

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3284, 32 pp., 16 figures, 2 tables
December 8, 1999

Preliminary Assessment of the Tribe Lemoniini (Lepidoptera: Riodinidae) Based on Adult Morphology

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ABSTRACT

A cladistic analysis of 97 characters taken from adult morphology was used to assess the higher-level phylogeny of the butterfly tribe Lemoniini (*sensu* Harvey, 1987). Many of our characters are described and illustrated in detail to assist future work in riodinid systematics. To evaluate the monophyly of Lemoniini, representative species of five genera in the putative sister tribe Nymphidiini were included in the analysis. Our results indicated that the Lemoniini was not monophyletic, and that some Nymphidiini grouped within Lemoniini. As this study provided no support for maintaining Lemoniini and Nymphidiini as separate taxa, we propose the amalgamation of these two tribes. Our analysis also suggested that not all genera currently placed in Lemoniini are monophyletic.

INTRODUCTION

The utility of evolutionary theory no longer just concerns theoreticians, ecologists, or naturalists. As recently pointed out by Bull and Wichman (1998), the principles of evolutionary biology are now used (consciously

or unconsciously) by molecular, cell, developmental, and medical biologists, as well as by anthropologists, corporate agro-businesses, and even the criminal courts. It is evident that many advances in evolutionary biology can be attributed directly to the development and use of methods that were pioneered by

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systematists (e.g., Hennig, 1966; Farris, 1970, 1983; Nelson and Platnick, 1981) who provided the basis upon which to construct phylogenies for understanding the evolution of particular groups. Although it may call forth the image of 19th-century biology to some (i.e., Bull and Wichman, 1998), museum-based systematic work clearly remains an essential part of modern evolutionary biology. Accordingly, the focus of this study concerns the evolution of a particular group of butterflies, and it derives directly from field and museum work.

Among butterflies, the ability to form symbiotic associations with ants occurs only in the lycaenids and riodinids (DeVries, 1991a; Fiedler, 1991). In contrast to the lycaenids, which may have upwards of 40% of the species being myrmecophilous (Pierce, 1987; Fiedler, 1991), only about 25–30% of riodinid species are thought to form symbioses with ants, all of which are Neotropical (DeVries, 1991a, 1997). Although most work on butterfly myrmecophily has focused on lycaenids, recent studies of riodinids have made significant strides toward understanding general butterfly myrmecophily, and the riodinid tribe Lemoniini has been particularly important. For example, studies on members of the Lemoniini have provided critical insights into the function and evolution of caterpillar organs that produce food secretions (Ross, 1966; DeVries, 1988; DeVries and Baker, 1989), semiochemicals (DeVries, 1988, 1997), and acoustical calls important to maintaining ant symbionts (DeVries, 1988, 1990, 1991a, b, c, 1997; DeVries and Poinar, 1997).

Our interest in Lemoniini relationships derives from the fact that, despite their importance as subjects for ecological and evolutionary studies, this tribe has never been subject to modern systematic analysis (something that is applicable to most riodinids). Phylogenetic studies of Lemoniini can provide a template for studies on the evolution of myrmecophily in riodinids while increasing our understanding of their diversification.

As the first effort of its kind, this study seeks to enhance understanding of the Lemoniini in four ways. Herein, we: (1) evaluate the classification and monophyly of Lemoniini sensu Harvey (1987) by cladistic

analysis of many more characters than ever considered previously, (2) assess the monophyly of particular genera used in our analysis, (3) discuss the influence of character variability on our analytical results, and (4) point to areas where future work on riodinid systematics is needed.

ACKNOWLEDGMENTS

Any work of this nature benefits from the enthusiasm and kindness of many colleagues and institutions. For loan of material critical to this study we gratefully acknowledge the assistance of G. Austin (Nevada State Museum), B. Brown (Natural History Museum of Los Angeles County), J. Hall (University of Florida), J. S. Miller (American Museum of Natural History), and L. D. and J. Miller (Allyn Museum of Entomology). Over the past 10 years the Smithsonian Tropical Research Institute, American Museum of Natural History, and especially Eric Schwartz of the La Selva Lodge, Ecuador, provided field support that was fundamental to many of our observations on riodinid butterflies. This research was supported in part by a Guggenheim Fellowship to DeVries. For discussion and critical comments that improved previous drafts of this manuscript, we thank P. Ackery, J. Cadle, D. Campbell, D. Grimaldi, J. Hall, J. S. Miller, and two anonymous reviewers.

HISTORICAL BACKGROUND

Although some discussion exists as to whether the riodinids should be considered as a separate family or as a subfamily of the Lycaenidae, all evidence indicates that the riodinid butterflies form a monophyletic group (Ehrlich, 1958; Eliot, 1973; Ackery, 1984; Harvey, 1987; DeJong et al., 1996; Campbell, 1998). Our current understanding of riodinid classification stems from work by three investigators. Bates (1868) provided the first higher classification of the riodinids, and subsequently Stichel (1910–1911, 1930–31) catalogued all the species and divided Riodinidae into two subfamilies and seven tribes, some which he further divided into *stirps* (from Latin, meaning twig or small branch, and clearly used to indicate subtribe). Most recently, Harvey (1987) synthesized

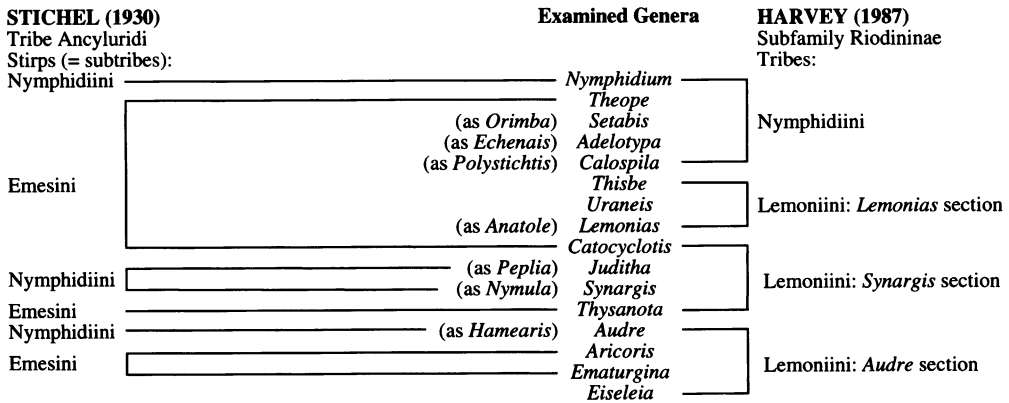


Fig. 1. A comparison between the classifications of Harvey (1987) and Stichel (1930) with emphasis on the riodinid taxa included in this study. The genus *Eiseleia* was described after the publication of Stichel's classification and is included here for completeness (compiled in part from Harvey, 1987).

and reorganized the classifications of Bates and Stichel into five monophyletic subfamilies, one of which (the Riodiniinae) was divided into 10 tribes. Harvey's work represents the first modern riodinid classification, and it has been widely used in systematic, faunistic, and ecological investigations (e.g., Campbell, 1998; DeJong et al., 1996; DeVries, 1991c, 1997; Hall and Willmott, 1996; Hall and Harvey, 1998; Hanner, 1997).

The 11 genera currently classified in the Lemoniini sensu Harvey (1987) were grouped by Stichel (1930–31) in the Ancylyruidi, the largest tribe in his classification. Stichel's Ancylyruidi (89 genera) contained six subtribes (or *stirps*), two of which are important in the context of this study: the Emesini (31 genera) and the Nymphidiini (5 genera). Harvey examined 57 species from Stichel's Emesini and Nymphidiini, and he placed taxa possessing bifurcated rami (paired projections on the male eighth abdominal sternite) in his tribe Lemoniini, which was adapted from the abandoned name Lemoniidae (Kirby, 1871). As established by Harvey (1987), the Lemoniini embraces about 70 species divided into three sections (fig. 1): the *Lemonias* section (12 species) containing *Lemonias* Hübner, 1807; *Thisbe* Hübner, 1814; and *Uraneis* Bates, 1868 (fig. 2); the *Synargis* section (30 species) containing *Catocyclotis* Stichel, 1911; *Juditha* Hemming, 1964; *Synargis* Hübner, 1819, and *Thysanota* Stichel, 1910 (figs. 3, 4); and the *Audre* section (28 species) con-

taining *Ematurgina* Röber, 1903; *Audre* Hemming, 1934; *Aricoris* Westwood, 1851; and *Eiseleia* Miller and Miller, 1972 (fig. 4). Based on the ventral displacement of the third abdominal spiracle, Harvey (1987) placed most of the remaining genera in Stichel's subtribe Emesini into his redefined tribe Nymphidiini. The residual Emesini was maintained as an incertae sedis group to accommodate an assemblage of genera that lacked apomorphic characters of other Riodiniinae, and it was not considered monophyletic (Harvey, 1987). As noted elsewhere (DeVries, 1997), the riodinid tribal name Emesini (Stichel, 1911; type genus *Emesia* F.) is preoccupied by the senior name Emesini (Amyot and Serville, 1843; type genus *Emesa* F. in the Reduviidae), and within the context of Harvey's classification of the Riodiniidae, this group might be more correctly regarded as incertae sedis group 2. However, for convenience sake we use Emesini here to discuss the classifications of Stichel (1930) and Harvey (1987).

