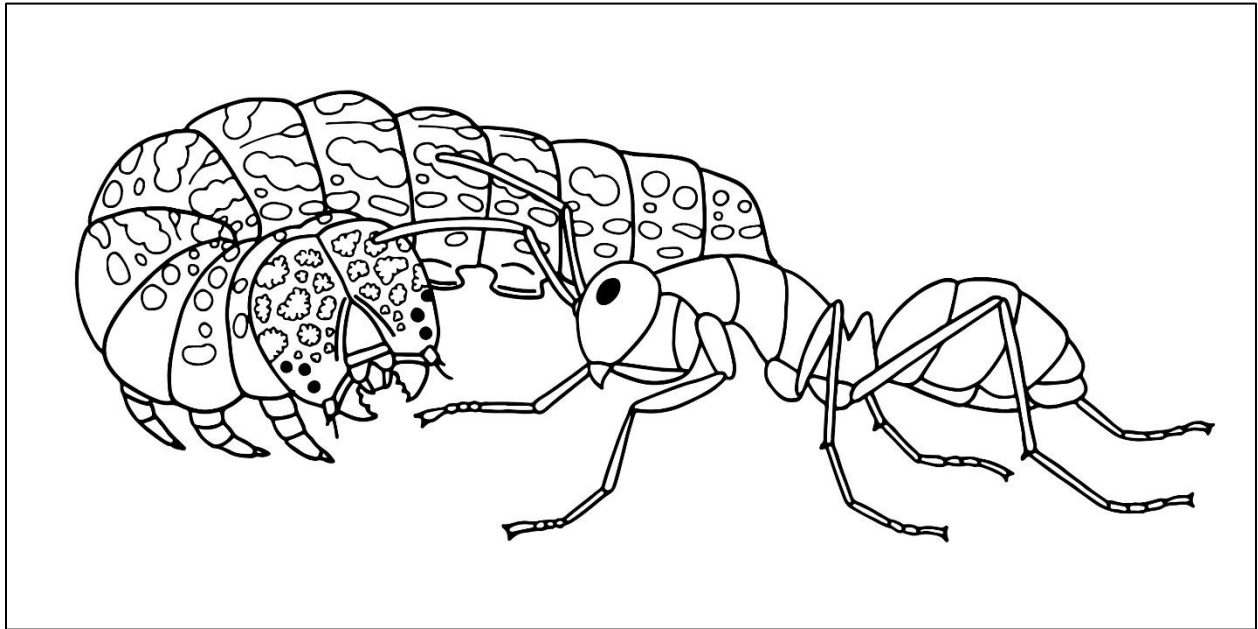
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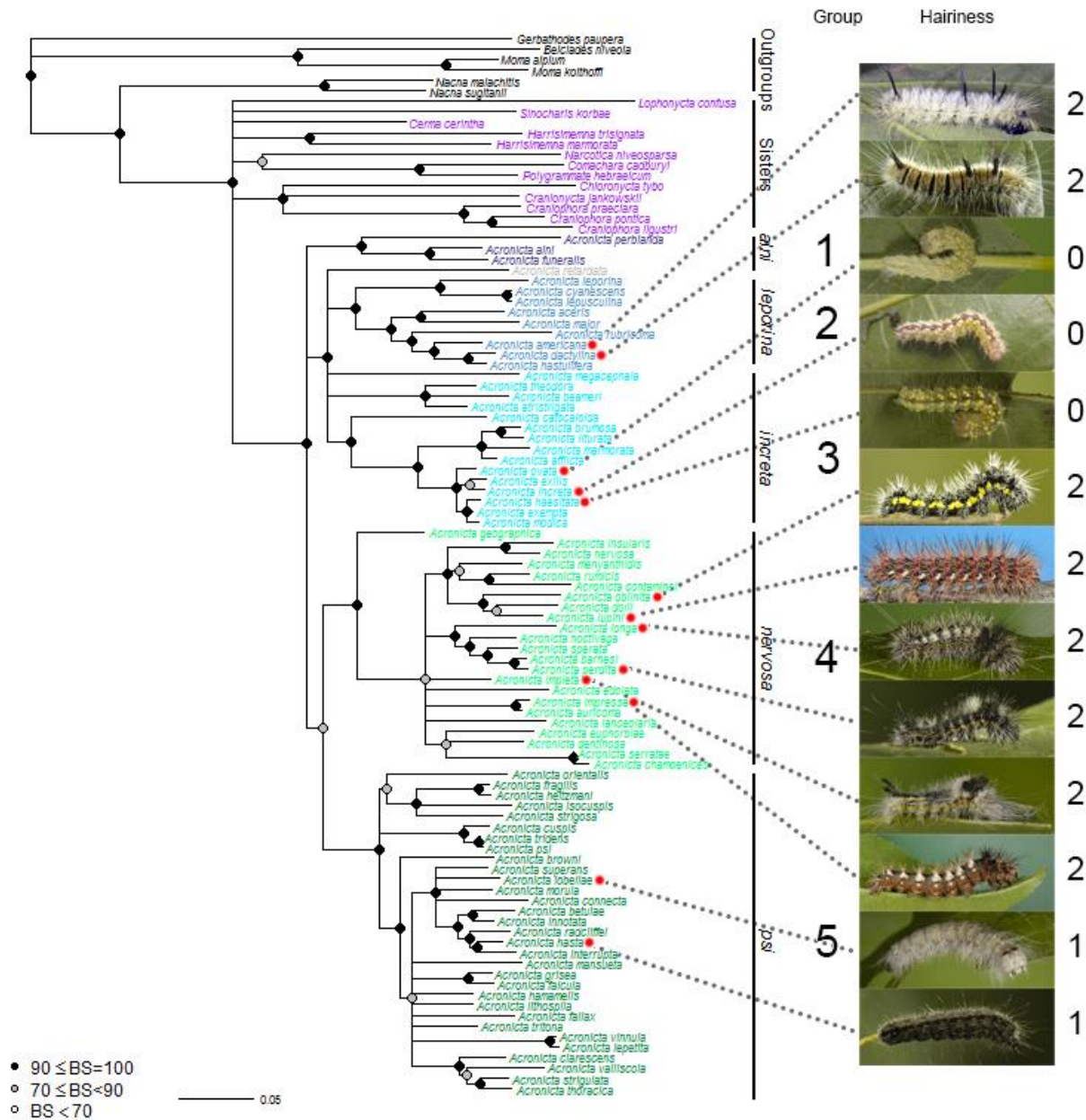
## Tables and Figures



**Figure 1.** Illustration of *Acronicta ovata* opening its jaws in response to the antennation of a potential invertebrate predator,<sup>9</sup>.

**Table 1.** Number of individuals and interactions recorded for each species tested. Species group numbers correspond to the species groups illustrated in Figure 2.

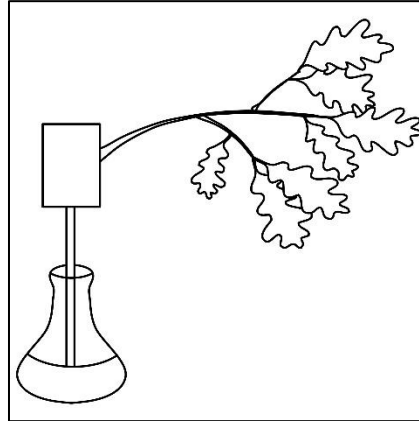
Species	Ant trials			Pinch test trials			Species group	Hairiness
	# Individuals	# Interactions	Year(s)	# Individuals	# Interactions	Year(s)		
<i>A. americana</i>	15	34	2013, 2014	9	16	2014	2	2
<i>A. dactylina</i>	23	63	2013, 2014	10	50	2014	2	2
<i>A. haesitata</i>	5	10	2013, 2014	30	40	2014, 2015	3	0
<i>A. hasta</i>	4	7	2013	-	-	-	5	1
<i>A. impleta</i>	14	35	2013, 2014	32	50	2014, 2015	4	2
<i>A. impressa</i>	9	19	2013	-	-	-	4	2
<i>A. increta</i>	5	9	2014	-	-	-	3	0
<i>A. lobeliae</i>	18	30	2013, 2014	4	4	2014	5	1
<i>A. longa</i>	5	7	2014	7	10	2014	4	2
<i>A. lupini</i>	5	13	2014	7	7	2014	4	2
<i>A. oblinita</i>	-	-	-	17	67	2015	4	2
<i>A. ovata</i>	10	22	2013	-	-	-	3	0
<i>A. perditia</i>	5	17	2013	-	-	-	4	2
<b>Totals</b>	<b>118</b>	<b>266</b>		<b>116</b>	<b>244</b>			



**Figure 2.** *Acronicta* phylogeny and the species used for this study. Maximum likelihood tree (101 taxa) with all genes analyzed using 12 partitions. Nodes are colored according to Bootstrap Support values. Nodes with <70% support are collapsed. Species groups are numbered for ease of reference. Species tested for this study marked with a red dot, and connected to their corresponding photo and hairiness category value.

**Table 2.** Hairiness categories for *Acronicta* larvae.

Score	Hairiness	Setal characters
0	Modest	Sparse secondary setae, no barbed setae/bristles/undercoat. No abundant secondary setae on integument or warts.
1	Moderate	Barbed setae, with abundant lateral setae
2	Hirsute	Barbed setae with secondary setae on integument, or barbed setae with bristles (may also include undercoat).

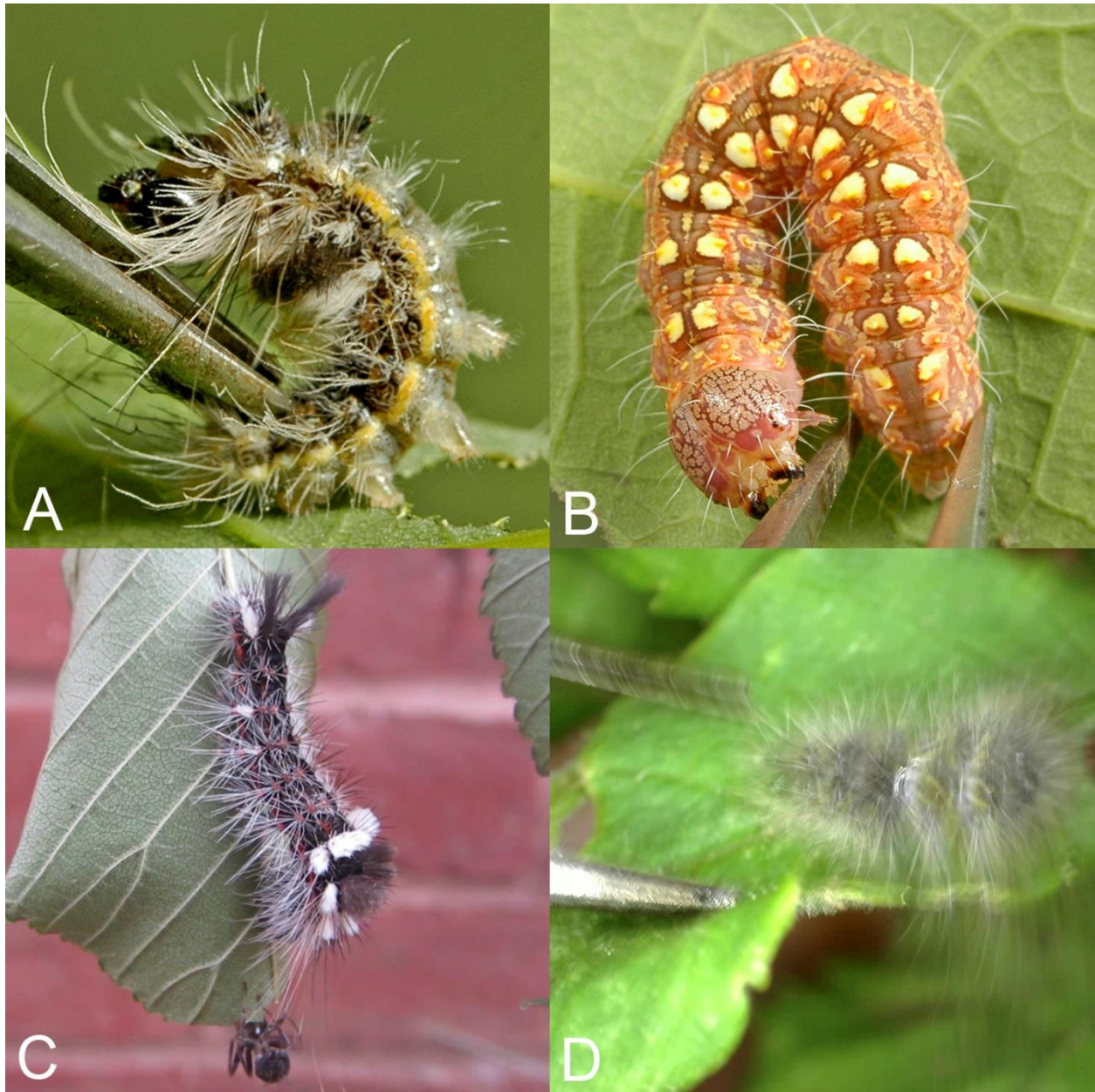


**Figure 3.** Experimental set-up for invertebrate trials. Each branch was positioned horizontally so as to emulate the natural leaf positions.

**Table 3.** Caterpillar behavior scale.

Score	Behavior	Category
4	Bite	↑ More Aggressive
3	Thrash several times	
2	Thrash once	
1	Wave or twitch	
0	No reaction	
-1	Turn away	More Evasive ↓
-2	Partially curl	
-3	Crawl away	
-4	Curl and drop	

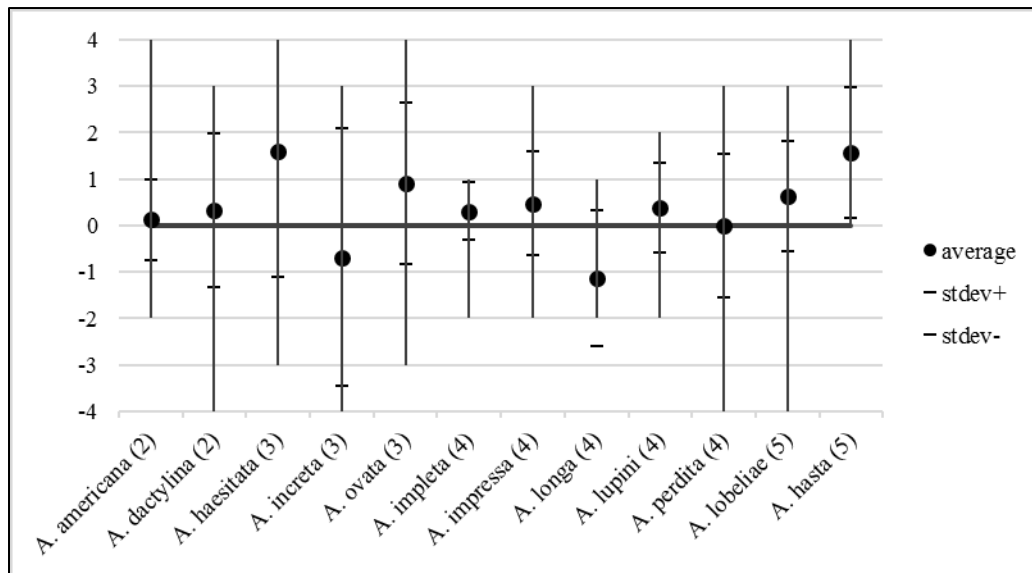




**Figure 4.** Examples of larval defensive behaviors. **A:** *A. impleta* thrashing toward the forceps, which would score a 2 on the scale for one thrash, or a 3 if multiple. **B:** *A. haesitata* biting the forceps, which would score a 4 on the scale. **C:** *A. impleta* tucking its head downward and under under prothorax after being contacted by ant, this would score a -2 for a partial curl. **D:** *A. oblinita* in the process of curling and dropping after being pinched, this would score a -4 on the scale.

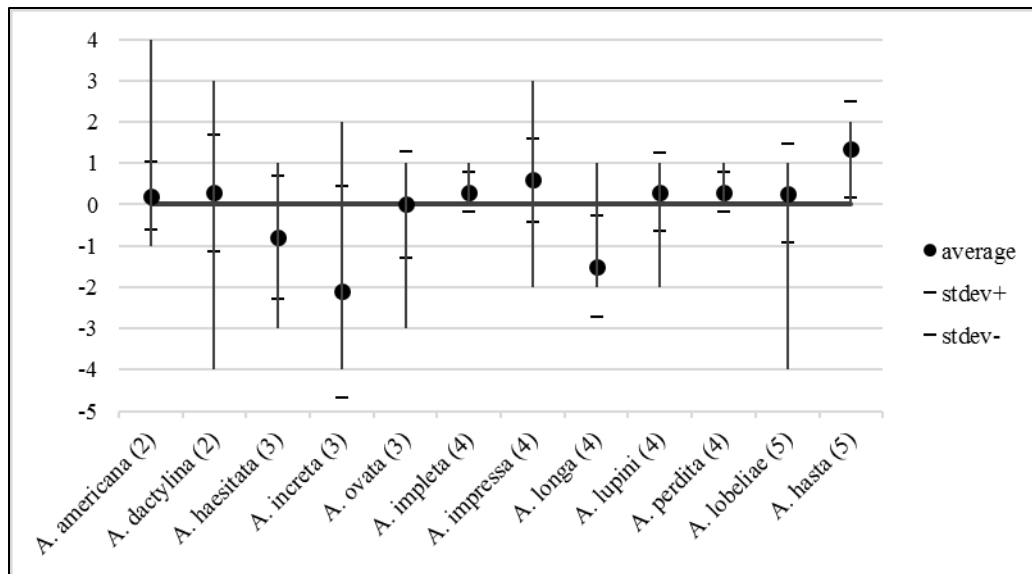
**Table 4.** Data for Invertebrate predator trials, separated by incidental and directed touching by ants.

Species	Ant - All					Ant - Incidental touching					Ant - Directed touching				
	# Int.	Avg.	Max	Min	Range	# Int.	Avg.	Max	Min	Range	# Int.	Avg.	Max	Min	Range
<i>A. americana</i>	39	0.13	4	-2	6	28	0.21	4	-1	5	11	-0.09	1	-2	3
<i>A. dactylina</i>	63	0.32	3	-4	7	42	0.29	3	-4	7	21	0.38	2	-4	6
<i>A. haesitata</i>	10	1.60	4	-3	7	5	-0.80	1	-3	4	5	4.00	4	4	0
<i>A. hasta</i>	7	1.57	4	0	4	3	1.33	2	0	2	3	2.33	4	1	3
<i>A. impleta</i>	35	0.31	1	-2	3	26	0.31	1	0	1	9	0.33	1	-2	3
<i>A. impressa</i>	19	0.47	3	-2	5	17	0.59	3	-2	5	2	-0.50	1	-2	3
<i>A. increta</i>	16	-0.69	3	-4	7	10	-2.10	2	-4	6	6	1.67	3	1	2
<i>A. lobeliae</i>	30	0.63	3	-4	7	19	0.26	1	-4	5	11	1.27	3	0	3
<i>A. longa</i>	7	-1.14	1	-2	3	6	-1.50	1	-2	3	1	1.00	1	1	0
<i>A. lupini</i>	13	0.38	2	-2	4	10	0.30	1	-2	3	3	0.67	2	0	2
<i>A. ovata</i>	22	0.91	4	-3	7	12	0.00	1	-3	4	10	2.00	4	0	4
<i>A. perditia</i>	17	0.00	3	-4	7	13	0.31	1	0	1	4	-1.00	3	-4	7

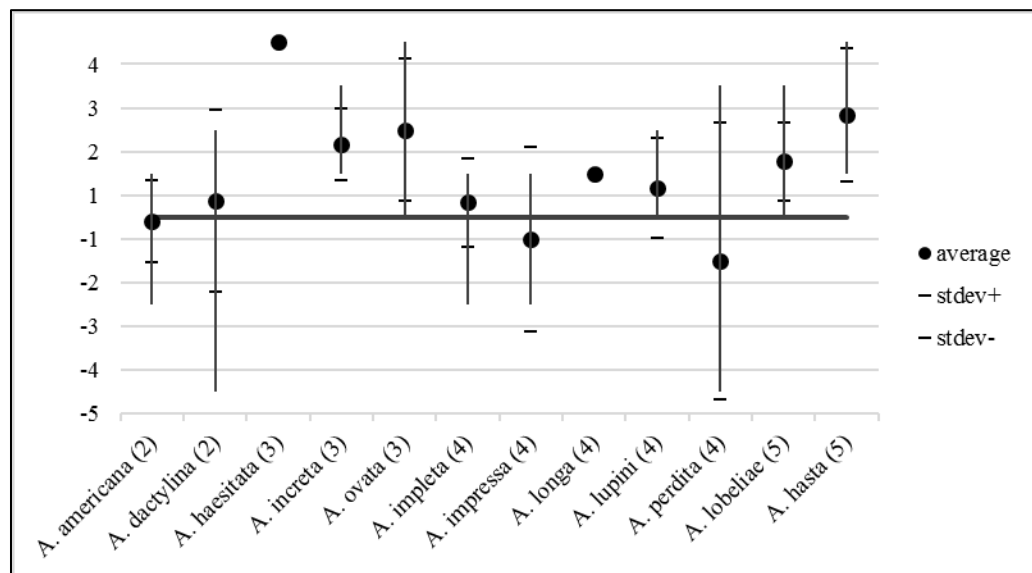


**Figure 5.** Defensive behaviors of *Acronicta* species when touched by an ant, combined data. Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.





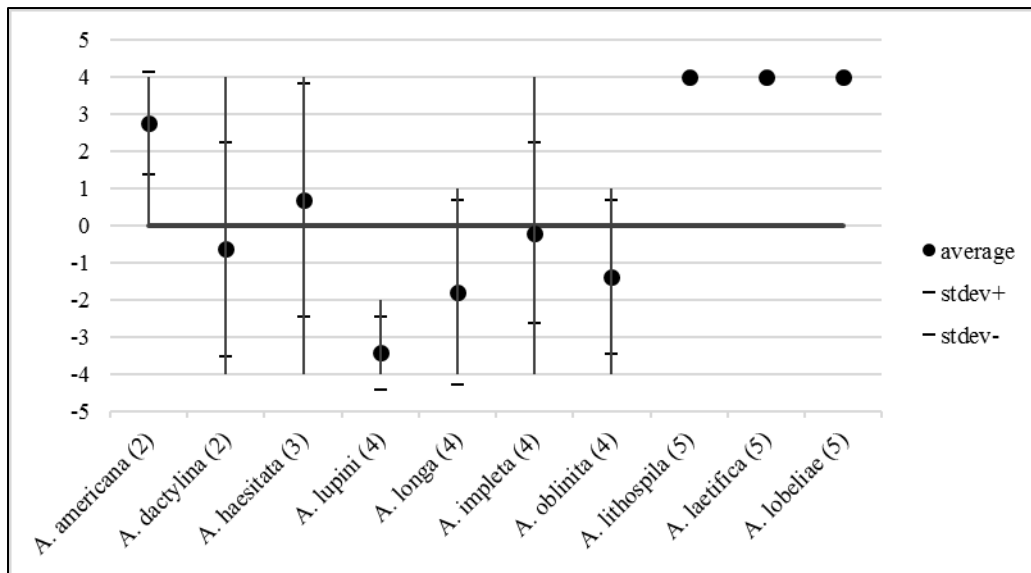
**Figure 6.** Defensive behaviors of *Acronicta* species when touched incidentally by an ant. Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.



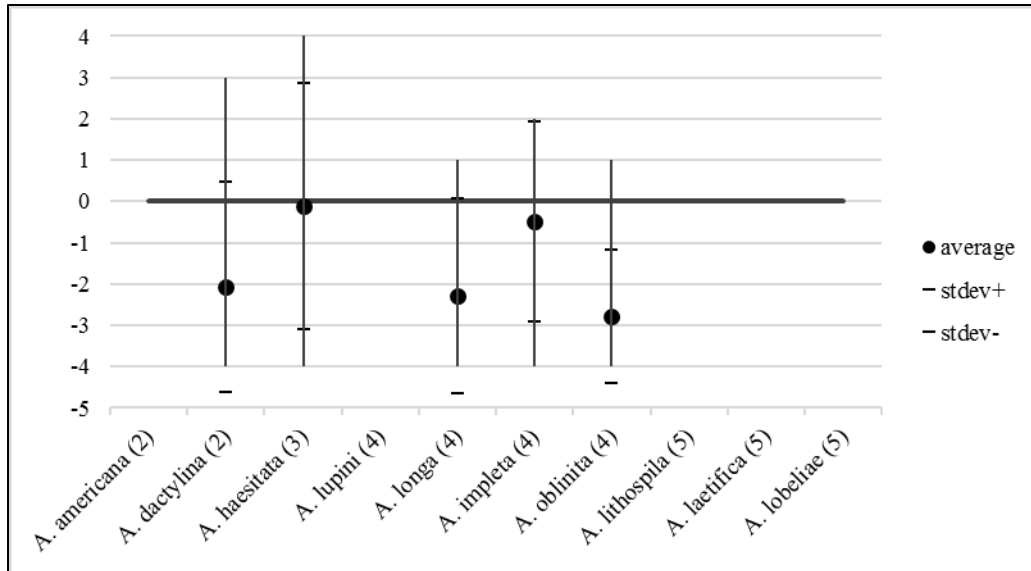
**Figure 7.** Defensive behaviors of *Acronicta* species when touched by an ant through directed movements. Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.

**Table 5.** Data for pinch test trials, separated by early and late instars.

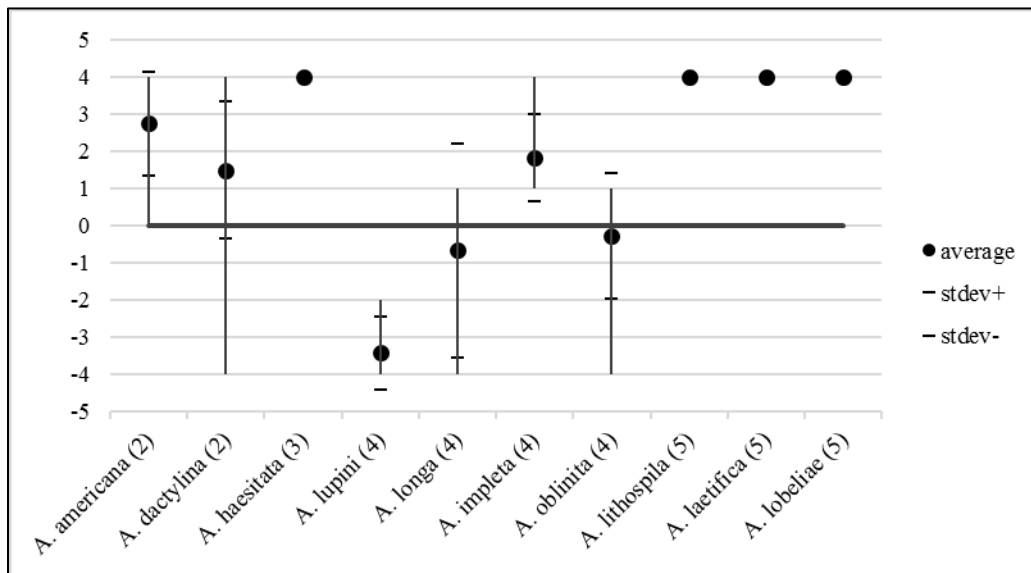
Species	Pinch - All					Pinch - Early instars (1-3)					Pinch - Late instars (4-5)				
	# Int.	Avg.	Max	Min	Range	# Int.	Avg.	Max	Min	Range	# Int.	Avg.	Max	Min	Range
<i>A. americana</i>	16	2.75	4	0	4	0	-	-	-	-	16	2.75	4	0	4
<i>A. dactylina</i>	50	-0.64	4	-4	8	30	-2.07	3	-4	7	20	1.50	4	-4	8
<i>A. haesitata</i>	40	0.70	4	-4	8	32	-0.13	4	-4	8	8	4.00	4	4	0
<i>A. impleta</i>	50	-0.20	4	-4	8	44	-0.48	2	-4	6	6	1.83	4	1	3
<i>A. laetifica</i>	5	4.00	4	4	0	0	-	-	-	-	5	4.00	4	4	0
<i>A. lithospila</i>	5	4.00	4	4	0	0	-	-	-	-	5	4.00	4	4	0
<i>A. lobeliae</i>	4	4.00	4	4	0	0	-	-	-	-	4	4.00	4	4	0
<i>A. longa</i>	10	-1.80	1	-4	5	7	-2.29	1	-4	5	3	-0.67	1	-4	5
<i>A. lupini</i>	7	-3.43	-2	-4	2	0	-	-	-	-	7	-3.43	-2	-4	2
<i>A. oblimita</i>	67	-1.37	1	-4	5	29	-2.79	1	-4	5	38	-0.28	1	-4	5



**Figure 8.** Defensive behaviors of *Acronicta* species when pinched by forceps, concatenated data. Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.



**Figure 9.** Defensive behaviors of *Acronicta* species when pinched by forceps, early instars (1-3). Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.



**Figure 10.** Defensive behaviors of *Acronicta* species when pinched by forceps, late instars (4-5). Each bar spans the maximum and minimum scored behavior. Black circles denote the average score. Short horizontal bars give the standard deviation for the average values. Species are arranged by species group.

**Table 6.** ANOVA summary data for comparisons between species, species groups, and hairiness categories for ant trials. Analyses were performed for All data, Incidental data, and Directed data.

All data					Incidental				
Species	Count	Sum	Average	Variance	Species	Count	Sum	Average	Variance
<i>A. americana</i>	39	5	0.1282	0.7463	<i>A. americana</i>	28	6	0.2143	0.6931
<i>A. dactylina</i>	63	20	0.3175	2.7363	<i>A. dactylina</i>	42	12	0.2857	2.0139
<i>A. haesitata</i>	10	16	1.6000	7.3778	<i>A. haesitata</i>	5	-4	-0.8000	2.2000
<i>A. hasta</i>	7	11	1.5714	1.9524	<i>A. hasta</i>	3	4	1.3333	1.3333
<i>A. impleta</i>	35	11	0.3143	0.3983	<i>A. impleta</i>	26	8	0.3077	0.2215
<i>A. impressa</i>	19	9	0.4737	1.2632	<i>A. impressa</i>	17	10	0.5882	1.0074
<i>A. increta</i>	16	-11	-0.6875	7.6958	<i>A. increta</i>	10	-21	-2.1000	6.5444
<i>A. lobeliae</i>	30	19	0.6333	1.4126	<i>A. lobeliae</i>	19	5	0.2632	1.4269
<i>A. longa</i>	7	-8	-1.1429	2.1429	<i>A. longa</i>	6	-9	-1.5000	1.5000
<i>A. lupini</i>	13	5	0.3846	0.9231	<i>A. lupini</i>	10	3	0.3000	0.9000
<i>A. ovata</i>	22	20	0.9091	3.0390	<i>A. ovata</i>	12	0	0.0000	1.6364
<i>A. perditia</i>	17	0	0.0000	2.3750	<i>A. perditia</i>	13	4	0.3077	0.2308
Species groups	Count	Sum	Average	Variance	Species groups	Count	Sum	Average	Variance
Group 2	102	25	0.2451	1.9690	Group 2	70	18	0.2571	1.4692
Group 3	48	25	0.5208	6.0421	Group 3	27	-25	-0.9259	4.2251
Group 4	91	17	0.1868	1.2647	Group 4	72	16	0.2222	0.8513
Group 5	37	30	0.8108	1.6021	Group 5	22	9	0.4091	1.4913
Hairiness	Count	Sum	Average	Variance	Hairiness	Count	Sum	Average	Variance
Type 0	48	25	0.5208	6.0421	Type 0	27	-26	-0.9630	4.1140
Type 1	37	30	0.8108	1.6021	Type 1	22	9	0.4091	1.4913
Type 2	193	42	0.2176	1.6295	Type 2	142	34	0.2394	1.1479
Directed									
Species	Count	Sum	Average	Variance					
<i>A. americana</i>	11	-1	-0.0909	0.8909					
<i>A. dactylina</i>	21	8	0.3810	4.3476					
<i>A. haesitata</i>	5	20	4.0000	0.0000					
<i>A. hasta</i>	3	7	2.3333	2.3333					
<i>A. impleta</i>	9	3	0.3333	1.0000					
<i>A. impressa</i>	2	-1	-0.5000	4.5000					
<i>A. increta</i>	6	10	1.6667	0.6667					
<i>A. lobeliae</i>	11	14	1.2727	0.8182					
<i>A. longa</i>	1	1	1.0000	-					
<i>A. lupini</i>	3	2	0.6667	1.3333					
<i>A. ovata</i>	10	20	2.0000	2.6667					
<i>A. perditia</i>	4	-4	-1.0000	10.0000					
Species groups	Count	Sum	Average	Variance					
Group 2	32	7	0.2188	3.1442					
Group 3	21	50	2.3810	2.2476					
Group 4	19	1	0.0526	2.9415					
Group 5	14	21	1.5000	1.1923					
Hairiness	Count	Sum	Average	Variance					
Type 0	21	50	2.3810	2.2476					
Type 1	14	21	1.5000	1.1923					
Type 2	51	8	0.1569	3.0149					

**Table 7.** ANOVA results for comparisons between species, species groups, and hairiness categories for Ant trials. Analyses were performed for All data, Incidental data, and Directed data. Bold p-values are significant ( $p < 0.05$ ).

All data						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	72.5945	11.0000	6.5995	2.9525	<b>0.0010</b>	1.8248
Within Groups	594.5602	266.0000	2.2352			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	12.8031	3.0000	4.2677	1.7870	0.1499	2.6375
Within Groups	654.3516	274.0000	2.3881			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	12.6397	2.0000	6.3199	2.6553	0.0721	3.0286
Within Groups	654.5149	275.0000	2.3801			
Incidental						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	80.9417	11.0000	7.3583	5.1579	<b>5.11E-07</b>	1.8425
Within Groups	255.3619	179.0000	1.4266			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	33.3178	3.0000	11.1059	6.8545	<b>2.09E-04</b>	2.6529
Within Groups	302.9859	187.0000	1.6202			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	35.3466	2.0000	17.6733	11.0701	<b>2.85E-05</b>	3.0440
Within Groups	300.1403	188.0000	1.5965			
Directed						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	109.2203	11.0000	9.9291	4.0547	<b>1.19E-04</b>	1.9206
Within Groups	181.2100	74.0000	2.4488			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	79.5617	3.0000	26.5206	10.3130	<b>7.84E-06</b>	2.7159
Within Groups	210.8685	82.0000	2.5716			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	79.2328	2.0000	39.6164	15.5691	<b>1.81E-06</b>	3.1065
Within Groups	211.1975	83.0000	2.5445			

**Table 8.** Two-tailed T-test results, comparing caterpillar behavioral responses to incidental (I) and directed (D) ant encounters in the ant trials. Bold p-values are significant ( $p < 0.05$ )

<i>Species</i>	<i>I - mean</i>	<i>D - mean</i>	<i>I - variance</i>	<i>D - variance</i>	<i>p value</i>
<i>A. americana</i>	0.2143	-0.0909	0.6931	0.8909	0.3619
<i>A. dactylina</i>	0.2857	0.3810	2.0139	4.3476	0.8517
<i>A. haesitata</i>	-0.8000	4.0000	2.2000	0.0000	<b>0.0019</b>
<i>A. hasta</i>	1.3333	2.3333	1.3333	2.3333	0.4169
<i>A. impleta</i>	0.3077	0.3333	0.2215	1.0000	0.9425
<i>A. impressa</i>	0.5882	-0.5000	1.0074	4.5000	0.6044
<i>A. increta</i>	-2.1000	1.6667	6.5444	0.6667	<b>0.0010</b>
<i>A. lobeliae</i>	0.2632	1.2727	1.4269	0.8182	<b>0.0148</b>
<i>A. longa</i>	-1.5000	1.0000	1.5000	0.0000	-
<i>A. lupini</i>	0.3000	0.6667	0.9000	1.3333	0.6505
<i>A. ovata</i>	0.0000	2.0000	1.6364	2.6667	<b>0.0058</b>
<i>A. perditia</i>	0.3077	-1.0000	0.2308	10.0000	0.4703

**Table 9.** Two-tailed T-test results, comparing caterpillar behavioral responses to directed ant trials (A) and late instar pinch trials (P). Bold p-values are significant ( $p < 0.05$ ).

<i>Species</i>	<i>A - mean</i>	<i>P - mean</i>	<i>A - variance</i>	<i>P - variance</i>	<i>p value</i>
<i>A. americana</i>	-0.0909	2.7500	0.8909	1.9333	<b>1.28E-06</b>
<i>A. dactylina</i>	0.3810	1.5000	4.3476	3.4211	0.0765
<i>A. haesitata</i>	4.0000	4.0000	0.0000	0.0000	-
<i>A. impleta</i>	0.3333	1.8333	1.0000	1.3667	<b>0.0276</b>
<i>A. lobeliae</i>	1.2727	4.0000	0.8182	0.0000	<b>1.59E-06</b>
<i>A. longa</i>	1.0000	-0.6667	0.0000	8.3333	-
<i>A. lupini</i>	0.6667	-3.4286	1.3333	0.9524	<b>0.0126</b>

**Table 10.** ANOVA summary data for comparisons between species, species groups, and hairiness categories for pinch test trials. Analyses were performed for All data, Early instars, and Late instars.

All data					Early instars				
<i>Species</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>	<i>Species</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
<i>A. americana</i>	16	44	2.7500	1.9333	<i>A. americana</i>	0	0	-	-
<i>A. dactylina</i>	50	-32	-0.6400	8.2759	<i>A. dactylina</i>	30	-62	-2.0667	6.4782
<i>A. haesitata</i>	40	28	0.7000	9.8564	<i>A. haesitata</i>	32	-4	-0.1250	8.8871
<i>A. lupini</i>	7	-24	-3.4286	0.9524	<i>A. lupini</i>	0	0	-	-
<i>A. longa</i>	10	-18	-1.8000	6.1778	<i>A. longa</i>	7	-16	-2.2857	5.5714
<i>A. impleta</i>	50	-10	-0.2000	5.9184	<i>A. impleta</i>	44	-21	-0.4773	5.9297
<i>A. obliterata</i>	62	-85	-1.3710	4.2700	<i>A. obliterata</i>	29	-81	-2.7931	2.5985
<i>A. lobeliae</i>	4	16	4.0000	0.0000	<i>A. lobeliae</i>	0	0	-	-
<i>Species groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>	<i>Species groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
Group 2	66	12	0.1818	8.8280	Group 2	30	-62	-2.0667	6.4782
Group 3	40	28	0.7000	9.8564	Group 3	32	-4	-0.1250	8.8871
Group 4	129	-137	-1.0620	5.4649	Group 4	80	-118	-1.4750	5.8222
Group 5	4	16	4.0000	0.0000	Group 5	0	0	-	-
<i>Hairiness</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>	<i>Hairiness</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
Type 0	40	28	0.7000	9.8564	Type 0	32	-4	-0.1250	8.8871
Type 1	4	16	4.0000	0.0000	Type 1	0	0	-	-
Type 2	195	-125	-0.6410	6.9117	Type 2	110	-180	-1.6364	6.0133
Late instars									
<i>Species</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>					
<i>A. americana</i>	16	44	2.75	1.933333					
<i>A. dactylina</i>	20	30	1.5	3.421053					
<i>A. haesitata</i>	8	32	4	0					
<i>A. lupini</i>	7	-24	-3.428571	0.952381					
<i>A. longa</i>	3	-2	-0.666667	8.333333					
<i>A. impleta</i>	6	11	1.833333	1.366667					
<i>A. obliterata</i>	36	-10	-0.277778	2.892063					
<i>A. lobeliae</i>	4	16	4	0					
<i>Species groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>					
Group 2	36	74	2.055556	3.08254					
Group 3	8	32	4	0					
Group 4	52	-25	-0.480769	4.411388					
Group 5	4	16	4	0					
<i>Hairiness</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>					
Type 0	8	32	4	0					
Type 1	4	16	4	0					
Type 2	88	49	0.556818	5.399033					

**Table 11.** ANOVA results for comparisons between species, species groups, and hairiness categories for pinch test trials. Analyses were performed for All data, Early instars, and Late instars. Bolded p-values are significant ( $p < 0.05$ ).

All data						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	430.8461	7.0000	61.5494	9.9377	<b>7.74E-11</b>	2.0494
Within Groups	1430.7020	231.0000	6.1935			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	203.8261	3.0000	67.9420	9.6315	<b>5.07E-06</b>	2.6430
Within Groups	1657.7221	235.0000	7.0541			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	136.2763	2.0000	68.1382	9.3206	<b>1.27E-04</b>	3.0341
Within Groups	1725.2718	236.0000	7.3105			
Early instars						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	163.0463	7.0000	23.2923	3.7854	<b>0.0009</b>	2.0786
Within Groups	824.5311	134.0000	6.1532			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	64.2608	3.0000	21.4203	3.2015	<b>0.0253</b>	2.6702
Within Groups	923.3167	138.0000	6.6907			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	56.6229	2.0000	28.3115	4.2272	<b>0.0165</b>	3.0612
Within Groups	930.9545	139.0000	6.6975			
Late instars						
<i>Species</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	370.4735	7.0000	52.9248	21.6947	<b>5.02E-17</b>	2.1108
Within Groups	224.4365	92.0000	2.4395			
<i>Species groups</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	262.0403	3.0000	87.3468	25.1909	<b>4.16E-12</b>	2.6994
Within Groups	332.8697	96.0000	3.4674			
<i>Hairiness</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	125.1941	2.0000	62.5970	12.9268	<b>1.05E-05</b>	3.0902
Within Groups	469.7159	97.0000	4.8424			



**Table 12.** Two-tailed T-test results, comparing caterpillar behavioral responses of early (E) and Late (L) instars to the pinch test trials. Bold p-values are significant ( $p < 0.05$ )

<i>Species</i>	<i>E - mean</i>	<i>L - mean</i>	<i>E - variance</i>	<i>L - variance</i>	<i>p value</i>
<i>A. americana</i>	-	2.7500	-	1.8125	-
<i>A. dactylina</i>	-2.0667	1.5000	6.4782	3.4211	<b>6.39E-07</b>
<i>A. haesitata</i>	-0.1250	4.0000	8.8871	0.0000	<b>7.82E-09</b>
<i>A. lupini</i>	-	-3.4286	-	0.8163	-
<i>A. longa</i>	-2.2857	-0.6667	5.5714	8.3333	0.4547
<i>A. impleta</i>	-0.4773	1.8333	5.9297	1.3667	<b>0.0024</b>
<i>A. oblonga</i>	-2.7931	-0.2778	2.5985	2.8921	<b>7.88E-08</b>
<i>A. lobeliae</i>	-	4.0000	-	0.0000	-

## **Chapter 4: Diet Breadth and the Evolution of Larval Defensive Morphology and Behavior in *Acronicta***

### **Introduction**

Determine the origins and causes of phenotypic (and species) diversity is a fundamental quest in evolutionary biology (Foote 1997). Some taxa remain conservative in their form and function, while other groups burst at the seams with morphological and behavioral diversity. Drivers of morphological diversity are legion, and include gene regulation (Carroll 2000), adaptive radiations (Warheit et al. 1999; Burns et al. 2002), habitat complexity (Willis et al. 2004; Farré et al. 2015), predation (Cordoba-Aguilar 2008; Ingley et al. 2014; Zanella et al. 2015), and host plant usage (Janz et al. 2006; Bennett and O’Grady 2012; Ebel et al. 2015). Phytophagous insects in particular are prone to rapid morphological and species diversification due to their ability to exploit the finely parsed niches provided by their hyperdiverse plant hosts with current estimates of species richness exceeding 300,000 species. The invasion of the phytophagous “adaptive zone” is associated with increased diversification rates in nearly all insect groups (Mitter et al. 1988). The best studied higher taxon of phytophagous insects are the butterflies and moths of the order Lepidoptera. A global gradient of lepidopteran larval diet breadth reveals increased dietary specialization among phytophagous insects with decreasing latitude; specialization, at least in part, may explain the extraordinary diversity of tropical ecosystems (Forister et al. 2015).

While there is much debate over the role of dietary specialization in species diversification (and how to measure diet breadth) (Janz and Nylin 2008; Hardy and Otto 2014; Hamm and Fordyce 2015; Fordyce et al. 2016; Hamm and Fordyce 2016; Janz et al. 2016), less is known about the relationships between dietary specialization and morphological and life history traits. The host

plant is not only a food source, but a habitat complete with associated diseases, predators, and anti-herbivory defenses (Dethier 1954). When a new diet evolves, herbivorous insects commit their fate to a new niche and associated selection pressures. Lepidopteran specialists have been found to differ from generalists in their defenses (Dyer and Floyd 1993; Dyer 1995), palatability (Bernays and Cornelius 1989), the strength of predation pressures (Singer et al. 2014), and responses to host plant quality (Mooney et al. 2012). Specialization is associated with increased crypsis and aposematism; while highly divergent strategies, both crypsis and aposematism are effective and much exploited anti-predator defenses. The combination of dietary specialization, aposematism, and stereotyped resting positions should result in the greatest amount of enemy-free-space (EFS) for larval lepidopterans to exploit (Singer et al. 2014). In order to understand these and other adaptations, and in particular their attendant advantages and disadvantages, species must be examined in multi-trophic frameworks: e.g., herbivorous insect morphology is mediated by both bottom-up (host plant) and top-down (predator and parasitoid) selection (Singer and Stireman 2005; Mooney et al. 2012; Singer et al. 2014). If this is true, changes in diet breadth should be associated with changes in defensive morphology to deal with new predation pressures on new host plants. Specialists may be driven in different morphological directions due to the niches they inhabit on their hosts; specialization can allow for more accurate camouflage, concealed resting positions, and defensive morphologies particular to the threats faced on that host. Specialists also tend to be more chemically protected, and less palatable to predators than generalists (Bernays and Cornelius 1989; Dyer 1995). Generalists typically cannot adapt to a particular niche on a particular host plant, and instead should have generalized defenses appropriate for a variety of threats.

Larval defenses are not just morphological; behavioral responses toward predators can also vary. These variations can be found among species, within species, and even within individuals (Greeney et al. 2012). Lepidopteran defenses can be categorized as either behaviors which serve to aid the larva in avoiding predators, or how they respond once detected. Responses to a potential attack by a predator typically fall into one of two main categories: evasive or aggressive (Gross 1993; Greeney et al. 2012). Importantly, these behaviors also may be mediated by the type of predator (or parasitoid) and the severity of the attack.

The owl moth genus *Acronicta* is an ideal lineage in which to use to evaluate the relationship between morphological diversity, behavior, and diet breadth. Within *Acronicta*, three phenomena are apparent: 1) it is a species-rich genus (among the top 10 largest genera of Nearctic Noctuoidea); 2) there is a remarkable amount of larval morphological variation within and between species groups; and 3) the species boast a wide range of diet breadths (that encompass a broad array of woody plant families). There are over 150 species distributed in temperate forests worldwide (Rota et al. 2016, Zacharczenko unpublished checklist), making *Acronicta* an unusually large genus. For most species, the larvae and their host plants are known. The larvae sport an astounding array of morphological features: they may be bristly or nearly hairless, aposematic or camouflaged, and have a variety of setal types (long wisps, tufts, spines, paddles, and others) (see Wagner 2005; Wagner et al. 2011). Some appear to mimic larvae of several other lepidopteran families. Many exhibit drastic color changes in their final instar that border on hypermetamorphic developments. Behaviorally they differ in their apparency (whether they remain exposed or hidden) and responses to predators. Diet breadths vary from strict specialization to broad generalization.

How did *Acronicta* come to be so morphologically diverse? This study seeks to address the following question: *Is diet breadth associated with defensive adaptations of Acronicta larvae, potentially explaining their morphological radiation via tri-trophic interactions and the quest for enemy-free space?* Based upon my experiences rearing *Acronicta* larvae, I hypothesize that increased hairiness is associated with an increase in diet breadth, due to the need to be more generally defended against an array of predators. In addition to elucidating evolutionary patterns within *Acronicta*, this study compares different methods of assessing lepidopteran diet breadths across different methodological frameworks.

## Methods

### *Taxon sampling and phylogeny*

This study utilized the most recent molecular phylogeny of *Acronicta* and related genera in the subfamily Acronictinae (Rota et al. 2016, Zacharczenko in prep.) A total of 101 taxa were sampled: 82 *Acronicta* species, 13 other species (in 10 genera) of Acronictinae, and 6 outgroup taxa. While many acronictine species have yet to be sequenced, the chosen taxa represent nearly all known genera and species groups, with taxon sampling from North America, Europe, and Asia (although focused on the Nearctic fauna). The species groups recognized for this study (but not formally named) are: *leporina*, *increta*, *alni*, *nervosa*, and *psi*. These names were utilized for the Rota et al. (2016) study, except for the *increta* group which is recognized here as distinct from the *leporina* group. Included taxa were sequenced for 1 mitochondrial and 7 nuclear genes (*COI*, *CAD*, *EF1 $\alpha$* , *GADPH*, *IDH*, *MDH*, *RpS5*, and *wingless*) with a proven history of utility in lepidopteran phylogenetics (Mitchell et al. 2006; Zahiri et al. 2011, 2013; Rota et al. 2016).