Previous systematic studies (Stichel, 1930–31; Harvey, 1987; Campbell, 1998) strongly suggest that consideration of the Nymphidiini is vital to testing the monophyly of Lemoniini. Based on shared larval characters associated with myrmecophily (position of the first abdominal spiracle and possession of ant-organs), Lemoniini and Nymphidiini were inferred to be sister taxa by Harvey (1987), and a recent study of DNA sequence data also suggested a close rela-

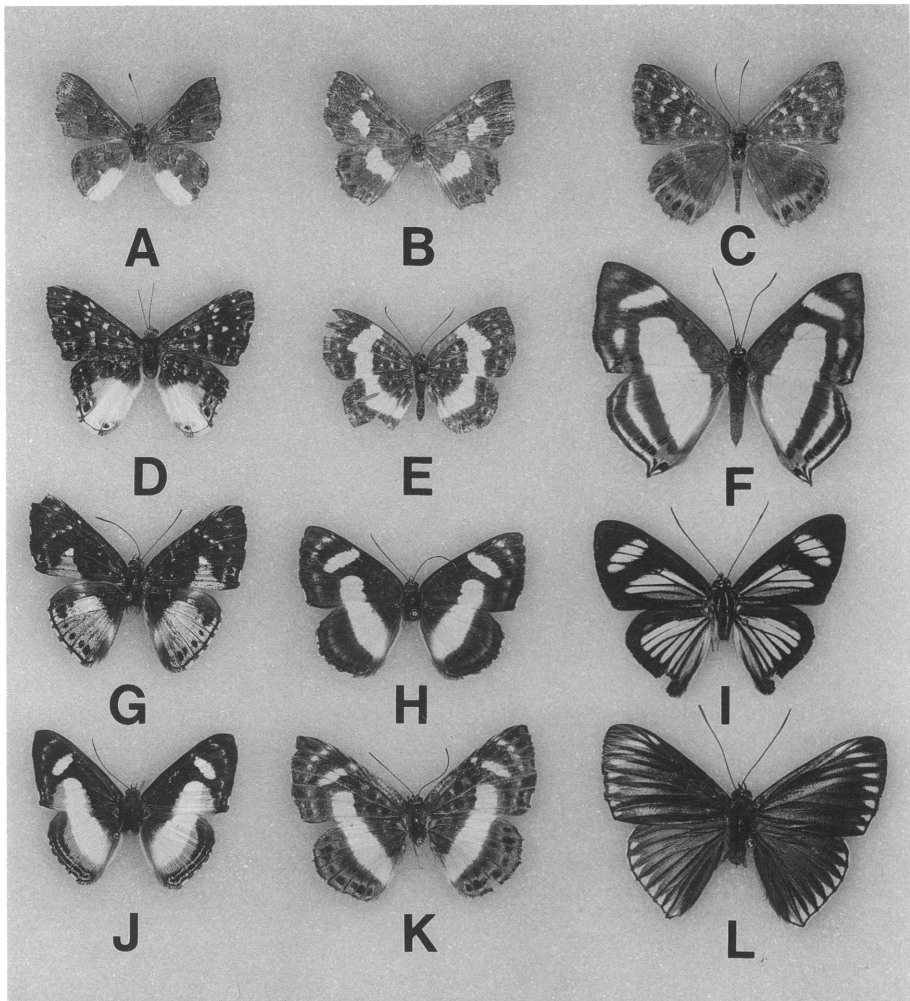


Fig. 2. Ingroup taxa (*Lemonias* section of Harvey, 1987). **A**, *Lemonias agave* (male) [Mexico, Veracruz, Presidio (AMNH)]; **B**, *Lemonias agave* (female) [Mexico, Veracruz, Presidio (AMNH)]; **C**, *Lemonias caliginea* (male) [Mexico, Veracruz (LACM)]; **D**, *Lemonias zygia* (male) [Brazil, Rondônia, Fazenda Rancho Grande (LACM)]; **E**, *Lemonias zygia* (female) [Brazil, Rondônia, Fazenda Rancho Grande (LACM)]; **F**, *Thisbe lycorias* (male) [Costa Rica, Heredia, Finca La Selva (PJD)]; **G**, *Thisbe molela* (male) [Peru, Madre de Dios, Shintuya (PJD)]; **H**, *Thisbe irenea* (female) [Panama, Barro Colorado Island (PJD)]; **I**, *Uraneis hyalina* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **J**, *Thisbe irenea* (male) [Panama, Barro Colorado Island (PJD)]; **K**, *Thisbe molela* (female) [Venezuela, Canaima (LACM)]; **L**, *Uraneis ucubis* (male) [Costa Rica, Heredia, Cariblanco (PJD)].

tionship (Campbell, 1998). We note, however, that Campbell's tree with *Nymphidium* as a sister taxon to *Thisbe* (Lemoniini) plus *Helicopsis* (Helicopini) warrants further investigation as it opposes all previous hypotheses (i.e., Bates, 1868; Stichel, 1930–31; Harvey, 1987).

This investigation considers the higher-level phylogeny of the rioidinid tribe Lemon-

iini sensu Harvey (1987) in light of a cladistic analysis of adult morphological characters. After reassessing the single character justifying the monophyly of Lemoniini, we provide a cladistic analysis of 97 characters and ask if Harvey's Lemoniini sections *Lemonias*, *Synargis*, and *Audre* (fig. 1) are supported by our results. We then compare our results to the classifications of Stichel (1930–

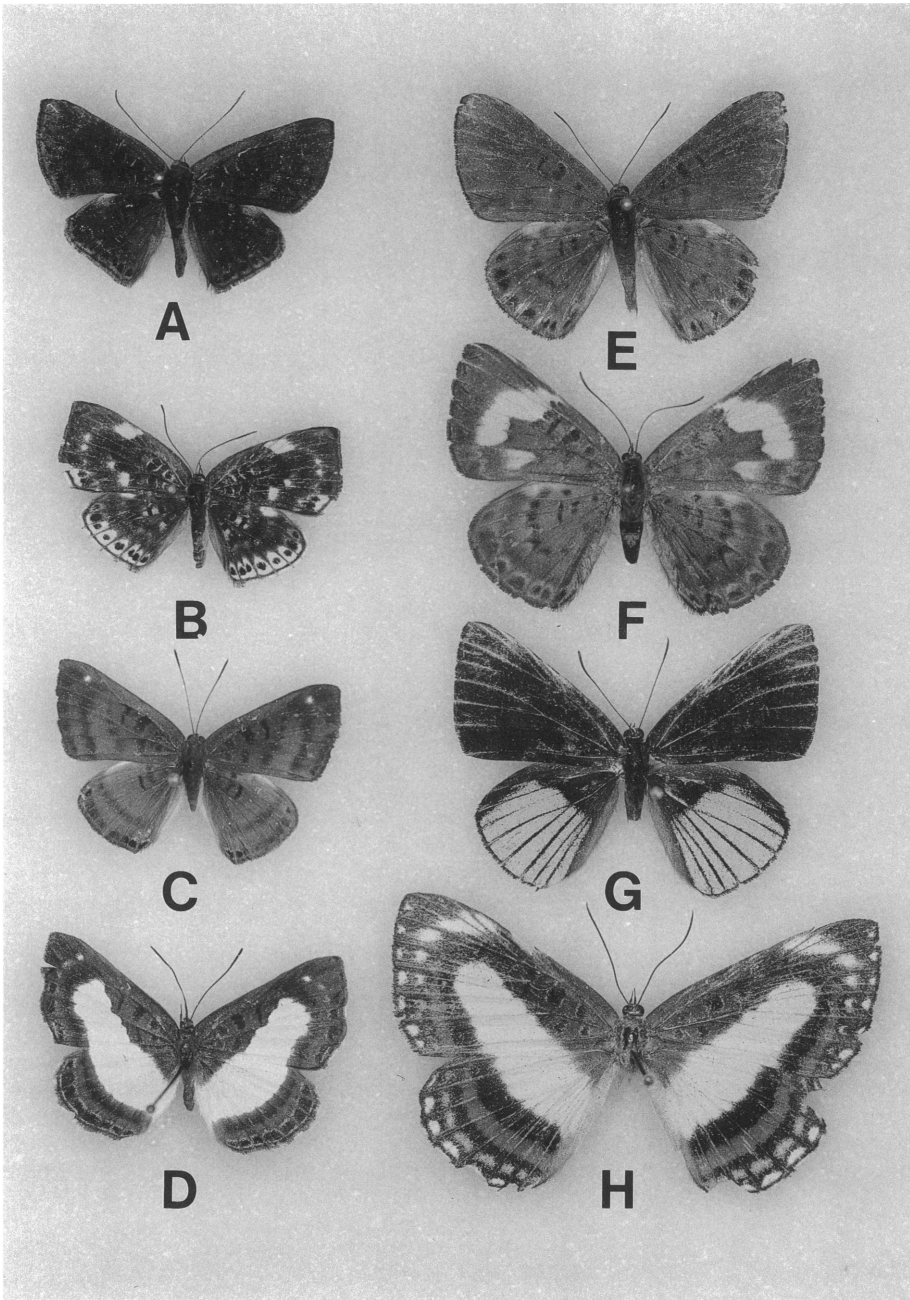


Fig. 3. Ingroup taxa (*Synargis* section of Harvey, 1987, in part). **A**, *Synargis abaris* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **B**, *Synargis abaris* (female) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **C**, *Synargis mycone* (male) [Panama, Barro Colorado Island (PJD)]; **D**, *Synargis mycone* (female) [Panama, Barro Colorado Island (PJD)]; **E**, *Synargis orestes* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **F**, *Synargis orestes* (female) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **G**, *Synargis palaeste* (male) [Costa Rica, Parque Nacional Corcovado (PJD)]; **H**, *Synargis palaeste* (female) [Panama, Darién, Pivesal (PJD)].

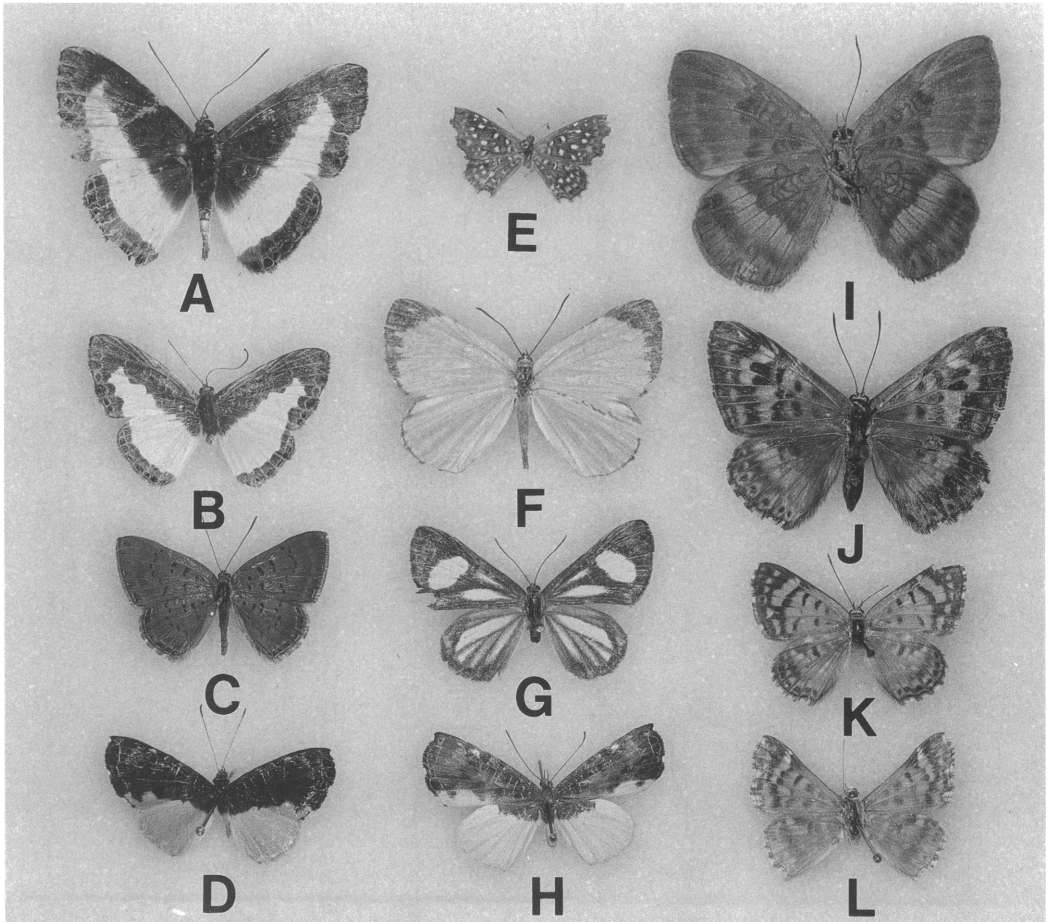


Fig. 4. Ingroup taxa (*Synargis* section (in part) and *Audre* section of Harvey, 1987). **A**, *Juditha azan* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **B**, *Juditha molpe* (male) [Costa Rica, Puntarenas, Parque Corcovado (PJD)]; **C**, *Thysanota galena* (male) [Brazil, Rondônia, Fazenda Rancho Grande (AMNH)]; **D**, *Catocyclotis aemulius* (male) [Costa Rica, Puntarenas, Las Alturas (PJD)]; **E**, *Audre guttata* (male) [Argentina, Salta, Pichanal (LACM)]; **F**, *Eiseleia pinchanalensis* (male) [Paraguay, Cordillera Santísima Trinidad (AMNH)]; **G**, *Ematurgina* nr. *leucotopus* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **H**, *Catocyclotis aemulius* (female) [Costa Rica, Puntarenas, Las Alturas (PJD)]; **I**, *Aricoris tutana* (male), ventral aspect [Jaraguá do Sul, Santa Catarina, Brasil (AME)]; **J**, *Audre domina* (male) [Panama, Pipeline Road (PJD)]; **K**, *Audre erostratus* (male) [Panama, Panama, Corozal (AMNH)]; **L**, *Audre* sp. (male) [Argentina, Mendoza, San Rafael (PJD)].

31) and Harvey (1987). Based on our morphological and systematic analyses we propose the amalgamation of Lemoniini and Nymphidiini. As no genus included here has been subject to a systematic revision, the monophyly of these taxa has not been evaluated previously. Although the restricted number of our study taxa precludes defining all genera considered in this work, the character analysis may prove useful in future revisionary studies.

METHODS

SPECIES EXAMINED

To test the monophyly of Lemoniini we analyzed 23 species in 11 genera (33% of all species in the tribe) plus 8 species from the putative sister tribe Nymphidiini (fig. 5). These taxa included (1) 4 out of 5 genera in Stichel's subtribe Nymphidiini, and 10 out of 31 of his Emesini (Stichel, 1930–31); and (2) all genera of Harvey's Lemoniini, and 5 of

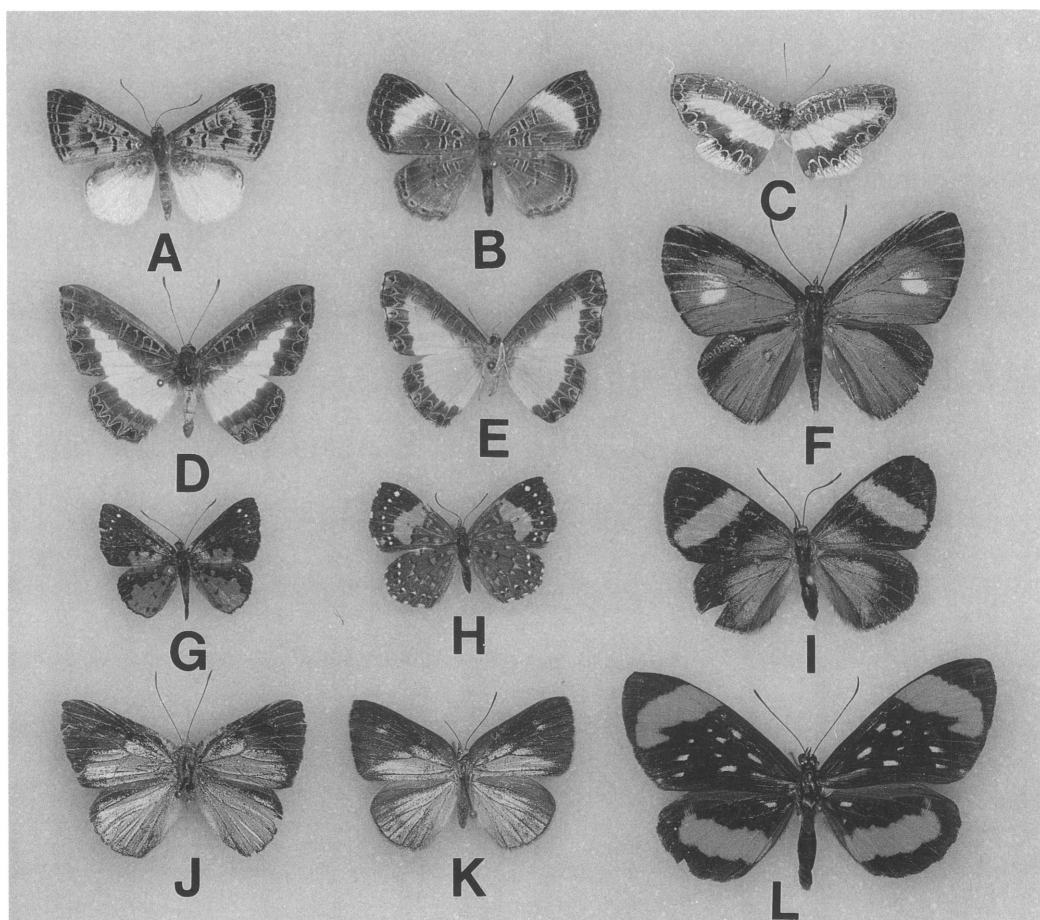


Fig. 5. Outgroup taxa (all placed in Nymphidiini except *Stalactis*, which is in Stalactini). **A**, *Adelotypa alector* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **B**, *Adelotypa alector* (female) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **C**, *Nymphidium mantus* (male) [Panama, Panama, Pipeline Road (PJD)]; **D**, *Nymphidium azanoides* (male) [Costa Rica, Heredia, La Selva (PJD)]; **E**, *Nymphidium cachrus* (male), ventral aspect [Ecuador, Sucumbios, Garza Cocha (PJD)]; **F**, *Setabis lagus* (male) [Costa Rica, Puntarenas, Las Cruces (PJD)]; **G**, *Calospila emylius* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **H**, *Calospila emylius* (female) [Ecuador, Sucumbios, Garza Cocha (PJD)]; **I**, *Setabis lagus* (female) [Costa Rica, Puntarenas, Las Cruces (PJD)]; **J**, *Theope publius* (male) [Costa Rica, Puntarenas, Parque Corcovado (PJD)]; **K**, *Theope virgilius* (female) [Costa Rica, Puntarenas, Isla del Caño (PJD)]; **L**, *Stalactis euterpe* (male) [Ecuador, Sucumbios, Garza Cocha (PJD)].

16 within his Nymphidiini (Harvey, 1987). Genera were sampled to represent the taxonomic diversity of the groups according to classifications by Stichel and Harvey, and species were chosen based on availability of material. *Stalactis euterpe* (Linnaeus, 1758) (Stalactini) was selected as an outgroup species for rooting the tree because all evidence suggests that it belongs to a group separate from the Lemoniini and Nymphidiini (Stichel, 1910–11, 1930–31; Harvey, 1987).

The spellings of generic and species names considered here follow Bridges (1994), excepting *Thysanota* (see Hemming, 1967). All taxa and specimens included in this study are listed in table 1 and illustrated in figures 2–5.

We examined males and females for taxa representing all 11 genera of Lemoniini except *Ematurgina* Röber, 1903 and *Aricoris* Westwood, 1851, for which females were unavailable. Our analyses include twice as many Lemoniini species as considered pre-