Sequences were analyzed with Maximum Likelihood, Bayesian, and SVD Quartet methods to generate trees (see Chapter 2 of this dissertation). The tree used for mapping traits was created using Maximum Likelihood with Garli (Zwickl 2006); concatenated sequences were split into 12 partitions according to PartitionFinder, which also determined the model for each partition (Lanfear et al. 2012).

### *Host plant records*

Host plant records at the genus and family level were gathered from 217 sources. An extensive search included primary literature, secondary literature (field guides, monographs, etc.), rearing notes (including the extensive records of David Wagner), personal observations, and websites. Host data collected by 118 individual entomologists, both professional and amateur, were pulled from rearing records; 100 of those individuals published photographic records on BugGuide.net. Reference dates ranged from 1797 to 2015. Of these sources 145 were found to be primary (directly reporting wild observation(s) or rearing record(s)), 51 secondary (repeating host records from the literature), 8 had a combination of both primary and secondary records, and 15 were indeterminate. Indeterminate records were primarily published in other languages where the distinctions between original and repeated records were unclear. For this study, no distinction was made between wild observations and rearing records, as it was seldom made clear in publications. There are cases where lab-rearing utilizes plants which larvae were directly collected from, while in other cases larvae may be fed (and successfully reared to adulthood) on plants they would never encounter or choose to feed upon in the wild. All plant families and genera were recorded and updated according to recent taxonomic decisions in order to standardize the dataset (Stevens 2001; The Angiosperm Phylogeny Group 2009). For sources

that referenced other publications for individual host records, such as the Larvae of Northern European Noctuidae, all cited references were also credited with records (Ahola and Silvonen 2005). One source (Tietz 1972) referenced 45 sources for acronictines in a life history index; however, none were directly associated with particular host records (i.e., for each *Acronicta* species there was a list of host plants, and a separate alphabetical list of references). Five of these sources were independently verified and recorded as additional sources, while the remaining 40 remained unverified. The unverified sources were old (the majority were published <1900) and of a lower priority due to the likelihood of error (e.g., either larval or hostplant misidentifications) in older literature.

#### *Relational database*

A relational database was created in Microsoft Access to relate acronictine species, host plant genera, host plant families, and references. Each species to host relationship related to multiple references. Each reference was marked according to its status as a primary or secondary source. This database is searchable and easy to query and update. A total of 78 plant families, 228 plant genera, 904 species-to-genus relationships, and 5596 species-to-genus-to-reference relationships was recorded. See Figure 1 for a schematic of the relationship table. A report of the database, including all genera/families/references (166 pages of data) can be viewed at the following link: [https://www.dropbox.com/s/86yt6goe6krzkys/Host\\_database\\_report\\_BVZ.xls?dl=0](https://www.dropbox.com/s/86yt6goe6krzkys/Host_database_report_BVZ.xls?dl=0).

#### *Database curation*

The database was curated for two analyses: *Complete Dataset* and *Authority-Driven Dataset*. The *Complete Dataset* includes all records regardless of source. This includes primary,

secondary, and potentially unreliable records – therefore representing what is currently available in the literature (and especially on-line compendia). The *Authority-Driven Dataset* includes only those records determined to be reliable based upon expert curation. Cleaning the data in this way is essential for the removal of erroneous records, which could significantly skew results (Ehrlich and Raven 1964; Wagner and Todd 2016). Multiple lepidopterists were consulted due to their experience with larval collection, rearing, and familiarity with the host record literature. The following authorities assisted in the curation of this dataset: David Wagner (North America), Tim McCabe (North America), Matti Ahola (Europe), and Kimmo Silvonen (Europe). These collaborating authorities offered their opinions on the validity of acronictine species-host plant relationships for their geographical area of expertise. These datasets were pooled into one *Authority-Driven Dataset*. In cases where the authorities disagreed, the record was removed. In cases where none of the authorities had an opinion on a record, it was included if it had at least two primary records in the literature. Any records without an expert opinion, and without at least two primary records, were removed.

#### *Diet breadth measures*

Six different diet breadth measures were utilized to compare their utility: *Family Category*, *Genus Richness*, *Family Richness*, *Phylodiversity*, and *Genus and Family Level Diet Breadth Ordination* (Table 1). While many publications use the terms “specialist” and “generalist,” they can have a multitude of meanings, making it difficult to compare results across studies (Symons and Beccaloni 1999). The *Family Category* analyses use a multistate dataset with three categories: Monophagous (specialist feeding on plants in a single host family), Oligophagous (intermediate diet breadth feeding on two to three plant families), and Polyphagous (generalist



feeding on four or more plant families). This categorization is consistent with Fiedler (1998), and roughly consistent with the multitude of other studies measuring diet breadth at the family level (Ehrlich and Raven 1964; Niemelä et al. 1982; Dyer and Floyd 1993; Janz et al. 2006; Hardy and Otto 2014; Hamm and Fordyce 2015, and others). This *Family Category* analysis represents a classical approach to diet breadth measures. The *Genus Richness* analyses use a continuous dataset, ranging from 1 genus (specialist) to 119 genera. The *Family Richness* analyses use a continuous dataset, ranging from 1 family to 41 families. The *Phylodiversity* analyses were used to put diet breadth into a phylogenetic context, an increasingly common consideration in studies exploring the diet breadths of herbivorous insects (Singer et al. 2014). Phylodiversity was measured using *pd* (Faith 1992) with the package ‘picante’ (Kembel et al. 2010) in R (R. Development Core Team 2008), using the Angiosperm megatree phylogeny (Davies et al. 2004). The root of the tree was not included in the measurements (`include.root = FALSE`). Values represent the sum of branch lengths (in millions of years) joining the host plant genera. Thus, lower values = the host genera are more closely related, higher values = the genera are more distantly related. A value of one is given to species feeding on only one genus of plants. *Diet Breadth Ordination* is a recently developed tool which does not include host relatedness, but looks for groups of hosts which are commonly utilized by a set of herbivores. Using this method, species with a large *Diet Breadth Ordination* value have a diet that is divergent from the other focal species. These measures are then scaled on a range from 0 to 1. *Diet Breadth Ordination* for both families and genera of hosts was implemented using the package ‘ordi.Breadth’ (Fordyce et al. 2016) in R (R. Development Core Team 2008).

#### *Host plant phylogeny*

An Angiosperm megatree phylogeny with fossil calibration was utilized for host phylodiversity analyses (Davies et al. 2013a). Davies et al. assembled DNA data from 1246 genera from multiple published phylogenies, with taxonomy based upon the most recent Angiosperm Phylogeny Working Group publication (The Angiosperm Phylogeny Group 2009). Their maximum likelihood tree is available as a Dryad package at <http://dx.doi.org/10.5061/dryad.td03p886> (Davies et al. 2013b).

Acronictine species and outgroups used for this study were reported to feed on a total of 228 plant genera from 78 families. The complete dataset was used for ordination analyses. For phylodiversity analyses, 34 of these genera were not represented in the Angiosperm megatree phylogeny. The missing genera affected 24 species, for a total of 45 affected records. Each diet breadth analysis was performed in two iterations: *Strict* analyses used the 194 plant genera represented in the phylogeny, *Replacement* analyses used those plus replacement plant genera for a total of host plant 210 genera. Replacement genera were chosen by consulting other published phylogenies to determine closely related genera within the same family. Of the 34 genera, 24 had a sister genus, or a genus in the same clade, represented in the Angiosperm megatree phylogeny (Supplementary Table S1). Eight of these were already present in the data, while 16 were new records. The remaining 10 genera were not included in any phylodiversity analyses.

#### *Larval morphology and behavior*

Larval characters were scored from whole specimens, dissections, photographs, and published literature. Larval specimens were obtained for 64 of the 101 species used for this study (for 10 species the larvae are unknown). Specimens were collected by BVZ (author) and DLW (David

L. Wagner), and borrowed from the CUIC (Cornell University Insect Collection) and NMNH (National Museum of Natural History). Characters were also scored from literature accounts for 73 species, and from photographs (unpublished or posted online) for 64 species. Setae were removed from specimens of 58 species and slide mounted with Euparal. With these combined methods, all known species were scored for at least some morphological characters (aside from three species for which larval host plants were documented, but no morphology or images recorded). See Supplementary Table S2 for the list of larval specimen data sources.

Larval morphological characters were selected according to their likelihood of being used as defensive measures against either vertebrate or invertebrate predation. These primarily relate to setal type and location. Other broad visual cues include head color, mimicry, and color/pattern changes during the ultimate instar. See Table 2 for a list of the 20 morphological characters, their states, and descriptions. Figures 2 – 10 illustrate most of these characters.

*Acronicta* larvae, while having a variety of setal traits, have different levels of “hairiness”. In terms of their perception by a predator, the overall setal density of the larva may be more important than whether the setae originate from warts or from the integument. In order to capture this variation, *Acronicta* species were scored for three levels of hairiness, based on previously scored characters (Figure 2). The first level, the least hairy, includes species with sparse unbarbed setae. The second level, moderately hairy, have barbed setae with abundant lateral setae. The third level, the hairiest, occurs under two combinations of traits. They may have barbed setae with setae covering the integument, or barbed setae with abundant secondary setae on warts (often, but not always, including bristles and/or undercoat).

Larval behavior was also measured for a limited number of *Acronicta* species. Characters were scored from literature, photos, wild observations, personal rearing, and field/lab experiments. Resting positions and locations can reveal the degree to which a caterpillar is adapted to its host, and whether it rests in a concealed position (presumably hiding from visual predators). Pupation behaviors may relate to qualities of the plant host(s), as these larvae do not travel far from their host to pupate (i.e., providing suitable leaf litter or bark). Erucism, the irritation of human skin caused by caterpillars, is a proximate indicator of how many mammalian and avian predators of lepidopterans (such as mice and songbirds) would react to larval setae. The full protocol for quantifying defensive behaviors in response to invertebrate (live carpenter ants) and vertebrate/pinching invertebrate (forceps as a simulated bird beak or invertebrate mouthparts) attacks is detailed in Chapter 3 . The results are broken into four categories: average defensive behavior scores for incidental ant encounters, directed ant encounters, pinch tests with early instars, and pinch tests with late instars. Six behavioral characters and their states are described in Table 3, and illustrated in Figures 11 – 14.

### *Mapping Characters*

All characters (diet breadth, morphology, and behavior) were drawn onto a phylogenetic tree generated by Zacharczenko (Chapter 2) using the packages *ape* (Paradis et al. 2004), *phangorn* (Schliep 2011), and *phytools* (Revell 2012) in R (R. Development Core Team 2008).

### *Character Correlations*

Characters were compared to determine if any morphological or behavioral character(s) are correlated with diet breadth, taking into account phylogenetic non-independence of observed species. Diet breadth is treated as the dependent variable, which is continuous for all measures except family category (which has ordered categories, and may be considered pseudo-continuous). All measures of diet breadth and all scored characters were first tested for phylogenetic signal using Pagel's lambda (Pagel 1999) using the function `phylosig` in the package `phytools` (Revell 2012) in R (R. Development Core Team 2008). The presence of strong phylogenetic signal indicates that closely related species have similar traits due to shared ancestry. The phylogenetic generalized least squares (PGLS) function in the package `caper` (Orme et al. 2013) was then used to analyze character correlations while taking phylogenetic signal into account. This method is appropriate for datasets in which the dependent variable is continuous, and the independent variable is either continuous or categorical (Martins and Hansen 1997). PGLS has been used to compare other life-history traits such as herbivory and diversification (Wiens et al. 2015), habitat and morphology (Blankers et al. 2012), pollination syndromes (Ballesteros-Mejia et al. 2016), and caterpillar traits offering defense against bird predation (Lichter-Marck et al. 2015).

## **Results**

### ***Diet Breadth Measures***

Diet breadth measures were calculated in multiple iterations: for the *Complete* and *Authority-driven* datasets, and for the *Strict* and *Replacement* datasets. Results from all diet breadth analyses can be viewed in Supplementary Tables S3 – S4.

## ***Authority-Driven Database Curation***

### *Plant Family Category*

When considering family-level categories (1=monophagous, 2=oligophagous, 3=polyphagous), the *Authority-Driven* dataset resulted in changes to 31 (*Strict*) and 32 (*Replacement*) species. In 16 (*Strict*)/16 (*Replacement*) cases the category changed from 2 to 1, in 7/8 cases the category changed from 3 to 2, in 4/3 cases the category changed from 1 to 0, in 3/3 cases the category changed from 3 to 1, in 1/2 cases the category changed from 2 to 0, and in 1/1 cases the category changed from 3 to 0.

### *Plant Genus and Family Richness*

In the *Strict* dataset, *Authority-Driven* curation resulted in generic plant richness changes to 49 *Acronicta* species; this resulted in 167 fewer generic records in the *Authority-Driven* dataset. In the *Replacement* dataset, *Authority-Driven* curation resulted in generic changes to 51 species; this resulted in 165 fewer generic records in the *Authority-Driven* dataset. The largest difference was in *Acronicta aceris*, which lost 19 genera. Among species which lost genera in the *Authority-Driven* dataset, the average number of genera lost were 3.4 (*Strict*) and 3.2 (*Replacement*).

The Authority-driven data were incorporated into both the *Strict* and *Replacement* host plant datasets. At the plant family level in the *Strict* dataset, *Authority-Driven* curation resulted in changes to 47 *Acronicta* species; this resulted in 96 fewer familial records in the *Authority-Driven* dataset. In the *Replacement* dataset, *Authority-Driven* curation resulted in familial changes to 49 species; this resulted in 97 fewer familial records in the *Authority-Driven* dataset.

Among species which lost families in the *Authority-Driven* dataset, the average number of families lost were 2 (for both *Strict* and *Replacement*).

### *Phylodiversity*

Phylodiversity measures ranged from 1 (specialist on one genus) to 3592.5 (broad generalist).

*Authority-Driven* curation resulted in reductions to Phylodiversity measures for 49 (*Strict*) and 50 (*Replacement*) species. On average, *Authority-Driven* curation reduced phylodiversity values by 188 (*Strict*) and 209 (*Replacement*).

### *Diet Breadth Ordination*

Ordinated diet breadth (ODB) was scaled; however it is still difficult to compare data among datasets. The results from each analysis are dependent upon the input data. Different sets of taxa in the analysis will result in a different ordination space and affect the clustering of the host plant data points. When comparing the *Complete* vs. *Authority-Driven* datasets for host plants at the generic level there were 41 species with an increase in ODB value, and 25 species with a decrease in ODB value. At the family level, there were 37 species with an increase in ODB value, and 25 species with a decrease in ODB value.

### ***Mapping Characters***

#### *Mapping Diet breadth*

In order to compare diet breadth measures, bar graph values for each measure (from the *Replacement* datasets) were mapped in a series alongside the acronictine phylogeny (Figure 15). This was done for both the *Complete* dataset and *Authority-Driven* dataset, so they could be

compared. They are figured separately in Figures 16 and 17 to see species trends more clearly. The Family-level category gave the crudest results, within which species-group patterns are not easily discerned. The remaining categories (Genus Richness, Family Richness, Phylodiversity, and Diet Breadth Ordination for both genera and families) give qualitatively similar results to each other when considering species-group patterns.

### *Mapping Morphology and Behavior*

Morphological and behavioral characters were mapped as color-coded squares alongside the acronictine phylogeny (Figure 18). Legends for character states are listed in the figure caption. Colored bars delineate *Acronicta* species groups.

### *Phylogenetic Signal*

Of the 36 diet breadth, morphological, and behavioral characters tested, 9 had a lambda value above 0.3 (Table 4). For the behavioral characters (resting position and pinch defense – early instar) there are so many missing data points (only scored for a few taxa) as to render the results unreliable until further data are collected. Among the morphological characters the setal characters hairiness, paddles, and tufts had lambda values between 0.5 and 0.8.

### *Character Correlations*

Each morphological and behavioral character was tested as an independent variable on each measure of diet breadth as dependent variables using the PGLS method, resulting in 180 different comparisons. The direction of each relationship (positive or negative) was recorded (Table 5) as well as the p-values, coefficients, lambdas, and adjusted R-squared values



(Supplementary Tables S5a – S5c). A lambda above zero was only found for 3 (out of 180) comparisons. Based upon a p-value of 0.05, four characters had a significant relationship for all diet breadth measures: Hairy (+), Undercoat (+), Bristles (+), and Ant defense – directed (-). Nine other characters were significant for one to five diet breadth measures: Smooth setae (-), Lateral setae abundant (-), Secondary setae on integument (+), Tufts (+), Head color (-), A8 shape (+), Color variation (+), Pupation (+), and Erucism (+).

Two methods were used to account for Type I errors while running multiple tests. A Bonferoni correction was calculated based upon the 180 comparisons and an original p-value of 0.05, resulting in an adjusted p-value of 0.00028. With this new value, fewer relationships met the significance threshold (Table 6); only Bristles (+) was significantly related to all diet breadth measures. Undercoat (+) was significant for five measures, and Hairy (+) was significant for two. However, this method is not always appropriate for multiple tests, and important results may be overlooked and deemed non-significant (Type II error) (Perneger 1998). A second method was used, the Benjamini-Hochberg correction, which accounts for the false discovery rate (of falsely rejected hypotheses) when considering p-values of multiple tests (Benjamini and Hochberg 1995). With the false discovery rate set to 0.05, the resulting significant comparisons (Table 7) were found to be similar to the original calculations, with a few characters dropping off in significance. It was noted that ant defense – directed was close to achieving significance in each case, but fell just below the threshold.

## Discussion

*Is diet breadth associated with defensive adaptations of Acronicta larvae, potentially explaining their morphological radiation via tri-trophic interactions and the quest for enemy-free space?*

Among *Acronicta* larvae, a pattern emerges connecting their diet breadth, morphology, and behavior. These trends persist between species groups: species with greater diet breadth have an increase in morphological protection, and display more evasive defensive behaviors. Likewise, specialization is associated with larvae sparsely covered in hairs, and increased defensive behaviors when directly attacked by an ant. The selection forces driving these morphological and behavioral traits are emanating from bottom-up (host plant) and top-down (predator) interactions.

Several morphological characters were significantly correlated with diet breadth in the PGLS analyses (Tables 5 – 7). Overall hairiness had a positive relationship; as diet breadth measures increase, hairiness of larvae likewise increases. Other setal characters positively correlated with at least one diet breadth measure (which are included in the Hairy character) include the Undercoat, Bristles, and Secondary setae on integument. Negatively correlated characters include Smooth setae, and Lateral setae abundant. Barbed setae did not significantly predict any diet breadth measure, likely due to the broad spread of barbed setae throughout the subfamily. These data provide a few clues that could be used to estimate the diet breadth of *Acronicta* larvae based on their morphological characters. However the adjusted R-squared values for morphological measure are wide ranging and relatively low (from 2% to 25%), suggesting that other factors are impacting diet breadth.

Behavioral data were only collected for a few species, but offer some interesting avenues for future exploration. Pupation is difficult to quantify, as some species exhibit multiple behaviors depending on their environment. For example, larvae which may ordinarily tunnel into soft wood, may use leaf litter or carve a shallow channel into hard wood if that is all they are provided when lab-reared. These data tentatively suggest that as diet breadth increases, the use of leaves in pupation increases, which is commonly seen in the *nervosa* clade of primarily generalist larvae.

Erucism is correlated with five measures of diet breadth (broader diet = more likely to cause erucism). Erucism (an itchy response on human skin caused by caterpillars) is caused by setae, which may be barbed or bristly to irritate the skin. Therefore as diet breadth increases, hairiness increases, and the possibility for erucism increases. These data were recorded as my reactions to larvae were discovered in the rearing process; a more robust testing protocol with different human subjects would be necessary to quantify the generality of erucism in *Acronicta*. The only *Acronicta* species with published reports of erucism is *A. americana* (Wray 1963; Alexander 1984; Wagner et al. 2011).

Of the experimental defensive behavior trials, one had a significant relationship with all diet breadth measures (though after Benjamini-Hochberg correction, only for phylodiversity); as diet breadth increases, caterpillar defensive behavior towards directed ant attacks decreases in aggressiveness. Since larvae with broader diets tend to be more hairy, this supports the observation that caterpillars that are well defended physically don't spend energy on behavioral

defenses. Instead of reacting aggressively, they are more apt to engage in avoidance behaviors such as curling their head or turning away from the ant.

### *Characters to Consider in the Future*

One character not measured here but anecdotally observed during data collection is body size. There appeared to be a relationship between body size and hairiness: hairier larvae achieve a larger size at the ultimate instar than larvae with fewer setae. It is possible that body size may be a better predictor of diet breadth (Wasserman and Mitter 1978), or it may combine with hairiness to a greater percentage of the data. Davis et al. (2013) studied lepidopterans within another family, Geometridae, and found a positive relationship between body size and diet breadth. Diet breadth was measured by both richness and phylodiversity; body size was measured by body mass (female) and wing length (male) of adult moths. While there should be a relationship between larval and adult body sizes, larval body mass may be a more appropriate measure when diet breadth is concerned. Future analyses for my studies of morphology and diet breadth will incorporate both larval and adult measures of body size.

### *Comparisons of Diet Breadth Measures*

The measurement of diet breadth is not straight forward; measures vary depending on researchers, available data, and the question being asked. While some cases offer clear distinctions between specialists and generalists, it is often found that [dietary] “specialization must lie in the eye of the beholder” (Futuyma and Moreno 1988). The level of specialization must be considered (family? genus? species?), keeping in mind that these taxonomic categories are our own constructs. This study examined six different methods of measuring diet breadth,

which were compared by mapping onto a maximum likelihood estimate of acronictine phylogeny. The family category, split into monophagous/oligophagous/polyphagous designations, offers a basic ranking system. This differs from methods that utilize a binary ranking, which may be more biologically relevant for Lepidoptera. Forister et al. (2015) proposed that a Pareto distribution is more suitable for describing patterns of host use in lepidopteran diet breadths; the distribution of diet breadth within *Acronicta* appears to follow this trend, with the majority of species feeding upon 1 family of plants, and a long tail ranging from 2 to 39 families. However the three category ranking was kept to examine its utility and comparison to other diet breadth measures.

Several distinctions can be made between family categorization and the other approaches used here (genus and family richness, phylodiversity, and diet breadth ordination). Comparing these methods across the tree (Figures 15, 16, and 17), nuanced differences between clades are lost with the family-category measure. While this measure scores much of the *psi* clade as generalized as the *nervosa* clade, the other measures display drastic differences between their diet breadths. If one were to draw ecological conclusions about *Acronicta* clades or subgenera from diet breadth as measured by family category, important detail would be lost. In the PGLS results, there were characters which were only correlated with family category and not any other diet breadth measure. Conversely, there were characters for which family category was the only measure not correlated. While other measures showed some variability, none were as divergent as family category when compared to the other methods. Based on these results, I recommend that whenever possible, more detailed measures of diet breadth should be used as opposed to a generalist/specialist or otherwise categorical ranking of diet breadth for lepidopteran species.

One encouraging result of this study is that genus/family richness, phylodiversity, and diet breadth ordination measures all give proportionally similar results for species across the acronictine tree. However, there were some differences between PGLS analyses using different diet breadth measures. Utilizing multiple methods may be considered beneficial for determining the robustness of data correlations with diet breadth.

This study also offers a cautionary tale. These results demonstrate the amount of detail which would be obscured by generalizing diet breadth data across a large, diverse lepidopteran genus. *Acronicta* species range from strict specialists to broad generalists; it would be difficult to choose an appropriate designation for the genus as a whole. This poses a problem for studies which intend to compare diet breadth across genera or higher level taxa, as collecting species-level data for all taxa can be a daunting task. For large genera it may be more meaningful to score diet breadth for subgenera or species groups; in the case of *Acronicta*, the five major species groups (*alni*, *leporina*, *increta*, *nervosa*, and *psi*) have clear diet breadth patterns that would be obscured by combining their data.

### *The Effect of Host Plant Curation*

Curating host plant data with a combination of expert authority and primary literature can affect datasets in different ways. For basic counts of genera and families, *Authority-Driven* curation led to a decrease in values for about half of the species studied. There were several species which appear to be generalists according to the literature, but which when captured or reared are found to actually to be specialists. This discrepancy may be due to misidentifications of the larvae or

plants, changing nomenclature, mistakes during field collecting, mistakes during literature summation, or other errors (described in Table 8). The effects of expert curation are made clearest in the comparisons of family-level categories, the most commonly used diet breadth measure. In this study, 30% of taxa were moved to a different category as a result of curation. While in a few cases these category shifts were to zero (due to no reliable records or expert knowledge available), for most species the shift reflects a better understanding of their ecological diet breadths in the wild. The remaining 20% of taxa for which there was a change in diet breadth but no change in family-level category were generalists. While some problematic hosts may have been pruned from their records, they did not drop below the 4-family threshold for polyphagous insects. It is also likely that different methods of assigning family-level categories would impact these results (i.e., binary specialist/generalist labels may obscure or amplify changes).

The effects of *Authority-Driven* curation can also be seen in the remaining methods: genus richness, family richness, phylodiversity, and ordination of genera and families (Figure 15). The clearest differences are in the *increta* clade, which is primarily composed of specialists on *Quercus* (Wagner 2005; Wagner et al. 2011). After expert curation, their values (as show in the bar graphs) all drop to low levels. A few groups within the *psi* clade had the same effect, as expert curation removed erroneous records for specialists. While differences are also noted among generalist taxa, they are not as drastic. Removing a few records from a broadly polyphagous insect's repertoire does not have a great impact on their reported richness, phylodiversity, or diet breadth ordination.

There were cases where expert curation could have resulted in an increase in generic and family records. For example, *A. edolata* is suspected to be a widely polyphagous larva; captive larvae consume several woody plants, but no wild records are known. Works on acronictines sometimes stop listing acceptable hostplant genera when it is clear that a large taxonomic range of woody plants are consumed. But without verified records to enter into a database, there is no way to calculate diet breadth measures for a species merely believed to be “polyphagous.” This was a problem repeatedly encountered when consulting the literature for host plant records. In many cases species were described as “polyphagous” but without any particular genera or families mentioned. For several taxa in this study it is likely their diet breadth measures were an underestimation.

### *The Importance of Expert Curation*

While I believe that expert curation is valuable for diet breadth studies, the depth of curation required depends on the purpose of the study and the species involved. This study revealed that specialists are most drastically impacted by erroneous records; even one or two bad records can boost a species from a monophagous to an oligophagous or polyphagous category. However, generalists have more of a buffer against bad records. Whether a larva is feeding on 20 or 21 plant genera may be of less concern for an ecological study. Measures of phylogenetic distance appear to be the most likely to change with the removal of bad records, but species-group patterns remain. If one is concerned with rearing larva, and wish to use the literature to obtain accurate records for collecting and feeding larvae, records should be detailed (and vetted) as thoroughly as possible to avoid wasted efforts and dead larvae. The same is recommended for any conservation efforts; the perils of using un-checked host records for conservation purposes is



discussed in Wagner and Todd (2016). If one is concerned with an evolutionary or ecological study, at least some curation should be done in order to remove erroneous records. Focus could be placed on taxa suspected to have narrow diet breadths, as they are the most adversely affected by reporting errors. Care can be taken to consult primary sources instead of secondary checklists; one straight-forward method is to only include records with a certain number of primary references (2 or more). While the HOSTS online database (Robinson et al. 2015) is popular, it is too often unreliable and should not be used exclusively for data-mining host plant records. The printed versions of HOSTS for North American (Robinson et al. 2002) and Oriental taxa (Robinson et al. 2001) can be consulted to obtain references for every record, from which deductions can be made as to the reliability of the records. While it may not be possible to obtain the cooperation of multiple academic experts to curate one's data, there are many larval enthusiasts throughout the world who may be willing to offer their opinions. Carefully pulling records from online forums and crowd-sourced websites, such as BugGuide.org, may be fruitful. Even primary rearing records (your own included!) may have errors, and care should be taken to weed out mistakes in record-keeping. One finding by Wagner and Todd (2016) was that historical host records (because of erroneous larval and host identifications) were the most likely to be problematic; they recommended that host records that had not been verified in the last fifty years, be used with caution. No dataset, no matter how carefully poured over, will be free from errors. However, with critical, authority-driven review, plant use data can be more confidently supported and, hopefully, more accurately reflect the true diet breadths of the taxa in question.

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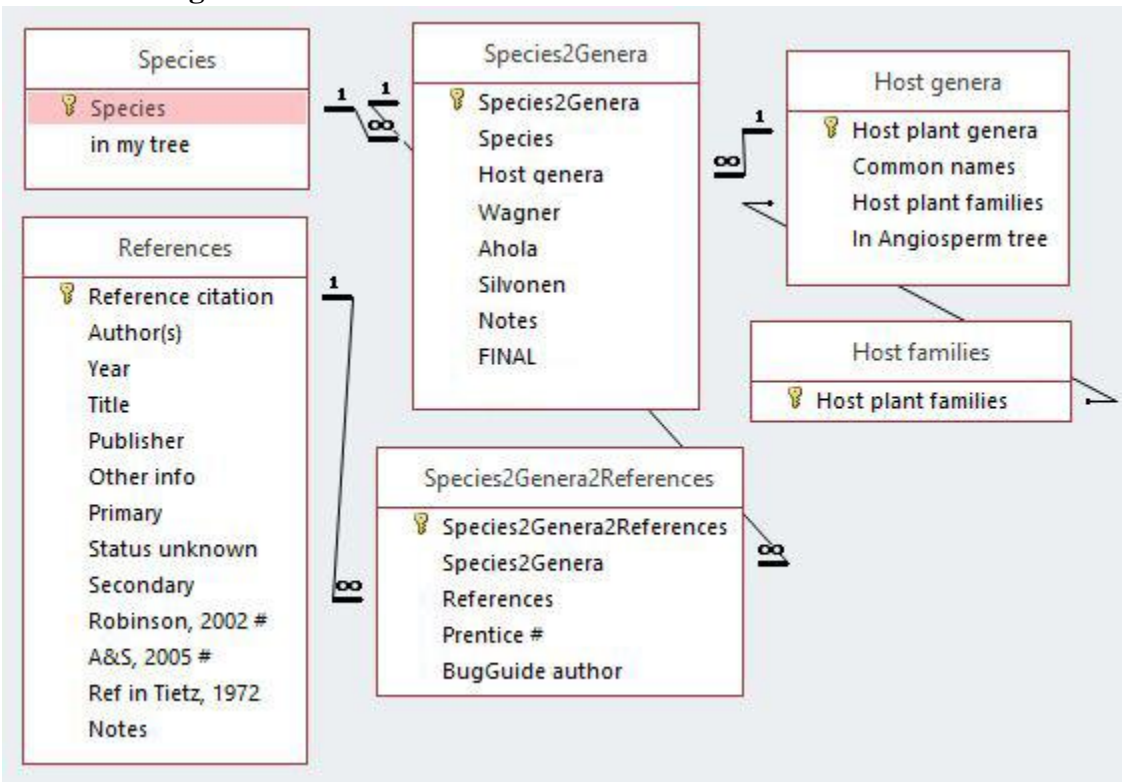
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## Tables and Figures



**Figure 1.** Microsoft Access relationship table for the Acronictinae host plant database.

**Table 1.** Diet breadth measures.

Method	Range	Description
Family Category	1: Monophagous	One family of plants
	2: Oligophagous	Two to three families of plants
	3: Polyphagous	Four or more families of plants
Genus Richness	1 to 119	Number of plant genera
Family Richness	1 to 41	Number of plant families
Phylodiversity	0 to 3608	Branch length measure of phylogenetic distance between plant genera
Diet Breadth Ordination: Families	0 to 1	Scaled diet breadth relating to the diet breadth of other species sampled. 0 = similar diet breadth as other species; 1 = completely disparate diet breadth.
Diet Breadth Ordination: Genera	0 to 1	Scaled diet breadth relating to the diet breadth of other species sampled. 0 = similar diet breadth as other species; 1 = completely disparate diet breadth.



**Table 2.** Morphological characters scored for *Acronicta* larvae, with descriptions. Characters are either binary, or multistate (none continuous).

Character	#	States	Description
Hairiness	0	Mild	Smooth setae only, no barbed setae/bristles/undercoat. No abundant secondary setae on integument or warts.
	1	Moderate	Barbed setae, with abundant lateral setae
	2	Hirsute	Two conditions. Barbed setae with secondary setae from integument, or barbed setae with bristles (may also include undercoat).
Mimicry	0	No	No larval mimicry
	1	Yes	Presumed larval mimicry of another caterpillar
Ultimate instar change	0	No	No appreciable phenotypic change
	1	Color	Change in color
	2	Color and morphology	Change in color and morphology
Smooth setae	0	No	Smooth setae absent
	1	Yes	Smooth setae present
Barbed setae	0	No	Barbed setae absent
	1	Yes	Barbed setae present
Paddles	0	No	Paddle setae absent
	1	Yes	Paddle setae present
Undercoat	0	No	Undercoat setae absent
	1	Yes	Undercoat setae present
Bristles	0	No	Bristle setae absent
	1	Yes	Bristle setae present
	2	On horn	Bristle setae on A1 horn only
Lateral setae more abundant	0	No	Lateral setae not more abundant
	1	Yes	Lateral setae more abundant
Secondary setae from integument (i.e., free from pinacula or verrucae)	0	No	No secondary setae from integument (i.e., free from pinacula or verrucae)
	1	Yes	Secondary setae from integument (i.e., free from pinacula or verrucae)
	2	Tufts only	Secondary setae outside from integument present only as tufts
Dorsal tufts	0	No	Dorsal tufts absent
	1	Yes	Dorsal tufts present
A1 horn	0	No	A1 horn absent
	1	Yes	A1 horn present
Head color (ultimate)	0	Solid	Solid color, usually black
	1	Spotted	Snowflake-type spots
	2	Red patch	Red patches on top of head
	3	Multi-colored	Stripes or other coloration, not including red patch
A8 shape	0	Smooth	A8 segment same as other segments

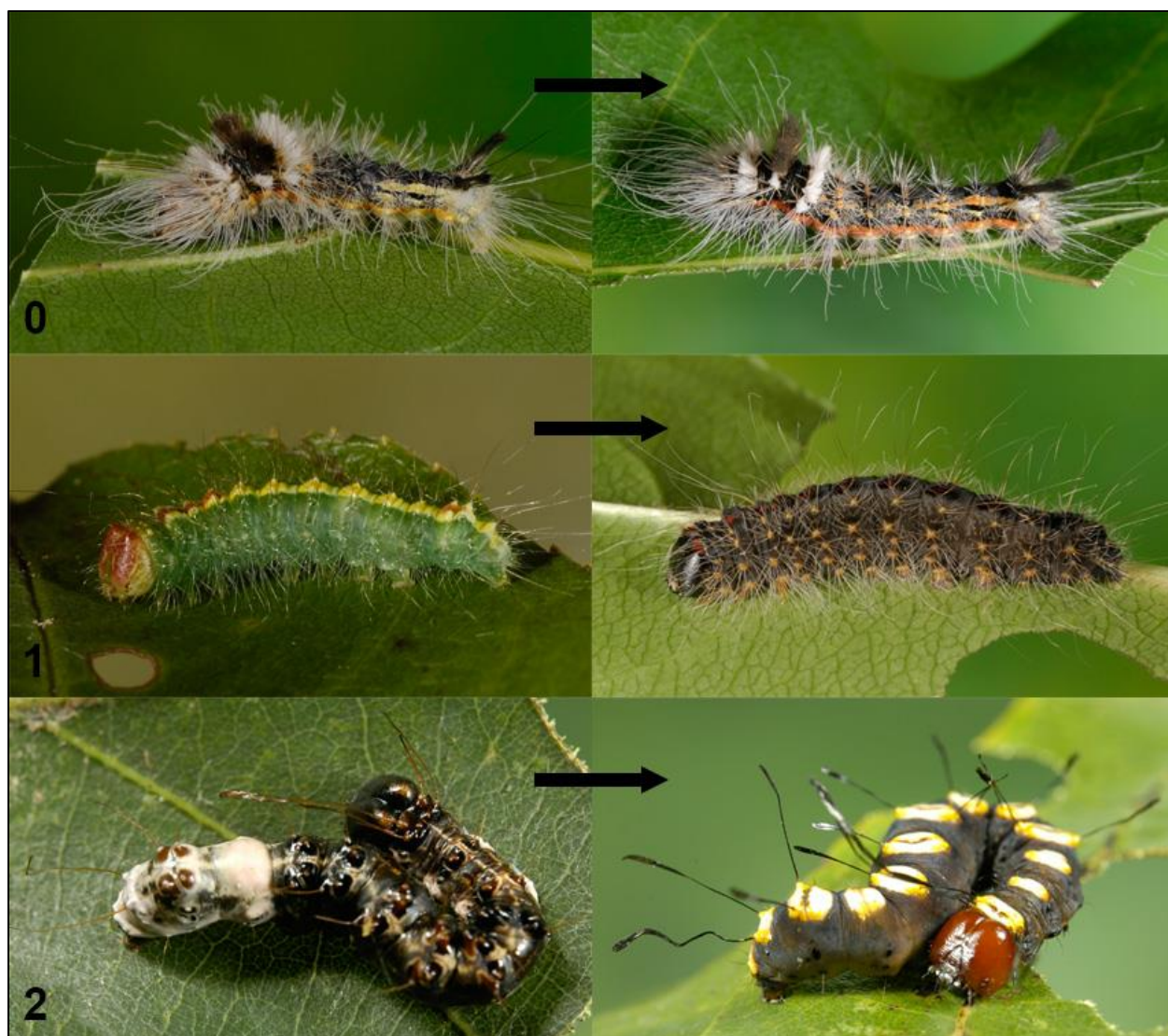
	1	Humped	A8 noticeably humped
A1 warts enlarged	0	No	A1 warts same size as adjacent warts
	1	Yes	A1 warts larger than adjacent warts
A5 warts enlarged	0	No	A5 warts same size as adjacent warts
	1	Yes	A5 warts larger than adjacent warts
A4 warts enlarged	0	No	A4 warts same size as adjacent warts
	1	Yes	A4 warts larger than adjacent warts
Paddle location	0	n/a	Not applicable (no paddles)
	1	D1	D1
	2	D2	D2
	3	SD1, SD2	SD1, SD2
	4	XD1, XD2	XD1, XD2
	5	L1, L2	L1, L2
Loss of secondary setae	0	No	Keep secondary setae throughout development
	1	Yes	Loss of secondary setae by ultimate instar
Color variation	0	No	No appreciable intraspecific larval color variation
	1	Yes	Appreciable intraspecific larval color variation
Secondary setae on head	0	No	Secondary setae on head absent
	1	Yes	Secondary setae on head present



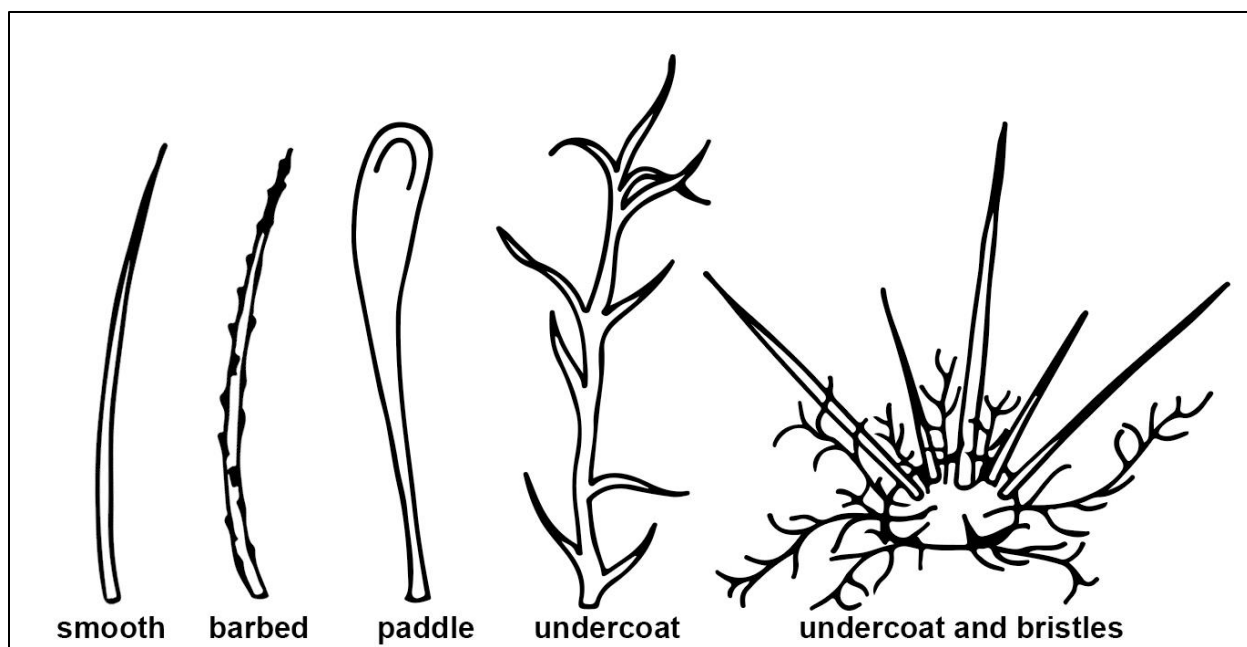
**Figure 2.** Larval morphological character suite: hairiness. Number corresponds to multistate scoring in Table 2. Species top to bottom: *A. increta*, *A. lobeliae*, *A. dactylina*. Image credit B. Zacharczenko.



**Figure 3.** Larval morphological character: mimicry. Number corresponds to binary scoring in Table 2. Left photo: *A. radcliffei*, image credit: B. Zacharczenko. Right photo: *Datana* sp., family Notodontidae, image credit: D. L. Wagner.

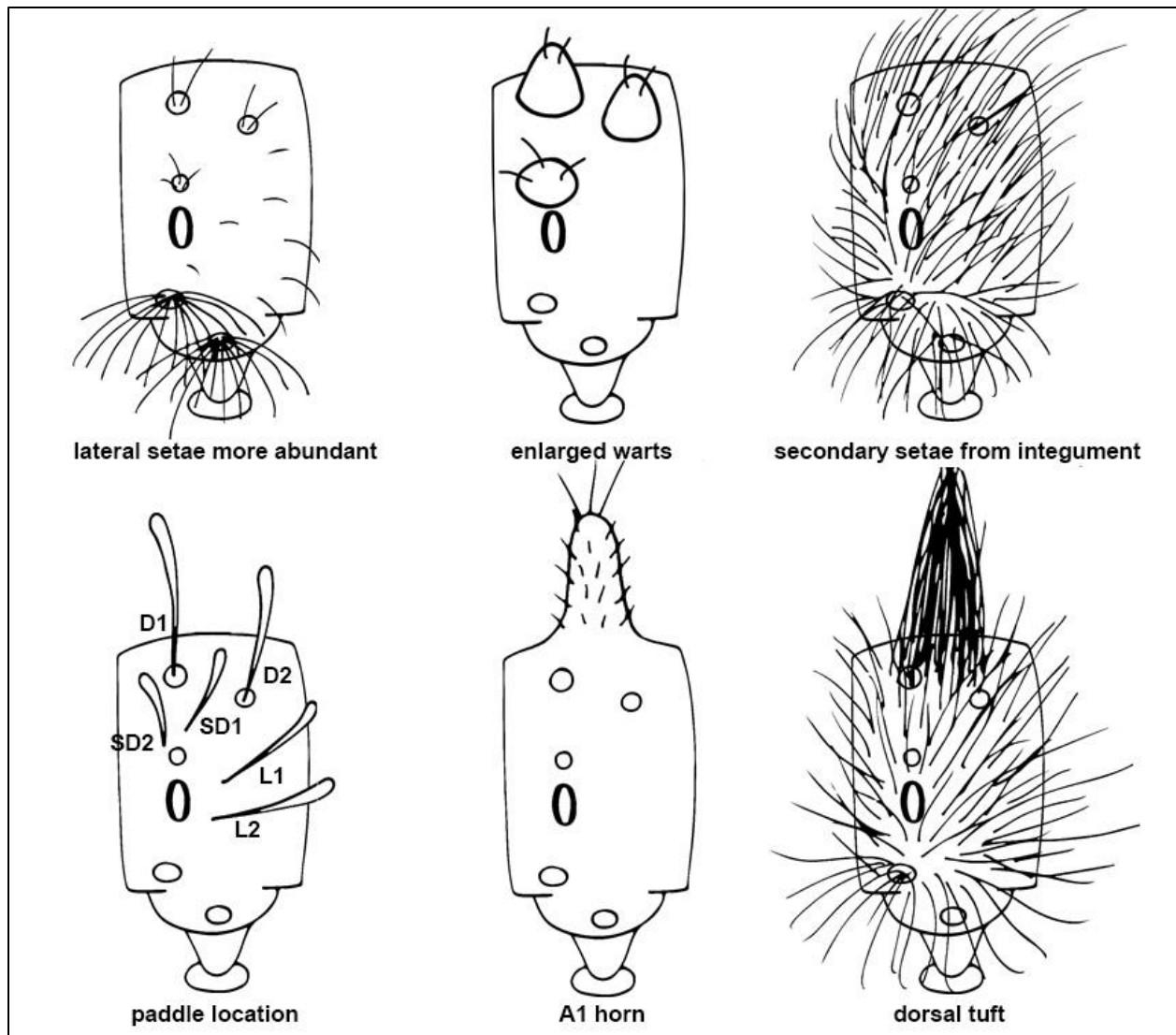


**Figure 4.** Larval morphological character: ultimate instar change. Numbers correspond to multistate scoring in Table 2. Species (top to bottom): *A. impleta*, *A. hasta*, *A. funeralis*. Image credit: B. Zacharczenko.

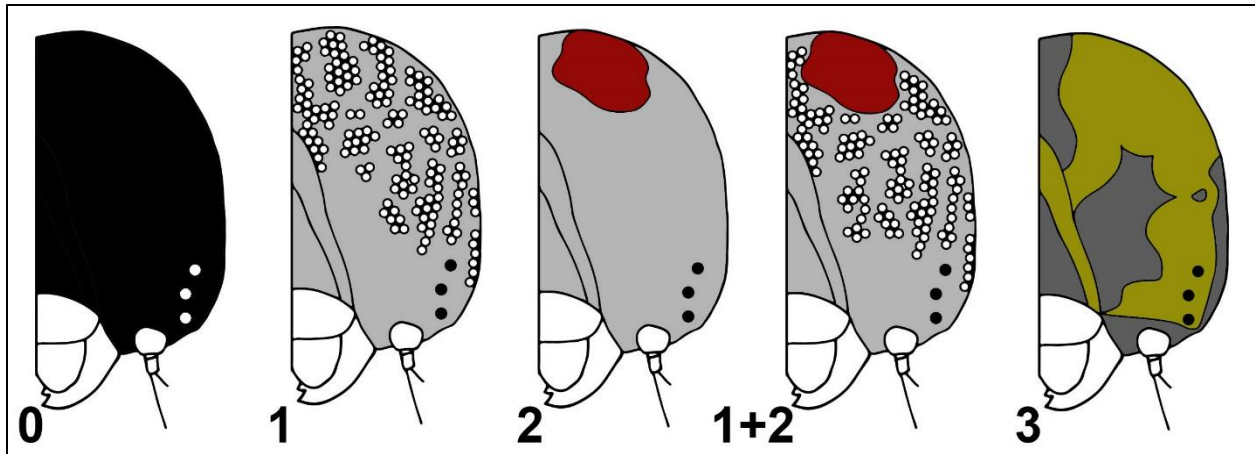


**Figure 5.** Larval morphological characters: setal types. Illustration credit: B. Zacharczenko.





**Figure 6.** Larval morphological characters: setal arrangements on abdominal segments.  
Illustration credit: B. Zacharczenko.



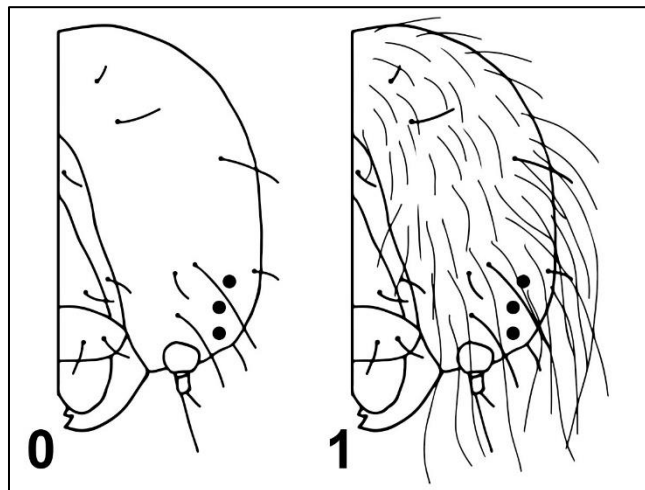
**Figure 7.** Larval morphological character: head color. Numbers correspond to multistate scoring in Table 2. Illustration credit: B. Zacharczenko.



**Figure 8.** Larval morphological character: color variation. Number corresponds to binary scoring in Table 2 (state 0 not pictured). All individuals pictured were siblings reared under the same conditions. Species: *A. increta*. Image credit: B. Zacharczenko.