TABLE 1
Study Taxa and Individuals Dissected*

Taxa	Source of dissected material
Ingroup	
Lemoniini	
<i>Aricoris</i> Westwood, 1851 (2)	
<i>A. tutana</i> (Godart, 1824)	1 male: Brasil, Santa Catarina, Jaraguá do Sul (AME); 1 male: Brasil, Santa Catarina, São Bento do Sul(AME)
<i>Audre</i> Hemming, 1934 (20)	
<i>A. domina</i> (Bates, 1864)	1 male: Panama, Panama, Pipeline Road (PJD); 1 female: Panama, Panama, Gamboa (PJD)
<i>A. erostratus</i> (Westwood, 1851)	1 male: Panama, Panama, Corozal (AMNH); 1 female: Panama, Panama, Nueva Gorgona (AMNH)
<i>A. guttata</i> (Stichel, 1910)	1 male and 1 female: Argentina, Salta, Pichanal (LACM)
<i>Audre</i> sp.	1 male and 1 female: Argentina, Mendoza, San Rafael (PJD)
<i>Catocyclotis</i> Stichel, 1911 (1)	
<i>C. aemulius</i> (Fabricius, 1793)	1 male: Costa Rica, Puntarenas, Las Alturas (PJD); 1 female: Costa Rica, San Miguel (PJD)
<i>Eiseleia</i> Miller and Miller, 1972 (2)	
<i>E. pinchanalensis</i> Miller and Miller, 1972	1 male: Paraguay, Cordillera Santísima Trinidad (AME); 1 female: Argentina, Salta, Pichanal (AME)
<i>Ematurgina</i> Röber, 1903 (5)	
<i>E. nr. leucotopus</i> Stichel, 1910	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>Juditha</i> Hemming, 1934 (5)	
<i>J. azan</i> (Stoll, 1780)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>J. molpe</i> (Hübner, 1808)	1 male and 1 female: Costa Rica, Puntarenas, Parque Nacional Corcovado (PJD)
Lemonias Hübner, 1806 (6)	
<i>L. agave</i> (Godman and Salvin, 1886)	1 male and 1 female: Mexico, Veracruz, Presidio (AMNH)
<i>L. caliginea</i> (Butler, 1867)	1 male and 1 female: Mexico, Veracruz (LACM)
<i>L. zygia</i> (Hübner, 1806)	1 male and 1 female: Brazil, Rondônia, Fazenda Rancho Grande (LACM)
<i>Synargis</i> Hübner, 1819 (23)	
<i>S. abaris</i> (Cramer, 1776)	1 male: Peru, Madre de Dios, Shintuya (PJD); 1 female: Ecuador, Napo, Jatun Sacha (PJD)
<i>S. mycone</i> (Hewitson, 1865)	1 male: Costa Rica, Guanacaste, Parque Santa Rosa; 1 female: Panama, Panama, Barro Colorado Island (PJD); 1 female: Costa Rica Limon, Tortuguero (PJD)
<i>S. orestes</i> (Cramer, 1780)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>S. palaeste</i> (Hewitson, 1911)	1 male: Costa Rica, Puntarenas, Parque Nacional Corcovado (PJD); 1 male: Costa Rica, Puntarenas, Rincón (PJD); 1 female: Panama, Darién, Pivesal (PJD)
<i>Thisbe</i> Hübner, 1819 (4)	
<i>T. irenea</i> (Stoll, 1780–1782)	1 male: Costa Rica, Heredia, Chilamate (PJD); 1 male: Panama, Panama, Pipeline Road (PJD); 1 female: Panama, Panama, Barro Colorado Island (PJD)
<i>T. lycorias</i> (Hewitson, 1853)	1 male: Costa Rica, Guanacaste, Parque Santa Rosa (PJD); 1 female: Costa Rica, Heredia, Finca La Selva (PJD)
<i>T. molela</i> (Hewitson, 1865)	1 male: Peru, Madre de Dios, Shintuya (PJD); 1 female: Venezuela, Canaima (LACM)
<i>Thysanota</i> Stichel, 1911 (1)	
<i>T. galena</i> (Bates, 1868)	1 male: Brazil, Rondônia, Fazenda Rancho Grande (AMNH); 1 female: Brazil, Rondônia, Fazenda Rancho Grande (AMNH)
Uraneis Bates, 1868 (3)	
<i>U. hyalina</i> (Butler, 1867)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>U. ucubis</i> Hewitson, 1870	1 male: Costa Rica, Heredia, Cariblanco (PJD); 1 female: Costa Rica, Cartago, Turrialba (PJD)

TABLE 1—(Continued)

Taxa	Source of dissected material
Outgroups	
Nymphidiini	
<i>Adelotypa alector</i> (Butler, 1867)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>Calospila emylius</i> (Cramer, 1775)	1 male, 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>Nymphidium azanoides</i> Butler, 1867	1 male: Panama, Darién, Cerro Pirre (PJD); 1 male: Costa Rica, Heredia, La Selva (PJD); 1 female: Costa Rica, Heredia, La Selva (PJD)
<i>Nymphidium cachrus</i> (Fabricius, 1787)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
<i>Nymphidium mantus</i> (Cramer, 1775)	1 male: Ecuador, Sucumbios, Garza Cocha (PJD); 1 male: Panama, Darién, Cerro Pirre (PJD); 1 male: Panama, Panama, Barro Colorado Island (PJD); 1 female: Panama, Panama, Pipeline Road (PJD)
<i>Setabis lagus</i> (Cramer, 1777)	1 male: Costa Rica, Puntarenas, Las Alturas (PJD); 1 female: Costa Rica, Puntarenas, Las Cruces (PJD)
<i>Theope publius</i> Felder and Felder, 1861	1 male: Costa Rica, Puntarenas, Punta Quepos (PJD); 1 female: Costa Rica, Puntarenas, Corcovado (PJD)
<i>Theope virgilius</i> (Fabricius, 1793)	1 male and 1 female: Costa Rica, Puntarenas, Isla del Caño (PJD)
Stalachtini	
<i>Stalachtis euterpe</i> (Linnaeus, 1758)	1 male and 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)

^a Numbers in bold indicate the numbers of species in each genus according to Harvey (1987, except for the genus *Thisbe*). References to original descriptions are in Stichel (1930) and Bridges (1994). Abbreviations for source collections are : AMNH, American Museum of Natural History; AME, Allyn Museum of Entomology; LACM, Natural History Museum of Los Angeles County; and PJD, P. J. DeVries.

viously (Harvey, 1987), thus providing a new starting point for future systematic work on riordinid tribes.

PREPARATION OF MATERIAL

Dissections were performed using a standard treatment with a 10% solution of potassium hydroxide. Specimens were subsequently examined and stored in glycerol. Whenever possible we examined the following parts with light microscopy (stereomicroscope and compound microscope): male genitalia and left mesoleg (when not available, the right mesoleg was prepared); female genitalia and left foreleg (when not available, the right foreleg was prepared); and male and female proboscis, chaetostemmata, wings, and tegula.

CHARACTERS AND TERMINOLOGY

The nomenclature for adult morphology (i.e., wings veins, legs, head) follows Scoble (1992). Terminology for male and female genitalia follows Klots (1970), with alternative terms of other authors given in the list

of abbreviations. The following abbreviations are used throughout the text and appendices:

Ae aedeagus; **Am** ampulla; **Antr** antrum; **Cha** chaetostemmata; **Coe** coecum penis; **Crn** cornuti; **Crp.bu** corpus bursa; **Cu** cucullus; **D.fen** dorsal fenestrella; **Du.bu** ductus bursa; **Du.sml** ductus seminalis; **Gn** gnathos (= brachia sensu Muschamp in Ogata et al., 1957; falci sensu Bethune-Baker, 1910); **Jx** juxta (= pedunculi sensu Harvey, 1987); **L1** foreleg; **L.fen** lateral fenestrella; **Ob** ostium bursa; **Pap.a** papilla analis; **Prob** proboscis; **Sa** saccus; **Sig** signum; **Sl** sacculus; **Spr** spiracle; **Ssca** subscaphium; **Stn** sternite (numbers may follow abbreviation; e.g., Stn7, seventh sternite); **Teg** tegumen; **Tg** tergite (numbers may follow abbreviation; e.g., Tg7, seventh tergite); **Tra** transtilla; **Tsm** tarsomere (numbers may follow abbreviation; e.g., Tsm1, first tarsomere); **Un** uncus; **Va** valva; **Ves** vesica; **Vin** vinculum.

Of the characters considered here, nine were compiled from previous riordinid studies (Harvey, 1987; Hanner, 1997), some were adapted from studies of other butterfly fam-

ilies (references follow the characters in appendix 1), but within the context of riodinids, 86% are described here for the first time. We examined all 97 characters firsthand, and none of the interpretations of characters were drawn from descriptions in the literature. We illustrate most characters used in our analysis (figs. 8–16) to provide future workers a foundation upon which to refine the entire higher level phylogeny of riodinid butterflies. A small number of autapomorphic characters were included in the analysis because they are either potentially useful for future phylogenetic studies (e.g., characters 37, 62, 92) or they represent tribal level synapomorphies (e.g., 38).

We found few informative characters on the head, legs, and wings. For example, the male mesolegs yielded a small number of characters (e.g., extent of the distal fringe of the pulvilli, number of setae and scales on the tibial spur), but because they were difficult to examine and score with optical microscopy, they were not included in our analysis. In contrast, male and female genitalic morphology provided many informative characters, as in other studies (e.g., Miller, 1991; Penz, 1999). Therefore, most of the characters in our analysis (92%) were derived from genitalia.

PHYLOGENETIC ANALYSIS

Our character matrix comprised 97 characters (71 binary, 26 multistate): 33 derived from females (3 from forelegs, 30 from genitalia), 60 from males (1 from proboscis, 59 from genitalia), and 4 from both sexes (chaetostemmata, tegula, venation; appendix 1). Parsimony analysis was used with the following settings: all characters were given equal weight, multistate characters were unordered, and polymorphic characters were treated as exhibiting both states. An heuristic search with 50 TBR replicates was performed as implemented in PAUP 4.0b1 (Swofford, 1998), and strength of branch support was estimated by means of 500 bootstrap replicates (Felsenstein, 1985). Characters were mapped onto trees using MacClade 3.01 (Maddison and Maddison, 1992), and character reconstruction for polytomies was performed using the “hard polytomies” op-

tion. A complete character list is provided in appendix 1 and our data matrix is presented in appendix 2.

RESULTS

MONOPHYLY OF THE LEMONIINI

Our analysis produced 12 equally parsimonious trees (tree length = 385, CI = 0.33, RI = 0.60). The strict consensus of these trees is presented in figure 6, and two equally parsimonious trees in figure 7 show uncertainty in the systematic position of *Catocyclotis aemulius* and *Thisbe* plus *Uraneis*. In contrast to deep nodes of the tree, subterminal groupings were generally well supported (see bootstrap values in fig. 6).

We found that, as presently conceived, the genera comprising Lemoniini do not form a monophyletic group (figs. 6, 7). The Nymphidiini genera *Nymphidium* and *Theope* consistently grouped with the Lemoniini *Synargis* and *Thysanota* (fig. 6; for character justification, see table 2, clade 13). *Catocyclotis aemulius* (Lemoniini) grouped with *Adelotypa alector*, *Setabis lagus*, and *Calospila emylius* (Nymphidiini) in some of our trees (fig. 7A; table 2, clade 2), and appeared as basal taxon in others (fig. 7B; table 2, clade 20). Finally, the genera *Adelotypa*, *Setabis*, and *Calospila* either appeared as basal to all taxa except *Audre guttata* in some trees (figure 7A; table 2, clade 1) or appeared as basal to all taxa except for *Thisbe*, *Uraneis*, *Audre guttata*, and *Catocyclotis aemulius* in others (figure 7B; table 2, clade 22). Although not central to our study, we note that the small number of species of Nymphidiini in our sample also did not form a monophyletic group (figs. 6, 7). Therefore, in lieu of a more comprehensive analysis we conclude that Lemoniini and Nymphidiini do not constitute natural taxa.

GROUPS OF GENERA

Our results indicate that within Lemoniini the following genera are closely related (fig. 6): (1) *Thisbe* and *Uraneis* (table 2, clade 6), (2) *Synargis* and *Thysanota* (table 2, clade 17), (3) *Audre*, *Aricoris*, *Eiseleia* and *Ematurgina* (table 2, clade 19), and (4) *Juditha* and *Lemonias* (table 2, clade 10). Furthermore, the Nymphidiini as considered here

TABLE 2
Characters Justifying Groups of Species and Genera

Clade 1. <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> , <i>Catocyclotis</i> , <i>Thisbe</i> , <i>Uraneis</i> , <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i> (24:0) Du.bu adorned with longitudinal ribs. (44:0) Male Stn8 with terminal abdominal projection extending beyond edge of pleural membrane (figs. 10L, 11E). (65:0) Ssca uniformly narrow (figs. 14A, 15A). (71:1) Vin extending along most of the anterior edge of Teg (figs. 12C, 12E).	(32:1) Base of Sig elongated (figs. 9H, 9K, 9L). (48:1) Abdominal projection on male Stn8 well sclerotized both externally and internally. (58:0) In ventral view, lateral margins of Un widened.
Clade 2. <i>Catocyclotis</i> , <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> (73:0) In ventrolateral view, Vin laterally widened to form a blade (fig. 14D). (90:0) Am split (fig. 13C).	Clade 10. <i>Lemonias</i> , <i>Juditha</i> (8:3) Sensilla on Tsm1 of female L1: distributed over less than one half of the length of Tsm1 (fig. 8H). (9:0) Female Stn7 elongated posteriorly to cover Ob (fig. 9B). (11:0) Genital plate equally well developed anteriorly and posteriorly (fig. 8J). (77:0) Distal end of Ae acute.
Clade 3. <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> (13:1) Genital plate thin, arched rim (fig. 8L). (40:0) Third abdominal Spr located closer to Stn3 than to Tg3 (fig. 10A). (45:0) Abdominal projection on male Stn8 simple (figs. 10E, 10F, 10G, 10H, 10J, 10L). (78:1) Tapering tip of Ae elongated.	Clade 11. <i>Juditha azan</i> , <i>J. molpe</i> , <i>Lemonias zygia</i> , <i>L. caliginea</i> (6:2) Spurs on Tsm of female L1 present on Tsm2-4 (fig. 8H). (7:0) In lateral view of female L1, spur on Tsm2 approaches the length of Tsm1 (figs. 8F and 8H). (14:0) Genital plate with one or more transverse ribs (figs. 9A, 9B). (63:0) Posterior end of Ssca forming a narrow lobe (fig. 14C).
Clade 4. <i>Thisbe</i> , <i>Uraneis</i> , <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i> (23:1) Spiny sculpturing on Du.bu vestigial or absent at midlength.	Clade 12. <i>Juditha</i> (35:1) Sig with spiny sculpturing restricted to base. (54:1) Un split (figs. 12C, 12E). (60:2) Posterior edge of Teg with a prong that projects into anterior edge of Un (fig. 12C). (72:2) Vin connected to anterior edge of Teg entirely by weakly sclerotized tissue (fig. 12C). (89:1) Sl asymmetrical (fig. 14C). (93:0) Inner base of Va adorned with patches of setae that are almost as long as Va itself (fig. 14C). (94:1) Inner base of Va devoid of thickened cuticular bracing. (96:0) Posterolateral ends of Sa elongated to connect with anterior portion of Vin. (97:1) In lateral view, anterior end of Sa not widened dorsoventrally.
Clade 5. <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i> (18:0) Antr well sclerotized both dorsally and ventrally. (97:0) In lateral view, anterior end of Sa widened dorsoventrally.	Clade 13. <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> (41:2) Male Tg8 about 2 times as long as Tg7. (57:1) Posterior margin of Un slightly concave (fig. 12D). (61:0) Lateral margins of Teg thickened at edges of L.fen to form ribs (fig. 13D). (69:0) Distal portion of Gn wide (fig. 16B). (73:0) In ventrolateral view, Vin laterally widened to form a blade (fig. 14D). (82:1) Coe present (figs. 16E, 16G).
Clade 6. <i>Thisbe</i> , <i>Uraneis</i> (5:0) Hindwing A2 produced to form a tail in at least one sex (fig. 8D). (22:0) Connection of Du.bu with Crp.bu narrow (fig. 9I). (24:1) Du.bu adorned with ribs forming a honeycomb pattern. (26:0) Crp.bu rounded (figs. 9I, 9J). (28:2) Spiny sculpturing of Crp.bu composed of groups of spines organized in clusters.	Clade 14. <i>Nymphidium</i> , <i>Theope</i> (17:3) Antr completely membranous. (24:1) Du.bu adorned with ribs forming a honeycomb pattern. (26:0) Crp.bu rounded (figs. 9I, 9J). (40:0) Third abdominal Spr located closer to Stn3 than to Tg3 (fig. 10A). (45:0) Abdominal projection on male Stn8 simple (figs. 10E, 10F, 10G, 10H, 10J, 10L). (72:2) Vin connected to anterior edge of Teg entirely by weakly sclerotized tissue (fig. 12C).
Clade 7. <i>Uraneis hyalina</i> , <i>U. ucubis</i> , <i>Thisbe lycorias</i> (3:0) Base of tegula bright orange or red, clearly contrasting with thorax. (8:1) Distribution of sensilla on Tsm1 of female L1: along the distal two thirds (fig. 8G). (44:1) Male Stn8 devoid of terminal abdominal projection (figs. 10D, 11A, 11L, 11N, 11O). (78:1) Tapering tip of Ae elongated.	
Clade 8. <i>Uraneis</i> (4:1) Forewing R4 meets wing margin posterior to apex (fig. 8B).	
Clade 9. <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i>	

TABLE 2—(Continued)

(74:1) Tra sclerotized (figs. 13A, 13D).	(84:2) Coe long (fig. 14D).
(75:0) Ves with conspicuous cuticular sculpturing (fig. 13D).	(91:0) Va fused ventrally (fig. 14D).
Clade 15. <i>Nymphidium</i>	Clade 18. <i>Synargis</i>
(6:2) Spurs on Tsm of female L1 present on Tsm2-4 (fig. 8H).	(21:0) Portion of Du.bu bordering Antr well sclerotized.
(35:1) Sig with spiny sculpturing restricted to base.	(65:3) Ssca broad anteriorly and narrowed posteriorly (fig. 14D).
(43:1) Genital capsule attached dorsally to male Tg8 by a sclerotized plate.	(67:1) Cuticular sculpturing restricted to posterior end of Ssca (fig. 14C).
(46:0) Abdominal projection on male Stn8 asymmetrical (fig. 10F).	(96:0) Posterolateral ends of Sa elongated to connect with anterior portion of Vin.
(57:2) Posterior margin of Un strongly concave, Un apparently four-lobed (fig. 12B).	Clade 19. <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i>
(60:2) Posterior edge of Teg with a prong that projects into anterior edge of Un (fig. 12C).	(50:0) Posteromedial margin of male Stn8 with a conspicuous v-shaped notch that is markedly deeper than edges of pleural membrane (fig. 11K).
(69:2) Distal portion of Gn narrow (fig. 16D).	(70:1) Distal portion of Gn about twice as long as proximal portion (figs. 16C, 16D).
(80:0) Distal opening of Ae dorsal.	(76:3) Crn composed of a broad thin plate (fig. 13B).
(83:1) Coe much wider than the Ae shaft, bulb-shaped (fig. 13A).	(96:0) Posterolateral ends of Sa elongated to connect with anterior portion of Vin.
Clade 16. <i>Theope</i>	Clade 20. <i>Audre guttata</i> , <i>Thisbe</i> , <i>Uraneis</i> , <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> , <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i>
(39:1) Number of male abdominal Stn reduced to seven.	(36:1) Spiny sculpturing of Sig small.
(42:0) Posterolateral margin of male Tg8 adorned with projections (fig. 10I).	(59:0) Posterior edge of Teg completely fused to Un.
(48:0) Abdominal projection on male Stn8 well sclerotized in its external portion, membranous along entire length of its internal portion.	(61:1) Lateral margins of Teg devoid of thickening at edges of L.fen (fig. 14B).
(59:1) Posterior edge of Teg not completely fused to Un.	(74:0) Tra membranous.
(87:1) Va reduced to a medial compact prong (fig. 13B).	Clade 21. <i>Thisbe</i> , <i>Uraneis</i> , <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> , <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i>
(95:0) Sa absent (fig. 13B).	(23:1) Spiny sculpturing on Du.bu vestigial or absent at midlength.
Clade 17. <i>Synargis</i> , <i>Thysanota</i>	(65:0) Ssca uniformly narrow (figs. 14A, 15A).
(34:1) Sig compressed transversely (fig. 9L).	Clade 22. <i>Adelotypa</i> , <i>Setabis</i> , <i>Calospila</i> , <i>Nymphidium</i> , <i>Theope</i> , <i>Synargis</i> , <i>Thysanota</i> , <i>Audre</i> (excepting <i>A. guttata</i>), <i>Aricoris</i> , <i>Eiseleia</i> , <i>Ematurgina</i> , <i>Lemonias</i> , <i>Juditha</i>
(49:0) Tip of bifurcated abdominal projection on male Stn8 adorned with spines (fig. 11E).	(2:1) Setae on Cha of lighter color than cuticle.
(52:0) Weakly sclerotized posteromedial margin of male Stn8 extending to reach anterior edge of Stn8 (figs. 11E, 11I).	
(53:1) Ventrolateral sclerotized cuticular bars forming an internal rib.	
(77:2) Distal end of Ae blunt (fig. 15A).	

MacClade (Maddison and Maddison, 1992) was used to map characters onto two of the 12 equally parsimonious trees, and clade numbers refer to fig. 7A (1–19) and 7B (20–22). Characters indicated in bold type were unique to the group they support (independent of reversals).

MONOPHYLY OF GENERA

Of the eight genera represented by more than one species in our analysis, five appear as monophyletic groups: *Uraneis*, *Juditha*, *Nymphidium*, *Theope*, and *Synargis* (fig. 6; table 2, clades 8, 12, 15, 16, and 18, respectively). We note that not all characters used to justify the monophyly of these genera are

universal, but they are potentially useful for future species-level studies.