**Figure 9.** Larval morphological character: loss of secondary setae. Number corresponds to binary scoring in Table 2 (state 0 not pictured). Species: *A. afflictata*. Image credit: B. Zacharczenko.

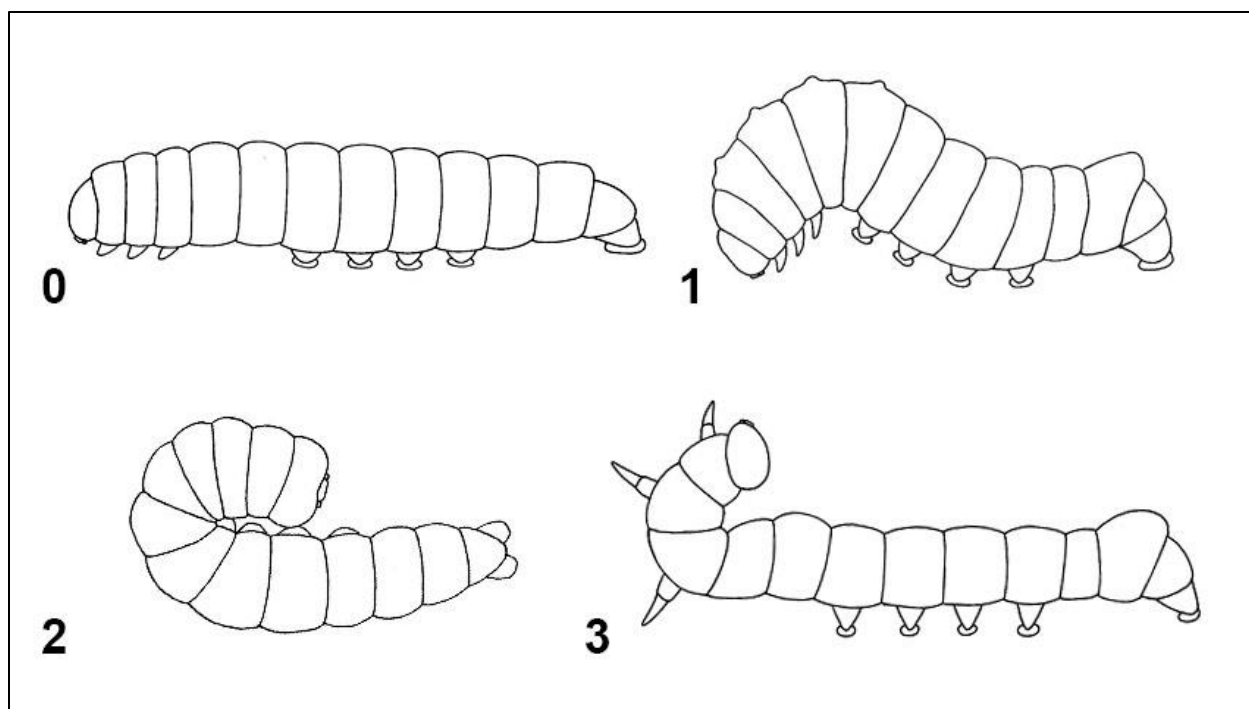


**Figure 10.** Larval morphological character: secondary setae on head. Numbers correspond to binary scoring in Table XX. Illustration credit: B. Zacharczenko.

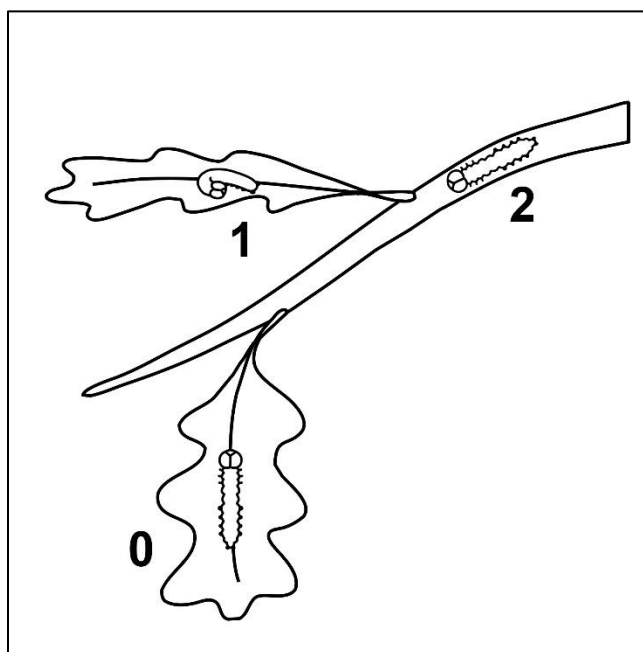


**Table 3.** Behavioral characters scored for *Acronicta* larvae, with descriptions. Characters are either binary, or multistate (none continuous).

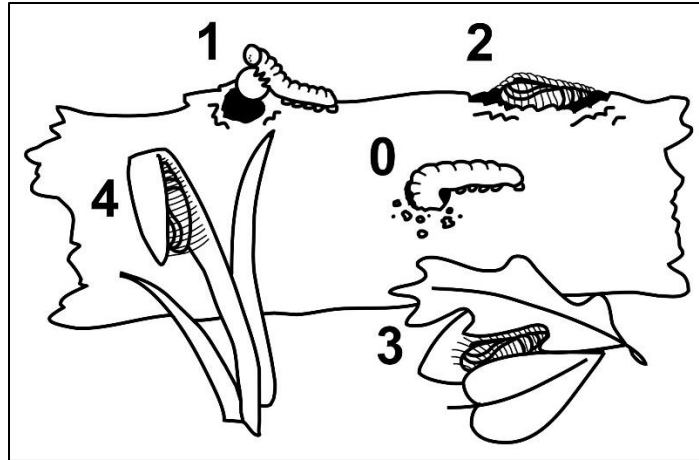
Character	#	States	Description
Resting positions	0	Straight	Rest with body straight
	1	Hunch	Rest with front of body hunched upward
	2	J-shape	Rest with body in a C- or J-shape
	3	Rear back	Rest with head (and maybe anal segment) raised off substrate
Location - early instars	0	Leaf-upper	Early instar rests on the upper side of a leaf
	1	Leaf-lower	Early instar rests on the lower side of a leaf
	2	Branch	Early instar rests on a branch
Location - ultimate instar	0	Leaf-upper	Ultimate instar rests on the upper side of a leaf
	1	Leaf-lower	Ultimate instar rests on the lower side of a leaf
	2	Branch	Ultimate instar rests on a branch or stem
Pupation	0	Wood-chewing	Chews vertical chamber in wood for pupation
	1	Wood-ball rolling	Chews vertical chamber in wood for pupation, forming balls of sawdust
	2	Wood-on surface	Chews a shallow channel on the surface of wood for pupation
	3	Leaf litter	Forms a cocoon in leaf litter
	4	Living leaves	Forms a cocoon using living leaves, or dying leaves on host plant
Erucism	0	No	Does not cause erucism in Brigitte ☺
	1	Yes	Has caused erucism in humans
Defensive behavior	-4	Curl and drop	Most evasive
	-3	Crawl away	Evasive
	-2	Partially curl	Evasive
	-1	Turn away	Evasive
	0	No reaction	No reaction
	1	Wave or twitch	Aggressive
	2	Thrash once	Aggressive
	3	Thrash several times	Aggressive
	4	Bite	Most aggressive, with thrashing



**Figure 11.** Larval behavioral character: resting position. Numbers correspond to multistate scoring in Table 2. Illustration credit: B. Zacharczenko.



**Figure 12.** Larval behavioral character: location (early and ultimate instars). Numbers correspond to multistate scoring in Table 2. Illustration credit: B. Zacharczenko.



**Figure 13.** Larval behavioral character: pupation. Numbers correspond to multistate scoring in Table 2. Illustration credit: B. Zacharczenko.

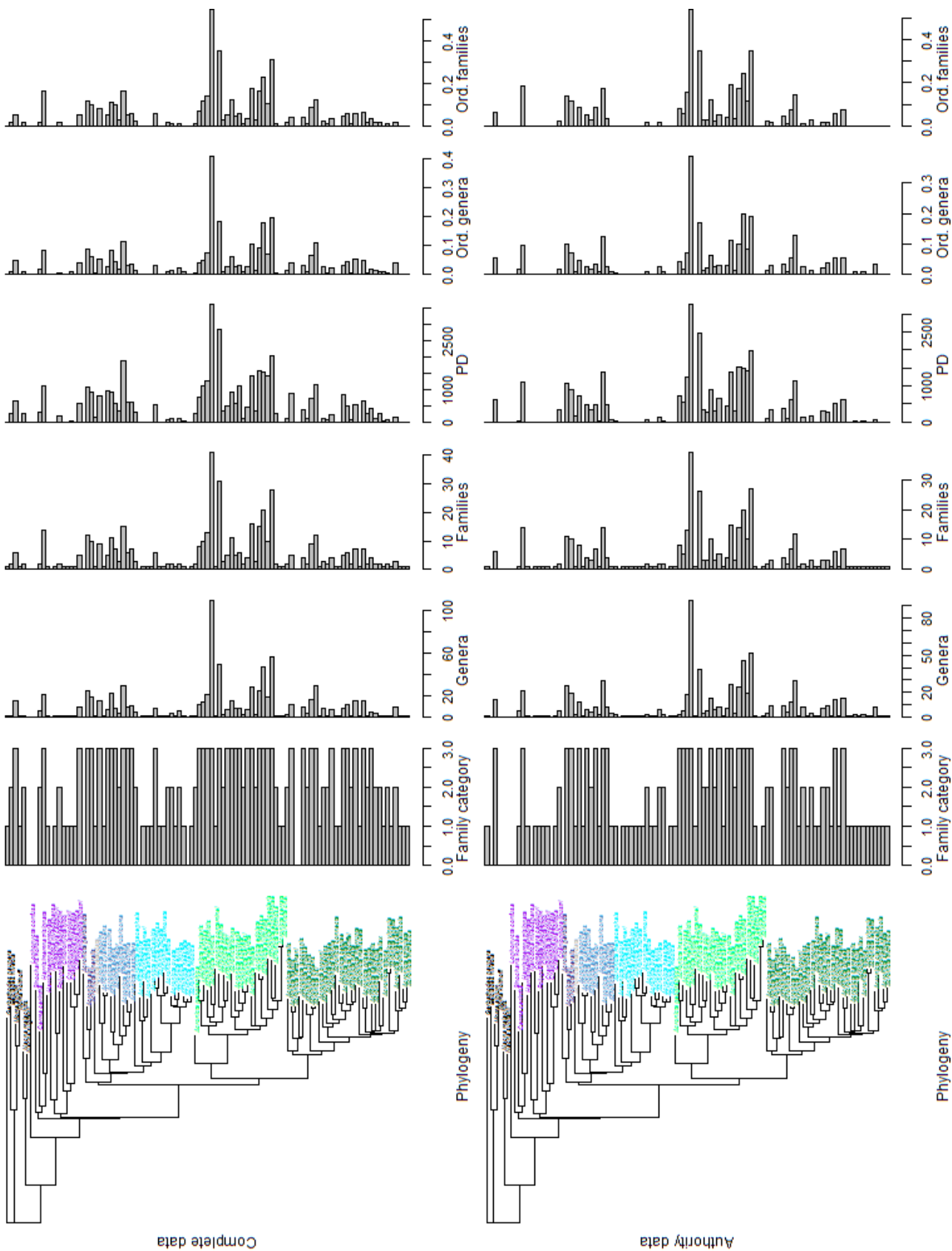


**Figure 14.** Larval behavioral character: erucism. These three forearm rashes were caused by (left to right) *A. edolata*, *A. impleta*, and *A. longa*. Image credit: B. Zacharczenko.

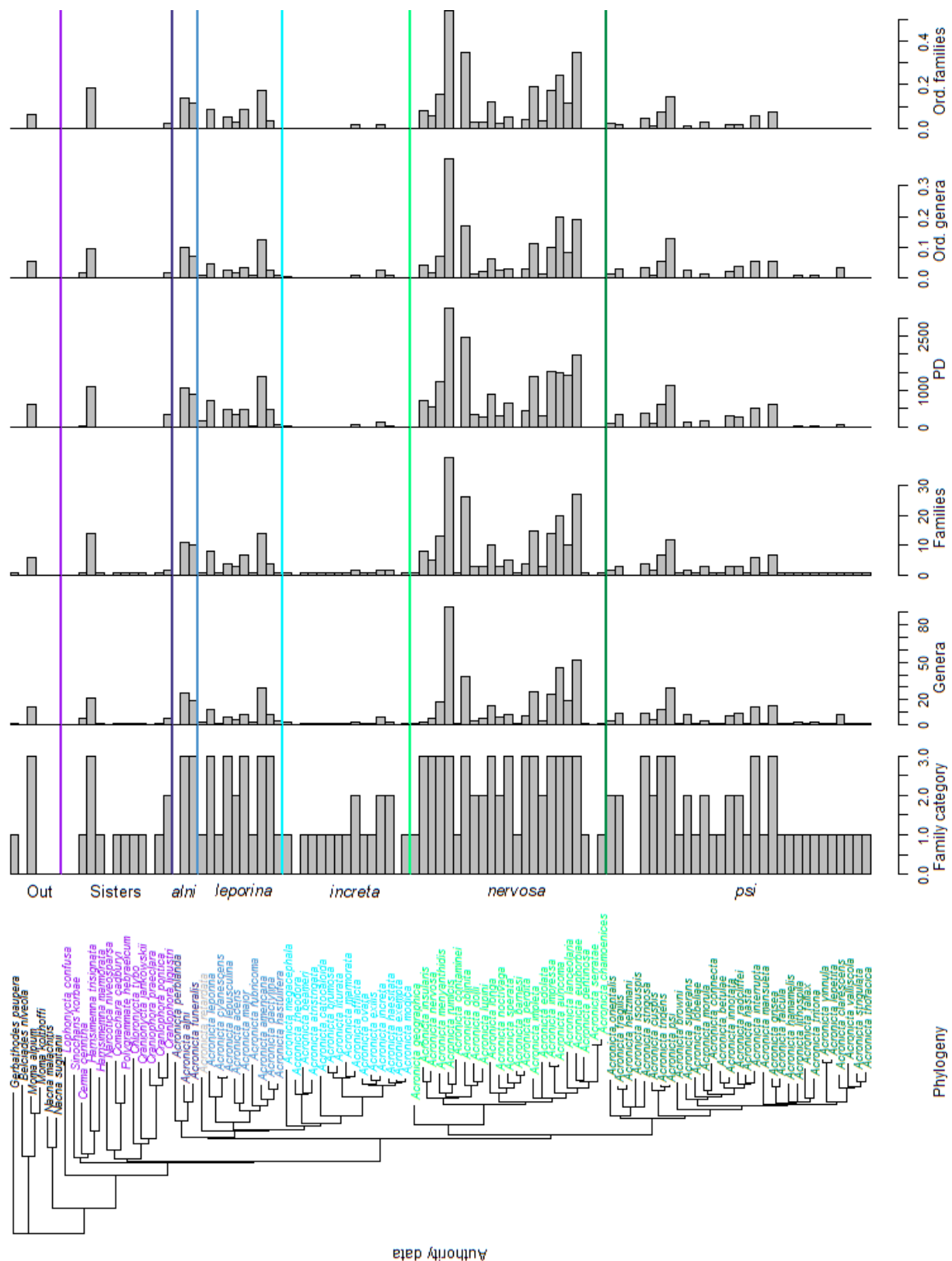
**Figure 15.** Mapping of larval diet breadth measures. The top half of the figure represents results from the *Complete* dataset. The bottom half of the figure represents results from the *Authority-Driven* dataset. Data for each species is mapped to its position on the phylogeny (left). Scales for each measure are figured. Diet breadth measures include (left to right) family category, genus richness, family richness, phylodiversity, ordination with genera, and ordination with families.

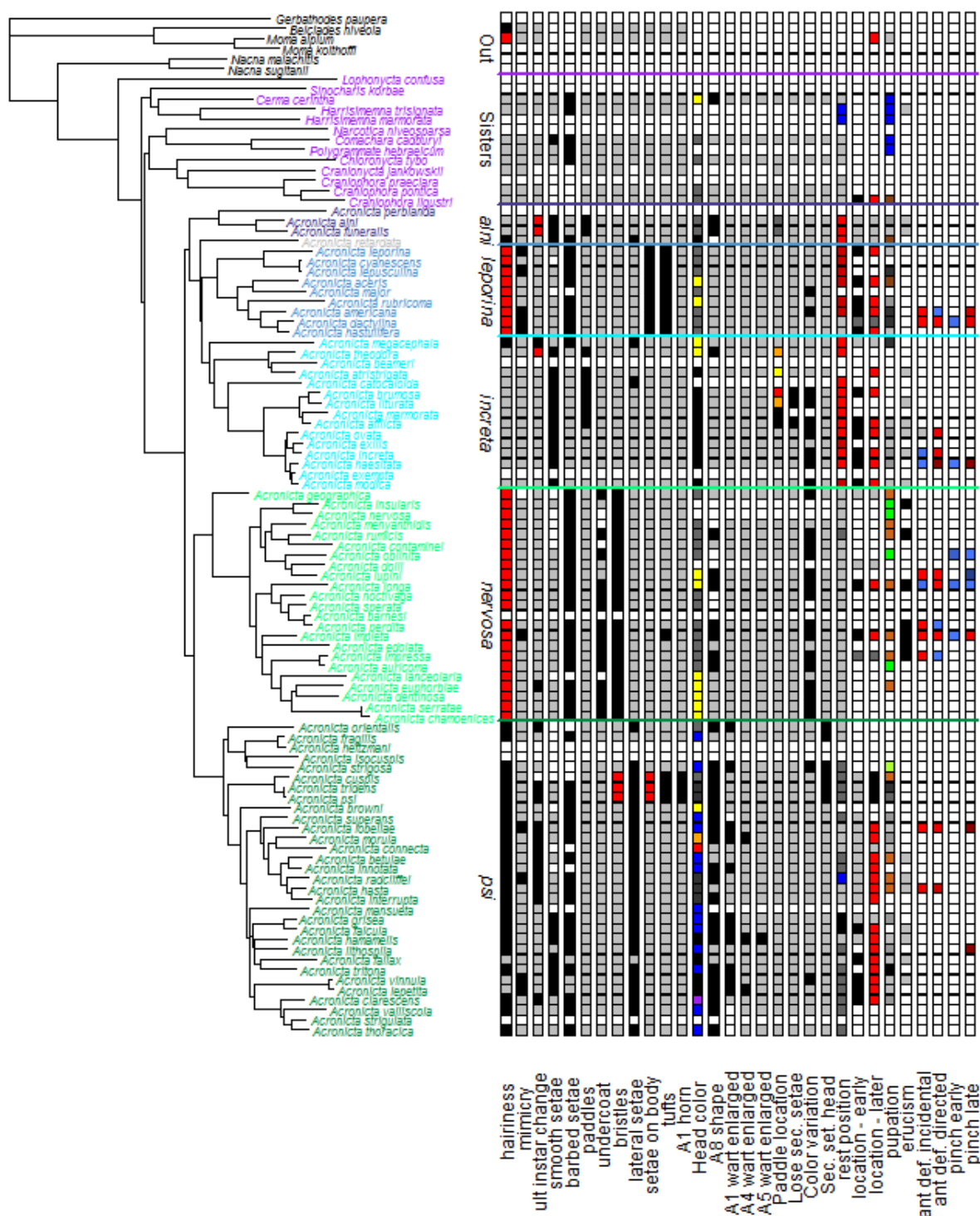
**Figure 16.** Expanded view of the *Complete* dataset from Figure XX. Species groups are labeled, and horizontal lines are added to delineate groups.

**Figure 17.** Expanded view of the *Authority-Driven* dataset from Figure XX. Species groups are labeled, and horizontal lines are added to delineate groups.









**Figure 18.** Morphological and behavioral traits mapped to the Acronictinae phylogeny. Phylogeny is colored by species groups, matching colored horizontal bars are added to the character map to delineate the groups. For all characters, white = unknown. Color coding is as follows. **MORPHOLOGY. Hairiness:** gray = mild, black = moderate, red = hirsute. **Mimicry:**



gray = no, black = yes. **Ultimate instar change:** gray = no, black = color, red = color and morphology. **Smooth setae:** gray = absent, black = present. **Barbed setae:** gray = absent, black = present. **Paddles:** gray = absent, black = present. **Undercoat:** gray = absent, black = present. **Bristles:** gray = absent, black = present, red = present on horn only. **Lateral setae more abundant:** gray = no, black = yes. **Secondary setae on body:** gray = no, black = yes, red = tufts only. **Dorsal tufts:** gray = absent, black = present. **A1 horn:** gray = absent, black = present. **Head color:** gray = solid, dark gray = solid and red patch, black = spotted, blue = spotted and red patch, purple = spotted and multi-colored, red = red patch, orange = red patch and multi-colored, yellow = multicolored. **A8 shape:** gray = smooth, black = humped. **A1 warts enlarged:** gray = no, black = yes. **A4 warts enlarged:** gray = no, black = yes. **A5 warts enlarged:** gray = no, black = yes. **Paddle location:** gray = n/a, red = D1 and D2, orange = D1, D2, SD1, SD2, XD1, and XD2, yellow = D1, D2, SD1, SD2, XD1, XD2, L1, and L2, black = D2, dark gray = D2, XD1, and XD2. **Lose secondary setae:** gray = no, black = yes. **Color variation:** gray = no, black = yes. **Secondary setae on head:** gray = no, black = yes. **BEHAVIOR. Resting position:** gray = straight, dark gray = straight and hunch, dark red = straight and J-shape, black = hunch, red = J-shape, blue = rear back. **Resting location, early instars:** gray = leaf upper side, dark gray = leaf upper or lower side, black = leaf lower side. **Resting location, later instars:** gray = leaf upper side, dark gray = leaf upper or lower side, black = leaf lower side, red = branch. **Pupation:** dark gray = chewing tunnel and surface, dark mid-gray = chewing tunnel, light mid-gray = chewing tunnel, surface, and leaf litter, light gray = chewing tunnel and leaf litter, greenyellow = chewing tunnel and living leaves, blue = ball rolling, black = wood surface, dark brown = surface and leaf litter, brown = leaf litter, green = living leaves. **Erucism:** gray = none observed, black = observed in BVZ. **DEFENSIVE BEHAVIOR. For all tests (ant test incidental and directed touching, pinch test early and later instars):** average score -4 to -3 = dark blue, -3 to -2 = dark mid-blue, -2 to -1 = light mid-blue, -1 to 0 = light blue, 0 = gray, 0 to 1 = light red, 1 to 2 = light mid-red, 2 to 3 = dark mid-red, 3 to 4 = dark red.

**Table 4.** Phylogenetic signal measured using Pagel's lambda for diet breadth, behavioral characters, and morphological characters. Values closer to zero = no phylogenetic signal, values closer to 1 = the character follows a Brownian Motion model of evolution.

<b>Diet Breadth</b>	<b>lambda</b>	<b>Morphology</b>	<b>lambda</b>
Genera	0.000066	Ultimate instar change	0.000066
Families	0.000066	Smooth setae	0.000041
Family category	0.000079	Barbed setae	0.000065
Phylodiversity	0.000066	Paddles	0.532645
Ordination - Genera	0.000066	Undercoat	0.000066
Ordination - Families	0.000066	Bristles	0.000073
<b>Behavior</b>	<b>lambda</b>	Lateral setae abundant	0.000066
Resting position	0.951628	Secondary setae on integument	0.000067
Location - early	0.000066	Tufts	0.594048
Location - ultimate	0.000066	A1 horn	0.000066
Pupation	0.000080	Head color	0.321998
Erucism	0.000066	A8 shape	0.379295
Ant defense - incidental	0.000066	A1 wart enlarged	0.000066
Ant defense - directed	0.000044	A5 wart enlarged	0.000066
Pinch defense - early instar	0.999934	A4 wart enlarged	0.000066
Pinch defense - late instar	0.000066	Paddle location	0.758674
<b>Morphology</b>	<b>lambda</b>	Lose secondary setae	0.449448
Hairy	0.771447	Color variation	0.000051
Mimicry	0.000066	Secondary setae on head	0.000066

**Table 5.** Summary of Phylogenetic Generalized Least Squares (PGLS) results, with diet breadth measures as the dependent variables and morphological and behavioral characters as the independent variables (all tested separately). Relationship (+/-) denotes the direction of the association. Filled boxes represent a significant result ( $p > 0.05$ ) for the relationship between a character and a diet breadth measure. Detailed results in Supplementary Tables S5a – S5c.

	Relationship	Family Category	Genera	Families	Phylodiversity	Ordin. Genera	Ordin. Families
Hairy	+						
Mimicry	+						
Ultimate instar change	+						
Smooth setae	-						
Barbed setae	+						
Paddles	-						
Undercoat	+						
Bristles	+						
Lateral setae abundant	-						
Secondary setae on integument	+						
Tufts	+						
A1 horn	+						
Head color	-						
A8 shape	+						
A1 wart enlarged	-						
A5 wart enlarged	-						
A4 wart enlarged	-						
Paddle location	+						
Lose secondary setae	-						
Color variation	+						
Secondary setae on head	+						
Resting position	-						
Location - early	-						
Location - ultimate	-						
Pupation	+						
Erucism	+						
Ant defense - incidental	+ / -						
Ant defense - directed	-						
Pinch defense - early instar	-						
Pinch defense - late instar	-						

**Table 6.** Summary of Phylogenetic Generalized Least Squares (PGLS) results, with diet breadth measures as the dependent variables and morphological and behavioral characters as the independent variables (all tested separately). Relationship (+/-) denotes the direction of the association. Filled boxes represent a significant result after Bonferoni correction accounting for the 180 individual tests ( $p > 0.00028$ ).

	Relationship	Family Category	Genera	Families	Phylodiversity	Ordi. Genera	Ordi. Families
Hairy	+						
Mimicry	+						
Ultimate instar change	+						
Smooth setae	-						
Barbed setae	+						
Paddles	-						
Undercoat	+						
Bristles	+						
Lateral setae abundant	-						
Secondary setae on integument	+						
Tufts	+						
A1 horn	+						
Head color	-						
A8 shape	+						
A1 wart enlarged	-						
A5 wart enlarged	-						
A4 wart enlarged	-						
Paddle location	+						
Lose secondary setae	-						
Color variation	+						
Secondary setae on head	+						
Resting position	-						
Location - early	-						
Location - ultimate	-						
Pupation	+						
Erucism	+						
Ant defense - incidental	+ / -						
Ant defense - directed	-						
Pinch defense - early instar	-						
Pinch defense - late instar	-						

**Table 7.** Summary of Phylogenetic Generalized Least Squares (PGLS) results, with diet breadth measures as the dependent variables and morphological and behavioral characters as the independent variables (all tested separately). Relationship (+/-) denotes the direction of the association. Filled boxes represent a significant result after Benjamini-Hochberg correction of p-values within each diet breadth column, with a false discovery rate (FDR) of 0.05.

	Relationship	Family Category	Genera	Families	Phylodiversity	Ordi. Genera	Ordi. Families
Hairy	+						
Mimicry	+						
Ultimate instar change	+						
Smooth setae	-						
Barbed setae	+						
Paddles	-						
Undercoat	+						
Bristles	+						
Lateral setae abundant	-						
Secondary setae on integument	+						
Tufts	+						
A1 horn	+						
Head color	-						
A8 shape	+						
A1 wart enlarged	-						
A5 wart enlarged	-						
A4 wart enlarged	-						
Paddle location	+						
Lose secondary setae	-						
Color variation	+						
Secondary setae on head	+						
Resting position	-						
Location - early	-						
Location - ultimate	-						
Pupation	+						
Erucism	+						
Ant defense - incidental	+ / -						
Ant defense - directed	-						
Pinch defense - early instar	-						
Pinch defense - late instar	-						

**Table 8.** Common error types encountered in the host plant record literature. Partially adapted from Table 2 of (Wagner and Todd 2016).

Error Type	Explanation
Larval misidentification	Cryptic or closely related species may be confused by amateurs and experts alike. Especially problematic for older publications with differing taxonomic treatments and species concepts. Some <i>Acronicta</i> species are mimics; the hosts of their models may be recorded.
Host misidentification	Plants may be difficult for non-botanists to identify.
Incidental associations	Larva found on a plant they do not feed on. May be due to wandering to a suitable pupation site or falling from their true host.
Lab rearing	Larvae may feed upon plants in a laboratory setting they would not otherwise eat in the wild.
Misreporting	Record-keeping errors.
Misattributions	Inappropriate interpretation of primary literature. For example, a primary record may list host plants the larvae rejected or failed to thrive upon, yet those are recorded in subsequent publications as viable records.
Missing references	Typical for secondary sources.
Inadequate sample size	Generalists mistakenly regarded to be specialized due to inadequate sampling. The species may be rare, or undercollected.

## Supplementary Tables and Figures

**Table S1.** Genera missing from the Angiosperm megatree phylogeny, and their replacements for the *Replacement* analyses. If a replacement genus was found to already be in the dataset, it was only scored if it was not already scored for a particular species.

Missing genus	Replacement genus	Status	Reference
<i>Abies</i>	<i>Tsuga</i>	New	Wang et al. 2000
<i>Alhagi</i>		NONE CLOSE ENOUGH	Ahangarian et al., 2007
<i>Armeria</i>	<i>Limonium</i>	Already in dataset	Moharrek et al. 2014
<i>Aronia</i>	<i>Chaenomeles</i>	Already in dataset	Potter et al. 2007
<i>Begonia</i>		NONE CLOSE ENOUGH	Clement et al., 2004
<i>Bergenia</i>	<i>Chrysopenium</i>	New	Xiang et al. 2012
<i>Beta</i>		NONE CLOSE ENOUGH	Kadereit and Borsch 2003
<i>Buxus</i>	<i>Pachysandra</i>	New	Balthazar et al. 2000
<i>Calligonum</i>	<i>Persicaria</i>	New	Tavakkoli et al., 2010
<i>Cedrela</i>		NONE CLOSE ENOUGH	Muellner et al. 2009
<i>Chamaemelum</i>		NONE CLOSE ENOUGH	Oberprieler, 2002
<i>Chondrilla</i>	<i>Taraxacum</i>	Already in dataset	van Dijk 2003
<i>Citrus</i>		NONE CLOSE ENOUGH	Grosso et al., 2008
<i>Cotinus</i>	<i>Toxicodendron</i>	New	Miller et al. 2001
<i>Cydonia</i>	<i>Photinia</i>	New	Potter et al. 2007
<i>Dahlia</i>	<i>Coreopsis</i>	New	Mort et al. 2008
<i>Dorycnium</i>	<i>Anthyllis</i>	New	Allan and Porter 2000
<i>Eubotrys</i>	<i>Leucothoe</i>	New	Bush et al. 2010
<i>Eucalyptus</i>		NONE CLOSE ENOUGH	Udovicic and Ladiges 2000
<i>Euphrasia</i>	<i>Odontites</i>	New	Bennett and Mathews 2006
<i>Fuchsia</i>	<i>Circaea</i>	New	Berry et al. 2004
<i>Heptacodium</i>	<i>Lonicera</i>	Already in dataset	Jacobs et al. 2011
<i>Heteromeles</i>	<i>Cotoneaster</i>	Already in dataset	Campbell et al. 2007
<i>Isodon</i>		NONE CLOSE ENOUGH	Zhong et al., 2010
<i>Jasminum</i>	<i>Menodora</i>	New	Wallander and Albert 2000
<i>Myricaria</i>	<i>Tamarix</i>	New	Wang et al. 2009
<i>Ocimum</i>		NONE CLOSE ENOUGH	Paton et al. 2004
<i>Paliurus</i>	<i>Ziziphus</i>	New	Richardson et al. 1999
<i>Pseudotsuga</i>	<i>Larix</i>	Already in dataset	Wang et al. 2000
<i>Purshia</i>	<i>Cercocarpus</i>	Already in dataset	Potter et al. 2007
<i>Pyracantha</i>	<i>Chaenomeles</i>	Already in dataset	Potter et al. 2007
<i>Sorbaria</i>		NONE CLOSE ENOUGH	Potter et al. 2007
<i>Wrightia</i>	<i>Trachelospermum</i>	New	Sennblad et al. 1998
<i>Zea</i>	<i>Andropogon</i>	New	Bouchenak-Khelladi et al. 2008

**Table S2.** Larval specimen data sources. n/a for species where the larvae are unknown.

<b>Taxon</b>	<b>Specimen(s)</b>	<b>Literature</b>	<b>Online or unpublished photos</b>	<b>Setal slide prep.</b>
<i>Acronicta aceris</i>	CUIC (no data)	Ahola & Silvonen, 2005; Nippe, 2000; Porter, 1997; Beck, 2000		BVZ (no data)
<i>Acronicta afflicta</i>	DLW (TX, 2012), BVZ (NC, 2011; CT, 2011; NC, 2012; NC, 2013), CUIC (NC, 1949)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (NC, 2013)
<i>Acronicta alni</i>		Ahola & Silvonen, 2005; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893; Buckler, 1891		
<i>Acronicta americana</i>	DLW (NY, 2008; NJ, 2011), BVZ (NH, 2013)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (NJ, 2011)
<i>Acronicta atristrigata</i>	DLW (AZ, 2012; AZ, 2014)		DLW	BVZ (AZ, 2012)
<i>Acronicta auricoma</i>	CUIC (no data)	Ahola & Silvonen, 2005; Nippe, 2000; Beck, 2000; Chapman, 1893; Buckler, 1891		BVZ (no data)
<i>Acronicta barnesi</i>				
<i>Acronicta beameri</i>				
<i>Acronicta betulae</i>	DLW (NC, 2011), BVZ (NC, 2012)	Wagner, 2011; Smith & Dyar, 1898	DLW, BVZ	BVZ (NC, 2012)
<i>Acronicta browni</i>	n/a			
<i>Acronicta brumosa</i>	DLW (AZ, 2012)	Smith & Dyar, 1898; Wagner, 2011; Wagner, 2005	DLW	
<i>Acronicta catocaloida</i>		Sugi, 1987	<a href="http://JPMoth.org">http://JPMoth.org</a>	
<i>Acronicta chamoenices</i>			<a href="http://insecta.pro">http://insecta.pro</a> (Diego Reggianti), <a href="http://lepiforum.de">http://lepiforum.de</a> (Karin Vogt), <a href="http://pyrgus.de">http://pyrgus.de</a>	
<i>Acronicta clarescens</i>	DLW (CT, 2008)	Wagner, 2011; Wagner, 2005	DLW	BVZ (CT, 2008)
<i>Acronicta connecta</i>	DLW	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	



<i>Acronicta contaminiei</i>		Ahola & Silvonen, 2005; Nippe, 2000; Beck, 2000	<a href="http://molbiol.ru">http://molbiol.ru</a> (Vladimir Savchuk)	
<i>Acronicta cuspis</i>		Ahola & Silvonen, 2005; Beck, 2000; Sugi, 1987		
<i>Acronicta cyanescens</i>	CUIC (AZ, 1964)	Miller & Hammond, 2003		
<i>Acronicta dactylina</i>	DLW (CT, 1997; NY, 2003), BVZ (MA, 2013), NMNH (NY, 1977), CUIC (NY, 1968)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (MA, 2013)
<i>Acronicta dentinosa</i>	CUIC (no data)	Ahola & Silvonen, 2005; Nippe, 2000; Beck, 2000	<a href="http://lepiforum.de">http://lepiforum.de</a> (multiple photographers)	BVZ (no data)
<i>Acronicta dolli</i>	DLW	Wagner, 2011	DLW	BVZ (?)
<i>Acronicta edolata</i>	DLW (AZ, 2012), CUIC (AZ, 1965)		DLW	BVZ (AZ, 2012)
<i>Acronicta euphorbiae</i>	CUIC (no data)	Ahola & Silvonen, 2005; Nippe, 2000; Porter, 1997; Beck, 2000; Chapman, 1893; Buckler, 1891		BVZ (no data)
<i>Acronicta exempta</i>	n/a			
<i>Acronicta exilis</i>	DLW, BVZ (NC, 2013)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (NC, 2013)
<i>Acronicta falcata</i>	DLW (CT, 2008), BVZ (NC, 2012; CT, 2014)	Wagner, 2011; Smith & Dyar, 1898	DLW, BVZ	BVZ (CT, 2012)
<i>Acronicta fallax</i>	DLW (NY, 1998), TLM (NY, 1977)	Wagner, 2011	DLW	BVZ (NY, 1998)
<i>Acronicta fragilis</i>	DLW (AB [Canada], 2002), NMNH (WA, 1938)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (AB [Canada], 2002)
<i>Acronicta funeralis</i>	BVZ (ME, 2011)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (ME, 2011)
<i>Acronicta geographica</i>		Ahola & Silvonen, 2005; Nippe, 2000; Beck, 2000	<a href="http://www.biolib.cz">http://www.biolib.cz</a> (Josef Dvořák)	
<i>Acronicta grisea</i>	DLW, NMNH (WA, 1937; NY, 1977)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (WA, 1937)
<i>Acronicta haesitata</i>	DLW (NJ, 2009)	Wagner, 2011	DLW, BVZ	BVZ (NJ, 2009)
<i>Acronicta hamamelis</i>	DLW (WV, 2008; NC, 2009)	Wagner, 2011; Smith & Dyar, 1898 (ovata); Wagner, 2005	DLW	BVZ (NC, 2009)

<i>Acronicta hasta</i>	BVZ (MA, 2011; CT, 2012; NC, 2012; CT, 2013)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (CT, 2012)
<i>Acronicta hastulifera</i>	DLW (WV, 2007), BVZ (CT, 2012)	Wagner, 2011; Smith & Dyar, 1898	DLW, BVZ	BVZ (CT, 2012)
<i>Acronicta heitzmani</i>	n/a			
<i>Acronicta impleta</i>	DLW (WV, 2008; TX, 2012), BVZ (NC, 2011; NC, 2013)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (NC, 2011)
<i>Acronicta impressa</i>	DLW (CT, 2008), BVZ (MA, 2013), NMNH (no data), CUIIC (AZ, 1965)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (MA, 2013)
<i>Acronicta increta</i>	DLW (NJ, 2005; NY, 2008), BVZ (CT, 2012; NC, 2011; NC, 2012; CT, 2013)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (NC, 2011)
<i>Acronicta innotata</i>	DLW, CUIIC (VT, 1980)	Wagner, 2011; Smith & Dyar, 1898	DLW	
<i>Acronicta insularis</i>	DLW, BVZ (CT, 2011; NC, 2011; CT, 2012)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (CT, 2012)
<i>Acronicta interrupta</i>	DLW (OH, 2006), NMNH (MD, 1943), CUIIC (NY, 1934)	Wagner, 2011; Wagner, 2005	DLW	BVZ (OH, 2006)
<i>Acronicta isocuspis</i>	n/a			
<i>Acronicta lanceolaria</i>		Wagner, 2011		
<i>Acronicta lepetita</i>	BVZ (TX, 2013)		DLW, BVZ	BVZ (TX, 2013)
<i>Acronicta leporina</i>	CUIIC (no data), NMNH (WA, 1935)	Ahola & Silvonen, 2005; Nippe, 2000; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893; Buckler, 1891		BVZ (WA, 1935, no data)
<i>Acronicta lepusculina</i>	DLW (CT, 1998; NH, 1998; NY, 2008)	Wagner, 2011; Wagner, 2005; Smith & Dyar 1898 (A. populi)		BVZ (NH, 1998)

<i>Acronicta lithospila</i>	DLW (MA, 1998), BVZ (NC, 2011)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (NC, 2011)
<i>Acronicta liturata</i>	DLW (AZ, 2011; AZ, 2012)		DLW	BVZ (AZ, 2011)
<i>Acronicta lobeliae</i>	DLW (PA, 2006), BVZ (CT, 2011; NC, 2012)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (PA, 2006; NC, 2012)
<i>Acronicta longa</i>	DLW (NC, 2004; OH, 2012), CUIC (TX, 1968)	Wagner, 2011; Wagner, 2005	DLW, BVZ	BVZ (NC, 2004)
<i>Acronicta lupini</i>	DLW (CO, 2014)		DLW	BVZ (CO, 2014)
<i>Acronicta major</i>		Zhu, 1979; Sugi, 1987	<a href="http://commons.wikimedia.org">http://commons.wikimedia.org</a> (Yasu)	
<i>Acronicta mansueta</i>				
<i>Acronicta marmorata</i>	NMNH (WA, 1935)	Miller & Hammond, 2003		
<i>Acronicta megacephala</i>	CUIC (no data)	Ahola & Silvonen, 2005; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893		BVZ (no data)
<i>Acronicta menyanthidis</i>		Ahola & Silvonen, 2005; Porter, 1997; Beck, 2000		
<i>Acronicta modica</i>	DLW (NJ, 2006; CT, 2011)	Wagner, 2011; Smith & Dyar, 1898	DLW	BVZ (CT, 2011)
<i>Acronicta morula</i>	DLW (CT, 1999; SC, 2009), BVZ (NC, 2012)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (NC, 2012)
<i>Acronicta nervosa</i>		Ahola & Silvonen, 2005; Beck, 2000	<a href="http://pyrgus.de">http://pyrgus.de</a> , <a href="http://lepiforum.de">http://lepiforum.de</a> (multiple photographers)	
<i>Acronicta noctivaga</i>	DLW (NH, 1998), BVZ (CT, 2014), CUIC (NY, 1990)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (NH, 1998)
<i>Acronicta obliterata</i>	DLW (CT, 1999; CT, 2000; MO, 2011; CT, 2012), BVZ (NJ, 2011)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (MO, 2011; NJ, 2011)
<i>Acronicta orientalis</i>			<a href="http://pyrgus.de">http://pyrgus.de</a>	
<i>Acronicta ovata</i>	DLW (CT, 2010), BVZ	Wagner, 2011; Smith & Dyar, 1898 (hamamelis); Wagner, 2005	DLW, BVZ	BVZ (CT, 2012)

	(CT, 2012; CT, 2014)			
<i>Acronicta perblanda</i>	n/a			
<i>Acronicta perdita</i>	DLW (CA, 2013), NMNH (CA, 1982)		DLW	BVZ (CA, 2013)
<i>Acronicta psi</i>	CUIC (no data)	Ahola & Silvonen, 2005; Porter, 1997; Beck, 2000; Chapman, 1893		BVZ (no data)
<i>Acronicta radcliffei</i>	DLW, NMNH (WA, 1934; VA, 1943), CUIC (VA, 1949)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (WA, 1934)
<i>Acronicta retardata</i>	DLW (NJ, 2002; MA, 2009), BVZ (NH, 2013), NMNH (VA, 1955; FL, 1975)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (NJ, 2002)
<i>Acronicta rubricoma</i>	DLW (TX, 2011), BVZ (NC, 2012)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (TX, 2011; NC, 2012)
<i>Acronicta rumicis</i>		Ahola & Silvonen, 2005; Nippe, 2000; Zhu, 1979; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893; Buckler, 1891		
<i>Acronicta serratae</i>		Beck, 2000	<a href="http://www.biolib.cz">http://www.biolib.cz</a> (Josef Dvořák)	
<i>Acronicta sperata</i>	DLW (WV, 2000), CUIC (NY, 1989)	Wagner, 2011	DLW	BVZ (WV, 2000)
<i>Acronicta strigosa</i>		Ahola & Silvonen, 2005; Zhu, 1979; Beck, 2000; Chapman, 1893; Buckler, 1891		
<i>Acronicta strigulata</i>	DLW		DLW	
<i>Acronicta superans</i>	DLW (CT, 2006)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (CT, 2006)
<i>Acronicta theodora</i>	n/a			
<i>Acronicta thoracica</i>	DLW (AZ, 2011; AZ, 2012; AZ, 2013)		DLW, BVZ	BVZ (AZ, 2012)
<i>Acronicta tridens</i>	CUIC (no data)	Ahola & Silvonen, 2005; Nippe, 2000; Porter, 1997; Beck, 2000; Chapman, 1893		BVZ (no data)

<i>Acronicta tritona</i>	DLW (NJ, 1997; NJ, 1999)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW	BVZ (NJ, 1999)
<i>Acronicta valliscola</i>	DLW (TX, 2013)		DLW	BVZ (TX, 2013)
<i>Acronicta vinnula</i>	DLW (CT, 1999), BVZ (NC, 2011)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (NC, 2011)
<i>Belciades niveola</i>		Sugi, 1987		
<i>Cerma cerintha</i>	DLW (CT, 2007)	Wagner, 2011; Wagner, 2005	DLW	BVZ (?)
<i>Chloronycta tybo</i>	DLW (AZ, 2012)	Schmidt et al., 2014	DLW	BVZ (AZ, 2012)
<i>Comachara cadburyi</i>	DLW (NJ, 2011)	Wagner, 2011; Wagner, 2005	DLW	BVZ (NJ, 2011)
<i>Cranionycta jankowskii</i>		Sugi, 1987		
<i>Craniophora ligustri</i>		Ahola & Silvonen, 2005; Nippe, 2000; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893		
<i>Craniophora pontica</i>		Beck, 2000		
<i>Craniophora praeclara</i>	no data found (host plant, but no larval images or descriptions)			
<i>Gerbathodes paupera</i>	no data found (host plant, but no larval images or descriptions)			
<i>Harrisimemna marmorata</i>		Sugi, 1987		
<i>Harrisimemna trisignata</i>	DLW (CT, 1999; CT, 2000; WV, 2007; MA, 2012), BVZ (NC, 2012; NC, 2013), CUIC (FL, 1978; NY, 1981)	Wagner, 2011; Smith & Dyar, 1898; Wagner, 2005	DLW, BVZ	BVZ (NC, 2012)
<i>Lophonycta confusa</i>	n/a			
<i>Moma alpium</i>		Ahola & Silvonen, 2005; Porter, 1997; Beck, 2000; Sugi, 1987; Chapman, 1893		
<i>Moma kolthoffi</i>	no data found (host plant, but no larval			

	images or descriptions)			
<i>Nacna malachitis</i>	n/a			
<i>Nacna sugitanii</i>	n/a			
<i>Narcotica niveosparsa</i>	n/a			
<i>Polygrammate hebraeicum</i>	DLW	Wagner, 2011; Wagner, 2005	DLW	BVZ (CT, 2011)
<i>Sinocharis korbae</i>	n/a			
<b>Total: 101</b>	<b>64</b>	<b>73</b>	<b>64</b>	<b>58</b>

**Table S3a.** Diet breadth measures for all taxa using the *Complete* dataset of diet breadth (prefix: 1). Taxa were tested using both the *Strict* (a) and *Replacement* (b) Angiosperm datasets. Ordinations were tested using all data regardless of inclusion in the Angiosperm tree.