Three genera in this study did not form monophyletic groups. *Thisbe* is paraphyletic with respect to *Uraneis* (table 2, clade 7), and *Lemonias* is paraphyletic with respect to *Juditha* (fig. 6; table 2, clades 10 and 11). As demonstrated by the basal position of *Audre guttata* and the grouping of the remain-

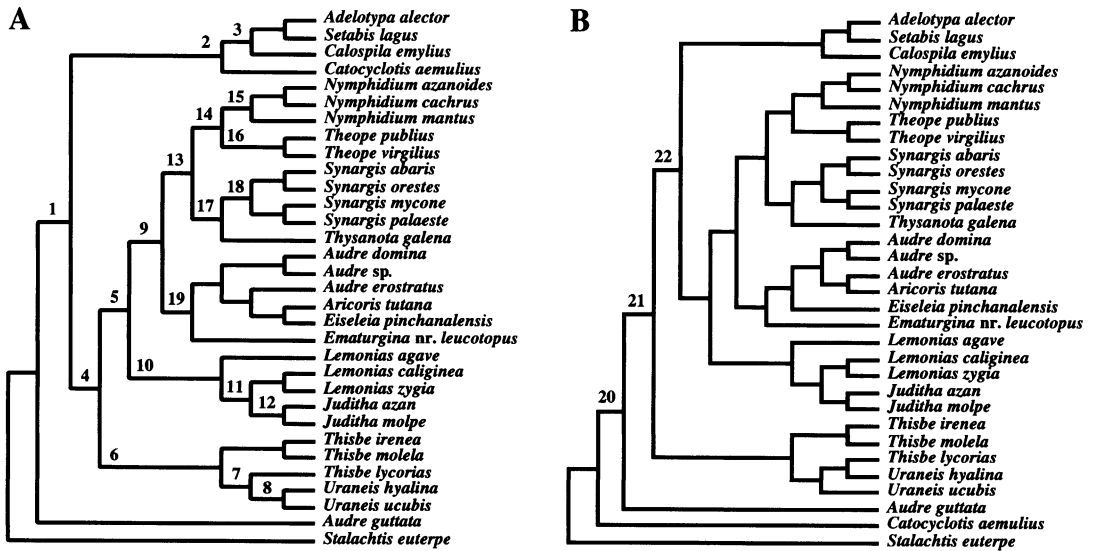


Fig. 7. Two selected equally parsimonious trees that show variation in the systematic position of Lemoniini taxa *Catocyclotis aemulius*, *Thisbe* plus *Uraneis*, and *Audre guttata*. These trees (A and B) were used for reconstruction of character changes, and numbers above branches correspond to clades discussed in table 2 (see Results).

ing *Audre* species with *Aricoris* and *Eiseleia* (figs. 6, 7; table 2, clades 1 and 19), *Audre* was the most problematic genus in our analysis.

DISCUSSION

This study is the first phylogenetic assessment of the tribe Lemoniini that evaluates characters defining this tribe and the relationships among genera. The impact that this study may have on riodinid systematics rests on three points: (1) How do our results differ from previous classifications? (2) How reliable are the characters supporting the Lemoniini and Nymphidiini? (3) What do our observations on character variability contribute to future systematics studies of riodinid butterflies?

COMPARISONS TO PREVIOUS CLASSIFICATIONS

Our study of 16 genera encompasses a substantial fraction of the ingroup, therefore allowing a comparison to existing classifications (fig. 1). The genera *Audre*, *Synargis*, *Juditha*, and *Nymphidium* were grouped under Nymphidiini by Stichel (fig. 1). We confirm Stichel's suggestion that these genera

are closely related, but they form a monophyletic group only in combination with *Lemonias*, *Theope*, *Thysanota*, *Aricoris*, and *Ematurgina*, which were classified by Stichel in his Emesini. Therefore, our results partly support Stichel's Nymphidiini, but not his Emesini (figs. 1, 6).

The monophyly of Lemoniini sensu Harvey (1987) was not supported by our analyses, as demonstrated by the grouping of *Nymphidium* and *Theope* with *Synargis* and *Thysanota*, and by the placement of *Catocyclotis* (fig. 7A, B). There was little agreement between our results and Harvey's division of Lemoniini into three sections. Genera in the *Lemonias* and *Synargis* sections do not form monophyletic groups (fig. 6), and although our results support the *Audre* section (except for *A. guttata*, fig. 6), the character defining this group (enlarged male proboscis, fig. 8A) is also present in *Thysanota galena* (*Synargis* section). Thirty-three additional steps (7.9%) were required to accommodate the monophyly of Lemoniini and Nymphidiini plus the infratribal classification of Lemoniini into three sections. Our results therefore weaken both the tribal and infratribal classification of Lemoniini as presently conceived.

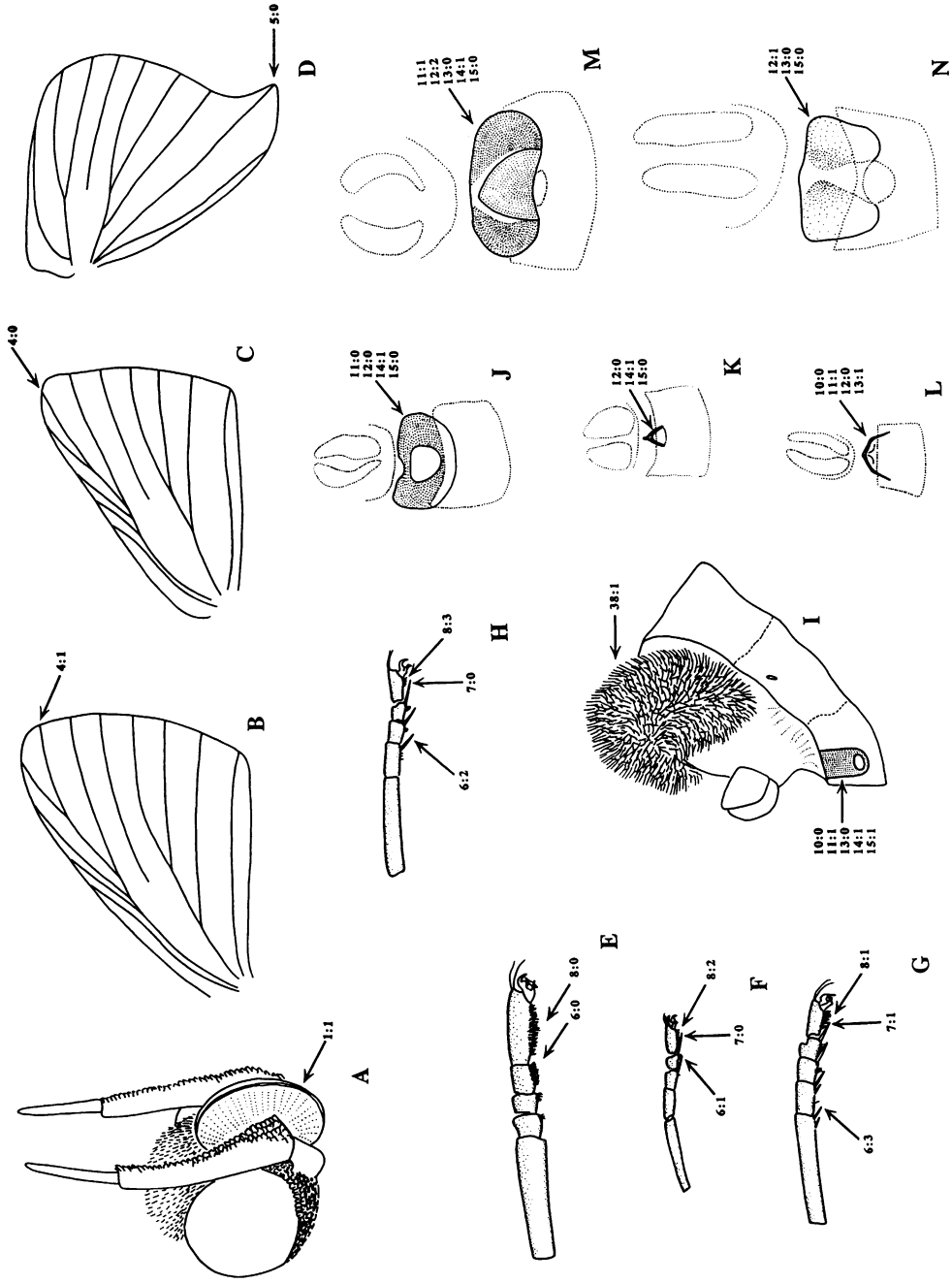


Fig. 8. Enlarged base of the proboscis of *Aricoris tutana*. Forewing venation of **B**, *Uraneis hyalina*; and **C**, *Synargis mycone*. Hindwing venation of **D**, *Thisbe lycorias*. Detail of the female left foreleg of **E**, *Stalachtis euterpe*; **F**, *Catocyclotus aemulius*; **G**, *Uraneis hyalina*; and **H**, *Juditha azan*. Terminal portion of the female abdomen of **I**, *Stalachtis euterpe* (hairs on the papilla anales were omitted). Genital plate of **J**, *Theope publius*; **K**, *Catocyclotus aemulius*; **L**, *Catospila emylius*; **M**, *Thisbe lycorias*; and **N**, *Uraneis hyalina*.