Taxa	1 total genera	1 total families	1a genera	1a families	1a fam. cat.	1a pd	1b genera	1b families	1b fam. cat.	1b pd	1 ordi. genera scaled	1 ordi. families scaled
<i>Acronicta aceris</i>	23	11	23	11	3	913.06218	23	11	3	913.06218	0.08148	0.11004
<i>Acronicta afflicta</i>	2	2	2	2	2	62.45518	2	2	2	62.45518	0.00538	0.01572
<i>Acronicta alni</i>	25	12	25	12	3	1074.27235	25	12	3	1074.27235	0.08385	0.11997
<i>Acronicta americana</i>	30	15	30	15	3	1859.11798	30	15	3	1859.11798	0.11119	0.16404
<i>Acronicta atristrigata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta auricoma</i>	47	21	47	21	3	1513.49922	47	21	3	1513.49922	0.17674	0.22812
<i>Acronicta barnesi</i>	3	2	3	2	2	83.57043	3	2	2	83.57043	0.00697	0.00849
<i>Acronicta beameri</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta betulae</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta browni</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta brumosa</i>	9	6	9	6	3	511.511	9	6	3	511.511	0.02934	0.05518
<i>Acronicta catocaloida</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta chamoenices</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta clarescens</i>	11	3	9	3	2	138.23398	10	3	2	141.27999	0.03583	0.01849
<i>Acronicta connecta</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta contaminiei</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta cuspidata</i>	4	2	4	2	2	101.70225	4	2	2	101.70225	0.00768	0.00849
<i>Acronicta cyanescens</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta dactylina</i>	10	6	10	6	3	617.89252	10	6	3	617.89252	0.02962	0.05375
<i>Acronicta dentinosa</i>	2	2	2	2	2	260.64733	2	2	2	260.64733	0.00431	0.01272
<i>Acronicta dolli</i>	3	3	3	3	2	342.58305	3	3	2	342.58305	0.00887	0.02677
<i>Acronicta edolata</i>	3	3	3	3	2	311.35404	3	3	2	311.35404	0.01059	0.03131
<i>Acronicta euphorbiae</i>	57	28	51	26	3	1752.6267	56	28	3	2010.4285	0.1937	0.31023
<i>Acronicta exempta</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta exilis</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta falcula</i>	2	2	2	2	2	260.64733	2	2	2	260.64733	0.00517	0.01722
<i>Acronicta fallax</i>	2	2	2	2	2	260.64733	2	2	2	260.64733	0.00534	0.01653
<i>Acronicta fragilis</i>	12	5	12	5	3	876.16242	12	5	3	876.16242	0.03617	0.04102
<i>Acronicta funeralis</i>	19	10	19	10	3	895.99408	19	10	3	895.99408	0.06153	0.09753
<i>Acronicta geographica</i>	2	2	2	2	2	260.64733	2	2	2	260.64733	0.00517	0.01378
<i>Acronicta grisea</i>	15	7	15	7	3	624.85605	15	7	3	624.85605	0.04494	0.06462
<i>Acronicta haesitata</i>	2	1	2	1	1	23.88938	2	1	1	23.88938	0.00526	0
<i>Acronicta hamamelis</i>	5	4	5	4	3	403.71817	5	4	3	403.71817	0.0173	0.03734
<i>Acronicta hasta</i>	2	2	2	2	2	75.80219	2	2	2	75.80219	0.00416	0.01162
<i>Acronicta hastulifera</i>	11	7	11	7	3	597.79231	11	7	3	597.79231	0.0331	0.0575
<i>Acronicta heitzmani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta impleta</i>	28	16	27	15	3	1341.334	28	16	3	1410.84478	0.10372	0.1772
<i>Acronicta impressa</i>	25	15	24	15	3	1531.72017	25	15	3	1551.99565	0.09048	0.16487
<i>Acronicta incerta</i>	6	2	6	2	2	117.31756	6	2	2	117.31756	0.01914	0.01186
<i>Acronicta innotata</i>	9	5	8	4	3	320.48341	9	5	3	841.93481	0.02839	0.04529
<i>Acronicta insularis</i>	12	8	11	8	3	731.82285	12	8	3	734.98085	0.03695	0.07223
<i>Acronicta interrupta</i>	16	7	15	7	3	537.79703	15	7	3	537.79703	0.05134	0.0575
<i>Acronicta isocuspis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta lanceolaria</i>	19	10	18	10	3	1403.26564	19	10	3	1407.85189	0.0702	0.1024
<i>Acronicta lepetita</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta leporina</i>	16	9	16	9	3	805.29812	16	9	3	805.29812	0.05006	0.08407
<i>Acronicta lepusculina</i>	7	5	6	4	3	483.8137	7	5	3	956.2667	0.02449	0.05481
<i>Acronicta lithospila</i>	4	2	4	2	2	83.28876	4	2	2	83.28876	0.01371	0.01572
<i>Acronicta liturata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta lobeliae</i>	2	2	2	2	2	75.80219	2	2	2	75.80219	0.00416	0.01162
<i>Acronicta longa</i>	16	11	16	11	3	923.26055	16	11	3	923.26055	0.05972	0.12191
<i>Acronicta lupini</i>	7	5	7	5	3	487.5368	7	5	3	487.5368	0.02603	0.05051
<i>Acronicta major</i>	11	9	9	7	3	548.69725	9	7	3	548.69725	0.04176	0.10037
<i>Acronicta mansueta</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta marmorata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta megacephala</i>	6	4	5	3	2	273.41562	5	3	2	273.41562	0.01357	0.025
<i>Acronicta menyanthidis</i>	21	13	21	13	3	1267.13729	21	13	3	1267.13729	0.07387	0.13771
<i>Acronicta modica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta morula</i>	7	4	7	4	3	219.98624	7	4	3	219.98624	0.01919	0.03168
<i>Acronicta nervosa</i>	16	11	13	10	3	1052.00102	14	10	3	1095.87808	0.04697	0.11566
<i>Acronicta noctivaga</i>	8	5	8	5	3	543.57583	8	5	3	543.57583	0.02676	0.04692
<i>Acronicta obliqua</i>	49	31	48	31	3	2827.93502	49	31	3	2849.92602	0.18301	0.3547
<i>Acronicta orientalis</i>	3	2	2	1	1	17.98906	3	2	2	84.07554	0.01008	0.01818
<i>Acronicta ovata</i>	4	2	4	2	2	99.55066	4	2	2	99.55066	0.01139	0.01186

Table S3b. (continued)

Taxa	1 total genera	1 total families	1a genera	1a families	1a fam. cat.	1a pd	1b genera	1b families	1b fam. cat.	1b pd	1 ordi. genera scaled	1 ordi. families scaled
<i>Acronicta perblanda</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta perdita</i>	7	4	5	4	3	408.14281	7	4	3	436.18653	0.02576	0.0362
<i>Acronicta psi</i>	30	12	29	12	3	1153.62355	29	12	3	1153.62355	0.10902	0.12559
<i>Acronicta radcliffei</i>	13	6	11	6	3	491.29521	12	6	3	494.38826	0.04402	0.05576
<i>Acronicta retardata</i>	2	1	2	1	1	155.33342	2	1	1	155.33342	0.00508	0
<i>Acronicta rubricoma</i>	4	3	4	3	2	326.4973	4	3	2	326.4973	0.01417	0.02685
<i>Acronicta rumicis</i>	119	49	103	39	3	3505.73289	109	41	3	3592.47847	0.40566	0.5503
<i>Acronicta serratae</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta sperata</i>	9	6	8	5	3	662.40132	9	6	3	1110.49873	0.02885	0.05963
<i>Acronicta strigosa</i>	10	4	10	4	3	377.73974	10	4	3	377.73974	0.0306	0.03796
<i>Acronicta strigulata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta superans</i>	9	3	8	3	2	113.77563	8	3	2	113.77563	0.02422	0.0204
<i>Acronicta theodora</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta thoracica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta tridens</i>	19	9	17	9	3	717.01676	17	9	3	717.01676	0.06542	0.08791
<i>Acronicta tritona</i>	2	1	2	1	1	13.69523	2	1	1	13.69523	0.00568	0
<i>Acronicta valliscola</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta vinnula</i>	2	2	2	2	2	75.80219	2	2	2	75.80219	0.00445	0.01334
<i>Belciades niveola</i>	2	2	1	1	1	1	2	2	2	260.6473	0.00641	0.01849
<i>Cerna cerintha</i>	6	2	6	2	2	285.26994	6	2	2	285.26994	0.01828	0.0152
<i>Chloronycta tybo</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Comachara cadburyi</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Cranionycta jankowskii</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Craniophora ligustri</i>	10	5	9	5	3	519.8067	10	5	3	546.0381	0.03623	0.05191
<i>Craniophora pontica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Craniophora praeclara</i>	2	1	2	1	1	40.87094	2	1	1	40.87094	0.00536	0
<i>Gerbathodes paupera</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Harrisimemna marmorata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Harrisimemna trisignata</i>	22	14	21	14	3	1098.75729	21	14	3	1098.75729	0.08321	0.16172
<i>Lophonycta confusa</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Moma alpium</i>	15	6	15	6	3	630.18639	15	6	3	630.18639	0.04676	0.04952
<i>Moma kolthoffi</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Nacna malachitis</i>	3	2	2	2	2	260.6473	2	2	2	260.6473	0.00854	0.0174
<i>Nacna sugitanii</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Narcotica niveosparsa</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Polygrammate hebraicum</i>	2	2	2	2	2	163.87143	2	2	2	163.87143	0.00517	0.01907
<i>Sinocharis korbae</i>	?	?	?	?	?	?	?	?	?	?	?	?



**Table S4a.** Diet breadth measures for all taxa using the *Authority-Driven* dataset of diet breadth (prefix: 2). Taxa were tested using both the *Strict* (a) and *Replacement* (b) Angiosperm datasets. Ordinations were tested using all data regardless of inclusion in the Angiosperm tree.

Taxa	2 total genera	2 total families	2a genera	2a families	2a fam. cat.	2a pd	2b genera	2b families	2b fam. cat.	2b pd	2 ordi. genera scaled	2 ordi. families scaled
<i>Acronicta aceris</i>	4	3	4	3	2	338.97138	4	3	2	338.97138	0.01462	0.02655
<i>Acronicta afflicta</i>	2	2	2	2	2	62.45518	2	2	2	62.45518	0.00665	0.0192
<i>Acronicta alni</i>	25	12	25	11	3	1074.27235	25	11	3	1074.27235	0.09647	0.13735
<i>Acronicta americana</i>	29	14	29	14	3	1386.66499	29	14	3	1386.66499	0.12201	0.17253
<i>Acronicta atristrigata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta auricoma</i>	46	20	46	20	3	1492.78126	46	20	3	1492.78126	0.19694	0.24287
<i>Acronicta barnesi</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta beameri</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta betulae</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta browni</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta brumosa</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta catocaloida</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta chamoenices</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta clarescens</i>	9	1	7	1	1	40.19873	8	1	1	43.24474	0.03341	0
<i>Acronicta connecta</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta contaminiei</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta cuspis</i>	4	2	4	2	2	101.70225	4	2	2	101.70225	0.00885	0.0096
<i>Acronicta cyanescens</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta dactylina</i>	8	4	8	4	3	473.98117	8	4	3	473.98117	0.02282	0.03357
<i>Acronicta dentinosa</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta dolli</i>	3	3	3	3	2	342.58305	3	3	2	342.58305	0.01001	0.03022
<i>Acronicta edolata</i>	3	3	3	3	2	311.35404	3	3	2	311.35404	0.01192	0.03627
<i>Acronicta euphorbiae</i>	53	28	47	24	3	1722.67041	52	27	3	1980.47219	0.19155	0.34675
<i>Acronicta exempta</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta exilis</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta falcula</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta fallax</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta fragilis</i>	9	3	9	3	3	318.71664	9	3	2	318.71664	0.02626	0.01609
<i>Acronicta funeralis</i>	19	10	19	10	3	895.99408	19	10	3	895.99408	0.07036	0.11376
<i>Acronicta geographica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta grisea</i>	15	7	15	7	3	624.85605	15	7	3	624.85605	0.05236	0.07705
<i>Acronicta haesitata</i>	2	1	2	2	2	23.88938	2	2	2	23.88938	0.00665	0
<i>Acronicta hamamelis</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta hasta</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta hastulifera</i>	3	1	3	1	1	41.93783	3	1	1	41.93783	0.00561	0
<i>Acronicta heitzmani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta impleta</i>	26	15	25	14	3	1298.77242	26	15	3	1388.55841	0.10967	0.19079
<i>Acronicta impressa</i>	24	14	23	14	3	1492.12874	24	14	3	1512.40422	0.09864	0.17458
<i>Acronicta increta</i>	6	2	6	2	2	117.31756	6	2	2	117.31756	0.02269	0.016
<i>Acronicta innotata</i>	7	3	7	3	2	293.3109	7	3	2	293.3109	0.01934	0.01609
<i>Acronicta insularis</i>	12	8	1	8	3	731.82285	2	8	3	734.98085	0.04112	0.08064
<i>Acronicta interrupta</i>	15	6	14	6	3	506.56944	14	6	3	506.56944	0.05474	0.05782
<i>Acronicta isocuspis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta lanceolaria</i>	19	10	18	10	3	1403.26564	19	10	3	1407.85189	0.08048	0.11569
<i>Acronicta lepetita</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta leporina</i>	12	8	12	8	3	704.86066	12	8	3	704.86066	0.04301	0.08846
<i>Acronicta lepusculina</i>	6	4	6	4	3	483.81369	6	4	3	483.81369	0.02187	0.04869
<i>Acronicta lithospila</i>	2	1	2	1	1	23.88938	2	1	1	23.88938	0.00665	0
<i>Acronicta liturata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta lobeliae</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta longa</i>	15	10	15	10	3	895.17238	15	10	3	895.17238	0.06267	0.12419
<i>Acronicta lupini</i>	5	3	5	3	2	273.16586	5	3	2	273.16586	0.02035	0.02625
<i>Acronicta major</i>	8	7	8	7	3	471.03054	8	7	3	471.03054	0.03395	0.08371
<i>Acronicta mansueta</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta marmorata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta megacephala</i>	2	1	2	1	1	29.38955	2	1	1	29.38955	0.00273	0
<i>Acronicta menyanthidis</i>	18	13	18	13	3	1253.331	18	13	3	1253.331	0.07084	0.15721
<i>Acronicta modica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta morula</i>	3	3	3	3	2	160.91618	3	3	2	160.91618	0.00928	0.02695
<i>Acronicta nervosa</i>	5	5	5	5	3	550.6788	5	5	3	550.6788	0.01369	0.05926
<i>Acronicta noctivaga</i>	6	3	6	3	2	306.72052	6	3	2	306.72052	0.02179	0.0244
<i>Acronicta obliqua</i>	39	27	38	25	3	2430.49826	39	26	3	2479.76034	0.16735	0.35084
<i>Acronicta orientalis</i>	3	2	2	1	1	17.98906	3	2	2	84.07554	0.01145	0.02115
<i>Acronicta ovata</i>	1	1	1	1	1	1	1	1	1	1	0	0

Table S4b. (continued)

Taxa	2 total genera	2 total families	2a genera	2a families	2a fam. cat.	2a pd	2b genera	2b families	2b fam. cat.	2b pd	2 ordi. genera scaled	2 ordi. families scaled
<i>Acronicta perblanda</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta perdita</i>	7	4	5	4	3	408.14281	7	4	3	436.18653	0.02934	0.0416
<i>Acronicta psi</i>	30	12	29	12	3	1153.62355	29	12	3	1153.62355	0.12557	0.14616
<i>Acronicta radcliffei</i>	10	3	8	3	2	277.46773	9	3	2	280.56077	0.0355	0.01609
<i>Acronicta retardata</i>	2	1	2	1	1	155.33342	2	1	1	155.33342	0.0061	0
<i>Acronicta rubricoma</i>	2	1	2	1	1	30.28652	2	1	1	30.28652	0.0074	0
<i>Acronicta rumicis</i>	98	42	89	36	3	3177.47127	94	39	3	3261.17085	0.38778	0.54301
<i>Acronicta serratae</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta sperata</i>	8	5	8	5	3	662.40132	8	5	3	662.40132	0.02678	0.05298
<i>Acronicta strigosa</i>	9	4	9	4	3	367.87747	9	4	3	367.87747	0.03175	0.04482
<i>Acronicta strigulata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta superans</i>	8	2	8	2	2	113.77563	8	2	2	113.77563	0.02287	0.0096
<i>Acronicta theodora</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Acronicta thoracica</i>	1	?	1	1	1	1	1	1	1	1	0	?
<i>Acronicta tridens</i>	14	7	12	7	3	618.49732	12	7	3	618.49732	0.05415	0.0752
<i>Acronicta tritona</i>	2	1	2	1	1	13.69523	2	1	1	13.69523	0.0068	0
<i>Acronicta valliscola</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Acronicta vinnula</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Belciades niveola</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cerna cerintha</i>	5	1	5	1	1	33.61713	5	1	1	33.61713	0.01503	0
<i>Chloronycta tybo</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Comachara cadburyi</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Cranionicta jankowskii</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Craniophora ligustri</i>	5	2	4	2	2	296.65566	5	2	2	322.88704	0.01657	0.0208
<i>Craniophora pontica</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Craniophora praeclara</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gerbathodes paupera</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Harrisimemna marmorata</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Harrisimemna trisignata</i>	22	14	21	14	3	1098.75729	21	14	3	1098.75729	0.09344	0.1839
<i>Lophonycta confusa</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Moma alpium</i>	14	6	14	6	3	622.28178	14	6	3	622.28178	0.05202	0.06089
<i>Moma kolthoffi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Nacna malachitis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Nacna sugitanii</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Narcotica niveosparsa</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Polygrammate hebraeicum</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Sinocharis korbae</i>	?	?	?	?	?	?	?	?	?	?	?	?

**Table S5a.** PGLS results with P-value, lambda, coefficient, and adjusted R-squared for each analysis.

Character	predict genera	genera lambda	genera coeff.	genera adj. R2	predict family	family lambda	family coeff.	family adj. R2
Hairy	0.0044	0	5.1067	8.59%	0.0007	0	2.8567	12.48%
Mimicry	0.7739	0	1.3872	-1.16%	0.7741	0	0.6561	-1.16%
Ultimate instar change	0.1835	0	4.3931	1.00%	0.3449	0	1.4804	-0.12%
Smooth setae	0.0085	0.689	-7.5719	9.51%	0.0497	0	-3.0482	4.70%
Barbed setae	0.1910	0	5.5486	1.07%	0.1420	0	2.9372	1.72%
Paddles	0.7306	0	-1.7779	-1.10%	0.6680	0	-1.0483	-1.02%
Undercoat	0.0000	0	17.2746	20.88%	0.0000	0	8.8824	25.27%
Bristles	0.0005	0	9.5905	13.05%	0.0001	0	5.1716	17.30%
Lateral setae abundant	0.1093	0	-5.1812	1.99%	0.0275	0	-3.3525	4.82%
Secondary setae on integument	0.6170	0	1.5816	-0.92%	0.6387	0	0.7031	-0.96%
Tufts	0.5958	0	2.1251	-0.89%	0.5007	0	1.2766	-0.67%
A1 horn	0.3899	0	7.1112	-0.31%	0.5107	0	2.5782	-0.70%
Head color	0.1324	0	-1.0115	1.77%	0.1182	0	-0.4936	2.02%
A8 shape	0.0241	0	7.8737	6.08%	0.0489	0	3.0789	4.32%
A1 wart enlarged	0.2203	0	-6.0477	0.76%	0.1856	0	-3.0645	1.13%
A5 wart enlarged	0.5927	0	-8.0513	-1.00%	0.5915	0	-3.7977	-1.00%
A4 wart enlarged	0.3862	0	-7.5745	-0.33%	0.4359	0	-3.2036	-0.54%
Paddle location	0.7804	0	0.4217	-1.28%	0.8130	0	0.1682	-1.31%
Lose secondary setae	0.3474	0	-8.0020	-0.15%	0.3739	0	-3.5610	-0.28%
Color variation	0.0146	0	8.8132	7.00%	0.0049	0	4.7382	9.60%
Secondary setae on head	0.7000	0	2.4229	-1.20%	0.9019	0	0.3647	-1.39%
Resting position	0.5987	0	-0.5284	-0.96%	0.4510	0	-0.3578	-0.56%
Location - early	0.4479	0	-1.0519	-1.04%	0.7364	0	-0.2310	-2.26%
Location - ultimate	0.1181	0	-1.4347	3.47%	0.0917	0	-0.7578	4.40%
Pupation	0.0332	0	1.4430	6.67%	0.0078	0	0.8402	11.15%
Erucism	0.0420	0	18.1677	14.36%	0.0089	0	9.7777	24.97%
Ant defense - incidental	0.7210	0	0.9257	-8.54%	0.7613	0	0.4258	-8.94%
Ant defense - directed	0.0147	0	-4.4883	41.09%	0.0232	0	-2.2993	35.92%
Pinch defense - early instar	0.2921	0	-10.4158	13.53%	0.2457	0	-7.3451	21.13%
Pinch defense - late instar	0.5115	0	-1.2492	-6.98%	0.4130	0	-0.9453	-3.13%

**Table S5b.** PGLS results with P-value, lambda, coefficient, and adjusted R-squared for each analysis.

Character	predict famcat	famcat lambda	famcat coeff.	famcat adj. R2	predict PD	PD lambda	PD coeff.	PD adj. R2
Hairy	0.0000	0	0.4933	20.97%	0.0001	0	304.1710	17.15%
Mimicry	0.3565	0	0.2845	-0.18%	0.6251	0	102.6550	-0.96%
Ultimate instar change	0.1776	0	0.2852	1.07%	0.4046	0	120.1320	-0.38%
Smooth setae	0.0190	0	-0.5515	7.31%	0.0252	0	-321.9530	6.54%
Barbed setae	0.0883	0	0.4376	2.80%	0.0826	0	313.2900	2.96%
Paddles	0.5712	0	-0.1878	-0.84%	0.5791	0	-124.6680	-0.86%
Undercoat	0.0041	0	0.7416	9.17%	0.0000	0	813.6200	26.03%
Bristles	0.0001	0	0.7053	17.46%	0.0000	0	510.9650	20.14%
Lateral setae abundant	0.0355	0	-0.4330	4.28%	0.0147	0	-340.0310	6.14%
Secondary setae on integument	0.0244	0	0.4523	4.94%	0.4705	0	99.3960	-0.58%
Tufts	0.0058	0.534	0.7106	8.00%	0.3277	0	170.4140	-0.04%
A1 horn	0.1007	0	0.8674	2.12%	0.4714	0	259.5990	-0.59%
Head color	0.0358	0	-0.0848	4.67%	0.1081	0	-46.6340	2.21%
A8 shape	0.0196	0	0.4857	6.59%	0.0507	0	276.4110	4.24%
A1 wart enlarged	0.3657	0	-0.2671	-0.25%	0.1328	0	-318.4420	1.87%
A5 wart enlarged	0.3404	0	-0.8630	-0.11%	0.5353	0	-402.7890	-0.86%
A4 wart enlarged	0.3072	0	-0.5374	0.08%	0.3426	0	-358.0210	-0.12%
Paddle location	0.5232	0	0.0584	-0.81%	0.8395	0	13.2380	-1.33%
Lose secondary setae	0.3309	0	-0.4969	-0.06%	0.2811	0	-395.7080	0.25%
Color variation	0.0948	0	0.3618	2.60%	0.0147	0	379.8950	7.00%
Secondary setae on head	0.0547	0	0.7193	3.77%	0.8403	0	54.7370	-1.35%
Resting position	0.5699	0	-0.0355	-0.90%	0.3423	0	-41.3440	-0.11%
Location - early	0.4519	0	-0.1016	-1.07%	0.7579	0	-22.0440	-2.31%
Location - ultimate	0.1423	0	-0.1362	2.79%	0.0639	0	-86.7850	5.75%
Pupation	0.1397	0	0.0575	2.30%	0.0065	0	77.0930	11.73%
Erucism	0.0011	0	1.2540	37.86%	0.0030	0	975.9100	31.85%
Ant defense - incidental	0.8312	0	-0.0459	-9.48%	0.6323	0	70.7920	-7.38%
Ant defense - directed	0.0115	0	-0.3811	43.69%	0.0078	0	-272.6900	47.58%
Pinch defense - early instar	0.3594	0	-0.2777	3.98%	0.2108	0	-761.0000	27.51%
Pinch defense - late instar	0.3279	0	-0.1122	1.31%	0.3888	0	-98.1500	-1.99%

**Table S5c.** PGLS results with P-value, lambda, coefficient, and adjusted R-squared for each analysis.

Character	predict ordigen	ordigen lambda	ordigen coeff.	ordigen adj. R2	predict ordifam	ordifam lambda	ordifam coeff.	ordifam adj. R2
Hairy	0.0029	0	0.0222	9.40%	0.0009	0	0.0386	11.95%
Mimicry	0.8054	0	0.0050	-1.19%	0.8134	0	0.0074	-1.19%
Ultimate instar change	0.2318	0	0.0165	0.57%	0.4087	0	0.0179	-0.39%
Smooth setae	0.0066	0.651	-0.0329	10.18%	0.0515	0	-0.0409	4.61%
Barbed setae	0.1643	0	0.0246	1.40%	0.1497	0	0.0398	1.60%
Paddles	0.6695	0	-0.0092	-1.02%	0.6908	0	-0.0134	-1.05%
Undercoat	0.0000	0	0.0725	21.05%	0.0000	0	0.1236	25.66%
Bristles	0.0002	0	0.0426	14.88%	0.0001	0	0.0701	16.70%
Lateral setae abundant	0.0971	0	-0.0225	2.22%	0.0257	0	-0.0467	4.96%
Secondary setae on integument	0.5612	0	0.0077	-0.81%	0.6864	0	0.0083	-1.03%
Tufts	0.5488	0	0.0101	-0.79%	0.5292	0	0.0164	-0.75%
A1 horn	0.3335	0	0.0335	-0.07%	0.5650	0	0.0311	-0.83%
Head color	0.1187	0	-0.0044	2.01%	0.1144	0	-0.0069	2.09%
A8 shape	0.0205	0	0.0336	6.48%	0.0561	0	0.0411	3.99%
A1 wart enlarged	0.1952	0	-0.0267	1.02%	0.1961	0	-0.0413	1.01%
A5 wart enlarged	0.5880	0	-0.0341	-0.99%	0.6024	0	-0.0508	-1.02%
A4 wart enlarged	0.3844	0	-0.0318	-0.33%	0.4502	0	-0.0428	-0.59%
Paddle location	0.8401	0	0.0013	-1.33%	0.8043	0	0.0024	-1.30%
Lose secondary setae	0.3554	0	-0.0329	-0.19%	0.4122	0	-0.0453	-0.45%
Color variation	0.0113	0	0.0382	7.61%	0.0043	0	0.0664	9.95%
Secondary setae on head	0.6723	0	0.0111	-1.15%	0.9326	0	0.0034	-1.40%
Resting position	0.5820	0	-0.0023	-0.92%	0.4552	0	-0.0049	-0.58%
Location - early	0.5589	0	-0.0035	-1.66%	0.8438	0	-0.0018	-2.46%
Location - ultimate	0.1642	0	-0.0055	2.28%	0.0808	0	-0.0105	4.87%
Pupation	0.0224	0	0.0064	7.90%	0.0082	0	0.0116	11.03%
Erucism	0.0233	0	0.0832	18.49%	0.0100	0	0.1362	24.20%
Ant defense - incidental	0.7568	0	0.0035	-8.90%	0.7656	0	0.0057	-8.98%
Ant defense - directed	0.0149	0	-0.0194	40.90%	0.0196	0	-0.0321	37.85%
Pinch defense - early instar	0.3116	0	-0.0449	10.59%	0.2379	0	-0.1079	22.50%
Pinch defense - late instar	0.4927	0	-0.0057	-6.33%	0.3911	0	-0.0139	-2.10%

## **Chapter 5: Tracking the Gain/Loss of Complex Courtship Structures in Noctuidae**

### **Introduction**

Most female moths use pheromones to attract a mate; males are thus outfitted with feathery, porous antennae to receive those long-distance chemical courtship signals. Less well appreciated are the short-range chemical cues used by males once they have approached a potential mate. Males of numerous moth species are adorned with courtship structures used to waft pheromones toward a female. These may be located on the wings, legs, abdomen, antennae, mouthparts, and other structures (Birch et al. 1990). Unlike primary sexual characters of the genitalia, these courtship structures are not necessarily essential for successful fertilization (Birch 1970a, 1972a), but are believed to be important in sexual selection. One particular set of secondary sexual structures, the triline brush organs (TBOs), are found throughout the largest family of moths: Noctuidae. With over 12,000 species worldwide, Noctuidae encompasses an enormous range of morphological diversity (van Nieukerken et al. 2011). However, the fundamental morphological aspects of TBO structures remain remarkably conserved where they appear (Poole 1995; Fibiger and Lafontaine 2005). On each side of the abdomen are a membranous pocket, a sclerotized lever, a long brush of specialized scales, and a glandular structure with associated scales (Figure 1), all of which are concealed when the moth is at rest. The gland releases its contents onto the brush while it sits within the pocket (evidently only once in the pharate adult); the androconial brush is then “charged” for a limited number of courtship attempts (Birch 1970b; Clearwater 1975a). During the final moments of courtship the lever activates, pulling the brush out of the pocket, dispersing the pheromones about the female (Birch 1970a).

While TBOs have not attracted the same attention and study as lepidopteran genitalia, many workers have been deeply captivated by the structure and function of these courtship characters. Some of the earliest mentions began as the mere description their presence in European noctuid taxa, typically as an addendum to describing features of the abdomen and genitalia (Petersen 1908; Swinton 1908; Pierce 1909) (Birch considered Pierce to be an unreliable source, and in many cases their findings conflicted [see caption for Table 1, Birch 1972b]). Stobbe worked extensively with the TBO gland, and eventually the gland was named for him. He provided detailed diagrams and descriptions, as well as a list of TBO presence in a list of trifine noctuid genera (Stobbe 1912).

In the 1960s, Varley published a description of TBOs and other courtship structures, accompanied by detailed illustrations. Within this paper was a plea to both professional entomologists and amateurs “to study the functions of the curious structures I have described.” He considered it a travesty that more was not yet known about the morphology and habits of moths due to a lack of experimentation and general curiosity. Luckily, one student took this plea to heart. In collaboration with Varley, Martin Birch set out to not only experiment with the use of TBOs in courtship, but to create a checklist of British moths with and without TBOs by personally dissecting them (Birch 1970a, 1970b, 1972a). He continued to work on TBOs throughout his career, gathering an incredible wealth of knowledge and setting the stage for further research (Alpin and Birch 1968; Birch et al. 1989, 1990; Poppy and Birch 1994). His list of British moths, with both presence and absence data for 131 species, is to date the most extensive TBO checklist. Meanwhile, more extensive morphological study was being done by

Clearwater, who focused on ultrastructure, pheromones, and development (Clearwater 1975a, 1975b).

The lepidopterist who eventually coined the acronym TBO was Alberto Zilli. His focus was turned toward aberrant structures found in the Leucaniini tribe, for which he coined several more terms for the genera *Leucania* Ochsenheimer 1816, *Hyphilare* Hübner 1821, and *Sablia* Sukhareva 1973 (LSO: *Leucania* brush organ, HBO: *Hyphilare* brush organ, SBO: *Sablia* brush organ). His own checklist focused on the species of Italy, and served to list those with known TBO or TBO-like structures (no absences were recorded) (Zilli 1996a). He has advocated a similar call to action as Varley, but this time to delve into more of the phylogenetics, ecology, and genetic underpinnings of the evolution of TBOs (Zilli 1992). While many noctuid workers are interested in TBOs (Fibiger, Goldstein, Lafontaine, McCabe, Wagner, Zilli, pers. comm.), these structures have not yet been addressed in a systematic or evolutionary framework.

TBO distribution through the phylogeny of Noctuidae is puzzling. TBOs appear in multiple subfamilies, and within those subfamilies are scattered among various tribes and genera (Scoble 1992; Zilli 1992; Poole 1995; Rota et al. 2016). Within genera they may show a mixture of presence and absence (McCabe 1980; Rota et al. 2016), and many species show reduced conditions (Birch 1972b; Birch et al. 1990). TBOs have been considered “an ancient device, but a very labile one” [within the Noctuidae] (McColl 1969). Despite these concerns, many taxonomic works of Lepidoptera use this character system to diagnose clades and assign species to higher level categories (Speidel et al. 1996; Fibiger and Lafontaine 2005), something which has been routinely advised against (Birch 1972b; Zilli 1992). This has led to several poorly

supported taxonomic decisions, which have been overturned by other morphological and/or genetic evidence (Rota et al. 2016).

It is unclear whether TBOs have multiple evolved origins, or represent an underlying pleisiomorphic condition that can be modified, lost, and regained (Zilli 1996a). The concept of an “underlying synapomorphy,” championed by Sæther, is defined as “parallelism as a result of common inherited genetic factors” (Tuomikoski 1967; Sæther 1977, 1979, 1988; Sluys 1989). This phenomenon, documented in groups ranging from plants (Funk 1982; Sanderson and Hufford 1996) to insects (Sæther 1977) to vertebrates (Bell et al. 1993; Sanderson and Hufford 1996), gives the appearance of repeated evolution of characters or character systems. I therefore hypothesize that the ability to express the set of TBO characters only evolved once in the Noctuidae. The lineage could then be said to inherit the capacity for expressing that character (Sanderson and Hufford 1996), though not all taxa do (Kitching 1998). Phrased another way, “the loss of a character commonly represents a loss of gene expression, not the loss of the genetic information necessary to produce the character” (Poole 1995). Figure 2 is a hypothetical cladogram illustrating the appearance of an underlying synapomorphy (adapted from Sanderson and Hufford, 1996). These parallelisms can be further classified as “inside” (restricted to the in-group) or “outside” (the character state is present in a distantly related group) (Sluys 1989). Whether the TBOs of noctuid moths could be considered inside or outside underlying synapomorphies is as yet untested; there are abdominal courtship brushes in other lepidopteran families, but their homologies are unknown.



One way to address the evolutionary puzzle of TBOs would be to determine their function. While they undoubtedly are involved in courtship, their necessity for successful mating varies between species (Birch 1970a; Birch et al. 1990; Poppy and Birch 1994). Only a few noctuid species have had their courtship behaviors monitored or experimentally altered. It has been hypothesized that courtship structures of moths are most common when the risk of mating mistakes are high (Phelan and Baker 1987). If closely related species have overlapping ranges and utilize the same host plants, rendezvous and/or oviposition sites, they may be more likely to make a mating mistake (especially as the courtships and mating behaviors of moths occur primarily at night), thus additional safeguards, such as TBOs and associated pheromones, would ensure pairing with the correct species. Likewise, the loss and reduction of these structures may be due to stabilizing selection and the lack of sympatric congeners, e.g., if resources would be better allocated to other functions. At a finer scale, even species with completely overlapping ranges may not encounter each other due to differences in host plant use, habitat preferences, timing of diel activity, etc. Early studies on these themes have suffered from lack of phylogenetic data, resulting in skepticism of Phelan and Baker's conclusions and calls for more evidence and experimentation (Zilli 1992). A few genera (*Apamea* Ochsenheimer 1816, *Sympistis* Hübner 1823, and others) show promise as future study subjects due to their well-known geographic ranges, host plant use, and variation in TBO presence and structures.

In order to address evolutionary questions about the significance of TBOs, there should be knowledge of their phylogenetic distribution. There has been great advancement in the systematics of Noctuidae in recent years (Zahiri et al. 2011, 2013; Mitter et al. 2016; Rota et al. 2016), with more expansive and robust trees on the horizon. A well-supported molecular

phylogeny of all noctuid subfamilies would be necessary in order to determine the evolutionary origination of TBOs. For evolutionary trends at a finer scale, species-level phylogenies of groups with dynamic expression of TBOs will be necessary. A comprehensive checklist of these structures, noted for their presence/absence and modifications, could then be mapped on the phylogenies. Currently, Birch's and Zilli's checklists are the only such compendia of organized and carefully evaluated TBO data. This study is the first initiative taken to work toward a worldwide checklist of TBOs across noctuid lineages. Over 1200 species were evaluated through examination of permanent slides and published literature. While this is approximately 1% of known noctuid species, the species examined represent 19 subfamilies and over 300 genera from most regions of the world. Additionally, all taxa were curated to the most recent lepidopteran classification schemes. With this database as a starting point, remaining taxa can be incorporated as data are collected. This effort also serves to illustrate the value of specimens held in biological collections; this research could not have been done without the efforts and deft hands of generations of entomologists preparing dissections and slides.

## **Methods**

### *Taxon Sampling*

This project focused primarily on moths in the family Noctuidae sensu stricto: 1234 species in 336 genera (Lafontaine and Schmidt 2010; Zahiri et al. 2013; Pohl et al. 2016). Some species formerly classified in Noctuidae, which are now members of Erebidae, were included: 40 species in 22 genera. It is recognized that some erebids have TBO-like structures, although it is unclear if these are homologous.

### *Data Collection: Literature*

Thirteen publications were used to glean TBO data: Petersen 1908; Swinton 1908; Pierce 1909; Stobbe 1912; Varley 1962; Birch 1972b; McCabe 1980; Zilli 1992, 1996b, 1997; Poole 1995; Lafontaine 2004; and Mikkola et al. 2009. Records from the earliest five sources were obtained via Birch's checklist. The majority of records were based upon the authors' own dissections. Both presence and absence data were collected, in addition to any notes concerning characteristics of the structures (size, position, abnormalities). In cases where Birch's checklist conflicted with earlier records, Birch's determination was considered authoritative. Some authors included data on the development of anterior apodemes on sternite 3, which are involved in TBO musculature (Birch 1970b). It was thought that the presence of the apodemes proved the "potential" for TBOs to occur in a taxon – it is unknown whether this means they are remnants, or a preliminary structure (Birch 1972b; Poole 1995; Poole pers. comm.). Since they were not specifically mentioned in all treatments, they were excluded from this checklist.

#### *Data Collection: Dissections*

Genitalic slide preparations for moths often (but not always) include the abdominal integument, or "pelt." The integument is cleared of setae and placed next to the dissected genitalic structures. This pelt is what houses the TBOs, which can be observed with the naked eye. Over 5000 slides were examined at the Canadian National Collection (CNC) and New York State Museum (NYSM). Slides were first examined for sex and presence/absence of TBOs. If TBOs were observed, the slide was examined under magnification to locate and scrutinize all structures. Dissections were also performed on select species, and the abdominal pelts stored in glycerin. In total, 1110 dissections were scored for the definitive presence or absence of TBOs. Slides were not included in scoring if they were female or lacked the abdominal pelt. Slides with an

incomplete pelt were included in the total count for species with TBOs, but could not be scored for each individual structure. In cases where published literature and slide data were found to conflict, direct examination of prepared slides were considered authoritative.

#### *Database Curation: TBO data*

A flat file was created to store TBO data. A scaffold taxonomy for Noctuidae was adapted from an electronic version of Poole's catalogue (Poole 1989). For each species for which data were collected, the source(s) of each data point were entered. [Literature sources were noted with a value from 1 to 13.] For dissection sources, the collection/preparator and slide number were entered. In cases where sources conflicted, the conflicting source was marked with an asterisk (\*). All TBO structures were described to indicate their completeness, size, and any abnormalities. These notes were transcribed to confer with Birch's (1972b) checklist method: each structure was denoted by a letter. Uppercase = full structure, lowercase = reduced structure, blank = absent, ? = unknown or undeterminable based on the material. Structures conforming to Zilli's categories for TBO modifications were noted in a column marked "other."

#### *Database Curation: Taxonomy*

Species were checked against several sources to determine accuracy, synonyms, and higher taxonomic reassignments. As most species were from North America, the latest Lepidopteran checklist served as the authority for the majority of taxonomic matters (Pohl et al. 2016).

European taxa were checked against volumes of Noctuidae Europaea, the Fauna Europaea website (<http://www.faunaeur.org/>), and the Barcode of Life Database BIN database ([http://www.boldsystems.org/index.php/Public\\_BINSearch](http://www.boldsystems.org/index.php/Public_BINSearch)). Taxa from other regions (Central

and South America, Asia, Australia) were searched on the BOLD BIN database, and the Natural History Museum's website for generic names of moths (<http://www.nhm.ac.uk/our-science/data/butmoth/search/>). The NHM website is considered less reliable than the other sources, as many of the input sources are outdated. It was used only when no other recent, authoritative sources for higher-level taxonomic placements could be found. In cases where the species could not be classified, it was left in the database with question marks for all checklist fields.

The subfamily and tribe were recorded for each species. Not all subfamilies are divided into tribes; in those cases, the tribe column was left blank. There were also cases where a genus had not yet been assigned to a tribe; for those the tribe column was left as a question mark.

Misidentification is always an issue in taxonomic matters especially when dealing with older determinations. For this study, species names on slide labels were accepted as accurate, and accordingly updated to new taxonomic standards. If species were not accurately identified on the slides, such mistakes could lead to errors in the TBO database. This may explain why there are some discrepancies between literature records and slides. In the cases observed here, more dissections of definitively identified individuals should be examined. This is an inherent problem in using specimens from biological collections for research – not all contributing scientists have had the same level of identification experience with noctuid moths, or agree on ever-changing species concepts.

## Results

### *The Numbers*

Of the 1274 species examined (including 1234 Noctuidae and 40 Erebidae), 473 (37%) were found to contain at least one element of the TBO structures. A similar proportion of noctuid genera (124/336, 37%) and species (472/1234, 38%) were found with TBOs. Within Noctuidae, TBOs were found in 8 out of 19 subfamilies (42%) and 13 out of 26 tribes (50%). These numbers comport with Birch's estimate of TBOs in British noctuids: 40% (Birch et al. 1990). Fewer erebids were examined, with only one genus (out of 7 subfamilies, 8 tribes, and 22 genera) found to have TBO-like structures. See Tables 1 and 2 for a list of all noctuid and erebid taxa examined, highlighting those for which TBOs were found.

### *The Table*

See Table 3 for a complete list of species examined and the scoring of their TBO characters.

### *Non-random Sampling*

While this study sought to generate a preliminary, comprehensive presence/absence database of TBO structures, the effort was decidedly non-random. A large portion of slides at the CNC with abdominal pelts were examined, but the collection has a strong focus on groups which happen to have TBOs (e.g. *Sympistis*). Not all of McCabe's slides at the NYSM were examined; priority was placed on subfamilies and lineages known to have TBOs. Published accounts of adult morphology typically do not denote the absence of a character unless it is noteworthy or distinctive compared to related taxa. Therefore, records pulled from the literature have a strong bias toward presence data. There is also a geographical bias. The CNC and NYSM hold

primarily North American specimens, and four of the published references were generated by North American taxonomists. The remaining published references were for European species. Of the species sampled, 888 (69.6%) were Nearctic taxa. The next largest group was Palaearctic species, with 306 (24%). A small number were marked as Holarctic (4), however it is likely that many in the Nearctic and Palaearctic groups actually have a Holarctic distribution. Other regions included Neotropical (4.4%), Australasian (1%), and Oriental (0.7%). Consequently, the proportion of species with TBOs reported here may be higher, or even lower, of the true proportion amongst noctuid moths – greater taxon sampling is required.

### *Morphology Summary*

*Stobbe's Gland:* The Stobbe's gland, a group of secretory cells, arises from an invagination of the cuticle adjacent to abdominal sternite 2. Each cell is associated with a hollow hair, through which the courtship pheromones are secreted. While they are small and may be difficult to detect in the adult, in the pharate adult the cells are swollen up to 30x their final size, filled with glycosides (Birch 1970b; Clearwater 1975a). Once the glycosides are dispersed to the brush upon eclosion, the gland collapses and remains dormant. The glycosides secreted by the Stobbe's gland are considered a stable "precursor" to the final pheromone scent. An enzyme is required to break down the glycosides into benzaldehyde, which has been identified in the TBOs of *Leucania*, *Mamestra* Ochsenheimer 1816, *Melanchra* Hübner 1820, *Persectania* Hampson 1905, *Phlogophora* Treitschke 1825, *Polia* Ochsenheimer 1816, and *Pseudaletia* Franclemont 1951 (Alpin and Birch 1968; Birch 1970b; Clearwater 1975b). Some species have also been found to have high amounts of phenyl ethanol, another downstream product of glycosides (Alpin and

Birch 1968). The production of the enzymes required to handle glycosides, and other chemicals present in the scent, may be occurring within the pocket. The intended purpose(s) of the scent are not known with certainty, and may differ among species. The male pheromones released from the TBO's have been postulated to serve as deterrents to other males, a confirmation of the correct species (to reduce mating mistakes), and as aphrodisiacs for the female (Alpin and Birch 1968).

*Lever:* The levers originate from the basal area of abdominal sternite 2. A weak point acts as a hinge at the base, while another area of weak sclerotization toward the middle of the lever allows it to bend (Birch 1970b). The brush is attached to an oblong sclerite at the end of the lever. The musculature involved in moving the lever, in order to revert and return the brush, has been described and illustrated in detail by Birch (1970b).

*Brush:* The brush scales are also known as androconia, hair-pencils, or scent-hairs (Birch 1970b). They do not themselves have any glandular or secretory cells, instead they are used to store and disperse courtship chemicals. The individual scales are elongated, with variations in diameter and ultrastructure along their length. Birch described three sections of a single androconial brush scale. The proximal-most (first) has longitudinal ridges and a pitted surface. The second has a reduced diameter, the ridges are reduced, and there are fewer pits. The third has the largest diameter, and the ridges form a zig-zag latticework – this increases the surface area for collecting scent and subsequently dispersing it (Birch 1970b). These sections may be more finely divided to include a transition zone between the second and third section, where the pores are significantly widened but the scale diameter is still narrow. The tip of each scale may also be considered a



separate section, as the diameter often abruptly tapers. Interspecific variation of scale morphology is thought to be minimal, with all studied species showing a similar progression of scale diameter changes and an increase in pore size. Differences are primarily noticed in the shape of the lattice-like ridges in the third section, and in the shape of the end of each scale (Birch 1970b; Rota et al. 2016). See Figure 3 for SEM images of brush scales for *Cerma cerintha* Treitschke 1826. It is likely there are many useful taxonomic characters here, if examined in detail across a wide range of taxa. The number of scales per brush varies widely, as well as their length in proportion to the pocket. In most cases the brush scales must be folded to fit into the pocket, but the degree of folding varies. These traits do not appear to be related to body size (Rota et al. 2016).

*Pocket:* The pockets are formed from cuticular invaginations of the pleural membrane of abdominal segments 3 and 4, sometimes extending internally into segment 5 (Birch 1970b; Rota et al. 2016). They are lined with inward-facing scales, which suggest a role in keeping brush scales inside the pocket. They may also serve to secrete chemicals to mix with those dispersed by the Stobbe's gland. In *Phlogophora meticulosa* Linnaeus 1758, the pocket scales contain glandular epidermal cells at their base, which are enlarged in the pharate adult. It has also been observed that males of this species will only emit a detectable scent (to humans) if both the Stobbe's gland and pocket scales are intact (Birch 1970a, 1970b). Since the Stobbe's gland emits only the precursor of the pheromone in the form of glycosides, it is likely that secretory cells in the pocket produce the necessary enzyme(s) to break the glycosides down into benzaldehyde or phenyl ethanol. They may also provide other scent components, accounting for the multiple peaks found in the mass spectra of some species (Alpin and Birch 1968; Clearwater 1975b).

### *Losses and Reductions*

TBOs typically come as a complete set: pocket, lever, brush, and Stobbe's gland. However, some species have missing or reduced structures. These reductions are not known to be variable within a species. It is currently unknown whether TBOs serve any function when parts of the suite of features are missing, or if a reduction in size is indicative of reduced importance in mating decisions. Results of experimental removal of TBO structures have been mixed; in some species TBOs appear required for mating, while other species achieve mating success with or without them (Birch et al. 1990). It has been documented that when TBO structures are lost evolutionarily, they are typically lost in the order of Stobbe's gland, brush, pocket, and lever (Birch 1972b). This was partially supported by the data collected for this study. Certain combinations of these four elements of the TBO were found to be more common than others.

Of the 473 species with TBO structures, 344 (73%) had the full complement. While only 5 species were listed as having the pocket, brush, and lever but no Stobbe's gland, 24 had a "?" for the gland. While it is possible those records were associated with a true loss of the gland, they may have been highly reduced or hidden. The next largest groups had the pocket and lever (28), lever only (19), and pocket only (12). There were also 21 species for which one or more structures were listed with a "?". Of all the other possible combinations, only two others were observed: one species with the lever and gland (*Archanara dissoluta* Treitschke 1825, as recorded by Birch), and one species with only the gland (*Harrisimemna trisignata* Walker 1856, personal observation). These data do suggest that when a structure is missing, it is more likely to be the Stobbe's gland and/or brush; depending on the phylogenetic relatedness of the taxa

studied, these may represent separate events or shared traits due to shared ancestry. There were also 20 LSO, 4 HBO, and 4 SBO records, representing a small group of alternative brush structures.

For species with all four structures, reductions either occurred in all structures (rendering them small or perhaps vestigial), or in one or two of the structures. For the 344 species examined with complete TBOs, 32 were found to have one or more structures highly reduced in size.

Reductions were most common in species with missing structures. Out of 363 species with a pocket, 16% had reduced pockets. Brushes were reduced in 8% of instances (of 347), levers 14% (of 372), and the gland 7% (of 332). The limitation of these data rests within the definition of a “reduction.” Different workers may use a different standard by which to determine whether a structure is within a normal size range or is reduced or even vestigial, and these standards may differ between taxa. Likewise as both small (yet functional) and vestigial structures are categorized in the same way, information is being lost. Birch claimed that the presence of any TBO structures without the Stobbe’s gland should be considered useless, as the brushes would have no pheromone to waft toward the female (Birch 1972b). It is unknown whether secretions from pocket gland cells would provide useful pheromones on their own, or if the Stobbe’s gland secretions are indeed required. Experimentation on the mating success of species with reduced or naturally missing structures have not yet been done – harkening back to the plea by Varley, and reiterated by Birch (Varley 1962; Birch 1972b). Whether every reduction in a species is considered a separate event, or can be traced back to a common ancestor of a genus or tribe, remains to be determined with phylogenetic study.

### *Minor Variations*

While TBOs are typically conservative in placement and orientation, there can be variations in size and shape. Figure 4 illustrates several examples of these differences. The Stobbe's gland (abdominal invagination with glands and associated long setae) may be a large and obvious structure, or barely detectable. The gland is typically round or oblong, with individual glandular cells visible. Species of several genera have elongated Stobbe's glands. Brush setal numbers range from under 10, to several dozen. The base of the brush, where it attaches to the lever, can range from small and round to a wide flat base. Brushes range from short and sparse to long and abundant. Some brush scales need to be folded in order to fit into the pockets. The levers typically have a single bend, but sometimes twist around entirely to hold the brush base closer to the body (Figure 4B). With the slide numbers recorded in this TBO database, a targeted approach could be made in the future to examine slide material in more detail.

### *Modifications*

A number of noctuid species were found to have strikingly divergent brush structures, which are likely to be modifications of TBOs. They still possess sclerotized levers and brushes in the anterior abdominal segments, but the brushes are anchored in an area forming an eversible coremata. They do not possess Stobbe's glands. They either do not have pockets, or utilize different abdominal folds than typical TBOs. This arrangement is known as the *Leucania* scent-organ (LSO), for the genus it is found in (extensively described and illustrated by Zilli 1996). These LSOs were found in 20 *Leucania* species (out of 26). Slightly divergent characters were found in the related noctuid genus *Mythimna* Ochsenheimer 1816, which Zilli had also designated with acronyms. The structures of former genus *Sablia* (now synonymized with

*Mythimna*) were named the *Sablia*-brush-organ (SBO). Similarly was the *Hyphilare*-brush-organ named (HBO), for another genus now synonymized with *Mythimna*. Thus all of the above, studied in detail by Zilli, derive from a single clade of noctuines. Structures similar to LSOs were found in several other related and unrelated genera: *Callopietria* (Eriopinae), *Haliophyle* (Noctuinae), *Hypopteridia* (Noctuinae, Leucaniini), and *Hypotrix* (Noctuinae, Eriopygini).

One species in the family Erebidae (*Hemeroplanis scopulepes* Haworth 1809) was found to have a set of structures similar to TBOs (Figure 5). These include a pocket, lever, and brush. A small nub-like structure is reminiscent of the Stobbe's gland, but its homology and function is unknown. There are additional sclerotized structures in the basal abdominal area which appear to be connected to or otherwise associated with the lever and brush. It is unknown if these are modified TBOs, or represent an independent evolution of courtship brushes. Should the condition in *H. scopulepes* prove to be homologous, the putative common origin of TBOs would be pushed back to a common ancestor.

### *Other Findings*

When a genus contains species with TBOs or TBO-like structures, they are typically common and widespread. For 12 genera with 10 or more species sampled in this study, where at least one member had TBOs, the percentage of species with TBOs ranged from 36 to 93% (avg. 68%). Stated differently, in no case were the structures present in all members of a given genus with ten or more species—a rather startling finding given the structural complexity and neural integration required to build a functional TBO system. Many genera with only one, two, or three species sampled had 100% TBO presence; however, in most cases these genera are undersampled.

### *Errors in Preparation and Scoring*

Abdominal pelts, while holding a wealth of morphological information, are not always kept or fully prepared. Due to the nature of abdominal removal for dissection, the anterior area may be torn or cut. Abdomens are usually cleared of all setae for slide mounting and study, which may result in the loss of brush and Stobbe's gland scales. This can be avoided if the preparator is concerned with the preservation of TBOs, but even careful cleaning can disrupt the delicate Stobbe's gland (personal observation).

Character scoring for TBOs was challenging due to the variation in slide preparation techniques and quality of the abdominal pelts. The most difficult structure to find was the Stobbe's gland. The positioning of the pelt may result in the glands becoming hidden amongst other structures, setae, or integument. For slides in the NYSM, eight were initially scored as missing the Stobbe's gland. Upon a second inspection, the gland was found in four of those slides. The slides had to be flipped upside down and observed under higher magnification.

In the literature, there is a possibility of "failure to mention." Within a treatment, it may not always be clear if the omission of a TBO description means the species lacks the structures. It is possible they were not noticed, ignored, or otherwise not pertinent to the work. This made scoring for absence of characters difficult. It was most helpful when authors specified the presence and absence of TBO characters for each species, which was most often done when TBOs appear sporadically throughout a genus. However for genera within which there are no

TBO structures, and no specific mention of their absence in the literature, dissections were required to demonstrate their definitive absence.

## Discussion

Evaluating the evolution of courtship structures in Lepidoptera requires two main pieces of evidence: a record of the presence/absence of the structures, and a molecular phylogeny.

Working toward the first piece, this preliminary study has produced a framework for the addition of further TBO data. For the first time, data from multiple collections and countries have been assembled – 1274 species were recorded via 1110 slides and 13 literature sources. While this dataset has a strong North American and European bias, specimens from Central and South America, Asia, Australia, the Middle East, the Caribbean, and islands of Southeast Asia were included. The focus was primarily placed on the family Noctuidae, with some representation from Erebidæ.

While the presence/absence of TBOs is problematic when accorded great weight in making higher-level taxonomic decisions, TBO structures are often helpful at the genus and species level (Birch 1972b; Zilli 1992). If a genus has species with and without TBOs, their presence can be a way to support species-level identifications – such as in the genus *Apamea*, where closely related species may have TBOs entirely present or absent (Birch 1972b). Within the large genus *Sympistis* there is a wide array of TBO variations and losses. This newly redefined supergenus is the result of synonymizing multiple genera, with the goal of creating a monophyletic grouping (Troubridge 2008). In the future, a molecular phylogeny of *Sympistis* and subsequent

reassignment to new/former genera may reveal clades with different patterns of TBO variation and absence.

Though TBOs are generally conserved in their basic morphology and arrangement, there can be considerable variation in the size and shape of each structure. For example, the Stobbe's gland may be spherical or elongated; the twists and bends in the levers may be more or less exaggerated; the brushes may have a wide or narrow base; the brush scales may be dense or sparse; the scales may be folded or not; the pockets may be short of or reach beyond the end of abdominal segment 4. These TBO deviations may provide genus-specific or species-level characters. Within a genus these traits can be generally conserved, e.g. in *Schinia* Hübner 1823, all species with full TBOs have an elongated or otherwise enlarged Stobbe's gland.

More extreme modifications, such as those present in *Leucania* (and related noctuid genera) and *Hemeroplanis* (Erebidae) (Figure 5), present puzzling scenarios. If the LSOs and TBO-like structures evolved independently, their present similarities to TBOs would be an example of convergent evolution. The likelihood of this scenario is dubious due to the complexity of the structures. The structures in *Hemeroplanis* suggest the underlying synapomorphy for TBOs has its origin deeper in the superfamily Noctuoidea. Due to their placement within the family Noctuidae, it is likely that LSOs represent highly modified TBO conditions. All *Leucania* are grass feeders with a high degree of sympatry and the potential for mating mistakes (Alpin and Birch 1968, Wagner, pers. comm.).



The progressive loss of structures commonly cited in the literature may be a reflection of preparation and/or examination, and not true loss of characters. The Stobbe's gland is said to be lost first, as evidenced by it being the character most often missing. Of most species for which the Stobbe's gland was reported missing for this study, it could not be said for certain if the gland was truly lost. Since the gland is only used once, it could potentially be reduced or even reabsorbed by the moth. The gland might also have been hidden or accidentally removed during the abdominal pelt preparation. The same could be said for the species for which both the gland and brush were reported lost. Brush scales may be wholly removed during abdominal slide preparations. The lever and pocket are more conspicuous structures; while the lever may be cut off, cut marks are typically distinguishable from the natural ends of the sclerotized structure. Pockets, even when small, are discerned by the presence of folds and the arrangement of inward-facing scales. Ultimately, if these absences (attributed to a given taxon) are to be trusted as true absences, more individuals should be dissected and examined. When conducting dissections to look for TBOs, care should be taken in the preparation of the abdomen to look for the Stobbe's gland and brush before the abdomen is cleared of setae. Whether the sequence of character loss can be demonstrated by the proportions of current TBO arrangements is questionable. Additionally, it is unknown whether common sequences of the structural losses noted above are meaningful in genetic or ecological terms.

### *Moving forward*

The circumscription of subfamilies within Noctuidae is an ongoing and highly dynamic area of study, with different outcomes resulting from the inclusion of different character data and different taxon sampling. There is also a bias towards European and North American taxa, a

problem being slowly rectified. A recent molecular phylogeny with worldwide sampling resulted in 19 subfamilies (Zahiri et al. 2013), however some taxa were missing (Eriopina and Oncocnemidinae) and some clades were too poorly represented to give a conclusive position. A more recent molecular phylogeny sampled 13 of “~20” subfamilies (Mitter et al. 2016), with some differences in subfamilial relationships (rendering Amphipyrinae and Noctuinae polyphyletic). These numbers are similar to surveys of noctuids in Thailand (17 subfamilies) (Kononenko and Pinratana 2013) and Europe (16 subfamilies) (<http://www.faunaeur.org>) – however it is likely some of these taxa are non-overlapping. Some works offer nearly twice these numbers; typically, this is due to including erebids (JPMoth 2015) or elevating tribes to the family level (Fibiger and Lafontaine 2005). The most recent North American lepidopteran checklist lists 20 subfamilies (Pohl et al. 2016). This TBO study primarily focused on North American taxa; 19 of the 20 noctuid subfamilies in Pohl’s list were examined. Eight of these subfamilies were found to have TBOs, or TBO-like structures. While these can be mapped onto the two most recent molecular phylogenies (Figures 6 and 7), trees with much greater taxon sampling are needed in order to address the evolutionary history of TBOs. Both treatments are missing subfamilies known to have TBOs. Based on the subfamilial relationships, the origin of TBOs on the Zahiri et al. tree is pushed back deeper compared to the Mitter et al. tree (Figures 6 and 7).

Based on the results of this study, several taxa emerge as especially promising for future research on the evolutionary significance of TBOs for courtship. Such complicated structures likely play an important role in mating success, but their distributions across subfamilies and genera are puzzling. Modifications and reductions also lack an explanation as to their utility for courtship

and mating. Birch's experiments have shown that the utility and requirement for TBOs can differ between species (Birch 1970a; Birch et al. 1990; Poppy and Birch 1994). Questions of the importance of ecology and geography also arise (Phelan and Baker 1987). If TBOs are used by females to recognize the correct mate, are TBOs more common in areas where related species overlap? According to Zilli (1992), the best group for such analyses requires all species be unambiguously related. One must know their geographic ranges, any geographic overlap between species, and presence/absence of TBOs. Three genera may fit these criteria: *Apamea* (Noctuinae), *Cucullia* Schrank 1802 (Cuculliinae), and *Sympistis* (Oncocnemidinae). They are large genera, with a high proportion of species bearing TBOs. *Apamea* has undergone thorough study of both morphology and species ranges (Mikkola et al. 2009). Tantalizingly, it so far appears that areas with the most *Apamea* species have the highest prevalence of TBO structures (Goldstein pers. comm., Zilli pers. comm.). Species-level molecular phylogenies for these genera have not yet been undertaken, but would provide a major piece required to map out the evolutionary history of TBOs in these taxa. By gathering more complete TBO data, geographical data, experimental mating results, and a molecular phylogeny, any (or all) of these could be viable candidates for studying the conditions under which TBOs are used.

As molecular techniques advance, so will the available data for constructing a broader phylogeny for noctuid subfamilies, tribes, and genera. Finer detail at the tribal and generic levels will be required in order to track the placement of TBOs and other courtship structures. Further work is also required to collect TBO data. Thousands of genitalic slide preparations reside in entomological collections, waiting to be analyzed. Millions of dried moths reside in pinned collections, available for dissection. While documenting the TBO and TBO-like structures of

every noctuid species is a daunting (and perhaps impossible) task, with concerted effort a sizable proportion can be examined and recorded. Within this framework other abdominal brushes and coremata can likewise be discovered and recorded, offering a more complete view of noctuid courtship. Ultimately these data will serve to not only tell us about insect mating systems, but lead to hypotheses about the evolutionary history of complex morphological characters. They also serve to remind us of the vast knowledge and potential held in the specimens of biological collections. Varley's plea bears repeating: we should fuel our curiosity and continue to delve deeper into the morphology and meaning within these structures.

### **Acknowledgements**

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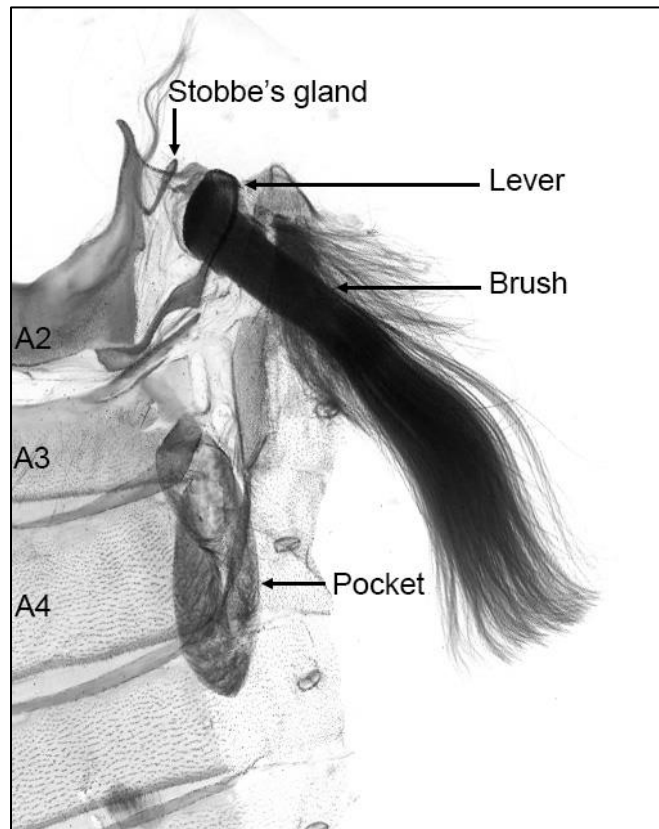
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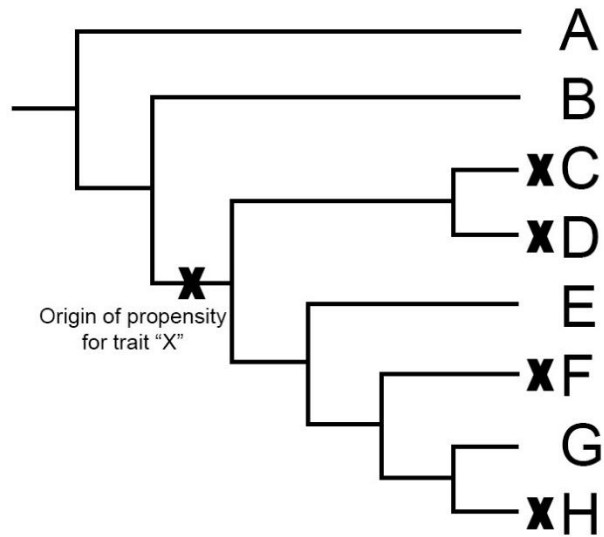
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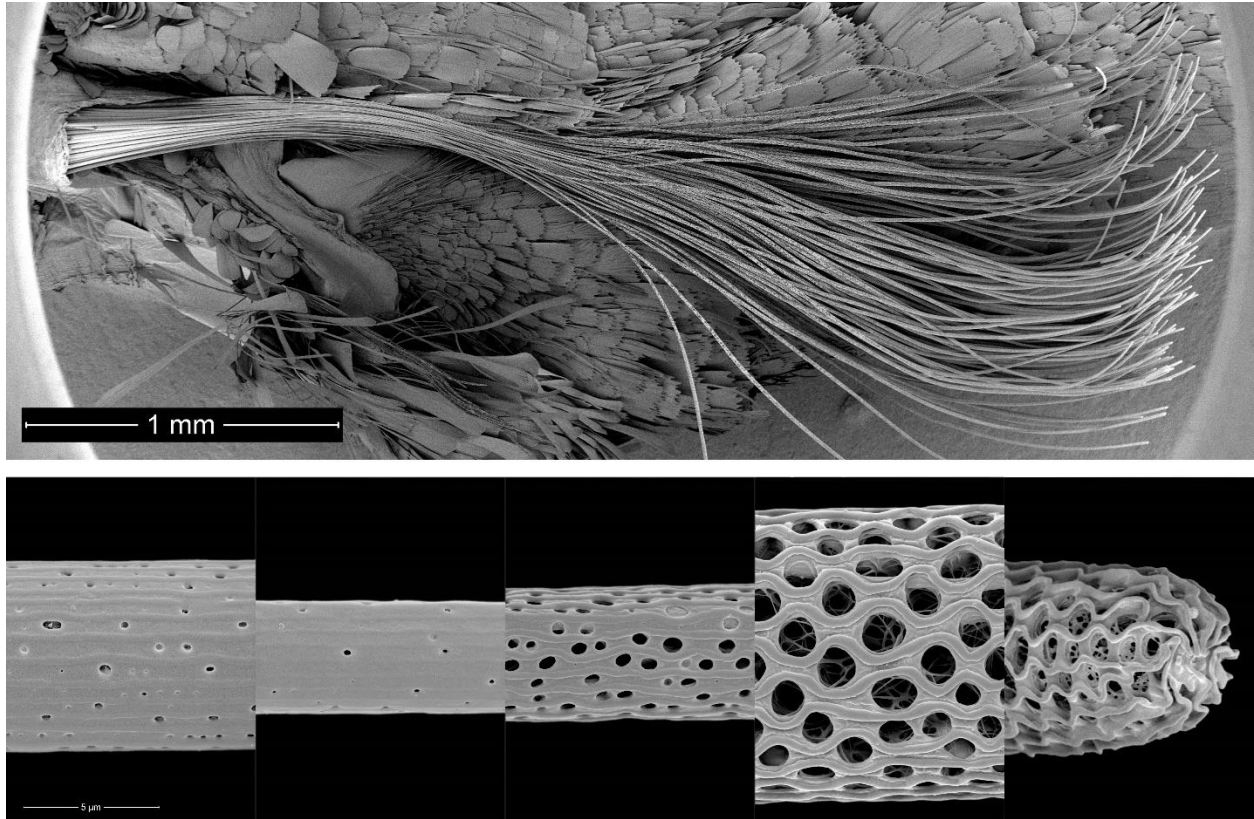
## Tables and Figures



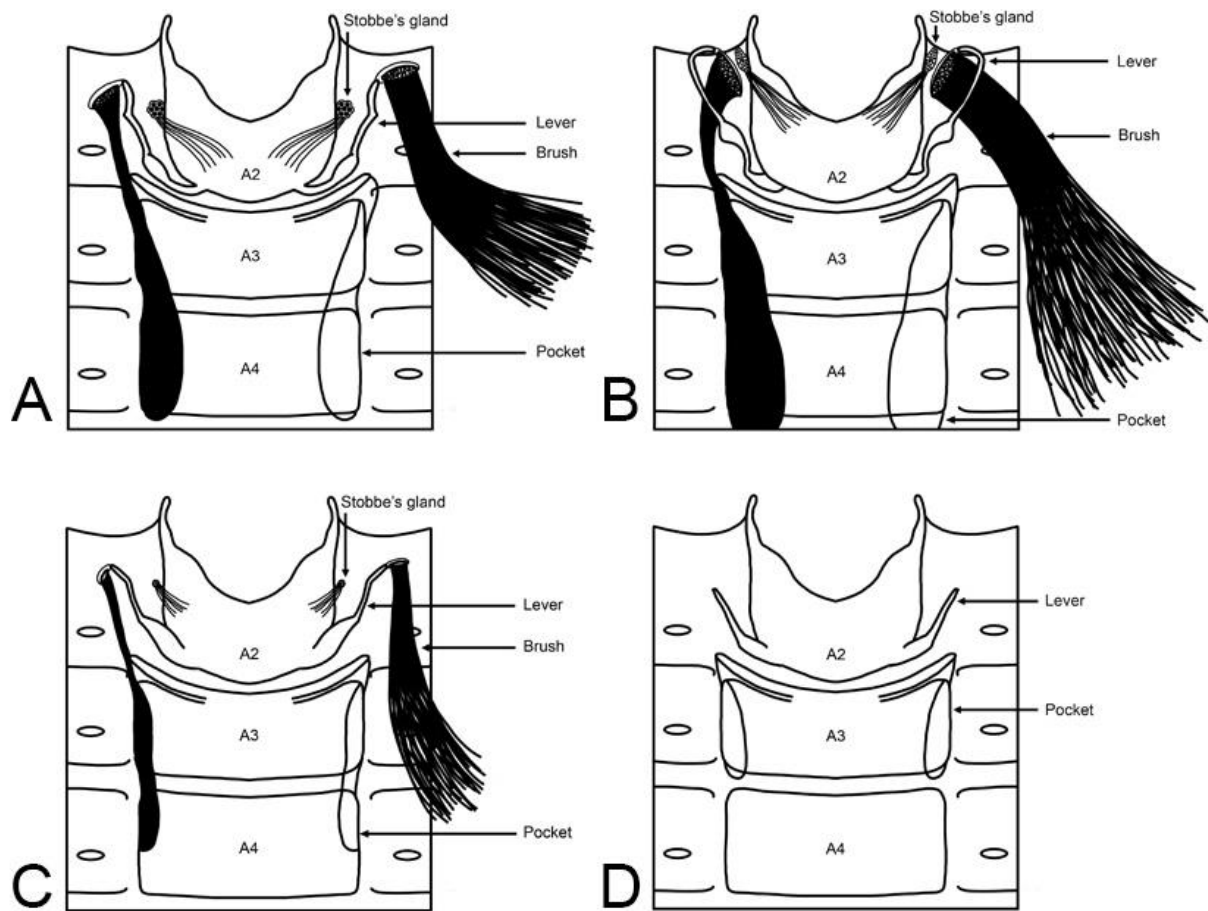
**Figure 1.** Scanned slide of a dissected abdominal pelt (*Graphania lignana* Walker 1857).



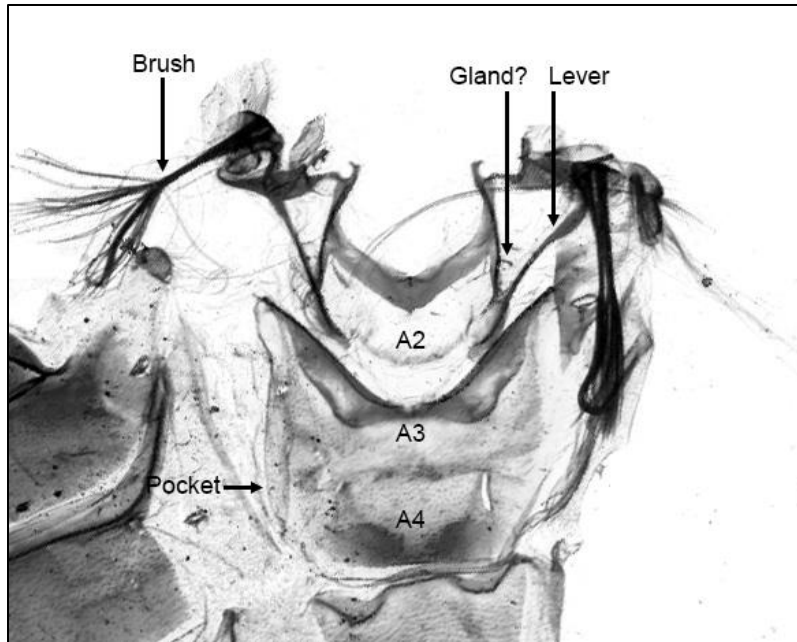
**Figure 2.** Hypothetical cladogram illustrating the concept of underlying synapomorphy. Once a clade has evolved a propensity for trait “X”, it may be expressed or not expressed in the resulting daughter taxa. Taxa with trait “X” appear to have evolved the homologous trait in parallel. Adapted from Sanderson and Hufford, 1996.



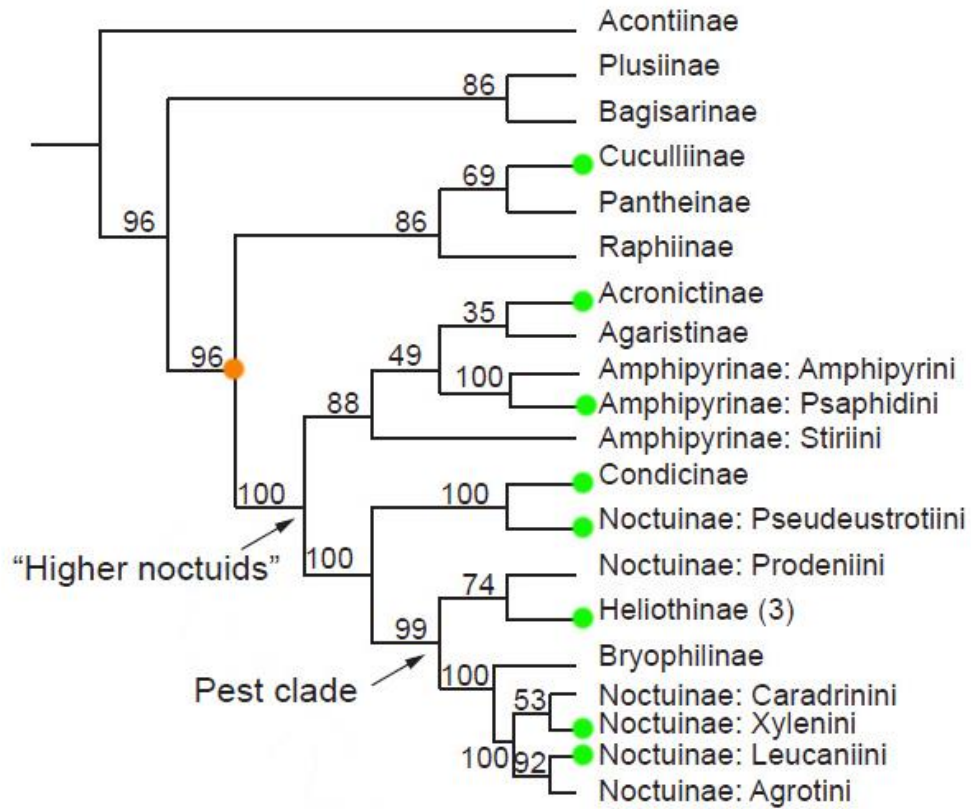
**Figure 3.** SEM images of brush scales of *Cerma cerintha*. Top image shows the entire brush pulled out of the pocket. Bottom images show, left to right: basal area (section 1), middle area start (section 2), middle area end (section 2), apical area (section 3), and the end (section 3). All bottom images were taken at the same magnification in order to illustrate the differences in diameter. They are also lined up to their approximate location on the brush above.



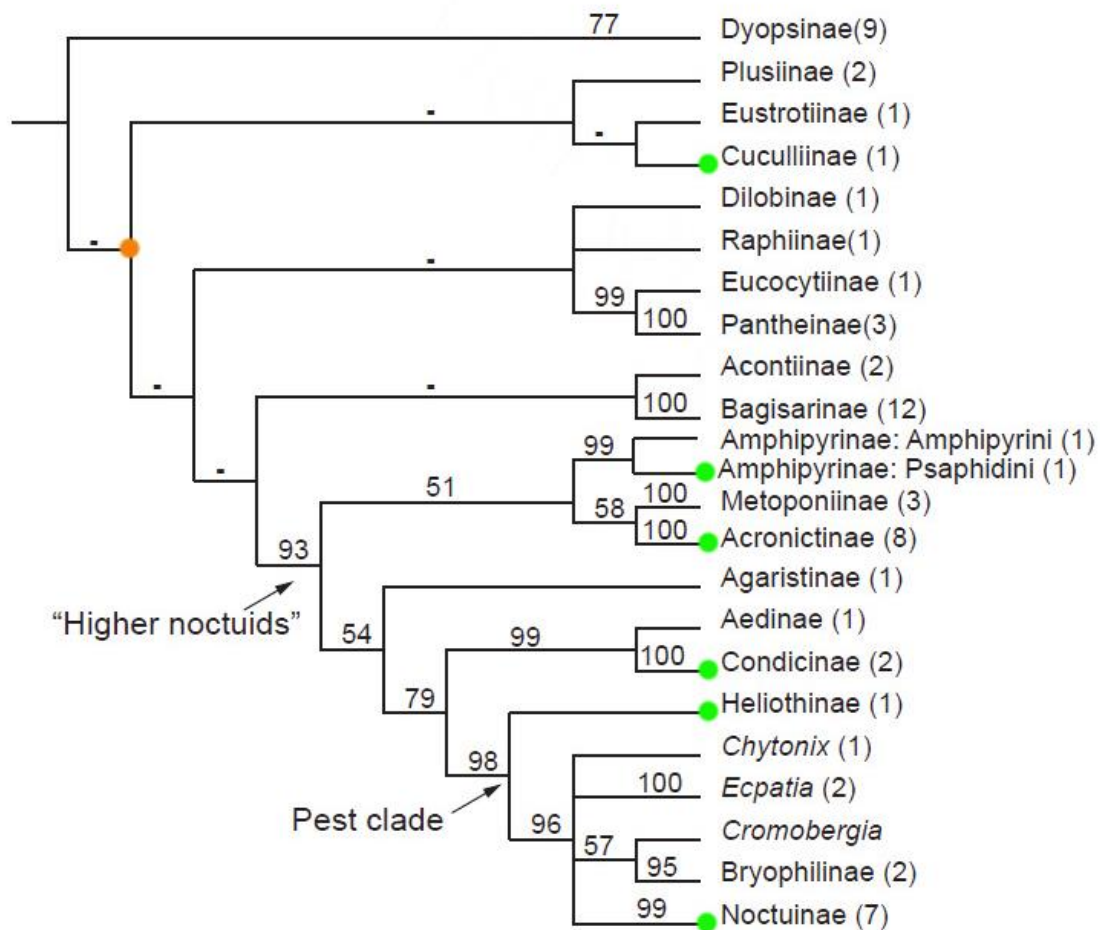
**Figure 4.** Generalizations of TBOs based on multiple species. A. Typical TBO arrangement in a dissected noctuid abdomen; B. Large TBO arrangement showing elongated Stobbe's gland, wide brush base, twisted lever, and pockets reaching beyond segment A4; C. Small TBO arrangement showing reduced structures; D. Reduced lever and pocket, gland and brush are missing.



**Figure 5.** Potential TBO structures of *Hemeroplanis scopulepes*. The pocket, brush, and lever are clearly visible, but with some added sclerotization in the anterior portion of the abdomen. There are paired nub-like structures on either side reminiscent of the Stobbe's gland, but the actual function is unknown.



**Figure 6.** Molecular phylogeny adapted from Mitter et al. (2016). Green dots represent TBO presence in the clade. Orange dot represents the hypothesized origin of TBOs based on this tree. Two subfamilies are missing: Eriopinae and Oncocnemidinae.



**Figure 7.** Molecular phylogeny from Zahiri et al. (2013), adapted from Mitter et al. (2016). Green dots represent TBO presence in the clade. Orange dot represents the hypothesized origin of TBOs based on this tree. Two subfamilies are missing: Eriopinae and Oncocnemidinae.

**Table 1.** Noctuidae subfamilies, tribes, and genera examined. The “Total” columns represent the number of species examined within that taxon. The “#” column gives the number of species with at least partial TBOs. Taxa names with TBOs present are highlighted for visibility. \* = LSOs or other TBO-like structures.

SUBFAMILY	Total	#	TRIBE	Total	#	GENUS	Total	#
Acontiinae	5	0	Acontiini	4	0	<i>Ponometia</i>	2	0
						<i>Tarache</i>	2	0
			Phytometrini	1	0	<i>Allerastria</i>	1	0
Acronictinae	36	5	(none)			<i>Acronicta</i>	28	0
						<i>Cerma</i>	2	2
						<i>Craniophora</i>	1	0
						<i>Harrisimemna</i>	1	1
						<i>Lophonycta</i>	1	1
						<i>Simyra</i>	2	0
						<i>Sinocharis</i>	1	1
Agaristinae	3	0	(none)			<i>Caularis</i>	1	0
						<i>Eudryas</i>	2	0
Amphipyrinae	132	5	Amphipyriini	4	0	<i>Amphipyra</i>	4	0
			Psaphidini	57	5	<i>Acopa</i>	2	0
						<i>Airamia</i>	1	0
						<i>Aleptina</i>	5	0
						<i>Allophyes</i>	1	0
						<i>Anycteola</i>	1	0
						<i>Brachionycha</i>	2	0
						<i>Copibryophila</i>	1	0
						<i>Copivaleria</i>	1	1
						<i>Crimona</i>	1	1
						<i>Emarginea</i>	1	1
						<i>Eviridemias</i>	1	0
						<i>Feralia</i>	6	0
						<i>Fota</i>	2	0
						<i>Gloanna</i>	2	0
						<i>Leucocnemis</i>	4	1
						<i>Metaponpneumata</i>	1	0
						<i>Nacopa</i>	2	0
						<i>Oxycnemis</i>	6	0
						<i>Pleromella</i>	1	0
						<i>Policocnemis</i>	1	0
						<i>Provia</i>	1	0
						<i>Psaphida</i>	7	0
						<i>Pseudocopivaleria</i>	2	0
						<i>Ruacodes</i>	1	1
						<i>Supralathosea</i>	1	0
						<i>Triocnemis</i>	1	0
						<i>Unciella</i>	2	0
			Stiriini	71	0	<i>Aleptinoides</i>	1	0
						<i>Argentostiria</i>	1	0
						<i>Azenia</i>	6	0
						<i>Bistica</i>	1	0



				<i>Chamaeclea</i>	2	0		
				<i>Cirrhophanus</i>	2	0		
				<i>Fala</i>	1	0		
				<i>Grotella</i>	17	0		
				<i>Grotellaforma</i>	1	0		
				<i>Hemigrotella</i>	1	0		
				<i>Heminocloa</i>	1	0		
				<i>Hemioslaria</i>	1	0		
				<i>Homolagoa</i>	1	0		
				<i>Lineostriastiria</i>	5	0		
				<i>Narthecophora</i>	1	0		
				<i>Neogrotella</i>	3	0		
				<i>Neumoegenia</i>	1	0		
				<i>Plagiomimicus</i>	19	0		
				<i>Podagra</i>	1	0		
				<i>Stiria</i>	1	0		
				<i>Thurberiphaga</i>	1	0		
				<i>Tristyla</i>	1	0		
				<i>Xanthothrix</i>	2	0		
Bagisarinae	2	0	(none)		<i>Amyna</i>	1	0	
					<i>Concana</i>	1	0	
Bryophilinae	3	0	(none)		<i>Bryophila</i>	1	0	
					<i>Cryphia</i>	1	0	
					<i>Nyctobrya</i>	1	0	
Condicinae	20	1	Condicini	16	1	<i>Acosmetia</i>	1	0
						<i>Codica</i>	10	0
						<i>Homophoberia</i>	2	0
						<i>Ogdoconta</i>	1	0
						<i>Perigea</i>	2	1
			Leuconyctini	4	0	<i>Crambodes</i>	1	0
						<i>Diastema</i>	1	0
						<i>Leuconycta</i>	2	0
Cuculliinae	41	24	(none)		<i>Cucullia</i>	39	24	
					<i>Emariannia</i>	1	0	
					<i>Opsigalea</i>	1	0	
Cydosiinae	1	0	(none)		<i>Cydosia</i>	1	0	
Dyopsinae	2	0	(none)		<i>Litoprosopus</i>	1	0	
					<i>Moma</i>	1	0	
Eriopinae	1	1	(none)		<i>Calloplistria</i>	1	*1	
Eustrotiinae	3	0	(none)		<i>Capis</i>	1	0	
					<i>Marimatha</i>	2	0	
Heliothinae	21	13	(none)		<i>Heliothis</i>	5	0	
					<i>Periphanes</i>	1	0	
					<i>Pyrhia</i>	1	0	
					<i>Schinia</i>	14	13	

Metoponiinae		Metoponiini	1	0	<i>Panemeria</i>	1	0
Noctuinae	802 311	(unknown)			<i>Actinotia</i>	2	1
					<i>Catephiodes</i>	1	0
					<i>Gonostygia</i>	1	1
					<i>Graphania</i>	4	1
					<i>Haliophyle</i>	2	*2
					<i>Hypaenistis</i>	1	0
					<i>Ichneutica</i>	1	0
					<i>Niaboma</i>	1	0
					<i>Priana</i>	4	0
					<i>Sarcopolia</i>	1	0
					<i>Sidemia authors</i>	1	1
					<i>Strigania</i>	1	0
		Actinotiini	3	1	<i>Alastria</i>	1	1
					<i>Iodopepla</i>	1	0
					<i>Nedra</i>	1	0
		Apameini	148	89	<i>Acrapex</i>	1	0
					<i>Amphipoea</i>	10	7
					<i>Apamea</i>	75	55
					<i>Archanara</i>	2	2
					<i>Arenostola</i>	1	0
					<i>Benjaminiola</i>	1	1
					<i>Capsula</i>	1	0
					<i>Celeana</i>	1	1
					<i>Coenobia</i>	1	0
					<i>Denticucullus</i>	1	0
					<i>Eremobia</i>	1	1
					<i>Eremobina</i>	1	0
					<i>Euros</i>	1	0
					<i>Franclemontia</i>	1	1
					<i>Globia</i>	2	2
					<i>Gortyna</i>	1	0
					<i>Helotrophia</i>	2	2
					<i>Hydraecia</i>	3	1
					<i>Hypocoena</i>	1	1
					<i>Laterologia</i>	1	1
					<i>Lemmeria</i>	1	0
					<i>Lenisa</i>	1	0
					<i>Litoligia</i>	1	1
					<i>Longalatedes</i>	1	0
					<i>Loscopia</i>	2	2
					<i>Luperina</i>	2	0
					<i>Macronoctua</i>	1	0
					<i>Melanapamea</i>	2	2
					<i>Meropleon</i>	1	0

			<i>Mesapamea</i>	1	1
			<i>Mesoligia</i>	1	1
			<i>Neoligia</i>	1	1
			<i>Nonagria</i>	1	1
			<i>Oligia</i>	6	2
			<i>Pabulatrix</i>	1	1
			<i>Papaipema</i>	4	0
			<i>Photedes</i>	6	0
			<i>Protapamea</i>	2	0
			<i>Protarchanara</i>	1	1
			<i>Resapamea</i>	2	0
			<i>Rhizedra</i>	1	0
			<i>Xylomoia</i>	1	1
Caradrinini	16	0	<i>Athetis</i>	2	0
			<i>Caradrina</i>	6	0
			<i>Charanyca</i>	1	0
			<i>Chilodes</i>	1	0
			<i>Hoplodrina</i>	4	0
			<i>Protoperigea</i>	1	0
			<i>Rusina</i>	1	0
Dypterygiini	8	5	<i>Dypterygia</i>	3	1
			<i>Magusa</i>	2	2
			<i>Mormo</i>	1	1
			<i>Thalpophila</i>	1	0
			<i>Trachea</i>	1	1
Elaphriini	13	7	<i>Bryolymnia</i>	2	2
			<i>Chytonix</i>	2	2
			<i>Elaphria</i>	8	3
			<i>Galgula</i>	1	0
Episemini	2	0	<i>Episema</i>	2	0
			<i>Leucochlaena</i>	1	0
Eriopygini	96	15	<i>Anhimella</i>	2	0
			<i>Anhypotrix</i>	1	0
			<i>Engelhardtia</i>	1	0
			<i>Eriopyga</i>	1	0
			<i>Hexorthodes</i>	2	0
			<i>Homorthodes</i>	5	0
			<i>Homorthodes</i>	5	0
			<i>Hyperepia</i>	1	0
			<i>Hypotrix</i>	11	*4
			<i>Lacinipolia</i>	25	10
			<i>Lasionycta</i>	16	0
			<i>Marilopteryx</i>	1	1
			<i>Mimobarathra</i>	1	0
			<i>Miodera</i>	1	0

			<i>Orthodes</i>	2	0
			<i>Protorthodes</i>	7	0
			<i>Psammopolia</i>	1	0
			<i>Pseudorthodes</i>	2	0
			<i>Synorthodes</i>	1	0
			<i>Trichocerapoda</i>	2	0
			<i>Trichofeltia</i>	1	0
			<i>Tricholita</i>	3	0
			<i>Trichopolia</i>	1	0
			<i>Ulolonche</i>	2	0
			<i>Zosteropoda</i>	1	0
Hadenini	105	43	<i>Anarta</i>	4	2
			<i>Ceramica</i>	1	1
			<i>Conisania</i>	2	0
			<i>Coranarta</i>	1	0
			<i>Dargida</i>	7	0
			<i>Dasygaster</i>	2	2
			<i>Dictyestra</i>	1	0
			<i>Feredayia</i>	1	0
			<i>Hada</i>	1	0
			<i>Hadena</i>	14	0
			<i>Hadula</i>	1	1
			<i>Hecatera</i>	3	1
			<i>Hyssia</i>	1	1
			<i>Lacanobia</i>	9	0
			<i>Mamestra</i>	3	3
			<i>Melanchra</i>	5	2
			<i>Metopiora</i>	1	0
			<i>Papestra</i>	6	5
			<i>Polia</i>	12	8
			<i>Poliodestra</i>	1	1
			<i>Saragossa</i>	2	0
			<i>Scriptania</i>	1	1
			<i>Sideridis</i>	13	9
			<i>Spiramater</i>	1	0
			<i>Tmetolophota</i>	2	1
			<i>Trichordestra</i>	8	3
			<i>Tridepia</i>	1	1
			<i>Trudestra</i>	1	1
Leucaniini	53	*41	<i>Hypopteridia</i>	1	*1
			<i>Leucania</i>	29	*20
			<i>Mythimna</i>	22	*19
			<i>Senta</i>	1	*1
Noctuini	187	19	<i>Abagrotis</i>	8	0
			<i>Actebia</i>	3	0

				<i>Agrotis</i>	8	0
				<i>Anaplectoides</i>	2	0
				<i>Anicla</i>	18	16
				<i>Aplectoides</i>	1	0
				<i>Axylia</i>	1	0
				<i>Cerastis</i>	2	0
				<i>Copablepharon</i>	23	0
				<i>Cryptocala</i>	2	0
				<i>Diarsia</i>	8	0
				<i>Dichagyris</i>	27	0
				<i>Eucoptocnemis</i>	6	0
				<i>Eugnorisma</i>	1	0
				<i>Eurois</i>	1	0
				<i>Euxoa</i>	8	0
				<i>Feltia</i>	3	0
				<i>Graphiphora</i>	1	0
				<i>Hemieuxoa</i>	1	0
				<i>Lycophotia</i>	2	0
				<i>Naenia</i>	1	0
				<i>Noctua</i>	6	0
				<i>Ochropleura</i>	1	0
				<i>Paradiarsia</i>	1	0
				<i>Peridroma</i>	3	3
				<i>Protogygia</i>	16	0
				<i>Protolampra</i>	3	0
				<i>Pseudohermonassa</i>	2	0
				<i>Rhyacia</i>	1	0
				<i>Richia</i>	2	0
				<i>Spaelotis</i>	1	0
				<i>Standfussiana</i>	1	0
				<i>Striacosta</i>	1	0
				<i>Xestia</i>	22	0
	Orthosiini	30	5	<i>Acerra</i>	1	0
				<i>Achatia</i>	1	1
				<i>Anorthoa</i>	1	0
				<i>Crocigrapha</i>	1	1
				<i>Egira</i>	6	0
				<i>Himella</i>	1	1
				<i>Morrisonia</i>	4	2
				<i>Orthosia</i>	12	0
				<i>Panolis</i>	1	0
				<i>Perigonica</i>	1	0
				<i>Perigrapha</i>	1	0
	Phlogophorini	4	3	<i>Conservula</i>	1	0
				<i>Euplexia</i>	1	1

			<i>Phlogophora</i>	2	2
Prodeniini	2	0	<i>Spodoptera</i>	2	0
Pseudeustrotiini	1	1	<i>Pseudeustrotia</i>	1	1
Tholerini	5	0	<i>Cerapteryx</i>	1	0
			<i>Nephelodes</i>	2	0
			<i>Tholera</i>	2	0
Xylenini	108	80	<i>Agrochola</i>	7	6
			<i>Ammoconia</i>	1	0
			<i>Andropolia</i>	2	2
			<i>Antitype</i>	1	1
			<i>Aporophyla</i>	3	3
			<i>Apterogenum</i>	1	1
			<i>Aseptis</i>	7	7
			<i>Atethmia</i>	1	0
			<i>Atypha</i>	1	1
			<i>Blepharita</i>	1	0
			<i>Brachylomia</i>	2	1
			<i>Conistra</i>	3	3
			<i>Cosmia</i>	5	2
			<i>Dasypolia</i>	1	0
			<i>Dicycla</i>	1	1
			<i>Dryobotodes</i>	1	1
			<i>Enargia</i>	4	4
			<i>Epiglaea</i>	1	1
			<i>Eupsilia</i>	4	1
			<i>Fagitana</i>	1	0
			<i>Fishia</i>	1	1
			<i>Griposia</i>	1	1
			<i>Hyppa</i>	4	4
			<i>Ipimorpha</i>	3	3
			<i>Lithomoia</i>	2	2
			<i>Lithophane</i>	12	6
			<i>Mesogona</i>	2	2
			<i>Metaxaglaea</i>	2	2
			<i>Mniotype</i>	4	3
			<i>Niphonyx</i>	1	1
			<i>Pachypolia</i>	1	1
			<i>Parastichtis</i>	1	1
			<i>Platypolia</i>	2	2
			<i>Polymixis</i>	4	1
			<i>Properigea</i>	2	2
			<i>Pseudanthoecia</i>	1	0
			<i>Pyreferra</i>	1	0
			<i>Rhizagrotis</i>	1	1
			<i>Sericaglaea</i>	1	1

				<i>Sunira</i>	3	3		
				<i>Sutyna</i>	1	1		
				<i>Tiliacea</i>	2	2		
				<i>Trigonophora</i>	1	1		
				<i>Ufeus</i>	1	0		
				<i>Xanthia</i>	3	3		
				<i>Xylena</i>	3	1		
<b>Oncocnemidinae</b>	146	112	(none)	<i>Behrensia</i>	1	0		
				<i>Calophasia</i>	1	0		
				<i>Catabenoides</i>	1	1		
				<i>Copanarta</i>	2	1		
				<i>Neogalea</i>	1	1		
				<i>Stilbia</i>	1	0		
				<i>Sympistis</i>	138	109		
				<i>Xylocampa</i>	1	0		
<b>Pantheinae</b>	3	0	(none)	<i>Anacronicta</i>	1	0		
				<i>Colocasia</i>	2	0		
<b>Plusiinae</b>	11	0	Argyrogrammatini	2	0	<i>Autographa</i>	1	0
						<i>Chrysodeixis</i>	1	0
			Plusiini	9	0	<i>Plusia</i>	2	0
						<i>Syngrapha</i>	7	0
<b>Raphiinae</b>	1	0	(none)			<i>Raphia</i>	1	0

**Table 2.** Erebidae subfamilies, tribes, and genera examined. The “Total” columns represent the number of species examined within that taxon. The “#” column gives the number of species with TBO-like structures.

SUBFAMILY	Total	#	TRIBE	Total	#	GENUS	Total	#
<b>Boletobiinae</b>	3	1	Boletobiini	1	0	<i>Metalectra</i>	1	0
			Phytometrini	2	1	<i>Hemeroplanis</i>	1	1
						<i>Isogona</i>	1	0
<b>Calpinae</b>	1	0	Calpini	1	0	<i>Plusiodonta</i>	1	0
<b>Erebinae</b>	20	0	Euclidiini	3	0	<i>Ptichodis</i>	2	0
						<i>Mocis</i>	1	0
			Melipotini	1	0	<i>Melipotis</i>	1	0
			Omopterini	15	0	<i>Lesmone</i>	1	0
						<i>Zale</i>	14	0
			Poaphilini	1	0	<i>Mimophis</i>	1	0
<b>Eulepidotinae</b>	5	0	(none)	5	0	<i>Eulepidotis</i>	1	0
						<i>Manbuta</i>	1	0
						<i>Massala</i>	1	0
						<i>Panopoda</i>	1	0
						<i>Phyprosopa</i>	1	0
<b>Hermiinae</b>	4	0	(none)			<i>Idia</i>	1	0
						<i>Macrochilo</i>	1	0
						<i>Zanclognatha</i>	2	0
<b>Hypenodinae</b>	2		(none)			<i>Dasyblemma</i>	1	0
						<i>Parahypenodes</i>	1	0
<b>Hypocalinae</b>	4	0	(none)			<i>Hypsoropha</i>	4	0
<b>Scoliopteryginae</b>	1	0	Scoliopterygini	1	0	<i>Scoliopteryx</i>	1	0

**Table 3.** Detailed TBO data for each species examined. Entries organized alphabetically by subfamily, tribe, genus, and species. P/p = normal/reduced pocket, B/b = normal/reduced brush, L/l = normal/reduced lever, G/g = normal/reduced Stobbe’s gland. Blank entries represent absence. Other observed structures are listed in column “O.” Question marks (?) mean the true status of a structure was unable to be determined. Slides are identified as follows: M##### = T. L. McCabe, New York State Museum; C##### = Various preparators, Canadian National Collection; Z##### = B. V. Zacharczenko. Literature is identified as follows: 1 = Petersen 1908; 2 = Swinton 1908; 3 = Pierce 1909; 4 = Stobbe 1912; 5 = Varley 1962; 6 = Birch 1972, 7 = McCabe 1980; 8 = Zilli 1992; 9 = Poole 1995; 10 = Zilli 1996; 11 = Zilli 1997; 12 = Lafontaine 2004; 13 = Mikkola 2009.