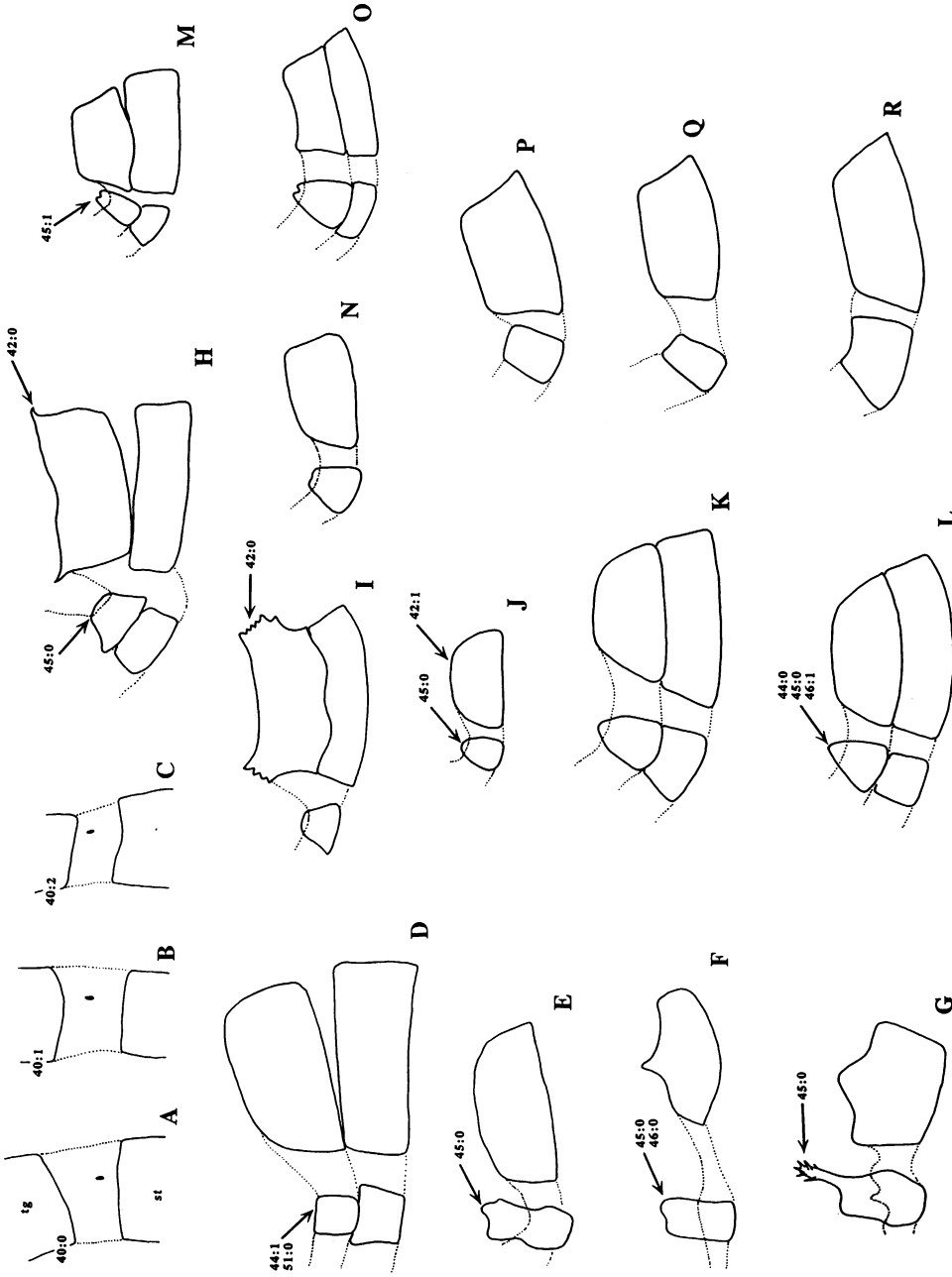


Fig. 10. Detail of the male third abdominal segment (tg = tergite, st = sternite, anterior portion to the left): **A**, *Setabis lagus*; **B**, *Thisbe irenea*; **C**, *Lemonias caliginea*. Male eighth abdominal tergum and sternum (dotted lines represent the pleural membrane and weakly sclerotized areas) with setae omitted: **D**, *Stalactis euterge*; **E**, *Nymphidium azanoides*; **F**, *Nymphidium cactrus*; **G**, *Nymphidium mantus*; **H**, *Theope publius*; **I**, *Theope virgilius*; **J**, *Calospila emylius*; **K**, *Setabis lagus*; **L**, *Adelotrypa alector*; **M**, *Catocyclotis aemulius*; **N**, *Thisbe irenea*; **O**, *Thisbe molela*; **P**, *Thisbe lycortias*; **Q**, *Uraneis hyalina*; **R**, *Uraneis ucubis*.

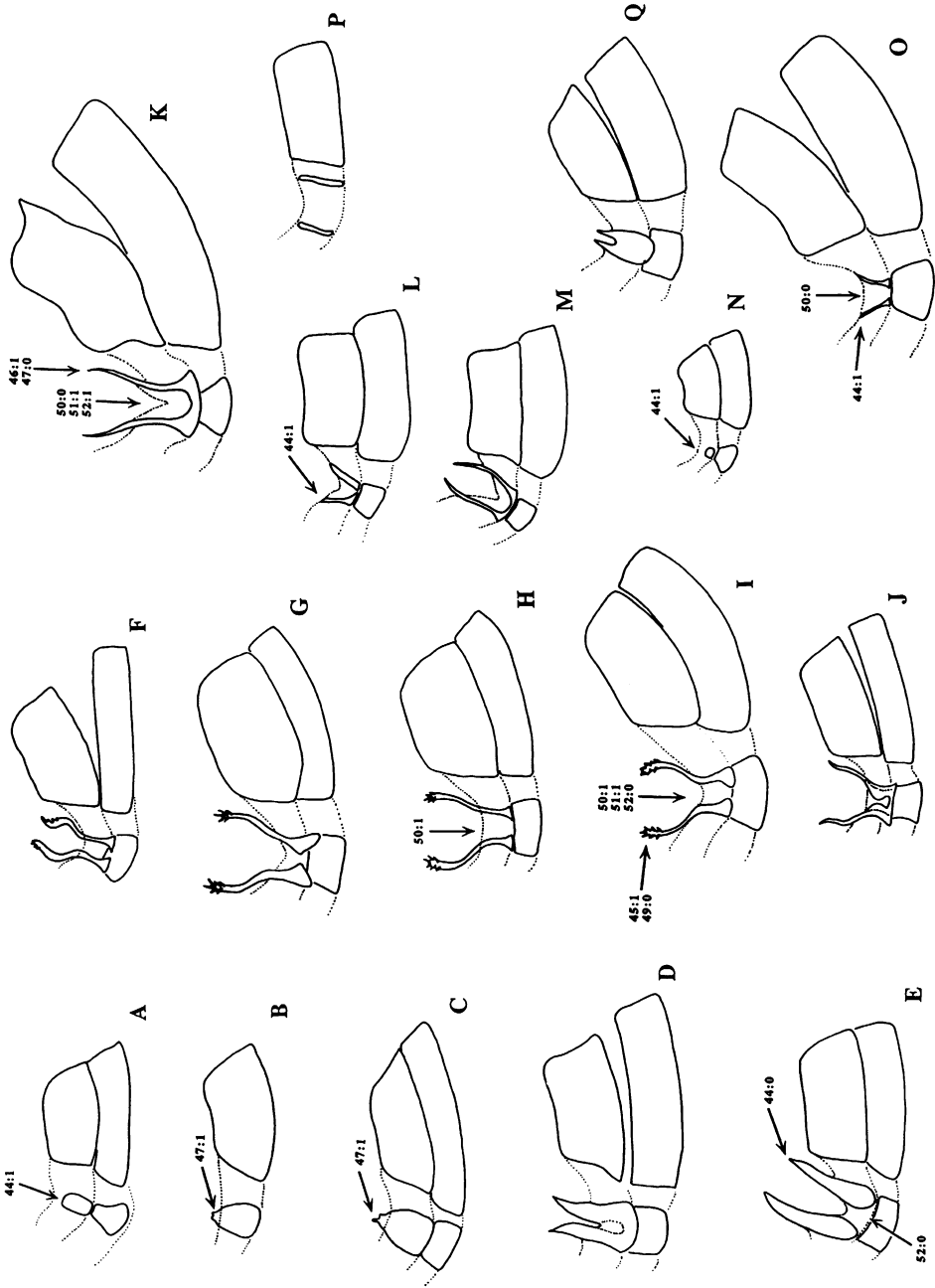


Fig. 11. Male eighth abdominal tergum and sternum (dotted lines represent the pleural membrane and weakly sclerotized areas) with setae omitted: **A**, *Lemonias agave*; **B**, *Lemonias caliginea*; **C**, *Lemonias zygia*; **D**, *Juditha azan*; **E**, *Juditha molpe*; **F**, *Synargis abaris*; **G**, *Synargis orestes*; **H**, *Synargis mycone*; **I**, *Synargis palaeste*; **J**, *Thysanota galena*; **K**, *Audre domina*; **L**, *Audre sp.*; **M**, *Audre erostratus*; **N**, *Audre guttata*; **O**, *Aricoris tutana*; **P**, *Eiseleta pinchanalensis*; **Q**, *Ematargina nr. leucotopus*.

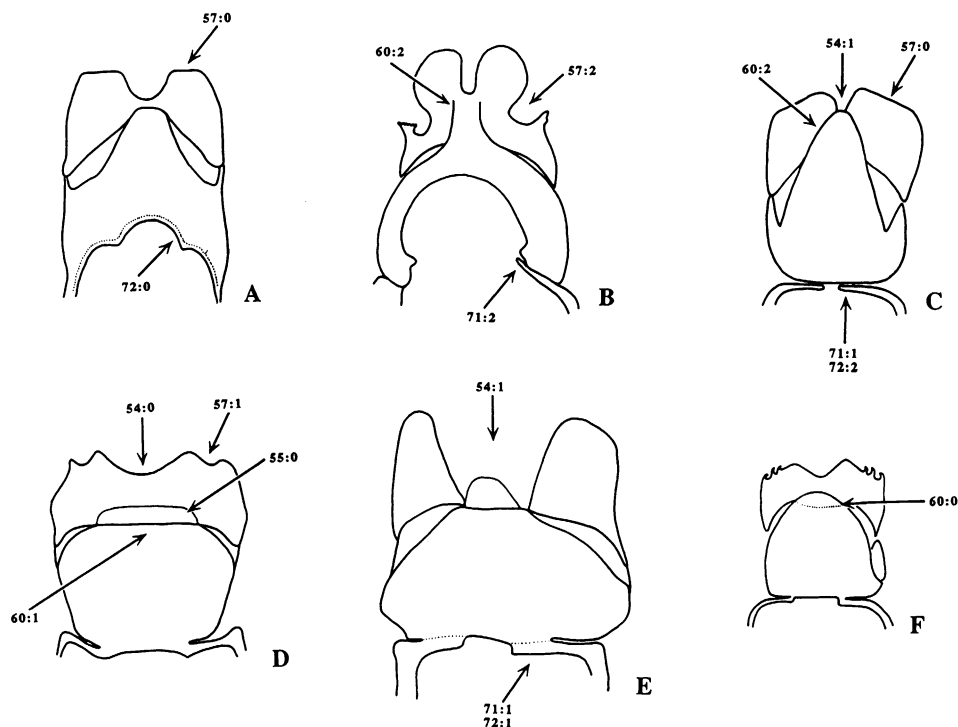


Fig. 12. Uncus, tegumen, and dorsal portion of vinculum with setae omitted: **A**, *Setabis lagus*; **B**, *Nymphidium cachrus*; **C**, *Juditha molpe*; **D**, *Synargis abaris*; **E**, *Audre domina*; **F**, *Catocyclotis aemulius*.