SUBFAMILY	TRIBE	GENUS	SPECIES	AUTHORS	DATE	REGION	P	B	L	G	O	SOURCES
Acronictinae	Acotini	<i>Ponomeria</i>	<i>elegantula</i>	Harvey	1876	Nearctic						C1722
Acronictinae	Acotini	<i>Ponomeria</i>	<i>semiflava</i>	Guenée	1852	Nearctic						M1995, M1996
Acronictinae	Acotini	<i>Tarache</i>	<i>aprica</i>	Hubner	[1808]	Nearctic						M1597, M1598
Acronictinae	Acotini	<i>Tarache</i>	<i>quadriplaga</i>	Smith	1900	Nearctic						M1608
Acronictinae	Phytometrii	<i>Allerastria</i>	<i>albiciliatus</i>	Smith	1903	Nearctic						M1562
Acronictinae		<i>Acronicta</i>	<i>aceris</i>	Linnaeus	1758	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>albarufa</i>	Grote	1874	Nearctic						M1781
Acronictinae		<i>Acronicta</i>	<i>alni</i>	Linnaeus	1767	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>auricoma</i>	Denis and Schiffmüller	1775	Palearctic						M1976
Acronictinae		<i>Acronicta</i>	<i>auricoma</i>	Denis and Schiffmüller	1775	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>brumosa</i>	Guenée	1852	Nearctic						M1406, M1506
Acronictinae		<i>Acronicta</i>	<i>dactylina</i>	Grote	1874	Nearctic						C17265, M364, M369, M370, M373
Acronictinae		<i>Acronicta</i>	<i>euphorbiae</i>	Denis and Schiffmüller	1775	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>fulcula</i>	Grote	1877	Nearctic						M1730, M1731
Acronictinae		<i>Acronicta</i>	<i>fallax</i>	Herrich-Schäffer	[1854]	Nearctic						M401, M467, M509
Acronictinae		<i>Acronicta</i>	<i>fragilis</i>	Guenée	1852	Nearctic						M367
Acronictinae		<i>Acronicta</i>	<i>grisea</i>	Walker	1856	Nearctic						M366
Acronictinae		<i>Acronicta</i>	<i>hastata</i>	Guenée	1852	Nearctic						M353, M377, M1498
Acronictinae		<i>Acronicta</i>	<i>impieta</i>	Walker	1856	Nearctic						M1501
Acronictinae		<i>Acronicta</i>	<i>impressa</i>	Walker	1856	Nearctic						M362, M372, M373, M374, M375, M376, M663, M1508
Acronictinae		<i>Acronicta</i>	<i>innotata</i>	Guenée	1852	Nearctic						M368
Acronictinae		<i>Acronicta</i>	<i>interrupta</i>	Guenée	1852	Nearctic						M1489, M1763
Acronictinae		<i>Acronicta</i>	<i>leporina</i>	Linnaeus	1758	Palearctic					3, 6	
Acronictinae		<i>Acronicta</i>	<i>lepusculina</i>	Guenée	1852	Nearctic						M1649, M1650, M1651, M1652
Acronictinae		<i>Acronicta</i>	<i>megacephala</i>	Denis and Schiffmüller	1775	Palearctic					3, 6	
Acronictinae		<i>Acronicta</i>	<i>menyanthidis</i>	Esper	1789	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>noctivaga</i>	Grote	1864	Nearctic						M359, M360, M361, M382, M383, M1300, M1307, M1977
Acronictinae		<i>Acronicta</i>	<i>oblinita</i>	J.E. Smith	1797	Nearctic						M1589
Acronictinae		<i>Acronicta</i>	<i>psi</i>	Linnaeus	1758	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>rumicis</i>	Linnaeus	1758	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>sperata</i>	Grote	1873	Nearctic						M1304, M1305
Acronictinae		<i>Acronicta</i>	<i>strigosa</i>	Denis and Schiffmüller	1775	Palearctic					6	
Acronictinae		<i>Acronicta</i>	<i>tridens</i>	Denis and Schiffmüller	1775	Palearctic					3, 6	
Acronictinae		<i>Cerna</i>	<i>cerintha</i>	Treitschke	1826	Nearctic						Z2014001, Z2014003, Z2014005

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Acronictinae		<i>Cerna</i>	<i>cora</i>	Hübner	1818	Nearctic	P	B	L	G		M1348, M1349
Acronictinae		<i>Craniophora</i>	<i>ligusni</i>	Denis and Schiffemüller	1775	Palearctic						6
Acronictinae		<i>Harrisinemina</i>	<i>trisinata</i>	Walker	1856	Nearctic				G		Z2014006, Z2014007
Acronictinae		<i>Lophonycta</i>	<i>confusa</i>	Leech	1889	Palearctic	p	b	l	g		Z2014
Acronictinae		<i>Sinyra</i>	<i>albovenosa</i>	Goeze	1781	Palearctic						6
Acronictinae		<i>Sinyra</i>	<i>insularis</i>	Grote	1873	Nearctic						M1658, M1661, M1662
Acronictinae		<i>Sinocharis</i>	<i>korbae</i>	Püngeler	1912	Palearctic	P	B	L	G		Z2014002
Agaristinae		<i>Caularis</i>	<i>lunata</i>	Hampson	1904	Neotropical						M1549
Agaristinae		<i>Eudryas</i>	<i>grata</i>	Fabricius	1793	Nearctic						M1379
Agaristinae		<i>Eudryas</i>	<i>unio</i>	Hübner	[1831]	Nearctic						M1383
Amphipyrimae	Amphipyrimini	<i>Amphipyra</i>	<i>berbera</i>	Rungs	1949	Palearctic						6
Amphipyrimae	Amphipyrimini	<i>Amphipyra</i>	<i>pyramidea</i>	Linnaeus	1758	Palearctic						3, 6
Amphipyrimae	Amphipyrimini	<i>Amphipyra</i>	<i>pyramidoidea</i>	Guenée	1852	Nearctic						M1621
Amphipyrimae	Amphipyrimini	<i>Amphipyra</i>	<i>tragopoginis</i>	Clerck	1759	Holarctic						3, 6, M1620
Amphipyrimae	Psaphidini	<i>Acopa</i>	<i>carina</i>	Harvey	1875	Nearctic						9
Amphipyrimae	Psaphidini	<i>Acopa</i>	<i>perpallida</i>	Grote	1878	Nearctic						9
Amphipyrimae	Psaphidini	<i>Airania</i>	<i>albiocula</i>	Barnes and McDunnough	1918	Nearctic						9
Amphipyrimae	Psaphidini	<i>Aleptina</i>	<i>aleptivoides</i>	Barnes and McDunnough	1912	Nearctic						9
Amphipyrimae	Psaphidini	<i>Aleptina</i>	<i>clinopetes</i>	Dyar	1920	Nearctic						9
Amphipyrimae	Psaphidini	<i>Aleptina</i>	<i>inca</i>	Dyar	1902	Nearctic						9
Amphipyrimae	Psaphidini	<i>Aleptina</i>	<i>junctimacula</i>	Blanchard	1984	Nearctic						9
Amphipyrimae	Psaphidini	<i>Aleptina</i>	<i>semiata</i>	Smith	1902	Nearctic						9
Amphipyrimae	Psaphidini	<i>Allophyes</i>	<i>oxyacanthae</i>	Linnaeus	1758	Palearctic						6
Amphipyrimae	Psaphidini	<i>Anysteola</i>	<i>foetelloides</i>	Barnes and McDunnough	1916	Nearctic						9
Amphipyrimae	Psaphidini	<i>Brachionycha</i>	<i>borealis</i>	Smith	1899	Nearctic						9
Amphipyrimae	Psaphidini	<i>Brachionycha</i>	<i>nubeculosa</i>	Esper	1785	Palearctic						6
Amphipyrimae	Psaphidini	<i>Copibryophila</i>	<i>angelica</i>	Smith	1900	Nearctic						9
Amphipyrimae	Psaphidini	<i>Copivaleria</i>	<i>grotei</i>	Morrison	1874	Nearctic	P	B	L	G		9, M1456, M1457
Amphipyrimae	Psaphidini	<i>Crimona</i>	<i>palimmedia</i>	Smith	1902	Nearctic	? ?	? ?	? ?			9
Amphipyrimae	Psaphidini	<i>Emarginea</i>	<i>percara</i>	Morrison	1875	Nearctic	p	b	l	g		M1228
Amphipyrimae	Psaphidini	<i>Evidemas</i>	<i>minuta</i>	Barnes and McDunnough	1910	Nearctic						9
Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>constocki</i>	Grote	1874	Nearctic						9
Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>deceptiva</i>	McDunnough	1920	Nearctic						9, M388, M698
Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>februalis</i>	Grote	1874	Nearctic						9

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Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>jocosa</i>	Guenée	1852	Nearctic						9, M394
Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>major</i>	Smith	1890	Nearctic						9, M387, M1164, C13521
Amphipyrimae	Psaphidini	<i>Feralia</i>	<i>meadowsi</i>	Buckett	[1968]	Nearctic						9
Amphipyrimae	Psaphidini	<i>Fota</i>	<i>armata</i>	Grote	1882	Nearctic						9
Amphipyrimae	Psaphidini	<i>Fota</i>	<i>minorata</i>	Grote	1882	Nearctic						9
Amphipyrimae	Psaphidini	<i>Glaenna</i>	<i>griseocens</i>	Barnes and Lindsey	1921	Nearctic						9
Amphipyrimae	Psaphidini	<i>Glaenna</i>	<i>hecate</i>	Blanchard	1983	Nearctic						9
Amphipyrimae	Psaphidini	<i>Leucocnemis</i>	<i>nivalis</i>	Smith	1894	Nearctic						9
Amphipyrimae	Psaphidini	<i>Leucocnemis</i>	<i>obsurella</i>	Barnes and McDunnough	1916	Nearctic	p	b	l	g		9*, M1917
Amphipyrimae	Psaphidini	<i>Leucocnemis</i>	<i>perfundis</i>	Smith	1894	Nearctic						9, C13905
Amphipyrimae	Psaphidini	<i>Leucocnemis</i>	<i>variabilis</i>	Barnes and McDunnough	1918	Nearctic						9
Amphipyrimae	Psaphidini	<i>Metaponopneumata</i>	<i>rogenhoferi</i>	Möschler	1890	Neotropical						9
Amphipyrimae	Psaphidini	<i>Nacopa</i>	<i>bisrigata</i>	Barnes and McDunnough	1918	Nearctic						9
Amphipyrimae	Psaphidini	<i>Nacopa</i>	<i>melanderi</i>	Barnes and Benjamin	1927	Nearctic						9
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>acuna</i>	Barnes	1907	Nearctic						9
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>advena</i>	Grote	1882	Nearctic						9, M1916
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>erratica</i>	Barnes and McDunnough	1913	Nearctic						9
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>fusimacula</i>	Smith	1902	Nearctic						9
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>gracillinea</i>	Grote	1881	Nearctic						9
Amphipyrimae	Psaphidini	<i>Oxycnemis</i>	<i>grandimacula</i>	Barnes and McDunnough	1910	Nearctic						9, C13898
Amphipyrimae	Psaphidini	<i>Pleromella</i>	<i>opter</i>	Dyar	1921	Nearctic						9
Amphipyrimae	Psaphidini	<i>Policocnemis</i>	<i>ungulatus</i>	Benjamin	1932	Nearctic						9
Amphipyrimae	Psaphidini	<i>Provia</i>	<i>argentata</i>	Barnes and McDunnough	1910	Nearctic						9
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>damalis</i>	Grote	1879	Nearctic						9
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>electilis</i>	Morrison	1875	Nearctic						9
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>grandis</i>	Smith	1898	Nearctic						9
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>resumens</i>	Walker	1865	Nearctic						9
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>rolandi</i>	Grote	1874	Nearctic						9, C17267, M1455
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>styracis</i>	Guenée	1852	Nearctic						9, C13949
Amphipyrimae	Psaphidini	<i>Psaphida</i>	<i>thaxterianus</i>	Grote	1874	Nearctic						9
Amphipyrimae	Psaphidini	<i>Pseudocopivaleria</i>	<i>anaverta</i>	Buckett and Bauer	1966	Nearctic						9
Amphipyrimae	Psaphidini	<i>Pseudocopivaleria</i>	<i>sonoma</i>	McDunnough	1941	Nearctic						9
Amphipyrimae	Psaphidini	<i>Ruacodes</i>	<i>tela</i>	Smith	1900	Nearctic	p	b	l	g		M1715
Amphipyrimae	Psaphidini	<i>Supralathosea</i>	<i>baboquivariensis</i>	Barnes and Benjamin	1924	Nearctic						C13940

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Amphipyrimae	Psaphidini	<i>Triocnemis</i>	<i>aporis</i>	Grote	1881	Nearctic						9
Amphipyrimae	Psaphidini	<i>Uciella</i>	<i>flagrantis</i>	Smith	1893	Nearctic						9, C13220
Amphipyrimae	Psaphidini	<i>Uciella</i>	<i>primula</i>	Barnes and McDunnough	1918	Nearctic						9
Amphipyrimae	Stirini	<i>Aleptinoides</i>	<i>ochrea</i>	Barnes and McDunnough	1912	Nearctic						9
Amphipyrimae	Stirini	<i>Argentostiria</i>	<i>koebeleri</i>	Riley	1893	Nearctic						9
Amphipyrimae	Stirini	<i>Azenia</i>	<i>edentata</i>	Grote	1883	Nearctic						9, C15448
Amphipyrimae	Stirini	<i>Azenia</i>	<i>implora</i>	Grote	1882	Nearctic						9
Amphipyrimae	Stirini	<i>Azenia</i>	<i>obtusa</i>	Herrich-Schäffer	[1854]	Nearctic						9, C15446
Amphipyrimae	Stirini	<i>Azenia</i>	<i>perflava</i>	Harvey	1875	Nearctic						9
Amphipyrimae	Stirini	<i>Azenia</i>	<i>templetonae</i>	Clarke	1937	Nearctic						9
Amphipyrimae	Stirini	<i>Azenia</i>	<i>virida</i>	Barnes and McDunnough	1916	Nearctic						9
Amphipyrimae	Stirini	<i>Bistica</i>	<i>noela</i>	Druce	1892	Neotropical						9
Amphipyrimae	Stirini	<i>Chamaeclea</i>	<i>basiochrea</i>	Barnes and McDunnough	1916	Nearctic						9
Amphipyrimae	Stirini	<i>Chamaeclea</i>	<i>permana</i>	Grote	1881	Nearctic						9
Amphipyrimae	Stirini	<i>Cirrhophanus</i>	<i>pretiosa</i>	Morrison	1875	Nearctic						M1981
Amphipyrimae	Stirini	<i>Cirrhophanus</i>	<i>triangulifer</i>	Grote	1872	Nearctic						M1980
Amphipyrimae	Stirini	<i>Fala</i>	<i>pychophora</i>	Grote	1875	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>binda</i>	Barnes	1907	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>blanca</i>	Barnes	1904	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>blanchardi</i>	McElvare	1966	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>citronella</i>	Barnes and McDunnough	1916	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>dis</i>	Grote	1883	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>griseus</i>	Barnes and McDunnough	1910	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>harveyi</i>	Barnes and Benjamin	1922	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>margueritaria</i>	Blanchard	1968	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>olivacea</i>	Barnes and McDunnough	1911	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>parvipuncta</i>	Barnes and McDunnough	1912	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>sampita</i>	Barnes	1907	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>sempunctata</i>	Harvey	1875	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>soror</i>	Barnes and McDunnough	1912	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>stretchi</i>	Barnes and Benjamin	1922	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>tricolor</i>	Barnes	1904	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>vaganis</i>	Barnes and Benjamin	1922	Nearctic						9
Amphipyrimae	Stirini	<i>Grotella</i>	<i>vauriae</i>	McElvare	1950	Nearctic						9

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Amphipyinae	Stirini	<i>Grotellaforma</i>	<i>lactea</i>	Stretch	1885	Nearctic					9	
Amphipyinae	Stirini	<i>Hemigrotella</i>	<i>argenteostriata</i>	Barnes and McDunnough	1918	Nearctic					9	
Amphipyinae	Stirini	<i>Heminocloa</i>	<i>mirabilis</i>	Neumoegen	1884	Nearctic					9	
Amphipyinae	Stirini	<i>Hemioslaria</i>	<i>pima</i>	Barnes and Benjamin	1924	Nearctic					9	
Amphipyinae	Stirini	<i>Homolagoa</i>	<i>grotelliformis</i>	Barnes and McDunnough	1912	Nearctic					9	
Amphipyinae	Stirini	<i>Lineostriastiria</i>	<i>biundulalis</i>	Zeller	1872	Nearctic					9	
Amphipyinae	Stirini	<i>Lineostriastiria</i>	<i>hachita</i>	Barnes	1904	Nearctic					9	
Amphipyinae	Stirini	<i>Lineostriastiria</i>	<i>huttoni</i>	Smith	1907	Nearctic					9	
Amphipyinae	Stirini	<i>Lineostriastiria</i>	<i>olivalis</i>	Barnes and McDunnough	1916	Nearctic					9	
Amphipyinae	Stirini	<i>Lineostriastiria</i>	<i>sexseriata</i>	Grote	1881	Nearctic					9	
Amphipyinae	Stirini	<i>Narthecophora</i>	<i>pulverea</i>	Smith	1900	Nearctic		1			9	
Amphipyinae	Stirini	<i>Neogrotella</i>	<i>confusa</i>	Barnes and Benjamin	1922	Nearctic					9	
Amphipyinae	Stirini	<i>Neogrotella</i>	<i>mcDunnoughi</i>	Barnes and Benjamin	1922	Nearctic					9	
Amphipyinae	Stirini	<i>Neogrotella</i>	<i>spladengi</i>	Barnes and McDunnough	1913	Nearctic					9	
Amphipyinae	Stirini	<i>Neumoegenia</i>	<i>poetica</i>	Grote	1882	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>astigmatosum</i>	Dyar	1921	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>aureolum</i>	H. Edwards	1882	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>caesium</i>	Blanchard & Knudson	1984	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>curiosum</i>	Neumoegen	1883	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>dimidiata</i>	Grote	1877	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>expallidus</i>	Grote	1882	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>heitzmani</i>	Poole	1995	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>hilli</i>	Barnes and Benjamin	1923	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>kathryae</i>	A dams	2009	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>mariti</i>	Barnes	1904	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>mimica</i>	Poole	1995	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>navia</i>	Harvey	1875	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>oc'hoa</i>	Barnes	1904	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>olvello</i>	Barnes	1907	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>pityochromus</i>	Grote	1873	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>pyralina</i>	Schaus	1904	Nearctic					C15467	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>spumosum</i>	Grote	1874	Nearctic					9, M1873	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>tepperi</i>	Morrison	1875	Nearctic					9	
Amphipyinae	Stirini	<i>Plagiomimicus</i>	<i>tripagiatus</i>	Smith	1890	Nearctic					9	

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Amphipyrimae	Stirini	<i>Podagra</i>	<i>crassipes</i>	Smith	1902	Nearctic					9	
Amphipyrimae	Stirini	<i>Stiria</i>	<i>rugifons</i>	Grote	1874	Nearctic						M1626, M1627
Amphipyrimae	Stirini	<i>Thurberiphaga</i>	<i>diffusa</i>	Barnes	1904	Nearctic					9	
Amphipyrimae	Stirini	<i>Tristyla</i>	<i>alboplagiata</i>	Smith	1893	Nearctic		1			9	
Amphipyrimae	Stirini	<i>Xanthothrix</i>	<i>neumoegeni</i>	H. Edwards	1881	Nearctic					9	
Amphipyrimae	Stirini	<i>Xanthothrix</i>	<i>ranunculi</i>	H. Edwards	1878	Nearctic					9	
Bagisarinae		<i>Amyia</i>	<i>axis</i>	Guenée	1852	Neotropical						M1961
Bagisarinae		<i>Concana</i>	<i>mundissima</i>	Walker	[1858]	Neotropical						M1751
Bryophilinae		<i>Bryophila</i>	<i>domestica</i>	Hufnagel	1766	Palearctic					6	
Bryophilinae		<i>Cryphia</i>	<i>flavipuncta</i>	Mustelin	2006	Nearctic						M1543
Bryophilinae		<i>Nyctobrya</i>	<i>muralis</i>	Forster	1771	Palearctic					6	
Condicinae	Condicini	<i>Acosmetia</i>	<i>caliginosa</i>	Hübner	1813	Palearctic					6	
Condicinae	Condicini	<i>Condica</i>	<i>albolabes</i>	Grote	1880	Nearctic						C15441
Condicinae	Condicini	<i>Condica</i>	<i>begallo</i>	Barnes	1905	Nearctic						C15459
Condicinae	Condicini	<i>Condica</i>	<i>concosa</i>	Walker	1856	Nearctic						M1039
Condicinae	Condicini	<i>Condica</i>	<i>cupentia</i>	Cramer	1780	Neotropical						M1356
Condicinae	Condicini	<i>Condica</i>	<i>discistriga</i>	Smith	1894	Nearctic						C15462
Condicinae	Condicini	<i>Condica</i>	<i>egestis</i>	Smith	1894	Nearctic						C15458
Condicinae	Condicini	<i>Condica</i>	<i>luxuriosa</i>	Dyar	1926	Nearctic						C15442
Condicinae	Condicini	<i>Condica</i>	<i>mobilis</i>	Walker	[1857]	Neotropical						M615, M1041, M1089
Condicinae	Condicini	<i>Condica</i>	<i>punctifera</i>	Walker	[1857]	Nearctic						M1038
Condicinae	Condicini	<i>Condica</i>	<i>sutor</i>	Guenée	1852	Neotropical						M1040
Condicinae	Condicini	<i>Homophoberia</i>	<i>apicosa</i>	Haworth	1809	Nearctic						M1520
Condicinae	Condicini	<i>Homophoberia</i>	<i>cristata</i>	Morrison	1875	Nearctic						M1523
Condicinae	Condicini	<i>Ogdoconta</i>	<i>cinereola</i>	Guenée	1852	Nearctic						M1703
Condicinae	Condicini	<i>Perigea</i>	<i>nr. berinda</i>	(according to McCabe)		Neotropical	P	B	L	G		M1850
Condicinae	Condicini	<i>Perigea</i>	<i>xanthioides</i>	Guenée	1852	Nearctic						M1037
Condicinae	Leuconyctini	<i>Crambodes</i>	<i>talidiformis</i>	Guenée	1852	Nearctic						M1950
Condicinae	Leuconyctini	<i>Diastema</i>	<i>tigris</i>	Guenée	1852	Neotropical						M1313, M1314
Condicinae	Leuconyctini	<i>Leuconycta</i>	<i>diptheroides</i>	Guenée	1852	Nearctic						M512
Condicinae	Leuconyctini	<i>Leuconycta</i>	<i>lepidula</i>	Grote	1874	Nearctic						M510
Cucullinae		<i>Cucullia</i>	<i>absinthii</i>	Linnaeus	1761	Palearctic	P	B	L	G		4, 5, 6
Cucullinae		<i>Cucullia</i>	<i>alfarata</i>	Strecker	1898	Nearctic	P	B	L	G		C10757
Cucullinae		<i>Cucullia</i>	<i>antipoda</i>	Strecker	1877	Nearctic						6, C14158, M1894, M1895

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Cucullinae		<i>Cucullia</i>	<i>asteris</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		5, 6
Cucullinae		<i>Cucullia</i>	<i>asteroides</i>	Guenée	1852	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>astigma</i>	Smith	1894	Nearctic						9, C14161
Cucullinae		<i>Cucullia</i>	<i>basipuncta</i>	Barnes and McDunnough	1918	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>chamomillae</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		4, 5, 6
Cucullinae		<i>Cucullia</i>	<i>charon</i>	Poole	1995	Nearctic	P	B	L	G		C10750, C10751, M444
Cucullinae		<i>Cucullia</i>	<i>convexipennis</i>	Grote and Robinson	1868	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>costaricensis</i>	Hampson	1918	Neotropical	P	B	L	G		M1865
Cucullinae		<i>Cucullia</i>	<i>cucullioides</i>	Barnes and Benjamin	1923	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>dammeri</i>	McDunnough	1935	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>dorsalis</i>	Smith	1892	Nearctic	P	B	L	G		C15910, C10772, M415
Cucullinae		<i>Cucullia</i>	<i>eccissima</i>	Dyar	1919	Nearctic	P	B	L	G		C10759
Cucullinae		<i>Cucullia</i>	<i>eucæna</i>	Dyar	1919	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>eulepis</i>	Grote	1876	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>eureka</i>	Poole	1995	Nearctic						9, M1892
Cucullinae		<i>Cucullia</i>	<i>floræ</i>	Guenée	1852	Nearctic	P	B	L	G		9, C16661
Cucullinae		<i>Cucullia</i>	<i>heinrichi</i>	Barnes and Benjamin	1924	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>increta</i>	Smith	1910	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>intermedia</i>	Speyer	1870	Nearctic	P	B	L	G		C13962, C17226, M416, M419
Cucullinae		<i>Cucullia</i>	<i>laetifica</i>	Lintner	1875	Nearctic	P	B	L	G		C10747, C10748, C10749
Cucullinae		<i>Cucullia</i>	<i>lethe</i>	Poole	1995	Nearctic	P	B	L	G		C10752
Cucullinae		<i>Cucullia</i>	<i>lilacina</i>	Schaus	1898	Nearctic	P	B	L	G		9, C16651, C16652, C16653, M1858, M1859
Cucullinae		<i>Cucullia</i>	<i>luna</i>	Morrison	1875	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>lychnitis</i>	Rambur	1833	Palearctic						4, 5, 6
Cucullinae		<i>Cucullia</i>	<i>mcDunnoughi</i>	Henne	1940	Nearctic						9, C15915, C15916
Cucullinae		<i>Cucullia</i>	<i>montanae</i>	Grote	1882	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>omissa</i>	Dod	1916	Nearctic	P	B	L	G		9, C16664
Cucullinae		<i>Cucullia</i>	<i>oribac</i>	Barnes	1904	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>postera</i>	Guenée	1852	Nearctic	P	B	L	G		9, C16665, C16666
Cucullinae		<i>Cucullia</i>	<i>pulla</i>	Grote	1881	Nearctic						9
Cucullinae		<i>Cucullia</i>	<i>scrophulariae</i>	Denis and Schiffemüller	1775	Palearctic						5, 6
Cucullinae		<i>Cucullia</i>	<i>similaris</i>	Smith	1892	Nearctic	P	B	L	G		9
Cucullinae		<i>Cucullia</i>	<i>speyeri</i>	Lintner	1874	Nearctic	P	B	L	G		C10758, C17231, C15911, C15912

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Cucullinae		<i>Cucullia</i>	<i>styx</i>	Poole	1995	Nearctic	P	B	L	G		C16735
Cucullinae		<i>Cucullia</i>	<i>umbratica</i>	Linnaeus	1758	Holarctic	P	B	L	G		4, 5, 6, C13961
Cucullinae		<i>Cucullia</i>	<i>verbasci</i>	Linnaeus	1758	Palearctic						4, 5, 6
Cucullinae		<i>Emariannia</i>	<i>cucullidea</i>	Benjamin	1933	Nearctic						9
Cucullinae		<i>Opsigalea</i>	<i>bianchardi</i>	Todd	1966	Nearctic						M1891
Cydosinae		<i>Cydosia</i>	<i>aurivitta</i>	Crote and Robinson	1868	Nearctic						C13009
Dyopsinae		<i>Litoprosopus</i>	<i>coachella</i>	Hill	1921	Nearctic						M1554
Dyopsinae		<i>Moma</i>	<i>alpinum</i>	Osbeck	1778	Palearctic						6
Eriopinae		<i>Callopietria</i>	<i>floridensis</i>	Guenée	1852	Nearctic					?	M1198
Eustrotinae		<i>Capis</i>	<i>curvata</i>	Crote	1882	Nearctic						C13556
Eustrotinae		<i>Marimatha</i>	<i>squala</i>	Ferns & Lafontaine	2010	Nearctic						C14892
Eustrotinae		<i>Marimatha</i>	<i>tripuncta</i>	Möschler	1890	Neotropical						C14893
Heliothinae		<i>Heliothis</i>	<i>acesias</i>	Felder and Rogenhofer	1874	Palearctic						C15920
Heliothinae		<i>Heliothis</i>	<i>maritima</i>	Graslin	1855	Palearctic						6
Heliothinae		<i>Heliothis</i>	<i>peltigera</i>	Denis and Schiffemüller	1775	Palearctic						4, 6
Heliothinae		<i>Heliothis</i>	<i>virescens</i>	Fabricius	1777	Palearctic						M1856, M1857
Heliothinae		<i>Heliothis</i>	<i>viripaca</i>	Hufnagel	1766	Palearctic						3
Heliothinae		<i>Periphanes</i>	<i>delphinii</i>	Linnaeus	1758	Palearctic						4
Heliothinae		<i>Pyrrhia</i>	<i>umbra</i>	Hufnagel	1766	Palearctic						4, 6, M1619
Heliothinae		<i>Schinia</i>	<i>anabelleae</i>	Pogue and Harp	2004	Nearctic	P	B	L	G		C16796
Heliothinae		<i>Schinia</i>	<i>apera</i>	Pogue and Harp	2004	Nearctic	p					C16793
Heliothinae		<i>Schinia</i>	<i>bina</i>	Guenée	1852	Nearctic	p	b	l	g		C16781, C16785, C16787
Heliothinae		<i>Schinia</i>	<i>errans</i>	Smith	1883	Nearctic	P	B	L	G		C11893
Heliothinae		<i>Schinia</i>	<i>felicitata</i>	Smith	1894	Nearctic	P	B	L	G		C12709
Heliothinae		<i>Schinia</i>	<i>ferrisi</i>	Pogue and Harp	2004	Nearctic	P	?	?	G		C13532
Heliothinae		<i>Schinia</i>	<i>fulleri</i>	McElvare	1961	Nearctic	P	B	L	G		C11895
Heliothinae		<i>Schinia</i>	<i>jaguarina</i>	Guenée	1852	Nearctic	P	B	L	G		C11891
Heliothinae		<i>Schinia</i>	<i>luxa</i>	Crote	1881	Nearctic	P	B	L	G		M835
Heliothinae		<i>Schinia</i>	<i>mitis</i>	Crote	1873	Nearctic						C13549
Heliothinae		<i>Schinia</i>	<i>scalena</i>	Pogue and Harp	2004	Nearctic	P	b	l	G		C16794
Heliothinae		<i>Schinia</i>	<i>scissoides</i>	Benjamin	1936	Nearctic	P	B	L	G		C16784
Heliothinae		<i>Schinia</i>	<i>sullivanii</i>	Pogue and Harp	2004	Nearctic	P	B	L	G		C16795
Heliothinae		<i>Schinia</i>	<i>volupia</i>	Fitch	1868	Nearctic	P	B	L	G		C11894



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Noctuinae	?	<i>Actinotia</i>	<i>hyperici</i>	Denis and Schiffemiller	1775	Palearctic	P	B	L	G		M1954
Noctuinae	?	<i>Actinotia</i>	<i>radiosa</i>	Esper	1804	Palearctic						M1957
Noctuinae	?	<i>Catephitodes</i>	<i>zuelana</i>	Schaus	1898	Neotropical						M1289
Noctuinae	?	<i>Gonostygia</i>	<i>agonax</i>	Druce	1890	Nearctic	P	B	L	G		M1783
Noctuinae	?	<i>Graphania</i>	<i>insignis</i>	Walker	1865	Australasia						M1719
Noctuinae	?	<i>Graphania</i>	<i>lignana</i>	Walker	1857	Australasia	P	B	L	G		M1502
Noctuinae	?	<i>Graphania</i>	<i>mutans</i>	Walker	1857	Australasia						M1718, M1721, M1722
Noctuinae	?	<i>Graphania</i>	<i>plena</i>	Walker	1865	Australasia						M1334
Noctuinae	?	<i>Haliophyle</i>	<i>*sp?</i>	?	?	Nearctic					?	C11157
Noctuinae	?	<i>Haliophyle</i>	<i>euclidias</i>	Meyrick	1899	Nearctic					?	C11158
Noctuinae	?	<i>Hypaenistis</i>	<i>purpurea</i>	Warren	1916	Australasia						M1462
Noctuinae	?	<i>Ichneutica</i>	<i>marmorata</i>	Hudson	1924	Australasia						M1474
Noctuinae	?	<i>Niabona</i>	<i>xena</i>	Staudinger	1895	Palearctic						M988
Noctuinae	?	<i>Praïna</i>	<i>irazuna</i>	Draudt	1924	Neotropical						C12053
Noctuinae	?	<i>Praïna</i>	<i>leucaniades</i>	Hampson	1913	Neotropical						C12052
Noctuinae	?	<i>Praïna</i>	<i>mexicana</i>	Lafontaine	?	Nearctic						C12043
Noctuinae	?	<i>Praïna</i>	<i>trifasciata</i>	Hampson	1909	Neotropical						C12054
Noctuinae	?	<i>Sarcopolia</i>	<i>illoba</i>	Butler	1878	Palearctic						M1624
Noctuinae	?	<i>Sidemia authors</i>	<i>hipparion</i>	Druce	1889	Neotropical	P	?	L	?		M1823
Noctuinae	?	<i>Strigania</i>	<i>calligrapha</i>	Butler	1882	Neotropical						M1297
Noctuinae	Actinotini	<i>Alasria</i>	<i>tropicalis</i>	Schaus	1911	Neotropical	P	B	L	G		C11760
Noctuinae	Actinotini	<i>Iodopepla</i>	<i>u-album</i>	Guenée	1852	Nearctic						M1677, M1754
Noctuinae	Actinotini	<i>Nedra</i>	<i>ramosula</i>	Guenée	1841	Nearctic						M1256
Noctuinae	Apameini	<i>Acrapex</i>	<i>exsanguis</i>	Lower	1901	Australasia						M1921
Noctuinae	Apameini	<i>Amphipoea</i>	<i>americana</i>	Speyer	1875	Nearctic	P	B	L	G		C16732, M437
Noctuinae	Apameini	<i>Amphipoea</i>	<i>crinensis</i>	Burrows	1908	Palearctic	P	B	L	G		3, 6
Noctuinae	Apameini	<i>Amphipoea</i>	<i>erepta</i>	Crote	1881	Nearctic	P	B	L	G		C13603
Noctuinae	Apameini	<i>Amphipoea</i>	<i>fucosa</i>	Freyer	1830	Palearctic	P	B	L	G		3, 6
Noctuinae	Apameini	<i>Amphipoea</i>	<i>interoceana</i>	Smith	1899	Nearctic	P	B	L	G		C16734, M438
Noctuinae	Apameini	<i>Amphipoea</i>	<i>keiferi</i>	Benjamin	1935	Nearctic						C15444
Noctuinae	Apameini	<i>Amphipoea</i>	<i>lucens</i>	Freyer	1845	Palearctic	P	B	L	G		3, 6
Noctuinae	Apameini	<i>Amphipoea</i>	<i>lunata</i>	Smith	1891	Nearctic						M1681
Noctuinae	Apameini	<i>Amphipoea</i>	<i>oculea</i>	Linnaeus	1761	Palearctic				I		6

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Noctuinae	Apameini	<i>Amphipoea</i>	<i>senilis</i>	Smith	1892	Nearctic						C15443
Noctuinae	Apameini	<i>Apamea</i>	<i>acera</i>	Smith	1900	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>albina</i>	Grote	1874	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>alia</i>	Guenee	1852	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>alticola</i>	Smith	1891	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>amputatrix</i>	Fitch	1856	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>anceps</i>	Denis and Schiffmüller	1775	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Apamea</i>	<i>antennata</i>	Smith	1891	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>apamiformis</i>	Guenee	1852	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>atricleava</i>	Barnes and McDunnough	1913	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>atrosuffusa</i>	Barnes and McDunnough	1913	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>auranticolor</i>	Grote	1873	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>bernardino</i>	Mikkola and Mustelin	2001	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>burgessi</i>	Morrison	1874	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>cariosa</i>	Guenee	1852	Nearctic	P	B	L	G		13, C17279
Noctuinae	Apameini	<i>Apamea</i>	<i>centralis</i>	Smith	1891	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>cinefacta</i>	Grote	1881	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>cogitata</i>	Smith	1891	Nearctic	P	B	L	G		13, C13638
Noctuinae	Apameini	<i>Apamea</i>	<i>commoda</i>	Walker	1857	Nearctic	P	B	L	G		13, M1377, M1483
Noctuinae	Apameini	<i>Apamea</i>	<i>contradicta</i>	Smith	1895	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>crenata</i>	Hufnagel	1766	Palearctic	P	B	L	G		3, 6
Noctuinae	Apameini	<i>Apamea</i>	<i>cristata</i>	Grote	1878	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>cuculiformis</i>	Grote	1875	Nearctic	P	B	L	G		13, C13585
Noctuinae	Apameini	<i>Apamea</i>	<i>devastator</i>	Brace	1819	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>digitula</i>	Mustelin and Mikkola	2006	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>dubitanis</i>	Walker	1856	Nearctic	P	B	L	G		13, C13566, M427, M464, M546, M1983
Noctuinae	Apameini	<i>Apamea</i>	<i>epomidion</i>	Haworth	1809	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Apamea</i>	<i>exilis</i>	Lefebvre	1836	Palearctic						3
Noctuinae	Apameini	<i>Apamea</i>	<i>fergusoni</i>	Mikkola & Lafontaine	2009	Nearctic						13, C17274
Noctuinae	Apameini	<i>Apamea</i>	<i>furva</i>	Denis and Schiffmüller	1775	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Apamea</i>	<i>geminimacula</i>	Dyar	1904	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>genialis</i>	Grote	1874	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>helva</i>	Grote	1875	Nearctic	P	B	L	G		13, M426

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Noctuinae	Apameini	<i>Apamea</i>	<i>impulsa</i>	Guenée	1852	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>indocilis</i>	Walker	1856	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>inebriata</i>	Ferguson	1977	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>inficita</i>	Walker	1857	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>inordinata</i>	Morrison	1875	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>lignicolora</i>	Guenée	1852	Nearctic	P	B	L	G		13, M463
Noctuinae	Apameini	<i>Apamea</i>	<i>lintheri</i>	Grote	1873	Nearctic			1			13, M1684
Noctuinae	Apameini	<i>Apamea</i>	<i>lithoxyloa</i>	Denis and Schiffmüller	1775	Palearctic	P	B	L	G		5, 6
Noctuinae	Apameini	<i>Apamea</i>	<i>longula</i>	Grote	1879	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>lutosa</i>	Andrews	1877	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>maroccana</i>	Zemy	1934	Palearctic	P		1			8
Noctuinae	Apameini	<i>Apamea</i>	<i>maxima</i>	Dyar	1904	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>monoglypha</i>	Hufnagel	1766	Palearctic	P	B	L	G		2, 3, 4, 5, 6, 8
Noctuinae	Apameini	<i>Apamea</i>	<i>nigrior</i>	Smith	1891	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>niveivenosa</i>	Grote	1879	Nearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>oblonga</i>	Haworth	1809	Palearctic	P		1			6
Noctuinae	Apameini	<i>Apamea</i>	<i>occidens</i>	Grote	1878	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>perpensa</i>	Grote	1881	Nearctic	P		L			13
Noctuinae	Apameini	<i>Apamea</i>	<i>plutonia</i>	Grote	1883	Nearctic	P		L			13
Noctuinae	Apameini	<i>Apamea</i>	<i>quinteri</i>	Mikkola & Lafontaine	2009	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>relicina</i>	Morrison	1875	Nearctic	P	B	L	G		13*, C17269
Noctuinae	Apameini	<i>Apamea</i>	<i>remissa</i>	Hubner	[1809]	Nearctic	P		L			4, 6, 13
Noctuinae	Apameini	<i>Apamea</i>	<i>robertsoni</i>	Mikkola and Mustelin	2006	Nearctic	P	B	L	G		13, C11888
Noctuinae	Apameini	<i>Apamea</i>	<i>rubirena</i>	Tretschke	1825	Palearctic						13
Noctuinae	Apameini	<i>Apamea</i>	<i>scolopacina</i>	Esper	1788	Palearctic						6, 13
Noctuinae	Apameini	<i>Apamea</i>	<i>scoparia</i>	Mikkola et al	2000	Nearctic	P	B	L	G		13, C17286
Noctuinae	Apameini	<i>Apamea</i>	<i>sicula</i>	Turati	1909	Palearctic	P	B	L	G		8
Noctuinae	Apameini	<i>Apamea</i>	<i>siskiyou</i>	Mikkola & Lafontaine	2009	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>smeythi</i>	Franclemont	1952	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>sora</i>	Smith	1903	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Apamea</i>	<i>sordens</i>	Hufnagel	1766	Palearctic	P	B	L	G		2, 6, 13, C13573, C17283
Noctuinae	Apameini	<i>Apamea</i>	<i>spaldingi</i>	Smith	1909	Nearctic	P	B	L	G		13

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Noctuinae	Apameini	<i>Apamea</i>	<i>subiustris</i>	Esper	1788	Palearctic	P	B	L	G	6	
Noctuinae	Apameini	<i>Apamea</i>	<i>syriaca</i>	Osthelder	1933	Palearctic	P	B	L	G	8	
Noctuinae	Apameini	<i>Apamea</i>	<i>tahoensis</i>	Mikkola & Lafontaine	2009	Nearctic	P	B	L	G	13	
Noctuinae	Apameini	<i>Apamea</i>	<i>unanimitis</i>	Hübner	[1813]	Nearctic	P	B	L	G	3, 6, C13583	
Noctuinae	Apameini	<i>Apamea</i>	<i>unita</i>	Smith	1904	Nearctic					13	
Noctuinae	Apameini	<i>Apamea</i>	<i>verbascoides</i>	Guenée	1852	Nearctic	P	B	L	G	13	
Noctuinae	Apameini	<i>Apamea</i>	<i>vulgaris</i>	Grote and Robinson	1866	Nearctic	P	B	L	G	13	
Noctuinae	Apameini	<i>Apamea</i>	<i>vultuosa</i>	Grote	1875	Nearctic	P	B	L	G	13, C17273	
Noctuinae	Apameini	<i>Apamea</i>	<i>wikeri</i>	Quinter & Lafontaine	2009	Nearctic	P	B	L	G	13	
Noctuinae	Apameini	<i>Apamea</i>	<i>xylodes</i>	Mikkola & Lafontaine	2009	Nearctic	P	B	L	G	13, C1227	
Noctuinae	Apameini	<i>Apamea</i>	<i>zeta</i>	Treitschke	1825	Nearctic					13	
Noctuinae	Apameini	<i>Archanara</i>	<i>dissoluta</i>	Treitschke	1825	Palearctic			1	g	6	
Noctuinae	Apameini	<i>Archanara</i>	<i>neurica</i>	Hübner	1808	Palearctic	P				3, 6	
Noctuinae	Apameini	<i>Arenostola</i>	<i>phragmitidis</i>	Hübner	1803	Palearctic	P	B	L	G	6	
Noctuinae	Apameini	<i>Benjaminiola</i>	<i>colorada</i>	Smith	1900	Nearctic			L		M1764	
Noctuinae	Apameini	<i>Capsula</i>	<i>subflava</i>	Grote	1882	Nearctic					M1276	
Noctuinae	Apameini	<i>Celaena</i>	<i>haworthii</i>	Curtis	1829	Palearctic			1		6	
Noctuinae	Apameini	<i>Coenobia</i>	<i>rufa</i>	Haworth	1809	Palearctic					3, 6	
Noctuinae	Apameini	<i>Denticucullus</i>	<i>pygmaea</i>	Haworth	1809	Palearctic					6	
Noctuinae	Apameini	<i>Eremobia</i>	<i>ochroleuca</i>	Denis and Schiffemüller	1775	Palearctic			1		6	
Noctuinae	Apameini	<i>Eremobia</i>	<i>claudens</i>	Walker	1857	Nearctic					M1716	
Noctuinae	Apameini	<i>Euros</i>	<i>proprius</i>	H. Edwards	1881	Nearctic					C13971	
Noctuinae	Apameini	<i>Franclemontia</i>	<i>interrogans</i>	Walker	1856	Nearctic	P	B	L	G	C13002	
Noctuinae	Apameini	<i>Globia</i>	<i>algae</i>	Esper	1789	Palearctic			1		6	
Noctuinae	Apameini	<i>Globia</i>	<i>sparganii</i>	Esper	1790	Palearctic	p	B	L	G	6	
Noctuinae	Apameini	<i>Gortyna</i>	<i>flavago</i>	Denis and Schiffemüller	1775	Palearctic					6	
Noctuinae	Apameini	<i>Helotrophia</i>	<i>leucostigma</i>	Hübner	1808	Palearctic	p	B	L	G	6	
Noctuinae	Apameini	<i>Helotrophia</i>	<i>reniformis</i>	Grote	1874	Nearctic	p	B	L	G	M1680	
Noctuinae	Apameini	<i>Hydraecia</i>	<i>hucherardi</i>	Mabille	1907	Palearctic					6	
Noctuinae	Apameini	<i>Hydraecia</i>	<i>medialis</i>	Smith	1892	Nearctic					M1618	
Noctuinae	Apameini	<i>Hydraecia</i>	<i>micacea</i>	Esper	1789	Palearctic	p		L		4, 6	
Noctuinae	Apameini	<i>Hypocœna</i>	<i>rufostrigata</i>	Packard	1867	Nearctic	p	b	l	g	M1706	
Noctuinae	Apameini	<i>Lateroligia</i>	<i>ophiogramma</i>	Esper	1794	Palearctic	p	B	L	G	4, 6*, 13, C15917	
Noctuinae	Apameini	<i>Lenneria</i>	<i>digitalis</i>	Grote	1882	Nearctic					M1707	

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Noctuinae	Apameini	<i>Lenisa</i>	<i>geminipuncta</i>	Haworth	1809	Palearctic						3, 6
Noctuinae	Apameini	<i>Litologia</i>	<i>litterosa</i>	Haworth	1809	Palearctic			1			6
Noctuinae	Apameini	<i>Longalatedes</i>	<i>elymi</i>	Treitschke	1825	Palearctic						6
Noctuinae	Apameini	<i>Loscopia</i>	<i>robilei</i>	Quinter & Lafontaine	2009	Nearctic	P	B	L	G		13, C13581, C13584
Noctuinae	Apameini	<i>Loscopia</i>	<i>velata</i>	Walker	1865	Nearctic	P	B	L	G		13, C13582
Noctuinae	Apameini	<i>Luperina</i>	<i>nickerlii</i>	Freyer	1845	Palearctic						6
Noctuinae	Apameini	<i>Luperina</i>	<i>testacea</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Apameini	<i>Macronoctua</i>	<i>onusta</i>	Grote	1874	Nearctic						M1696
Noctuinae	Apameini	<i>Melanapamea</i>	<i>mixta</i>	Grote	1881	Nearctic	P	B	L	G		13
Noctuinae	Apameini	<i>Meropleon</i>	<i>cosmion</i>	Dyar	1924	Nearctic						C13001
Noctuinae	Apameini	<i>Mesapamea</i>	<i>fractilinea</i>	Grote	1874	Nearctic	P	B	L	G		C14176, M1765
Noctuinae	Apameini	<i>Mesapamea</i>	<i>secalis</i>	Linnaeus	1758	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Mesoligia</i>	<i>furuncula</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		3, 6
Noctuinae	Apameini	<i>Neoligia</i>	<i>albirena</i>	Troubridge and Lafontaine	2002	Nearctic	p		1			C13438
Noctuinae	Apameini	<i>Nonagria</i>	<i>typhae</i>	Thunberg	1784	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Oligia</i>	<i>chlorostigma</i>	Harvey	1876	Nearctic	P	?	?	?		M1473
Noctuinae	Apameini	<i>Oligia</i>	<i>fasciuncula</i>	Denis and Schiffemüller	1809	Palearctic						6
Noctuinae	Apameini	<i>Oligia</i>	<i>latruncula</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Apameini	<i>Oligia</i>	<i>modica</i>	Guenée	1852	Nearctic	P	B	L	G		M545
Noctuinae	Apameini	<i>Oligia</i>	<i>strigilis</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Apameini	<i>Oligia</i>	<i>versicolor</i>	Borkhausen	1792	Palearctic						6
Noctuinae	Apameini	<i>Pabulatrix</i>	<i>pabulatrixcula</i>	Brahm	1791	Palearctic			1			1, 6
Noctuinae	Apameini	<i>Papaipema</i>	<i>appassionata</i>	Harvey	1876	Nearctic						M324
Noctuinae	Apameini	<i>Papaipema</i>	<i>nepheleptena</i>	Dyar	1908	Nearctic						M320
Noctuinae	Apameini	<i>Papaipema</i>	<i>pterisii</i>	Brad	1907	Nearctic						M323, M326, M327, M328
Noctuinae	Apameini	<i>Papaipema</i>	<i>rigida</i>	Grote	1877	Nearctic						M321
Noctuinae	Apameini	<i>Photodes</i>	<i>captiuncula</i>	Treitschke	1825	Palearctic						6
Noctuinae	Apameini	<i>Photodes</i>	<i>extrema</i>	Hübner	1809	Palearctic						3, 6
Noctuinae	Apameini	<i>Photodes</i>	<i>fluxa</i>	Hübner	1809	Palearctic						3, 6
Noctuinae	Apameini	<i>Photodes</i>	<i>inops</i>	Grote	1881	Nearctic						M1172
Noctuinae	Apameini	<i>Photodes</i>	<i>minima</i>	Haworth	1809	Palearctic						6
Noctuinae	Apameini	<i>Photodes</i>	<i>morrisii</i>	Dale	1837	Palearctic						6
Noctuinae	Apameini	<i>Protapamea</i>	<i>danieli</i>	Quinter	2009	Nearctic						13, C13582

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Noctuinae	Apameini	<i>Protapamea</i>	<i>louisae</i>	Quinter	2009	Nearctic						13, C13632
Noctuinae	Apameini	<i>Protarchanara</i>	<i>brevilinea</i>	Fenn	1864	Palearctic	P	B	L	G		6
Noctuinae	Apameini	<i>Resapamea</i>	<i>passer</i>	Guénée	1852	Nearctic						M774
Noctuinae	Apameini	<i>Resapamea</i>	<i>stipata</i>	Morrison	1875	Nearctic						M776
Noctuinae	Apameini	<i>Rhizedra</i>	<i>lutosa</i>	Hübner	[1803]	Palearctic						6, M1717
Noctuinae	Apameini	<i>Xylomoia</i>	<i>chiagnoni</i>	Barnes and McDunnough	1917	Nearctic	P	B	L	G		M1670
Noctuinae	Caradriniini	<i>Aethis</i>	<i>palustris</i>	Hübner	1808	Palearctic						6
Noctuinae	Caradriniini	<i>Aethis</i>	<i>tarda</i>	Guénée	1852	Nearctic						M1098
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>alana</i>	Druce	1890	Neotropical						M1819
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>clavipalpis</i>	Scopoli	1763	Palearctic						6
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>distinctoides</i>	Poole	1989	Nearctic						M1054
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>meralis</i>	Morrison	1875	Nearctic						M1053
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>morpheus</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Caradriniini	<i>Caradrina</i>	<i>multifera</i>	Walker	[1857]	Nearctic						C13527
Noctuinae	Caradriniini	<i>Charanyca</i>	<i>trigrammica</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Caradriniini	<i>Chilodes</i>	<i>maritima</i>	Tauscher	1806	Palearctic						3, 6
Noctuinae	Caradriniini	<i>Hoplodrina</i>	<i>ambigua</i>	Denis and Schiffemüller	1775	Palearctic						M753
Noctuinae	Caradriniini	<i>Hoplodrina</i>	<i>ambigua</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Caradriniini	<i>Hoplodrina</i>	<i>blanda</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Caradriniini	<i>Hoplodrina</i>	<i>octogenaria</i>	Goeze	1781	Palearctic						M751
Noctuinae	Caradriniini	<i>Protoperigea</i>	<i>umbratica</i>	Mustelin	2006	Nearctic						M1757
Noctuinae	Caradriniini	<i>Rustina</i>	<i>ferruginea</i>	Esper	1785	Palearctic						6
Noctuinae	Dypterygini	<i>Dypterygia</i>	<i>assuetus</i>	Butler	1879	Neotropical						M1202
Noctuinae	Dypterygini	<i>Dypterygia</i>	<i>patina</i>	Harvey	1875	Nearctic						M991, M1678
Noctuinae	Dypterygini	<i>Dypterygia</i>	<i>scabriuscula</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Dypterygini	<i>Magusa</i>	<i>divaricata</i>	Grote	1874	Nearctic	p					C12041
Noctuinae	Dypterygini	<i>Magusa</i>	<i>orbifera</i>	Walker	1857	Nearctic	P	B	L	G		M1242, M1243, M1245
Noctuinae	Dypterygini	<i>Mormo</i>	<i>maura</i>	Linnaeus	1758	Palearctic	p	B	L	G		1, 6
Noctuinae	Dypterygini	<i>Thalpoiphila</i>	<i>matura</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Dypterygini	<i>Trachea</i>	<i>atripilis</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Elaphriini	<i>Bryolymnia</i>	<i>anthracitaria</i>	Fenn and McFarland	2007	Nearctic	P	B	L	G		C13586
Noctuinae	Elaphriini	<i>Bryolymnia</i>	<i>ensina</i>	Barnes	1907	Nearctic	P	B	L	G		C14896
Noctuinae	Elaphriini	<i>Chytonix</i>	<i>albonotata</i>	Staudinger	1892	Palearctic	P	B	L	?		C16645

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Noctuinae	Elaphrini	<i>Chytonix</i>	<i>palliatricula</i>	Guenée	1852	Nearctic	P	?	L	G		M508
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>cornutus</i>	Pogue	2003	Nearctic	P	B	L	G		M1975
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>deltoides</i>	Möschler	1880	Neotropical	P					M1970
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>festivoides</i>	Guenée	1852	Nearctic						M1631, M1632
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>grata</i>	Hübner	1818	Nearctic				1		C12040*, M1965
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>nucicolora</i>	Guenée	1852	Nearctic						M1327, M1337, M1605
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>repanda</i>	Schaus	1904	Nearctic						M1893
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>venustula</i>	Hübner	1790	Palearctic	P	B	L	G		6
Noctuinae	Elaphrini	<i>Elaphria</i>	<i>versicolor</i>	Grote	1874	Nearctic						M1328, M1625
Noctuinae	Elaphrini	<i>Galgula</i>	<i>parita</i>	Guenée	1852	Nearctic						M1702
Noctuinae	Episenini	<i>Episema</i>	<i>glauca</i>	Esper	1789	Palearctic						C13014
Noctuinae	Episenini	<i>Episema</i>	<i>scoriacea</i>	Esper	[1789]	Palearctic						C13013
Noctuinae	Episenini	<i>Leucochaena</i>	<i>oditis</i>	Hübner	1822	Palearctic						6
Noctuinae	Eriopygini	<i>Anhimella</i>	<i>contrahens</i>	Walker	1860	Nearctic						C16672, M213
Noctuinae	Eriopygini	<i>Anhimella</i>	<i>pacifica</i>	McDunnough	1943	Nearctic						C16669, M1505
Noctuinae	Eriopygini	<i>Anhypotrix</i>	<i>tristis</i>	Barnes and McDunnough	1910	Nearctic						C15792, M972
Noctuinae	Eriopygini	<i>Engelhardtia</i>	<i>ursina</i>	Smith	1898	Nearctic						M1115
Noctuinae	Eriopygini	<i>Eriopyga</i>	<i>moesta</i>	Walker	1858	Neotropical						M1269
Noctuinae	Eriopygini	<i>Hexorthodes</i>	<i>agrotiformis</i>	Grote	1883	Nearctic						C15942
Noctuinae	Eriopygini	<i>Hexorthodes</i>	<i>tuana</i>	Smith	1906	Nearctic						M285
Noctuinae	Eriopygini	<i>Homorthodes</i>	<i>carneola</i>	McDunnough	1943	Nearctic						M951
Noctuinae	Eriopygini	<i>Homorthodes</i>	<i>fractura</i>	Smith	1906	Nearctic						M189, M1424
Noctuinae	Eriopygini	<i>Homorthodes</i>	<i>fufurata</i>	Grote	1874	Nearctic						M936, M1471, M1484, M1538
Noctuinae	Eriopygini	<i>Homorthodes</i>	<i>hanhami</i>	Barnes and McDunnough	1911	Nearctic						M171, M766
Noctuinae	Eriopygini	<i>Homorthodes</i>	<i>mania</i>	Strecker	1899	Nearctic						M765, M921
Noctuinae	Eriopygini	<i>Hydroecioides</i>	<i>aspasta</i>	Dyar	1918	Nearctic						M1812
Noctuinae	Eriopygini	<i>Hydroecioides</i>	<i>juvenilis</i>	Grote	1881	Nearctic						M1132
Noctuinae	Eriopygini	<i>Hydroecioides</i>	<i>ruxis</i>	Dyar	1916	Nearctic						M1000
Noctuinae	Eriopygini	<i>Hydroecioides</i>	<i>serrata</i>	Grote	1880	Nearctic						M783
Noctuinae	Eriopygini	<i>Hydroecioides</i>	<i>xanthina</i>	Hampson	1905	Nearctic						M1811
Noctuinae	Eriopygini	<i>Hyperopia</i>	<i>jugifera</i>	Dyar	1920	Nearctic						M986
Noctuinae	Eriopygini	<i>Hypotrix</i>	<i>*sp.?</i>	?	?	Neotropical	P	B	L	G		C15782
Noctuinae	Eriopygini	<i>Hypotrix</i>	<i>alamosa</i>	Barnes	1904	Nearctic						C15778

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Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>diplogramma</i>	Schaus	1903	Nearctic						C14867
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>ferricola</i>	Smith	1905	Nearctic						C15762, M1035
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>hueco</i>	Barnes	1904	Nearctic						C15785
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>lunata</i>	Smith	1906	Nearctic					?	C15786, C15788, M785*
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>ocularis</i>	Lafontaine, Ferris, Walsh	2010	Nearctic					?	C14949
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>optima</i>	Dyar	1920	Nearctic						C15779
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>paralella</i>	Grote	1883	Nearctic						C 15773, M974
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>purpurigera</i>	Guenee	1852	Neotropical					?	C15791
Noctuidae	Eriopygini	<i>Hypotrix</i>	<i>trifascia</i>	Smith	1891	Nearctic						C15776
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>acutipennis</i>	Grote	1880	Nearctic	P	B	L	G		C16860, C16861, C16862
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>agnata</i>	Smith	1905	Nearctic				I		M1394
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>anguina</i>	Grote	1881	Nearctic						M62, M1392, M1668, M1755
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>buscki</i>	Barnes and Benjamin	1927	Nearctic						C15479
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>cuneata</i>	Grote	1873	Nearctic						M227
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>davena</i>	Smith	1901	Nearctic						M223
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>dimocki</i>	Schmidt	2015	Nearctic	P	B	L	G		C16896, C16897, C16898, C16890
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>erecta</i>	Walker	[1857]	Nearctic	P	B	L	G		M997
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>incurva</i>	Smith	1888	Nearctic						M1674
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>laudabilis</i>	Guenee	1852	Nearctic						M6
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>leucogramma</i>	Grote	1873	Nearctic						M1422
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>longiclava</i>	Smith	1891	Nearctic						M1390
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>lustralis</i>	Grote	1875	Nearctic	P	B	L	G		M536
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>marinitincta</i>	Harvey	1875	Nearctic						C15477
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>meditata</i>	Grote	1873	Nearctic	P	B	L	G		M78
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>naevia</i>	Smith	1898	Nearctic						M1391, M1395, M1401
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>palilis</i>	Harvey	1875	Nearctic						M987
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>pensilis</i>	Grote	1874	Nearctic	P	B	L	G		C16879, M1752
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>renigera</i>	Stephens	1829	Nearctic						C13551
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>sareta</i>	Smith	1906	Nearctic	P	B	L	G		C16863, C16864, C16865, C16866, C16867, C16868
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>spiculosa</i>	Grote	1883	Nearctic						M1010
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>stenotis</i>	Hampson	1905	Nearctic						M1175, M1389
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>strigicollis</i>	Wallengren	1860	Nearctic						C15478, M805, M1672, M1673, M1753
Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>teligera</i>	Morrison	1875	Nearctic	P	B	L	G		C16886



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Noctuidae	Eriopygini	<i>Lacinipolia</i>	<i>vicina</i>	Grote	1874	Nearctic	P	B	L	G		C16884, M23, M76, M221, M222
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>albetta</i>	Barnes and Benjamin	1923	Nearctic						M725
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>benjamini</i>	Hill	1927	Nearctic						M1001
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>discolor</i>	Smith	1899	Nearctic						M922, M1125, M1126
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>exasperata</i>	Franclemont	1941	Nearctic						M1901
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>flava</i>	Grote	1874	Nearctic						M284
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>imbecilla</i>	Fabricius	1794	Palearctic						M801
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>impingens</i>	Walker	1857	Nearctic						M705, M706
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>leucocycla</i>	Staudinger	1857	Nearctic						M723, M726, M729, M924
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>luteola</i>	Smith	1893	Nearctic						M745
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>promulsa</i>	Morrison	1875	Nearctic						M746
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>secedens</i>	Walker	[1858]	Nearctic						M1009
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>singula</i>	Grote	1880	Nearctic						M1713
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>skraelingia</i>	Herrich-Schäffer	[1852]	Nearctic						C17254, M1287
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>staudingeri</i>	Aurivillius	1891	Palearctic						M707, M708, M708, M777, M925,
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>subdita</i>	Möschler	1860	Nearctic						M968, M1177
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>subfuscula</i>	Grote	1874	Nearctic						M1005, M1176
Noctuidae	Eriopygini	<i>Lasionycta</i>	<i>lutina</i>	Smith	1902	Nearctic	p	b	l			M167, M220, M1127
Noctuidae	Eriopygini	<i>Mimobara</i>	<i>antonito</i>	Barnes	1907	Nearctic						C15945
Noctuidae	Eriopygini	<i>Mimobara</i>	<i>stigmata</i>	Smith	1908	Nearctic						M900, M969
Noctuidae	Eriopygini	<i>Orthodes</i>	<i>lanaris</i>	Butler	1890	Neotropical						M779
Noctuidae	Eriopygini	<i>Orthodes</i>	<i>majuscula</i>	Herrich-Schäffer	1868	Neotropical						M1168, M1185
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>alfkenii</i>	Grote	1895	Nearctic						M156, M1999
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>incincta</i>	Morrison	1875	Nearctic						M1073, M1147, M1441, M1902
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>melanopsis</i>	Hampson	1905	Nearctic						C15952, M763, M935, M950, M1148,
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>mulina</i>	Schaus	1894	Nearctic						M1555
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>oviduca</i>	Guenée	1852	Nearctic						C10745, M1542
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>rufula</i>	Grote	1874	Nearctic						M9131
Noctuidae	Eriopygini	<i>Pratorhodes</i>	<i>texana</i>	Smith	1900	Nearctic						C13579, M155, M596, M1417, M1659,
Noctuidae	Eriopygini	<i>Psammopolia</i>	<i>sala</i>	Troutbridge and Mustelin	2006	Nearctic						M1660, M1789
Noctuidae	Eriopygini	<i>Pseudorthodes</i>	<i>puerilis</i>	Grote	1874	Nearctic						M1540
Noctuidae	Eriopygini	<i>Pseudorthodes</i>	<i>vecors</i>	Guenée	1852	Nearctic						C16658
Noctuidae	Eriopygini	<i>Synorthodes</i>	<i>melanops</i>	Dyar	1912	Nearctic						C13980

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Noctuinae	Eriopygini	<i>Trichocera</i>	<i>comstocki</i>	Benjamin	1932	Nearctic						M1412
Noctuinae	Eriopygini	<i>Trichocera</i>	<i>harbisoni</i>	Mustelin	2006	Nearctic						M1111
Noctuinae	Eriopygini	<i>Trichofelitia</i>	<i>circumdanta</i>	Grote	1883	Nearctic						C15798, M757
Noctuinae	Eriopygini	<i>Tricholita</i>	<i>bisulca</i>	Grote	1881	Nearctic						M710
Noctuinae	Eriopygini	<i>Tricholita</i>	<i>chipeta</i>	Barnes	1904	Nearctic						M1411
Noctuinae	Eriopygini	<i>Tricholita</i>	<i>signata</i>	Walker	1860	Nearctic						C17321, M784
Noctuinae	Eriopygini	<i>Trichopolia</i>	<i>dentatella</i>	Grote	1883	Nearctic						C15796, M1343
Noctuinae	Eriopygini	<i>Ulolonche</i>	<i>culea</i>	Guenée	1852	Nearctic						M505
Noctuinae	Eriopygini	<i>Ulolonche</i>	<i>orbiculata</i>	Smith	1891	Nearctic						C15947, M933
Noctuinae	Eriopygini	<i>Zosteropoda</i>	<i>hirtipes</i>	Grote	1874	Nearctic						M247
Noctuinae	Hadenini	<i>Anarta</i>	<i>crotchii</i>	Grote	1880	Nearctic			L			C13979
Noctuinae	Hadenini	<i>Anarta</i>	<i>melanopa</i>	Thunberg	1791	Palearctic						6
Noctuinae	Hadenini	<i>Anarta</i>	<i>myrtilli</i>	Linnaeus	1761	Palearctic	p		1			6
Noctuinae	Hadenini	<i>Anarta</i>	<i>trifolii</i>	Hufnagel	1766	Palearctic						3, 4, 6, M861
Noctuinae	Hadenini	<i>Ceramica</i>	<i>pisi</i>	Linnaeus	1758	Palearctic						4, 6
Noctuinae	Hadenini	<i>Conisania</i>	<i>leineri</i>	Freyer	1836	Palearctic						M1720
Noctuinae	Hadenini	<i>Conisania</i>	<i>poelli</i>	Stertz	1915	Palearctic						M909
Noctuinae	Hadenini	<i>Coranarta</i>	<i>cordigera</i>	Thunberg	1788	Palearctic						6
Noctuinae	Hadenini	<i>Dargida</i>	<i>diffusa</i>	Walker	1856	Nearctic						C16667
Noctuinae	Hadenini	<i>Dargida</i>	<i>diffusa</i>	Walker	1856	Nearctic						C16668, M957, M958, M1539
Noctuinae	Hadenini	<i>Dargida</i>	<i>egregia</i>	Draudt	1924	Neotropical						M1119
Noctuinae	Hadenini	<i>Dargida</i>	<i>grammivora</i>	Walker	1856	Neotropical						M1189, M1833
Noctuinae	Hadenini	<i>Dargida</i>	<i>juxta</i>	Pogue	2008	Neotropical						M1834
Noctuinae	Hadenini	<i>Dargida</i>	<i>procinctus</i>	Grote	1873	Nearctic						M744
Noctuinae	Hadenini	<i>Dargida</i>	<i>tetera</i>	Smith	1902	Nearctic						M1750
Noctuinae	Hadenini	<i>Dasygaster</i>	<i>hollandiae</i>	Guenée	1852	Australasia	p		1			M1466
Noctuinae	Hadenini	<i>Dasygaster</i>	<i>punctosa</i>	Walker	[1857]	Australasia			L			M1535
Noctuinae	Hadenini	<i>Dictyestra</i>	<i>dissectus</i>	Walker	1865	Oriental			1			M1215
Noctuinae	Hadenini	<i>Feredayia</i>	<i>graminosa</i>	Walker	1857	Australasia	p					M1465
Noctuinae	Hadenini	<i>Hada</i>	<i>plebeja</i>	Hufnagel	1766	Palearctic	p		B	L	G	4, 6, M489
Noctuinae	Hadenini	<i>Hadena</i>	<i>albimacula</i>	Borkhausen	1792	Palearctic						3, 6
Noctuinae	Hadenini	<i>Hadena</i>	<i>bicruris</i>	Hufnagel	1766	Palearctic						M759
Noctuinae	Hadenini	<i>Hadena</i>	<i>caesia</i>	Denis and Schiffemüller	1775	Palearctic						3, 6

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Noctuinae	Hadenini	<i>Hadena</i>	<i>circumvadis</i>	Smith	1902	Nearctic						M161, M1368
Noctuinae	Hadenini	<i>Hadena</i>	<i>compta</i>	Denis and Schiffemüller	1775	Palearctic						M965
Noctuinae	Hadenini	<i>Hadena</i>	<i>confusa</i>	Hufnagel	1766	Palearctic						6, M494
Noctuinae	Hadenini	<i>Hadena</i>	<i>eberti</i>	Boursin	1961	Palearctic						M1517, M1602
Noctuinae	Hadenini	<i>Hadena</i>	<i>ectrapela</i>	Smith	1898	Nearctic						C12611, M165
Noctuinae	Hadenini	<i>Hadena</i>	<i>ectrypa</i>	Morrison	1875	Nearctic						M1029
Noctuinae	Hadenini	<i>Hadena</i>	<i>irregularis</i>	Hufnagel	1766	Palearctic						6, C12591, M994
Noctuinae	Hadenini	<i>Hadena</i>	<i>macabei</i>	Troubridge and Crabo	2002	Nearctic						C12605
Noctuinae	Hadenini	<i>Hadena</i>	<i>perplexa</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Hadenini	<i>Hadena</i>	<i>silenes</i>	Hübner	[1822]	Palearctic						M1223
Noctuinae	Hadenini	<i>Hadena</i>	<i>variolata</i>	Smith	1888	Nearctic						C12582, C17221, M721, M1381
Noctuinae	Hadenini	<i>Hadula</i>	<i>perdentata</i>	Hampson	1894	Oriental	p					M1603
Noctuinae	Hadenini	<i>Hecatera</i>	<i>bicolorata</i>	Hufnagel	1766	Palearctic						6, C11700, M926, M927
Noctuinae	Hadenini	<i>Hecatera</i>	<i>cappa</i>	Hübner	[1809]	Palearctic						M384
Noctuinae	Hadenini	<i>Hecatera</i>	<i>dysoidea</i>	Denis and Schiffemüller	1775	Palearctic	p	B	L	G		6, M1365
Noctuinae	Hadenini	<i>Hyssia</i>	<i>cavernosa</i>	Eversmann	1842	Palearctic	p	b		l	g	M1212
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>atlantica</i>	Grote	1874	Nearctic						7, M42, M75, M267, M1496
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>contigua</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>grandis</i>	Guenée	1852	Nearctic						7, M65
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>nevadae</i>	Grote	1876	Nearctic						7, M174
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>radix</i>	Walker	[1857]	Nearctic						7, M97, M300
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>suasa</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>subjuncta</i>	Grote and Robinson	1868	Nearctic						7, M10, M226
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>thalassina</i>	Hufnagel	1766	Palearctic						4, 6
Noctuinae	Hadenini	<i>Lacanobia</i>	<i>w-latinum</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Hadenini	<i>Manestra</i>	<i>brassicae</i>	Linnaeus	1758	Palearctic	p	B	L	G		4, 5, 6, M280
Noctuinae	Hadenini	<i>Manestra</i>	<i>configurata</i>	Walker	1856	Nearctic	p	B	L	G		M747
Noctuinae	Hadenini	<i>Manestra</i>	<i>curialis</i>	Smith	1888	Nearctic	p	B	L	G		C11074
Noctuinae	Hadenini	<i>Melanchnra</i>	<i>adjuncta</i>	Boisduval	1852	Nearctic	p	B	L	G		7, M36, M219
Noctuinae	Hadenini	<i>Melanchnra</i>	<i>assimilis</i>	Morrison	1874	Nearctic						7, M168
Noctuinae	Hadenini	<i>Melanchnra</i>	<i>persicariae</i>	Linnaeus	1761	Palearctic	p	B	L	G		4, 5, 6
Noctuinae	Hadenini	<i>Melanchnra</i>	<i>picta</i>	Harris	1841	Nearctic						7, M38, M225
Noctuinae	Hadenini	<i>Melanchnra</i>	<i>pulverulenta</i>	Smith	1888	Nearctic						7

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Noctuinae	Hadenini	<i>Metopiora</i>	<i>sanguinata</i>	Lucas	1893	Palearctic						M1463
Noctuinae	Hadenini	<i>Pachetra</i>	<i>sagittigera</i>	Hufnagel	1766	Palearctic						M310
Noctuinae	Hadenini	<i>Papestra</i>	<i>biren</i>	Goeze	1781	Nearctic	P	b	L	G		6, 7, C17250
Noctuinae	Hadenini	<i>Papestra</i>	<i>brenda</i>	Barnes and McDunnough	1916	Nearctic			L			7, M256, M286, M308
Noctuinae	Hadenini	<i>Papestra</i>	<i>cristifera</i>	Walker	1858	Nearctic	P	B	L	G		7, M197, M236
Noctuinae	Hadenini	<i>Papestra</i>	<i>invalida</i>	Smith	1891	Nearctic	P	B	L	G		7, M287
Noctuinae	Hadenini	<i>Papestra</i>	<i>quadrata</i>	Smith	1891	Nearctic	P	B	L	G		7, M251, M252
Noctuinae	Hadenini	<i>Polia</i>	<i>bombycina</i>	Hufnagel	1766	Palearctic	p	b	L		6	
Noctuinae	Hadenini	<i>Polia</i>	<i>discalis</i>	Grote	1877	Nearctic	P	B	L	G	7	
Noctuinae	Hadenini	<i>Polia</i>	<i>hepatica</i>	Clerk	1759	Palearctic	P	B	L	G	3, 6	
Noctuinae	Hadenini	<i>Polia</i>	<i>imbrifera</i>	Guenée	1852	Nearctic					7, M194	
Noctuinae	Hadenini	<i>Polia</i>	<i>nimbosa</i>	Guenée	1852	Nearctic			1		7, M3, M24, M218	
Noctuinae	Hadenini	<i>Polia</i>	<i>nugatis</i>	Smith	1898	Nearctic					7	
Noctuinae	Hadenini	<i>Polia</i>	<i>piniae</i>	Buckett and Bauer	[1967]	Nearctic	P	B	L	G	7, M169, M170	
Noctuinae	Hadenini	<i>Polia</i>	<i>purpurissata</i>	Grote	1864	Nearctic					7, M2, M49, M166, M262	
Noctuinae	Hadenini	<i>Polia</i>	<i>richardsoni</i>	Curtis	1835	Nearctic	P	B	L	G	7, C17252, M724	
Noctuinae	Hadenini	<i>Polia</i>	<i>rogenhoferi</i>	Möschler	1870	Nearctic					7, M237	
Noctuinae	Hadenini	<i>Polia</i>	<i>serratilinea</i>	Ochsenheimer	1816	Palearctic	p	1			M1979	
Noctuinae	Hadenini	<i>Polia authors</i>	<i>marea</i>	Schaus	1894	Nearctic	P	B	L	G	M999	
Noctuinae	Hadenini	<i>Poliodesstra</i>	<i>glauippe</i>	Dognin	1907	Neotropical	P	B	L	G	M1445	
Noctuinae	Hadenini	<i>Saragossa</i>	<i>seeboldi</i>	Standing	1900	Palearctic					M907	
Noctuinae	Hadenini	<i>Saragossa</i>	<i>siccanorum</i>	Standing	1870	Palearctic					M1366	
Noctuinae	Hadenini	<i>Scriptania</i>	<i>nr. michaelsoni</i>	(according to McCabe)	?	Neotropical	P	B	L	G	M1301	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>artesta</i>	Smith	1903	Nearctic					M52	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>congermana</i>	Morrison	1874	Nearctic	P	B	L	G	M736	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>fuscolutea</i>	Smith	1892	Nearctic	P	B	L	G	M1409	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>maryx</i>	Guenée	1852	Nearctic	P	B	L	G	M50	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>mojave</i>	Benjamin	1932	Nearctic	P	B	L	G	M888, M1432	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>nr. u-scripta</i>	Smith	1891	Nearctic					M158	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>reticulata</i>	Villers	1789	Palearctic	P	B	L	G	6, M809	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>rivularis</i>	Fabricius	1775	Palearctic					6	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>rosea</i>	Harvey	1874	Nearctic	P	B	L	G	M9	
Noctuinae	Hadenini	<i>Sideridis</i>	<i>ruisa</i>	Forbes	1913	Nearctic	P	B	L	G	M1927	

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Noctuinae	Hadenini	<i>Sideridis</i>	<i>turbida</i>	Esper	1790	Palearctic	P	B	L	G		6, M1592
Noctuinae	Hadenini	<i>Sideridis</i>	<i>u-scripta</i>	Smith	1891	Nearctic						M1397
Noctuinae	Hadenini	<i>Sideridis</i>	<i>vindemialis</i>	Grote	1875	Nearctic	p	L				M1096
Noctuinae	Hadenini	<i>Spiramater</i>	<i>lutra</i>	Guenée	1852	Nearctic						7, M1, M173, M231
Noctuinae	Hadenini	<i>Tmetolophota</i>	<i>propria</i>	Walker	1856	Australasia	p	1				M1461
Noctuinae	Hadenini	<i>Tmetolophota</i>	<i>semivittata</i>	Walker	1865	Australasia						M1609
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>beanii</i>	Grote	1877	Nearctic						7, M141
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>dodii</i>	Smith	1904	Nearctic						7, M242
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>legitima</i>	Grote	1864	Nearctic						7, M98, M541, M542
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>lilacina</i>	Harvey	1874	Nearctic	P	B	L	G		7, M162, M163, M164
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>liquida</i>	Grote	1881	Nearctic	P	B	L	G		7
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>prodeniformis</i>	Smith	1888	Nearctic	P	B	L	G		7, M56
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>rugosa</i>	Morrison	1875	Nearctic						7, M41
Noctuinae	Hadenini	<i>Trichordestra</i>	<i>tacoma</i>	Strecker	1900	Nearctic						7, M21, M40, M198
Noctuinae	Hadenini	<i>Tridepia</i>	<i>nova</i>	Smith	1903	Nearctic	P	B	L	G		C17315
Noctuinae	Hadenini	<i>Trudestra</i>	<i>hadeniformis</i>	Smith	1894	Nearctic	P	B	L	G		C17317
Noctuinae	Leucanini	<i>Hypoptervidia</i>	<i>reversa</i>	Moore	[1885]	Oriental	P	B	L		?	11, M1219
Noctuinae	Leucanini	<i>Leucania</i>	<i>adjuta</i>	Grote	1874	Nearctic						M1415, M1420
Noctuinae	Leucanini	<i>Leucania</i>	<i>anteroclara</i>	Smith	1902	Nearctic					LSO	C13597, M205, M482, M560
Noctuinae	Leucanini	<i>Leucania</i>	<i>calidior</i>	Forbes	1936	Nearctic					LSO	M1108
Noctuinae	Leucanini	<i>Leucania</i>	<i>comma</i>	Linnaeus	1761	Palearctic					LSO	5, 6, 10, C13530, M1088
Noctuinae	Leucanini	<i>Leucania</i>	<i>commoides</i>	Guenée	1852	Nearctic					LSO	M380, M418
Noctuinae	Leucanini	<i>Leucania</i>	<i>dorsalis</i>	Walker	1856	Neotropical						M568
Noctuinae	Leucanini	<i>Leucania</i>	<i>extenuata</i>	Guenée	1852	Neotropical						M694
Noctuinae	Leucanini	<i>Leucania</i>	<i>farcta</i>	Grote	1881	Nearctic					LSO	C13598
Noctuinae	Leucanini	<i>Leucania</i>	<i>humidicola</i>	Guenée	1852	Neotropical					LSO	M514
Noctuinae	Leucanini	<i>Leucania</i>	<i>imperfecta</i>	Smith	1894	Nearctic						C13596
Noctuinae	Leucanini	<i>Leucania</i>	<i>incognita</i>	Barnes and McDunnough	1918	Nearctic					LSO	M1558
Noctuinae	Leucanini	<i>Leucania</i>	<i>insueta</i>	Guenée	1852	Nearctic					LSO	C13531, M204, M453, M454
Noctuinae	Leucanini	<i>Leucania</i>	<i>joannisi</i>	Boursin & Rungs	1952	Palearctic					Iso	10
Noctuinae	Leucanini	<i>Leucania</i>	<i>linita</i>	Guenée	1852	Nearctic						M660
Noctuinae	Leucanini	<i>Leucania</i>	<i>loreyi</i>	Duponchel	1827	Palearctic					Iso	10, M1046
Noctuinae	Leucanini	<i>Leucania</i>	<i>multilinea</i>	Walker	1856	Nearctic					LSO	C13599, M381, M607, M661, M742

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Noctuinae	Leucanini	<i>Leucania</i>	<i>oaxacana</i>	Schaus	1898	Nearctic					LSO	M1816
Noctuinae	Leucanini	<i>Leucania</i>	<i>obsolleta</i>	Hubner	1803	Palearctic					LSO	3, 5, 6, 10
Noctuinae	Leucanini	<i>Leucania</i>	<i>phragmitidicola</i>	Guenée	1852	Nearctic					LSO	M630, M1068
Noctuinae	Leucanini	<i>Leucania</i>	<i>pilipalpis</i>	Grote	1876	Nearctic					LSO	M1646
Noctuinae	Leucanini	<i>Leucania</i>	<i>polystrota</i>	Hampson	1905	Neotropical					LSO	M1813
Noctuinae	Leucanini	<i>Leucania</i>	<i>punctosa</i>	Treitschke	1825	Palearctic					iso	10
Noctuinae	Leucanini	<i>Leucania</i>	<i>putrescens</i>	Hubner	1824	Palearctic					LSO	5, 6, 10
Noctuinae	Leucanini	<i>Leucania</i>	<i>ravilinsi</i>	A dams	2001	Neotropical						M517, M1890
Noctuinae	Leucanini	<i>Leucania</i>	<i>roseilinea</i>	Walker	1862	Oriental						M1458, M1459
Noctuinae	Leucanini	<i>Leucania</i>	<i>subpunctata</i>	Harvey	1875	Nearctic						M1439
Noctuinae	Leucanini	<i>Leucania</i>	<i>ursula</i>	Forbes	1936	Nearctic					LSO	M1644, M1645
Noctuinae	Leucanini	<i>Leucania</i>	<i>venaliba</i>	Moore	1867	Oriental						M1460
Noctuinae	Leucanini	<i>Leucania</i>	<i>zeae</i>	Duponchel	1827	Palearctic					iso	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>albipuncta</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G	HBO	10, M814
Noctuinae	Leucanini	<i>Mythimna</i>	<i>alopecuri</i>	Boisduval	1840	Palearctic					SBO	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>andereggii</i>	Boisduval	1840	Palearctic					sbo	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>australis</i>	Franclemont	1951	Australasia	P	B	L	G		M1529
Noctuinae	Leucanini	<i>Mythimna</i>	<i>congrua</i>	Hubner	1817	Palearctic	P	B	L	G	HBO	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>conigera</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		3, 5, 6, 10, M1087
Noctuinae	Leucanini	<i>Mythimna</i>	<i>consanguis</i>	Guenée	1852	Oriental					?	M1013
Noctuinae	Leucanini	<i>Mythimna</i>	<i>ferrago</i>	Fabricius	1787	Oriental	P	B	L	G	HBO	3, 5, 6, 10, M1069
Noctuinae	Leucanini	<i>Mythimna</i>	<i>impura</i>	Hubner	[1808]	Oriental	P	B	L	G		5, 6, 10, M1048
Noctuinae	Leucanini	<i>Mythimna</i>	<i>l-album</i>	Linnaeus	1767	Oriental	P	B	L	G	HBO	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>oxygala</i>	Grote	1881	Nearctic	P	B	L	G		M964
Noctuinae	Leucanini	<i>Mythimna</i>	<i>pallens</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 5, 6, 10, M1047
Noctuinae	Leucanini	<i>Mythimna</i>	<i>prominens</i>	Walker	1856	Palearctic					SBO	10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>pudorina</i>	Denis and Schiffemüller	1775	Palearctic						10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>riparia</i>	Rambur	1829	Palearctic	P	B	L	G		10
Noctuinae	Leucanini	<i>Mythimna</i>	<i>rorainae</i>	Franclemont	1951	Neotropical	P	B	L	G		M1832
Noctuinae	Leucanini	<i>Mythimna</i>	<i>sequax</i>	Franclemont	1951	Nearctic	P	B	L	G		M798, M1836
Noctuinae	Leucanini	<i>Mythimna</i>	<i>sicula</i>	Treitschke	1835	Palearctic					SBO	10, M1043
Noctuinae	Leucanini	<i>Mythimna</i>	<i>straminea</i>	Treitschke	1825	Palearctic	P	B	L	G		6, 10, M1044
Noctuinae	Leucanini	<i>Mythimna</i>	<i>turca</i>	Linnaeus	1761	Palearctic						6, 10, M816

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Noctuinae	Leucanini	<i>Mythimna</i>	<i>unipuncta</i>	Haworth	1809	Palearctic	P	B	L	G		10, C11775, Z2014010
Noctuinae	Leucanini	<i>Mythimna</i>	<i>vitellina</i>	Hubner	[1808]	Palearctic	P	B	L	G		10, M1045
Noctuinae	Leucanini	<i>Senta</i>	<i>flammea</i>	Curtis	1828	Palearctic					LSO?	6*, 10, M808*
Noctuinae	Metoponiinae	<i>Panemeria</i>	<i>tenebrata</i>	Scopoli	1763	Palearctic						6
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>alternata</i>	Grote	1864	Nearctic						M551
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>cupida</i>	Grote	1864	Nearctic						M548
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>dickeli</i>	Lafontaine	1998	Nearctic						C14145
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>duanca</i>	Smith	1908	Nearctic						C16733
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>hermina</i>	Lafontaine	1998	Nearctic						C14147
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>magnicupida</i>	Lafontaine	1998	Nearctic						M1705
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>nefascia</i>	Smith	1908	Nearctic						C14141, M1919
Noctuinae	Noctuini	<i>Abagrotis</i>	<i>placida</i>	Grote	1876	Nearctic						C11077, C14143
Noctuinae	Noctuini	<i>Actebia</i>	<i>balanitis</i>	Grote	1873	Nearctic						12
Noctuinae	Noctuini	<i>Actebia</i>	<i>fennica</i>	Tauscher	1806	Palearctic						12
Noctuinae	Noctuini	<i>Actebia</i>	<i>praecox</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>clavis</i>	Hufnagel	1766	Palearctic						4, 6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>exclamationis</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>ipsilon</i>	Hufnagel	1766	Palearctic						4, 6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>puta</i>	Hubner	1803	Palearctic						4, 6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>ripae</i>	Hubner	1823	Palearctic						6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>segetum</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>trux</i>	Hubner	1824	Palearctic						6
Noctuinae	Noctuini	<i>Agrotis</i>	<i>vestigialis</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Noctuini	<i>Anaplectoides</i>	<i>prasina</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Noctuini	<i>Anaplectoides</i>	<i>pressus</i>	Grote	1874	Nearctic						M665
Noctuinae	Noctuini	<i>Anicla</i>	<i>*n. sp.</i>	?	?	Neotropical	P	B	L	G		C13591
Noctuinae	Noctuini	<i>Anicla</i>	<i>beata</i>	Grote	1883	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>biformata</i>	Lafontaine	2004	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>cemolia</i>	Franclemont	1967	Nearctic	P					12, C11892, M1880
Noctuinae	Noctuini	<i>Anicla</i>	<i>digna</i>	Morrison	1875	Nearctic	P	B	L	G		12, M1847
Noctuinae	Noctuini	<i>Anicla</i>	<i>espoetia</i>	Dyar	1910	Nearctic	P	B	L	G		12, C15959
Noctuinae	Noctuini	<i>Anicla</i>	<i>exuberans</i>	Smith	1898	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>forbesi</i>	Franclemont	1952	Nearctic	P	B	L	G		12, M547, M1477

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Noctuinae	Noctuini	<i>Anicla</i>	<i>ignicans</i>	Guénée	1852	Neotropical						C12051, M1884
Noctuinae	Noctuini	<i>Anicla</i>	<i>illapsa</i>	Walker	1857	Nearctic	P	B	L	G		12, C15953, C15954, C15955, M1479
Noctuinae	Noctuini	<i>Anicla</i>	<i>infecta</i>	Ochsenheimer	1816	Nearctic	P	B	L	G		12, M928, M929, M1881, M1882, M1883
Noctuinae	Noctuini	<i>Anicla</i>	<i>lubricans</i>	Guénée	1852	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>mus</i>	Lafontaine	2004	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>simplicius</i>	Morrison	1875	Nearctic	P	B	L	G		12, C15956, C15957
Noctuinae	Noctuini	<i>Anicla</i>	<i>sullivani</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Anicla</i>	<i>temperata</i>	Schaus	1894	Nearctic	P	B	L	G		C12050
Noctuinae	Noctuini	<i>Anicla</i>	<i>tenuescens</i>	Smith	1890	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Anicla</i>	<i>tepperi</i>	Smith	1888	Nearctic	P	B	L	G		12
Noctuinae	Noctuini	<i>Apictoides</i>	<i>condita</i>	Guénée	1852	Nearctic						M658, M659, M662, M822
Noctuinae	Noctuini	<i>Axytia</i>	<i>putris</i>	Linnaeus	1761	Palearctic						6, M1955
Noctuinae	Noctuini	<i>Cerastis</i>	<i>leucographa</i>	Denis and Schiffmüller	1775	Palearctic						6, M642
Noctuinae	Noctuini	<i>Cerastis</i>	<i>rubricosa</i>	Denis and Schiffmüller	1775	Palearctic						3, 6, M643
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>absidium</i>	Harvey	1875	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>alaskensis</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>albisericea</i>	Blanchard	1976	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>arinetum</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>canariana</i>	McDunnough	1932	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>columbia</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>flavum</i>	Fauske and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>fuscum</i>	Troubridge and Crabo	1996	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>gillaspys</i>	Blanchard	1976	Nearctic						12, M1533
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>grandis</i>	Strecker	1877	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>longipenne</i>	Grote	1882	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>michiganensis</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>muselini</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>mutans</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>nevada</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>opleri</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>pictum</i>	Fauske and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>robertsoni</i>	Crabo and Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>sanctaemonicae</i>	Dyar	1904	Nearctic						12



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Noctuinae	Noctuini	<i>Copablepharon</i>	<i>serrata</i>	McDunnough	1932	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>serratrigrande</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>spiritum</i>	Crabo and Fauske	2004	Nearctic						12
Noctuinae	Noctuini	<i>Copablepharon</i>	<i>viridisparva</i>	Dod	1916	Nearctic						12
Noctuinae	Noctuini	<i>Cryptocala</i>	<i>acadiensis</i>	Bethune	1869	Nearctic						M338
Noctuinae	Noctuini	<i>Cryptocala</i>	<i>chardinyi</i>	Boisduval	1829	Palearctic						M646
Noctuinae	Noctuini	<i>Diarsia</i>	<i>brunnea</i>	Denis and Schiffemüller	1775	Palearctic						3, 6
Noctuinae	Noctuini	<i>Diarsia</i>	<i>dahlia</i>	Hübner	1813	Palearctic						6
Noctuinae	Noctuini	<i>Diarsia</i>	<i>dislocata</i>	Smith	1904	Nearctic						C11062
Noctuinae	Noctuini	<i>Diarsia</i>	<i>esurialis</i>	Grote	1881	Nearctic						C11065
Noctuinae	Noctuini	<i>Diarsia</i>	<i>jucunda</i>	Walker	[1857]	Nearctic						C11063
Noctuinae	Noctuini	<i>Diarsia</i>	<i>mendica</i>	Fabricius	1775	Palearctic						6
Noctuinae	Noctuini	<i>Diarsia</i>	<i>rosaria</i>	Grote	1878	Nearctic						C11060
Noctuinae	Noctuini	<i>Diarsia</i>	<i>rubi</i>	Vieweg	1790	Palearctic						6
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>acclivis</i>	Morrison	1875	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>arabella</i>	Dyar	1901	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>broui</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>capota</i>	Smith	1908	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>cataclivis</i>	Dyar	1910	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>cyminoipristes</i>	Dyar	1912	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>dubitata</i>	McDunnough	1933	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>flammatra</i>	Denis and Schiffemüller	1775	Palearctic						3, 6
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>grandipennis</i>	Grote	1883	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>grotei</i>	Franclemont and Todd	1983	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>kyune</i>	Barnes	1904	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>larga</i>	Smith	1908	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>lobato</i>	Barnes	1904	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>longidens</i>	Smith	1890	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>madida</i>	Cuenée	1852	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>mizteca</i>	Schaus	1894	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>neoclivis</i>	Barnes and Benjamin	1924	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>polycala</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>proclivis</i>	Smith	1888	Nearctic						12

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Noctuinae	Noctuini	<i>Dichagyris</i>	<i>pyrsogramma</i>	Dyar	1916	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>reliqua</i>	Lafontaine and Schweitzer	2004	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>ruckesi</i>	Barnes and Benjamin	1927	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>salina</i>	Barnes	1904	Nearctic						12, C12058
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>socorro</i>	Barnes	1904	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>timbor</i>	Dyar	1919	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>triphaenoides</i>	Dyar	1912	Nearctic						12
Noctuinae	Noctuini	<i>Dichagyris</i>	<i>variabilis</i>	Grote	1874	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>canescens</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>dapsilis</i>	Grote	1882	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>dollii</i>	Grote	[1883]	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>elingua</i>	Smith	1903	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>fimbriaris</i>	Guenée	1852	Nearctic						12
Noctuinae	Noctuini	<i>Eucloptocnemis</i>	<i>rufula</i>	Lafontaine	2004	Nearctic						12
Noctuinae	Noctuini	<i>Eugnorisma</i>	<i>glareosa</i>	Esper	1788	Palearctic						6
Noctuinae	Noctuini	<i>Eurois</i>	<i>occulta</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Noctuini	<i>Euxoa</i>	<i>aequalis</i>	Harvey	1876	Nearctic						M8
Noctuinae	Noctuini	<i>Euxoa</i>	<i>cincta</i>	Barnes and McDunnough	1924	Nearctic						C13536
Noctuinae	Noctuini	<i>Euxoa</i>	<i>comosa</i>	Morrison	1876	Nearctic						C11073
Noctuinae	Noctuini	<i>Euxoa</i>	<i>cursoria</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Noctuini	<i>Euxoa</i>	<i>medialis</i>	Smith	1888	Nearctic						M1467, M1468
Noctuinae	Noctuini	<i>Euxoa</i>	<i>nigricans</i>	Linnaeus	1761	Palearctic						6
Noctuinae	Noctuini	<i>Euxoa</i>	<i>obelisca</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Noctuini	<i>Euxoa</i>	<i>tritici</i>	Linnaeus	1761	Palearctic						6
Noctuinae	Noctuini	<i>Feltia</i>	<i>herilis</i>	Grote	1873	Nearctic						C12047
Noctuinae	Noctuini	<i>Feltia</i>	<i>subgothica</i>	Haworth	1809	Nearctic						C12046
Noctuinae	Noctuini	<i>Feltia</i>	<i>tricolor</i>	Lintner	1874	Nearctic						C12044
Noctuinae	Noctuini	<i>Graphiphora</i>	<i>auger</i>	Fabricius	1775	Palearctic						6
Noctuinae	Noctuini	<i>Hemieuxoa</i>	<i>rudens</i>	Harvey	1875	Nearctic						12
Noctuinae	Noctuini	<i>Lycophotia</i>	<i>phyllophora</i>	Grote	1874	Nearctic						M406
Noctuinae	Noctuini	<i>Lycophotia</i>	<i>porphyrea</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Noctuini	<i>Naenia</i>	<i>typica</i>	Linnaeus	1758	Palearctic						4, 6
Noctuinae	Noctuini	<i>Noctua</i>	<i>comes</i>	Hübner	1813	Palearctic						6

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Noctuinae	Noctuini	<i>Noctua</i>	<i>fimbriata</i>	Schreber	1759	Palearctic					6	
Noctuinae	Noctuini	<i>Noctua</i>	<i>interjecta</i>	Hübner	1803	Palearctic					3, 6	
Noctuinae	Noctuini	<i>Noctua</i>	<i>janthina</i>	Denis and Schiffemiller	1775	Palearctic					6	
Noctuinae	Noctuini	<i>Noctua</i>	<i>orbana</i>	Hufnagel	1766	Palearctic					3	
Noctuinae	Noctuini	<i>Noctua</i>	<i>pronuba</i>	Linnaeus	1758	Palearctic					3, 6	
Noctuinae	Noctuini	<i>Ochropleura</i>	<i>plecta</i>	Linnaeus	1761	Palearctic					6	
Noctuinae	Noctuini	<i>Paradiarsia</i>	<i>littoralis</i>	Packard	1867	Nearctic					M47	
Noctuinae	Noctuini	<i>Peridroma</i>	<i>clerica</i>	Butler	1882	Neotropical	P	B	L	G		C7819
Noctuinae	Noctuini	<i>Peridroma</i>	<i>saucia</i>	Hübner	[1808]	Nearctic	P	B	L	G		4, 6, 12, M1385, Z2014008
Noctuinae	Noctuini	<i>Peridroma</i>	<i>semidolens</i>	Walker	1857	Neotropical	P	B	L	G		C12049
Noctuinae	Noctuini	<i>Protogygia</i>	<i>albata</i>	Trourbridge and Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>album</i>	Harvey	1876	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>arena</i>	Trourbridge and Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>biclavus</i>	Grote	1879	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>constocki</i>	McDunnough	1934	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>elevata</i>	Smith	1891	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>enalaga</i>	McDunnough	1932	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>lagena</i>	Grote	1875	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>milleri</i>	Grote	1876	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>pallida</i>	Fauske and Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>pectinata</i>	Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>polingi</i>	Barnes and Benjamin	1922	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>postera</i>	Fauske and Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>querula</i>	Dod	1915	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>rufescens</i>	Fauske and Lafontaine	2004	Nearctic					12	
Noctuinae	Noctuini	<i>Protogygia</i>	<i>whitesandsensis</i>	Metzler & Forbes	2009	Nearctic					12	
Noctuinae	Noctuini	<i>Protolampra</i>	<i>brunneicollis</i>	Grote	1864	Nearctic					M599, M652	
Noctuinae	Noctuini	<i>Protolampra</i>	<i>rufipectus</i>	Morrison	1875	Nearctic					M591, M650, M651, M701, M702	
Noctuinae	Noctuini	<i>Protolampra</i>	<i>sobrina</i>	Duponchel	1843	Palearctic					6, M677	
Noctuinae	Noctuini	<i>Pseudohermonassa</i>	<i>bicarnea</i>	Guenée	1852	Nearctic					M329	
Noctuinae	Noctuini	<i>Pseudohermonassa</i>	<i>tenuicula</i>	Morrison	1875	Nearctic					M334	
Noctuinae	Noctuini	<i>Rhyacia</i>	<i>simulans</i>	Hufnagel	1766	Palearctic					4, 6	
Noctuinae	Noctuini	<i>Richia</i>	<i>chortalis</i>	Harvey	1875	Nearctic					C12048	

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Noctuinae	Noctuini	<i>Richia</i>	<i>olearia</i>	Hampson	1918	Nearctic						C12057
Noctuinae	Noctuini	<i>Spaelotis</i>	<i>ravida</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Noctuini	<i>Standfussiana</i>	<i>lucerna</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Noctuini	<i>Siriaca</i>	<i>albica</i>	Smith	1888	Nearctic						12
Noctuinae	Noctuini	<i>Xestia</i>	<i>agathina</i>	Duponchel	1827	Palearctic						3, 6
Noctuinae	Noctuini	<i>Xestia</i>	<i>albuncula</i>	Eversmann	1851	Palearctic						C10777, C10778, C10779
Noctuinae	Noctuini	<i>Xestia</i>	<i>alpicola</i>	Zetterstedt	1839	Palearctic						3, 6
Noctuinae	Noctuini	<i>Xestia</i>	<i>ashworthii</i>	Doubleday	1855	Palearctic						3, 6
Noctuinae	Noctuini	<i>Xestia</i>	<i>badicollis</i>	Grote	1873	Nearctic						M344, M465
Noctuinae	Noctuini	<i>Xestia</i>	<i>baja</i>	Denis and Schiffemüller	1775	Palearctic						6, M645
Noctuinae	Noctuini	<i>Xestia</i>	<i>castanea</i>	Esper	1798	Palearctic						6
Noctuinae	Noctuini	<i>Xestia</i>	<i>cinerascens</i>	Smith	1891	Nearctic						M1110
Noctuinae	Noctuini	<i>Xestia</i>	<i>c-nigrum</i>	Linnaeus	1758	Palearctic						4, 6
Noctuinae	Noctuini	<i>Xestia</i>	<i>dilucida</i>	Morrison	1875	Nearctic						M346, m347
Noctuinae	Noctuini	<i>Xestia</i>	<i>ditrapezium</i>	Denis and Schiffemüller	1775	Palearctic						3, 6
Noctuinae	Noctuini	<i>Xestia</i>	<i>elimata</i>	Guenée	1852	Nearctic						M343, M466, M532
Noctuinae	Noctuini	<i>Xestia</i>	<i>fabulosa</i>	Ferguson	1965	Nearctic						M1006
Noctuinae	Noctuini	<i>Xestia</i>	<i>homogena</i>	McDunnough	1921	Nearctic						M1458
Noctuinae	Noctuini	<i>Xestia</i>	<i>normaniana</i>	Grote	1874	Nearctic						M648
Noctuinae	Noctuini	<i>Xestia</i>	<i>sexstrigata</i>	Haworth	1809	Palearctic						6
Noctuinae	Noctuini	<i>Xestia</i>	<i>smithii</i>	Snellen	1896	Nearctic						M647, M664
Noctuinae	Noctuini	<i>Xestia</i>	<i>stigmatica</i>	Hubner	1813	Palearctic						6
Noctuinae	Noctuini	<i>Xestia</i>	<i>triangulum</i>	Hufangel	1766	Palearctic						M644
Noctuinae	Noctuini	<i>Xestia</i>	<i>triangulum</i>	Hufangel	1766	Palearctic						6
Noctuinae	Noctuini	<i>Xestia</i>	<i>xanthographa</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Orthosini	<i>Acerra</i>	<i>normalis</i>	Grote	1874	Nearctic						M1296
Noctuinae	Orthosini	<i>Achatia</i>	<i>distincta</i>	Hübner	[1813]	Nearctic	P	B	L	G		C10755, C10756, M147, M148
Noctuinae	Orthosini	<i>Anorthia</i>	<i>munda</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Orthosini	<i>Crocigrapha</i>	<i>normani</i>	Grote	1874	Nearctic	P	B	L	G		C15941, M152
Noctuinae	Orthosini	<i>Egira</i>	<i>alternans</i>	Walker	[1857]	Nearctic						M399, M400, M1072
Noctuinae	Orthosini	<i>Egira</i>	<i>conspicillaris</i>	Linnaeus	1758	Palearctic						M955
Noctuinae	Orthosini	<i>Egira</i>	<i>dolosa</i>	Grote	1880	Nearctic						M151

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Noctuinae	Orthosiini	<i>Egira</i>	<i>purpurea</i>	Barnes and McDunnough	1910	Nearctic						M1034
Noctuinae	Orthosiini	<i>Egira</i>	<i>rubrica</i>	Harvey	1878	Nearctic						M1118, M1142
Noctuinae	Orthosiini	<i>Egira</i>	<i>simplex</i>	Walker	1865	Nearctic						C17323
Noctuinae	Orthosiini	<i>Himella</i>	<i>fidelis</i>	Grote	1874	Nearctic	p	b	l	g		C15940, M1169
Noctuinae	Orthosiini	<i>Morissonia</i>	<i>confusa</i>	Hübner	[1831]	Nearctic						C11711, M1141
Noctuinae	Orthosiini	<i>Morissonia</i>	<i>evicta</i>	Grote	1873	Nearctic	p	B	L	G		C13538, C11710, M301
Noctuinae	Orthosiini	<i>Morissonia</i>	<i>latex</i>	Guenée	1852	Nearctic						M68
Noctuinae	Orthosiini	<i>Morissonia</i>	<i>mucens</i>	Hübner	[1831]	Nearctic	p	B	L	G		M1100
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>alutina</i>	Smith	1902	Nearctic						M153, M504, M1686
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>cerasi</i>	Fabricius	1775	Palearctic						6, M806
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>cruda</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>flavimacula</i>	Smith	1899	Nearctic						M1134
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>gothica</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>incerta</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>miniosa</i>	Denis and Schiffemüller	1775	Palearctic						6, M800
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>opina</i>	Hübner	1909	Palearctic						6
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>populeti</i>	Fabricius	1775	Palearctic						6
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>revicta</i>	Morrison	1876	Nearctic						M309
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>rubescens</i>	Walker	1865	Nearctic						M154
Noctuinae	Orthosiini	<i>Orthosia</i>	<i>segregata</i>	Smith	1893	Nearctic						M709
Noctuinae	Orthosiini	<i>Panolis</i>	<i>flammea</i>	Denis and Schiffemüller	1775	Palearctic						6, M1018
Noctuinae	Orthosiini	<i>Perigonica</i>	<i>pectinata</i>	Smith	1888	Nearctic						C13533
Noctuinae	Orthosiini	<i>Perigrapha</i>	<i>i-cinctum</i>	Denis and Schiffemüller	1775	Palearctic						M758
Noctuinae	Phlogophorini	<i>Conservula</i>	<i>anodonta</i>	Guenée	1852	Nearctic						M1671
Noctuinae	Phlogophorini	<i>Euplexia</i>	<i>lucipara</i>	Linnaeus	1758	Palearctic				1		6
Noctuinae	Phlogophorini	<i>Phlogophora</i>	<i>meticulosa</i>	Linnaeus	1758	Palearctic	p	B	L	G		4, 6
Noctuinae	Phlogophorini	<i>Phlogophora</i>	<i>periculosa</i>	Guenée	1852	Nearctic	p	B	L	G		Z2014009
Noctuinae	Prodeniini	<i>Spodoptera</i>	<i>eridania</i>	Stoll	1782	Neotropical						M1278
Noctuinae	Prodeniini	<i>Spodoptera</i>	<i>exigua</i>	Hübner	1808	Palearctic						6
Noctuinae	Pseudeustrotiini	<i>Pseudeustrotia</i>	<i>carneola</i>	Guenée	1852	Nearctic	p	b	l	g		C13008
Noctuinae	Tholerini	<i>Cerapteryx</i>	<i>graminis</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Tholerini	<i>Nephelodes</i>	<i>carminata</i>	Smith	1890	Nearctic						M995
Noctuinae	Tholerini	<i>Nephelodes</i>	<i>minians</i>	Guenée	1852	Nearctic						M157, M216, M1158

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Noctuinae	Tholerini	<i>Tholera</i>	<i>cespitis</i>	Denis and Schiffemüller	1775	Palearctic						6, M807
Noctuinae	Tholerini	<i>Tholera</i>	<i>decimalis</i>	Poda	1761	Palearctic						6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>circellaris</i>	Hufnagel	1766	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>helvola</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>litura</i>	Linnaeus	1758	Palearctic						4, 6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>lota</i>	Clerck	1759	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>lunosa</i>	Haworth	1809	Palearctic						6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>lychnidis</i>	Denis and Schiffemüller	1775	Palearctic	p	b	l			2, 6
Noctuinae	Xylenini	<i>Agrochola</i>	<i>macilenta</i>	Hübner	1809	Palearctic	P	B	L	G		2, 6
Noctuinae	Xylenini	<i>Ammonoia</i>	<i>caecimacula</i>	Denis and Schiffemüller	1775	Palearctic						M1576
Noctuinae	Xylenini	<i>Andropolia</i>	<i>contacta</i>	Walker	1856	Nearctic	P	B	L	G		M1641, M1643
Noctuinae	Xylenini	<i>Andropolia</i>	<i>olorina</i>	Grote	1876	Nearctic	P	B	L	G		M1642
Noctuinae	Xylenini	<i>Antitype</i>	<i>chi</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Aporophyla</i>	<i>australis</i>	Boisduval	1829	Palearctic	p	b	l			6
Noctuinae	Xylenini	<i>Aporophyla</i>	<i>lutulenta</i>	Denis and Schiffemüller	1775	Palearctic	P		l			6
Noctuinae	Xylenini	<i>Aporophyla</i>	<i>nigra</i>	Haworth	1809	Palearctic	P	B	L	G		2, 6
Noctuinae	Xylenini	<i>Apterogenum</i>	<i>ypsilon</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Aseptis</i>	<i>binotata</i>	Walker	1865	Nearctic	P	B	L	G		C11737, M430, M431, M436, M1918
Noctuinae	Xylenini	<i>Aseptis</i>	<i>catalina</i>	Smith	1899	Nearctic	P	B	L	G		M1138
Noctuinae	Xylenini	<i>Aseptis</i>	<i>characta</i>	Grote	1880	Nearctic	P	B	L	G		C11704
Noctuinae	Xylenini	<i>Aseptis</i>	<i>ethnica</i>	Smith	1899	Nearctic	P	?	L	?		M429
Noctuinae	Xylenini	<i>Aseptis</i>	<i>fumosa</i>	Grote	1879	Nearctic	P	?	L	?		M432
Noctuinae	Xylenini	<i>Aseptis</i>	<i>perfumosa</i>	Hampson	1918	Nearctic	P	B	L	G		M610
Noctuinae	Xylenini	<i>Aseptis</i>	<i>susquesa</i>	Smith	1908	Nearctic	P	B	L	G		C11707, C11709
Noctuinae	Xylenini	<i>Atethmia</i>	<i>centrago</i>	Haworth	1809	Palearctic						3, 6
Noctuinae	Xylenini	<i>Atrypha</i>	<i>pulmonaris</i>	Esper	1790	Palearctic	P	B	L	G		C13012
Noctuinae	Xylenini	<i>Blepharita</i>	<i>amica</i>	Tretschke	1825	Palearctic						M1578
Noctuinae	Xylenini	<i>Brachylomia</i>	<i>elda</i>	French	1887	Nearctic						C13946
Noctuinae	Xylenini	<i>Brachylomia</i>	<i>viminalis</i>	Fabricius	1776	Palearctic	p	B	L			6
Noctuinae	Xylenini	<i>Conistra</i>	<i>ligula</i>	Esper	1791	Palearctic	p	b	l	g		6
Noctuinae	Xylenini	<i>Conistra</i>	<i>rubiginea</i>	Denis and Schiffemüller	1775	Palearctic	p	b	l	G		6
Noctuinae	Xylenini	<i>Conistra</i>	<i>vaccinii</i>	Linnaeus	1761	Palearctic	p	b	L	G		6
Noctuinae	Xylenini	<i>Cosmia</i>	<i>affinis</i>	Linnaeus	1767	Palearctic						3, 6

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Noctuinae	Xylenini	<i>Cosmia</i>	<i>calami</i>	Harvey	1876	Nearctic	P	B	L	G		M2901
Noctuinae	Xylenini	<i>Cosmia</i>	<i>diffinis</i>	Linnaeus	1767	Palearctic						3, 6
Noctuinae	Xylenini	<i>Cosmia</i>	<i>pyralina</i>	Denis and Schiffemüller	1775	Palearctic						3, 6
Noctuinae	Xylenini	<i>Cosmia</i>	<i>trapezina</i>	Linnaeus	1758	Palearctic						4, 6
Noctuinae	Xylenini	<i>Dasypolia</i>	<i>templi</i>	Thunberg	1792	Palearctic						6, M1687
Noctuinae	Xylenini	<i>Dicycla</i>	<i>oo</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Dryobotodes</i>	<i>eremita</i>	Fabricius	1775	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Enargia</i>	<i>decolor</i>	Walker	1858	Nearctic	P	?	?	?		M451
Noctuinae	Xylenini	<i>Enargia</i>	<i>infumata</i>	Grote	1874	Nearctic	P	B	L	G		M450, M496, M497, M498
Noctuinae	Xylenini	<i>Enargia</i>	<i>paleacea</i>	Esper	1788	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Enargia</i>	<i>ypsillon</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		M1633
Noctuinae	Xylenini	<i>Epiglaea</i>	<i>apiata</i>	Grote	1874	Nearctic	P	?	L	G		M395, M396
Noctuinae	Xylenini	<i>Eupsilia</i>	<i>sidus</i>	Guenée	1852	Nearctic						M495, M507, M518, M534, M740
Noctuinae	Xylenini	<i>Eupsilia</i>	<i>transversa</i>	Hufnagel	1766	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Eupsilia</i>	<i>tristigmata</i>	Grote	1877	Nearctic						M449, M713
Noctuinae	Xylenini	<i>Eupsilia</i>	<i>vinulenta</i>	Grote	1864	Nearctic						M448, M533
Noctuinae	Xylenini	<i>Fagitana</i>	<i>littera</i>	Guenée	1852	Nearctic						M1676
Noctuinae	Xylenini	<i>Fishia</i>	<i>yosemitae</i>	Grote	1873	Nearctic	p	b	l	g		M1640
Noctuinae	Xylenini	<i>Gripesia</i>	<i>aprilina</i>	Linnaeus	1758	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Hyppa</i>	<i>*n.sp. A</i>		?	Nearctic	P	B	L	G		C11146, M11147
Noctuinae	Xylenini	<i>Hyppa</i>	<i>indistincta</i>	Smith	1894	Nearctic	P	B	L	G		M609
Noctuinae	Xylenini	<i>Hyppa</i>	<i>rectilinea</i>	Esper	1788	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Hyppa</i>	<i>xylinoidea</i>	Guenée	1852	Nearctic	P	L				M392, M393
Noctuinae	Xylenini	<i>Ipimorpha</i>	<i>pleonectusa</i>	Grote	1873	Nearctic	P	B	L	G		C17263, M1679
Noctuinae	Xylenini	<i>Ipimorpha</i>	<i>retusa</i>	Linnaeus	1761	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Ipimorpha</i>	<i>subtrusa</i>	Denis and Schiffemüller	1775	Palearctic	P	B	L	G		3, 6
Noctuinae	Xylenini	<i>Lithomoia</i>	<i>germana</i>	Morrison	1874	Nearctic	P	B	L	g		M1282, M1283
Noctuinae	Xylenini	<i>Lithomoia</i>	<i>solidaginis</i>	Hübner	1803	Palearctic	p	B	L	g		4, 6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>disposita</i>	Morrison	1874	Nearctic	p	b	l	g		M1840, M1841
Noctuinae	Xylenini	<i>Lithophane</i>	<i>furcifera</i>	Hufnagel	1766	Palearctic						4, 6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>hemina</i>	Grote	1879	Nearctic	P	B	L	G		C13570, C13869
Noctuinae	Xylenini	<i>Lithophane</i>	<i>lamda</i>	Fabricius	1787	Palearctic						3, 6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>lanei</i>	Troubridge	2006	Nearctic	P	B	L	G		C13569, C13860

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Noctuinae	Xylenini	<i>Lithophane</i>	<i>leautieri</i>	Boisduval	1829	Palearctic						6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>ornitopus</i>	Hufnagel	1766	Palearctic						6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>querquera</i>	Grote	1874	Nearctic	p	b	l	g		C13190
Noctuinae	Xylenini	<i>Lithophane</i>	<i>semibrunnea</i>	Haworth	1809	Palearctic	p	b	l	g		6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>socia</i>	Hufnagel	1766	Palearctic	p	b	l	g		6
Noctuinae	Xylenini	<i>Lithophane</i>	<i>thaxteri</i>	Grote	1874	Nearctic						M716
Noctuinae	Xylenini	<i>Lithophane</i>	<i>viridipallens</i>	Grote	1877	Nearctic						C13520
Noctuinae	Xylenini	<i>Mesogona</i>	<i>olivata</i>	Harvey	1874	Nearctic	p	b	l	g		M1163
Noctuinae	Xylenini	<i>Mesogona</i>	<i>oxalina</i>	Hübner	[1803]	Palearctic	p	l				M1682
Noctuinae	Xylenini	<i>Metaxaglaea</i>	<i>australis</i>	Sweitzer	1979	Nearctic	p	b	l	g		M1700
Noctuinae	Xylenini	<i>Metaxaglaea</i>	<i>semitaria</i>	Franclemont	1968	Nearctic	p	b	l	g		M1689
Noctuinae	Xylenini	<i>Mniontype</i>	<i>adusta</i>	Esper	1790	Palearctic	p	b	l	g		6
Noctuinae	Xylenini	<i>Mniontype</i>	<i>ducta</i>	Grote	1878	Nearctic	p	b	l	g		M1664
Noctuinae	Xylenini	<i>Mniontype</i>	<i>satura</i>	Denis and Schiffemüller	1775	Palearctic						6
Noctuinae	Xylenini	<i>Mniontype</i>	<i>tenera</i>	Smith	1900	Nearctic	p	b	l	g		M1634
Noctuinae	Xylenini	<i>Niphonyx</i>	<i>segregata</i>	Butler	1878	Holarctic	p	b	l	g		C14173
Noctuinae	Xylenini	<i>Pachypolia</i>	<i>atricornis</i>	Grote	1874	Nearctic	p	b	l	?		M606
Noctuinae	Xylenini	<i>Parastichtis</i>	<i>suspecta</i>	Hübner	[1817]	Holarctic	p	b	l	g		1, 6, C14166, M1630
Noctuinae	Xylenini	<i>Platypolia</i>	<i>anceps</i>	Stephens	1850	Nearctic	p	b	l	g		M605
Noctuinae	Xylenini	<i>Platypolia</i>	<i>mactata</i>	Guenée	1852	Nearctic	p	?	l	g		M544
Noctuinae	Xylenini	<i>Polymixis</i>	<i>chlorographa</i>	Dognin	1907	Neotropical	p	?	l	g		M1264
Noctuinae	Xylenini	<i>Polymixis</i>	<i>faivicineta</i>	Denis and Schiffemüller	1775	Palearctic						4, 6
Noctuinae	Xylenini	<i>Polymixis</i>	<i>lichenae</i>	Hübner	1813	Palearctic						6
Noctuinae	Xylenini	<i>Polymixis</i>	<i>xanthomista</i>	Hübner	1819	Palearctic						3, 4, 6
Noctuinae	Xylenini	<i>Properigea</i>	<i>costa</i>	Barnes and Benjamin	1923	Nearctic	p	b	l	g		C10802, M1335
Noctuinae	Xylenini	<i>Properigea</i>	<i>tapeta</i>	Smith	1900	Nearctic	p	b	l	g		M1357
Noctuinae	Xylenini	<i>Pseudanthoecia</i>	<i>tumida</i>	Grote	1880	Nearctic						M1154
Noctuinae	Xylenini	<i>Pyreferra</i>	<i>citrombra</i>	Franclemont	1941	Nearctic						M443
Noctuinae	Xylenini	<i>Rhizagrotis</i>	<i>stylata</i>	Smith	1893	Nearctic	p	l				C13937
Noctuinae	Xylenini	<i>Sericaglaea</i>	<i>signata</i>	French	1879	Nearctic	p	b	l	g		M1728
Noctuinae	Xylenini	<i>Sunitra</i>	<i>bicolorago</i>	Guenée	1852	Nearctic	p	b	l	g		C17257
Noctuinae	Xylenini	<i>Sunitra</i>	<i>decipiens</i>	Grote	1881	Nearctic	p	b	l	g		C17255
Noctuinae	Xylenini	<i>Sunitra</i>	<i>verberata</i>	Smith	1904	Nearctic	p	b	l	g		C17256



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Noctuinae	Xylenini	<i>Sutyna</i>	<i>privata</i>	Walker	1857	Nearctic	P	B	L	G		M670, M671, M672, M673, M674
Noctuinae	Xylenini	<i>Tiliacea</i>	<i>aurogo</i>	Denis and Schiffemiller	1775	Palearctic	P	B	L	G		3, 6
Noctuinae	Xylenini	<i>Tiliacea</i>	<i>citrago</i>	Linnaeus	1758	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Trigonophora</i>	<i>flammea</i>	Esper	1785	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Ufeus</i>	<i>saryicus</i>	Grote	1873	Nearctic						M1688
Noctuinae	Xylenini	<i>Xanthia</i>	<i>givabo</i>	Denis and Schiffemiller	1775	Palearctic	P	B	L	G		4, 5, 6
Noctuinae	Xylenini	<i>Xanthia</i>	<i>icteritia</i>	Hufangl	1766	Palearctic	P	B	L	G		6
Noctuinae	Xylenini	<i>Xanthia</i>	<i>togata</i>	Esper	1788	Palearctic	P	B	L	G		4, 6
Noctuinae	Xylenini	<i>Xylena</i>	<i>exoleta</i>	Linnaeus	1758	Palearctic						6
Noctuinae	Xylenini	<i>Xylena</i>	<i>thoracica</i>	Putnam-Cramer	1886	Nearctic						M2000
Noctuinae	Xylenini	<i>Xylena</i>	<i>vetusta</i>	Hübner	1813	Palearctic	p	b	L	G		6
Oncocnemidinae		<i>Behrensia</i>	<i>conchiformis</i>	Grote	1875	Nearctic						C13217
Oncocnemidinae		<i>Calophasia</i>	<i>lunula</i>	Hufangl	1766	Palearctic						M1956
Oncocnemidinae		<i>Catabenoides</i>	<i>sp.?</i>	?	?	Nearctic	P	B	L	G		C16713, C16707
Oncocnemidinae		<i>Copanarta</i>	<i>aurea</i>	Grote	1879	Nearctic						C13884
Oncocnemidinae		<i>Copanarta</i>	<i>sexpunctata</i>	Barnes and McDunnough	1916	Nearctic	p	?	?	?		C13917
Oncocnemidinae		<i>Neogalea</i>	<i>sunia</i>	Guenée	1852	Neotropical	P	B	L	?	?	C13935, M1911
Oncocnemidinae		<i>Stilbia</i>	<i>anomala</i>	Haworth	1812	Palearctic						6
Oncocnemidinae		<i>Sympistis</i>	<i>acheron</i>	Troubridge	2008	Nearctic	P	B	L	G		C13985, C14032, C14034
Oncocnemidinae		<i>Sympistis</i>	<i>albifasciata</i>	Hampson	1906	Nearctic						C13870
Oncocnemidinae		<i>Sympistis</i>	<i>amenithes</i>	Troubridge	2008	Nearctic	P	B	L	G		C13907, C14050
Oncocnemidinae		<i>Sympistis</i>	<i>amun</i>	Troubridge	2008	Nearctic	P	B	L	G		C14056
Oncocnemidinae		<i>Sympistis</i>	<i>aepes</i>	Troubridge	2008	Nearctic	p					C13259
Oncocnemidinae		<i>Sympistis</i>	<i>apis</i>	Troubridge	2008	Nearctic	P	B	L	?		C13255, C14065
Oncocnemidinae		<i>Sympistis</i>	<i>apposita</i>	Barnes and McDunnough	1918	Nearctic	P	B	L	G		C13903
Oncocnemidinae		<i>Sympistis</i>	<i>arizonensis</i>	Barnes	1928	Nearctic	P	B	L	G		C13199
Oncocnemidinae		<i>Sympistis</i>	<i>astrigata</i>	Barnes and McDunnough	1912	Nearctic	P	B	L	?		C13442
Oncocnemidinae		<i>Sympistis</i>	<i>atricollaris</i>	Harvey	1875	Nearctic	P	B	L	G		C13206, C13416
Oncocnemidinae		<i>Sympistis</i>	<i>augustus</i>	Harvey	1875	Nearctic						C13369
Oncocnemidinae		<i>Sympistis</i>	<i>babi</i>	Troubridge	2008	Nearctic	P	B	L	G		C13876
Oncocnemidinae		<i>Sympistis</i>	<i>badistriga</i>	Grote	1872	Nearctic	P	B	L	G		C13919
Oncocnemidinae		<i>Sympistis</i>	<i>bakeri</i>	Dyar	1905	Nearctic	P	B	L	G		C13358, C13360
Oncocnemidinae		<i>Sympistis</i>	<i>baileata</i>	Smith	1902	Nearctic	P	B	L	G		C13495

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Oncocnemidinae		<i>Sympistis</i>	<i>barnesii</i>	Smith	1899	Nearctic	P	B	L	?		C13317
Oncocnemidinae		<i>Sympistis</i>	<i>behrensi</i>	Grote	1874	Nearctic	p			?		C13236
Oncocnemidinae		<i>Sympistis</i>	<i>benjamini</i>	Lindsey	1923	Nearctic	P	B	L	G		C13381
Oncocnemidinae		<i>Sympistis</i>	<i>bes</i>	Troubridge	2008	Nearctic						C13501
Oncocnemidinae		<i>Sympistis</i>	<i>buchis</i>	Troubridge	2008	Nearctic	P	B	L	?		C13254, C14060
Oncocnemidinae		<i>Sympistis</i>	<i>buto</i>	Troubridge	2008	Nearctic	p					C14077
Oncocnemidinae		<i>Sympistis</i>	<i>californiae</i>	McDunnough	1946	Nearctic	P	B	L	G		M1915
Oncocnemidinae		<i>Sympistis</i>	<i>chalybdis</i>	Troubridge and Crabo	1998	Nearctic	P	B	L	G		C13497
Oncocnemidinae		<i>Sympistis</i>	<i>chandleri</i>	Grote	1873	Nearctic						C13345
Oncocnemidinae		<i>Sympistis</i>	<i>cherti</i>	Troubridge	2008	Nearctic	P	B	L	G		C14089
Oncocnemidinae		<i>Sympistis</i>	<i>chionanthi</i>	J.E. Smith	1797	Nearctic	p	b	l	g		M214, M215, M433, M434, M468, C14130
Oncocnemidinae		<i>Sympistis</i>	<i>chons</i>	Troubridge	2008	Nearctic	P	B	L	G		C13450
Oncocnemidinae		<i>Sympistis</i>	<i>chorda</i>	Grote	1880	Nearctic	p					C14071
Oncocnemidinae		<i>Sympistis</i>	<i>cibalis</i>	Grote	1880	Nearctic	P	B	L	G		C13909
Oncocnemidinae		<i>Sympistis</i>	<i>ciliata</i>	Smith	1900	Nearctic						C13391
Oncocnemidinae		<i>Sympistis</i>	<i>cocytus</i>	Troubridge	2008	Nearctic	p	b	l	g		C13988, C14036
Oncocnemidinae		<i>Sympistis</i>	<i>collaris</i>	Troubridge	2008	Nearctic	P	B	L	?		C13406
Oncocnemidinae		<i>Sympistis</i>	<i>columbia</i>	McDunnough	1922	Nearctic	P	B	L	G		C14075
Oncocnemidinae		<i>Sympistis</i>	<i>confusa</i>	Freyer	1840	Palearctic						M632
Oncocnemidinae		<i>Sympistis</i>	<i>corusca</i>	Smith	1899	Nearctic	P	?	L	G		C13182
Oncocnemidinae		<i>Sympistis</i>	<i>cottami</i>	Blanchard	1972	Nearctic	P	B	L	?		C13425
Oncocnemidinae		<i>Sympistis</i>	<i>dayi</i>	Grote	1873	Nearctic	p	l				C13975
Oncocnemidinae		<i>Sympistis</i>	<i>deceptiva</i>	Barnes and Lindsey	1922	Nearctic	P	B	L	G		C13410
Oncocnemidinae		<i>Sympistis</i>	<i>dentata</i>	Grote	1875	Nearctic	P	B	L	G		M653, M657, M1306
Oncocnemidinae		<i>Sympistis</i>	<i>dinalda</i>	Smith	1908	Nearctic	P	B	L	G		C13925
Oncocnemidinae		<i>Sympistis</i>	<i>dischora</i>	Troubridge	2008	Nearctic	p					C14124
Oncocnemidinae		<i>Sympistis</i>	<i>disfigurata</i>	Troubridge	2008	Nearctic	P	B	L	?		C13337
Oncocnemidinae		<i>Sympistis</i>	<i>doris</i>	Dimock and Troubridge	2008	Nearctic	p					C14079, M14138
Oncocnemidinae		<i>Sympistis</i>	<i>duplex</i>	Troubridge and Mustelin	2006	Nearctic						C13274, C13379
Oncocnemidinae		<i>Sympistis</i>	<i>euta</i>	Smith	1903	Nearctic						C13197
Oncocnemidinae		<i>Sympistis</i>	<i>extremis</i>	Smith	1890	Nearctic	p					C14081
Oncocnemidinae		<i>Sympistis</i>	<i>fasciata</i>	Edwards	1886	Nearctic	p	b	l	?		C13193
Oncocnemidinae		<i>Sympistis</i>	<i>ffia</i>	Dyar	1904	Nearctic	P	B	L	G		C14113

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Oncocnemidinae		<i>Sympistis</i>	<i>figurata</i>	Harvey	1875	Nearctic	P	B	L	G		C13294, C13331, C13997
Oncocnemidinae		<i>Sympistis</i>	<i>fortis</i>	Grote	1880	Nearctic	P	B	L	G		C13931*, C13933
Oncocnemidinae		<i>Sympistis</i>	<i>funebis</i>	Hubner	[1809]	Nearctic	P	B	L	G		C14012, C17243
Oncocnemidinae		<i>Sympistis</i>	<i>glennyi</i>	Grote	1873	Nearctic	P	B	L	G		C13855, C14046
Oncocnemidinae		<i>Sympistis</i>	<i>goedeni</i>	Troubridge and Crabo	1998	Nearctic	P	B	L	?		C13853
Oncocnemidinae		<i>Sympistis</i>	<i>grevi</i>	Troubridge and Crabo	1998	Nearctic	P	B	L	G		M593
Oncocnemidinae		<i>Sympistis</i>	<i>hapi</i>	Troubridge	2008	Nearctic	P					C14080
Oncocnemidinae		<i>Sympistis</i>	<i>hathor</i>	Troubridge	2008	Nearctic	P	B	L	G		C14073
Oncocnemidinae		<i>Sympistis</i>	<i>hayesi</i>	Grote	1873	Nearctic	P		I			C13389
Oncocnemidinae		<i>Sympistis</i>	<i>heliophila</i>	Paykull	1793	Nearctic	P	B	L	G		C14009, C17242, M792
Oncocnemidinae		<i>Sympistis</i>	<i>heterogena</i>	Blanchard	1972	Nearctic	P	B	L	G		C13204
Oncocnemidinae		<i>Sympistis</i>	<i>horus</i>	Troubridge	2008	Nearctic						C14000
Oncocnemidinae		<i>Sympistis</i>	<i>ibapahensis</i>	Barnes and Benjamin	1924	Nearctic						C13343
Oncocnemidinae		<i>Sympistis</i>	<i>incomitata</i>	Harvey	1875	Nearctic	P	B	L	G		C13923
Oncocnemidinae		<i>Sympistis</i>	<i>incubus</i>	Troubridge	2008	Nearctic						C13373
Oncocnemidinae		<i>Sympistis</i>	<i>induta</i>	Harvey	1875	Nearctic	P	B	L	G		C13927
Oncocnemidinae		<i>Sympistis</i>	<i>infixa</i>	Walker	1856	Nearctic	P	B	L	G		C13929, M557, M587
Oncocnemidinae		<i>Sympistis</i>	<i>insanina</i>	Troubridge	2008	Nearctic						C13271
Oncocnemidinae		<i>Sympistis</i>	<i>iricolor</i>	Smith	1888	Nearctic	P	B	L	?		C13435*, C13282
Oncocnemidinae		<i>Sympistis</i>	<i>isis</i>	Troubridge	2008	Nearctic						C14022
Oncocnemidinae		<i>Sympistis</i>	<i>jenniferae</i>	Troubridge	2008	Nearctic						C13371
Oncocnemidinae		<i>Sympistis</i>	<i>jocelynae</i>	Troubridge	2008	Nearctic						C13998
Oncocnemidinae		<i>Sympistis</i>	<i>kappa</i>	Grote	1874	Nearctic	P	B	L	G		C14109
Oncocnemidinae		<i>Sympistis</i>	<i>lacrhymana</i>	Troubridge	2008	Nearctic	P	B	L	G		C13180
Oncocnemidinae		<i>Sympistis</i>	<i>lacticollis</i>	Smith	1908	Nearctic	P	B	L	G		C13429
Oncocnemidinae		<i>Sympistis</i>	<i>lapponica</i>	Thunberg	1791	Nearctic	P	B	L	G		C17246, C17247
Oncocnemidinae		<i>Sympistis</i>	<i>lepipoloides</i>	McDunnough	1922	Nearctic	P	B	L	G		C13851
Oncocnemidinae		<i>Sympistis</i>	<i>levis</i>	Grote	1880	Nearctic						C13276
Oncocnemidinae		<i>Sympistis</i>	<i>linda</i>	Barnes and McDunnough	1913	Nearctic	P	B	L	G		C13387
Oncocnemidinae		<i>Sympistis</i>	<i>major</i>	Grote	1881	Nearctic	P	B	L	G		C13446, C14028
Oncocnemidinae		<i>Sympistis</i>	<i>melantho</i>	Smith	1899	Nearctic	P	B	L	G		C13299
Oncocnemidinae		<i>Sympistis</i>	<i>min</i>	Troubridge	2008	Nearctic	P	B	L	G		C13872, C14097
Oncocnemidinae		<i>Sympistis</i>	<i>minor</i>	Barnes	1928	Nearctic	P	B	L	?		C13408

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Oncocnemidinae		<i>Sympistis</i>	<i>mirificalis</i>	Grote	1879	Nearctic						C13196, C13215
Oncocnemidinae		<i>Sympistis</i>	<i>modesta</i>	McDunnough	1933	Nearctic	p					C13412
Oncocnemidinae		<i>Sympistis</i>	<i>mut</i>	Troubridge	2008	Nearctic	p	B	L	G		C14058
Oncocnemidinae		<i>Sympistis</i>	<i>nenun</i>	Troubridge	2008	Nearctic	p	B	L	G		C14054
Oncocnemidinae		<i>Sympistis</i>	<i>nigrocaput</i>	Smith	1892	Nearctic	p	B	L	G		C13363
Oncocnemidinae		<i>Sympistis</i>	<i>nita</i>	Smith	1910	Nearctic						C13367
Oncocnemidinae		<i>Sympistis</i>	<i>obscurata</i>	Barnes and McDunnough	1912	Nearctic	p	B	L	G		C13240
Oncocnemidinae		<i>Sympistis</i>	<i>occata</i>	Grote	1875	Nearctic						C13324
Oncocnemidinae		<i>Sympistis</i>	<i>opleri</i>	Troubridge	2008	Nearctic	p					C13996
Oncocnemidinae		<i>Sympistis</i>	<i>orbicularis</i>	Barnes and McDunnough	1912	Nearctic						M1232, M1912
Oncocnemidinae		<i>Sympistis</i>	<i>osirus</i>	Troubridge	2008	Nearctic						C13464
Oncocnemidinae		<i>Sympistis</i>	<i>pachet</i>	Troubridge	2008	Nearctic	p	B	L	G		C13242, C14103
Oncocnemidinae		<i>Sympistis</i>	<i>pallidior</i>	Barnes	1928	Nearctic	p	B	L	G		C14336, C13456, M588
Oncocnemidinae		<i>Sympistis</i>	<i>pernotata</i>	Grote	1883	Nearctic	p	B	L	G		C14061
Oncocnemidinae		<i>Sympistis</i>	<i>perscripta</i>	Guénée	1852	Nearctic	p	B	L	G		C13234, C13235
Oncocnemidinae		<i>Sympistis</i>	<i>piffardi</i>	Walker	1862	Nearctic	p	B	L	G		C13498
Oncocnemidinae		<i>Sympistis</i>	<i>poliafascies</i>	Dyar	1910	Nearctic	p	b	L	?		C13226
Oncocnemidinae		<i>Sympistis</i>	<i>poliochroa</i>	Hampson	1906	Nearctic	p	B	L	G		C13210
Oncocnemidinae		<i>Sympistis</i>	<i>ptah</i>	Troubridge	2008	Nearctic	p	B	L	G		C14051
Oncocnemidinae		<i>Sympistis</i>	<i>pudorata</i>	Smith	1893	Nearctic	p	?	L	?		C13396
Oncocnemidinae		<i>Sympistis</i>	<i>punctilinea</i>	Hampson	1906	Nearctic	p	B	L	?		C13311
Oncocnemidinae		<i>Sympistis</i>	<i>ra</i>	Troubridge	2008	Nearctic	p	B	L	?		C13291
Oncocnemidinae		<i>Sympistis</i>	<i>ragani</i>	Barnes	1928	Nearctic	p	B	L	G		C13321
Oncocnemidinae		<i>Sympistis</i>	<i>rayata</i>	Smith	1908	Nearctic	p	B	L	G		C14119
Oncocnemidinae		<i>Sympistis</i>	<i>regina</i>	Smith	1902	Nearctic						C13385
Oncocnemidinae		<i>Sympistis</i>	<i>richersi</i>	Troubridge	2008	Nearctic	p	B	L	G		C41134
Oncocnemidinae		<i>Sympistis</i>	<i>riparia</i>	Morrison	1875	Nearctic	p	B	L	G		C13444
Oncocnemidinae		<i>Sympistis</i>	<i>rosea</i>	Smith	1903	Nearctic						C13224
Oncocnemidinae		<i>Sympistis</i>	<i>rudis</i>	Troubridge and Lafontaine	?	Nearctic	p					C13393
Oncocnemidinae		<i>Sympistis</i>	<i>rustica</i>	Barnes and McDunnough	1911	Nearctic	p	B	L	G		C14120
Oncocnemidinae		<i>Sympistis</i>	<i>sagittata</i>	Barnes and McDunnough	1916	Nearctic						C13247
Oncocnemidinae		<i>Sympistis</i>	<i>sakinet</i>	Troubridge	2008	Nearctic	p	B	L	G		C13499
Oncocnemidinae		<i>Sympistis</i>	<i>sandaraca</i>	Buckett and Bauer	[1967]	Nearctic	p					C13492

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Oncocnemidinae		<i>Sympistis</i>	<i>sanina</i>	Smith	1910	Nearctic						C14018, C14025
Oncocnemidinae		<i>Sympistis</i>	<i>sauandersiana</i>	Grote	1876	Nearctic	p					C13315
Oncocnemidinae		<i>Sympistis</i>	<i>sectilis</i>	Smith	1894	Nearctic	p	B	L	G		C13505, C13507
Oncocnemidinae		<i>Sympistis</i>	<i>sectiloides</i>	Barnes and McDunnough	1913	Nearctic	p	B	L	G		C13503
Oncocnemidinae		<i>Sympistis</i>	<i>semicollaris</i>	Smith	1909	Nearctic	p	B	L	?		C13295, C13485
Oncocnemidinae		<i>Sympistis</i>	<i>septa</i>	Troubridge	2008	Nearctic	p	B	L	G		C13874
Oncocnemidinae		<i>Sympistis</i>	<i>sesmu</i>	Troubridge	2008	Nearctic						C13404
Oncocnemidinae		<i>Sympistis</i>	<i>seth</i>	Troubridge	2008	Nearctic						C13296
Oncocnemidinae		<i>Sympistis</i>	<i>shait</i>	Troubridge	2008	Nearctic	p	B	L	G		C14053
Oncocnemidinae		<i>Sympistis</i>	<i>simplex</i>	Smith	1888	Nearctic	p	B	L	G		C13364, C13431
Oncocnemidinae		<i>Sympistis</i>	<i>singularis</i>	Barnes and McDunnough	1912	Nearctic	p	b	l	?		C13264
Oncocnemidinae		<i>Sympistis</i>	<i>sobek</i>	Troubridge	2008	Nearctic	p	B	L	G		C14092
Oncocnemidinae		<i>Sympistis</i>	<i>sokar</i>	Troubridge	2008	Nearctic	p					C13222, C14128
Oncocnemidinae		<i>Sympistis</i>	<i>sorapis</i>	Troubridge	2008	Nearctic						C13232
Oncocnemidinae		<i>Sympistis</i>	<i>stabilis</i>	Smith	1895	Nearctic	p	B	L	G		C13921, M597
Oncocnemidinae		<i>Sympistis</i>	<i>subsimplex</i>	Dyar	1904	Nearctic	p	B	L	G		C13901
Oncocnemidinae		<i>Sympistis</i>	<i>tenuifascia</i>	Smith	1888	Nearctic	p	l				C13260
Oncocnemidinae		<i>Sympistis</i>	<i>tetrops</i>	Dyar	1904	Nearctic	p	B	L	?		C13328
Oncocnemidinae		<i>Sympistis</i>	<i>umbri-fascia</i>	Smith	1894	Nearctic	p					C13230
Oncocnemidinae		<i>Sympistis</i>	<i>utahensis</i>	Barnes and Benjamin	1924	Nearctic						C13347
Oncocnemidinae		<i>Sympistis</i>	<i>viriditincta</i>	Smith	1894	Nearctic						C13865
Oncocnemidinae		<i>Sympistis</i>	<i>wilsonensis</i>	Hill	1924	Nearctic	p	b	l	?		C13228
Oncocnemidinae		<i>Sympistis</i>	<i>youngi</i>	McDunnough	1922	Nearctic	p	B	L	?		C13250
Oncocnemidinae		<i>Sympistis</i>	<i>zetterstedti</i>	Staudinger	1857	Nearctic	p	B	L	G		C17239
Oncocnemidinae		<i>Xyllocampa</i>	<i>areola</i>	Esper	1789	Palearctic						4, 6
Pantheinae		<i>Anacronicta</i>	<i>okinawensis</i>	Sugi	1970	Palearctic						M1614
Pantheinae		<i>Colocasia</i>	<i>flavicornis</i>	Smith	1884	Nearctic						M1103
Pantheinae		<i>Colocasia</i>	<i>propinquilinea</i>	Grote	1873	Nearctic						M1101
Plusinae	Axyrogrammatini	<i>Autographa</i>	<i>precatonis</i>	Guenee	1852	Nearctic						M350, M351
Plusinae	Axyrogrammatini	<i>Chrysodeixis</i>	<i>includens</i>	Walker	[1858]	Neotropical						M352
Plusinae	Plusini	<i>Plusia</i>	<i>magnimacula</i>	Handfield & Handfield	2006	Nearctic						C13559, C13590
Plusinae	Plusini	<i>Plusia</i>	<i>putnami</i>	Grote	1873	Nearctic						C13546
Plusinae	Plusini	<i>Syngrapha</i>	<i>abstrusa</i>	Eichlin and Cunningham	1978	Nearctic						M314

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Plusinae	Plusini	<i>Syngrapha</i>	<i>alias</i>	Ottolengui	1902	Nearctic						M317, M340, M342
Plusinae	Plusini	<i>Syngrapha</i>	<i>cryptica</i>	Eichlin and Cunningham	1978	Nearctic						M1559
Plusinae	Plusini	<i>Syngrapha</i>	<i>epigaea</i>	Grote	1874	Nearctic						M1274, M1272
Plusinae	Plusini	<i>Syngrapha</i>	<i>parilis</i>	Hübner	[1809]	Nearctic						C17236
Plusinae	Plusini	<i>Syngrapha</i>	<i>rectangula</i>	Kirby	1837	Nearctic						M1568
Plusinae	Plusini	<i>Syngrapha</i>	<i>sackenii</i>	Grote	1877	Nearctic						M703, M704
Raphiinae		<i>Raphia</i>	<i>abrupta</i>	Grote	1863	Nearctic						M1546
<b>Erebidae</b>												
Boletobinae	Boletobini	<i>Metalectra</i>	<i>discalis</i>	Grote	1876	Nearctic						M1231
Boletobinae	Phytometrini	<i>Hemeroplanis</i>	<i>scopulepes</i>	Haworth	1809	Neotropical	P	B	L	?		M799, M811, M1594
Boletobinae	Phytometrini	<i>Isogona</i>	<i>natatrix</i>	Guenée	1852	Nearctic						C13553
Calpinae	Calpini	<i>Plusiodonta</i>	<i>compressipalpis</i>	Guenée	1852	Nearctic						M1585
Erebinae	Euclidiini	<i>Mocis</i>	<i>latipes</i>	Guenée	1852	Neotropical						M1920
Erebinae	Euclidiini	<i>Ptichodis</i>	<i>basilans</i>	Guenée	1852	Neotropical						M1804
Erebinae	Euclidiini	<i>Ptichodis</i>	<i>bisrigata</i>	Hübner	1818	Nearctic						M1144
Erebinae	Melipotini	<i>Melipotis</i>	<i>famelica</i>	Guenée	1852	Nearctic						M154, M1565
Erebinae	Omopterini	<i>Lesmone</i>	<i>detransens</i>	Walker	1858	Nearctic						M682
Erebinae	Omopterini	<i>Zale</i>	<i>buchholzi</i>	McDunnough	1943	Nearctic						M522
Erebinae	Omopterini	<i>Zale</i>	<i>colorado</i>	Smith	1908	Nearctic						M530
Erebinae	Omopterini	<i>Zale</i>	<i>curema</i>	Smith	1908	Nearctic						M828, M827
Erebinae	Omopterini	<i>Zale</i>	<i>duplicata</i>	Bethune	1865	Nearctic						M830
Erebinae	Omopterini	<i>Zale</i>	<i>galbanata</i>	Morrison	1875	Nearctic						M836
Erebinae	Omopterini	<i>Zale</i>	<i>helata</i>	Smith	1908	Nearctic						M554, M829
Erebinae	Omopterini	<i>Zale</i>	<i>lunifera</i>	Hübner	1818	Nearctic						M523
Erebinae	Omopterini	<i>Zale</i>	<i>metatoides</i>	McDunnough	1943	Nearctic						M550, M823
Erebinae	Omopterini	<i>Zale</i>	<i>minerea</i>	Guenée	1852	Nearctic						M524, M1761, M1762
Erebinae	Omopterini	<i>Zale</i>	<i>obliqua</i>	Guenée	1852	Nearctic						M824
Erebinae	Omopterini	<i>Zale</i>	<i>phaeocapna</i>	Franclemont	1950	Nearctic						M837
Erebinae	Omopterini	<i>Zale</i>	<i>rubi</i>	H. Edwards	1881	Nearctic						M604
Erebinae	Omopterini	<i>Zale</i>	<i>submediana</i>	McDunnough	1938	Nearctic						M831
Erebinae	Omopterini	<i>Zale</i>	<i>undularis</i>	Drury	[1773]	Nearctic						M525, M526
Erebinae	Posphiliini	<i>Mimophisma</i>	<i>delunaris</i>	Guenée	1852	Neotropical						M1600
Eulepidotinae		<i>Eulepidotis</i>	<i>persimilis</i>	Guenée	1852	Neotropical						C15465

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Eulepidotinae		<i>Manbuta</i>	<i>pyraliformis</i>	Walker	1858	Neotropical						M1246
Eulepidotinae		<i>Massala</i>	<i>obvertens</i>	Walker	1858	Neotropical						M1592, M1741
Eulepidotinae		<i>Panopoda</i>	<i>repanda</i>	Walker	[1858]	Nearctic						M1552
Eulepidotinae		<i>Phyprosopus</i>	<i>callitrichoides</i>	Grote	1872	Nearctic						M1511
Heminiinae		<i>Idia</i>	<i>aemula</i>	Hübner	[1813]	Nearctic						M1993
Heminiinae		<i>Macrochilo</i>	<i>orciferalis</i>	Walker	[1859]	Nearctic						M1612
Heminiinae		<i>Zanclognatha</i>	<i>jachusalis</i>	Walker	[1859]	Nearctic						M1279
Heminiinae		<i>Zanclognatha</i>	<i>protumnusalis</i>	Walker	[1859]	Nearctic						M1280, M1281
Hypenodinae		<i>Dasybienna</i>	<i>straminea</i>	Dyar	1923	Nearctic						C13516
Hypenodinae		<i>Parahypenodes</i>	<i>quadralis</i>	Barnes and McDunnough	1918	Nearctic						M1992
Hypocalinae		<i>Hypsoropha</i>	<i>baja</i>	McCabe	1992	Nearctic						M1922
Hypocalinae		<i>Hypsoropha</i>	<i>franclemontii</i>	McCabe	1992	Neotropical						M1497
Hypocalinae		<i>Hypsoropha</i>	<i>hormos</i>	Hübner	1818	Nearctic						M1330, M1777
Hypocalinae		<i>Hypsoropha</i>	<i>monilis</i>	Fabricius	1777	Nearctic						M1513
Scoliopteryginae	Scoliopterygini	<i>Scoliopteryx</i>	<i>libatrix</i>	Linnaeus	1758	Nearctic						M579