BIFURCATED RAMI AND LEMONIINI

Systematic delimitation of both Lemoniini and Nymphidiini depends largely on accurately assessing the homology of male abdominal projections. From our study it appears that the utility of bifurcated rami for defining Lemoniini centers on two issues: (1) the absence of bifurcated rami in some Lemoniini, and (2) the occurrence of abdominal projections in Nymphidiini.

Harvey (1987) used bifurcated rami to justify the monophyly of Lemoniini and noted their absence in *Eiseleia terias*, *Aricoris tutana*, *Uraneis hyalina*, *U. ucubis* and *Thisbe irenea* (5 of the 13 species he examined). We found that these structures were also absent in *Eiseleia pinchanalensis* (potentially a synonym of *E. terias*, J. Hall, personal commun.), *Thisbe lycorias*, *Lemonias agave*, *Audre* sp., and *A. guttata*, all being taxa not examined by Harvey. However, in contrast to Harvey we found inconspicuous bifurcated rami in *Thisbe irenea* (fig. 10N). Our study

showed that members of 6 out of 11 genera in the Lemoniini lack bifurcated rami (35% of the species sampled), which suggests that they may be variable or absent in other taxa not examined here.

In both Lemoniini and Nymphidiini the eighth abdominal sternite was typically elongated independent of having a bifurcated outline (character 44:0; figs. 6, 10D–O, 11B–K, 11M, 11Q). We found asymmetrical abdominal projections in *Nymphidium mantus*, *N. cachrus* and *N. azanoides* that were similar in length or longer than those in some Lemoniini (e.g., *Thisbe irenea*; see figs. 10E–G, 10N), and that both the length of abdominal projections and the depth of the indentation producing a bifurcated outline may vary continuously in Lemoniini and Nymphidiini (compare figs. 10E–L, 10M–O, 11D–F, 11Q). Elongated abdominal projections have also been documented for several species of *Theope* and in *Archaeonympha* Hall, 1998 (Hall, 1999; Hall and Harvey,

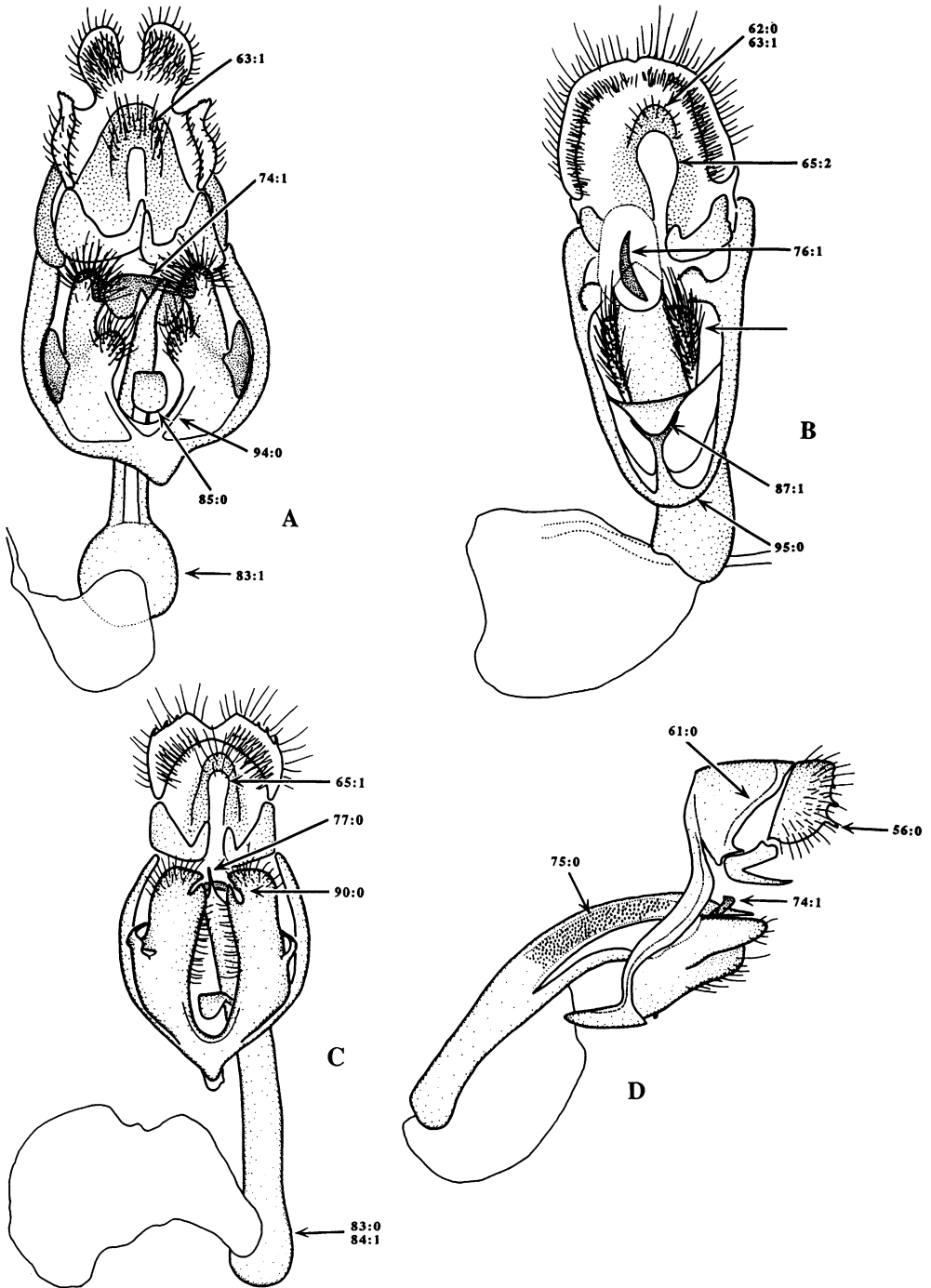


Fig. 13. Male genitalia in ventral view (except as indicated): **A**, *Nymphidium cachrus*; **B**, *Theope publius* (arrow lacking a character number represents a patch of setae similar to character 93:0); **C**, *Catocyclotis aemulius*; **D**, *Catocyclotis aemulius* (lateral view).

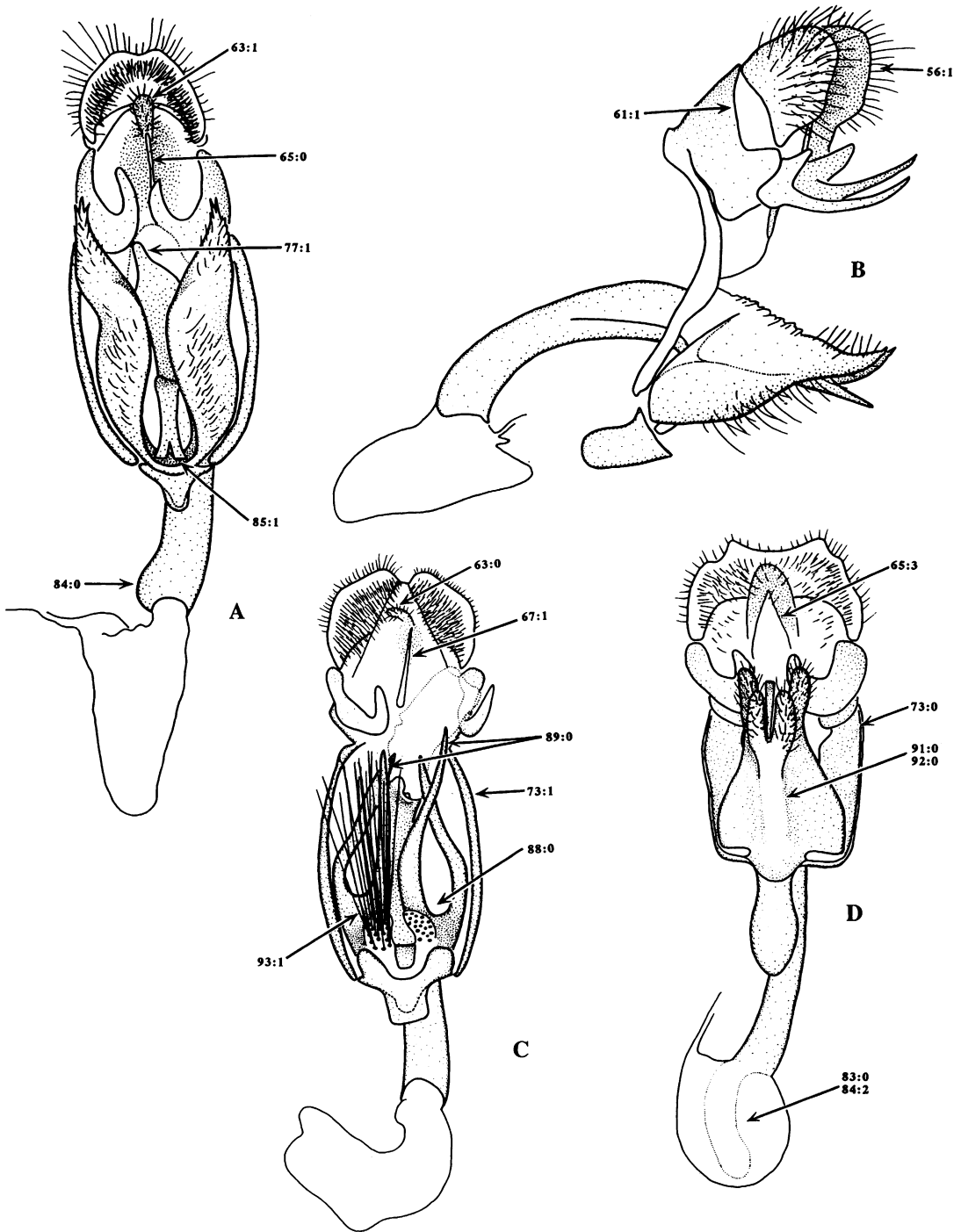


Fig. 14. Male genitalia in ventral view (except as indicated): **A**, *Uraneis hyalina*; **B**, *Aricoris tutana* (lateral view); **C**, *Juditha molpe*; **D**, *Synargis abaris*.

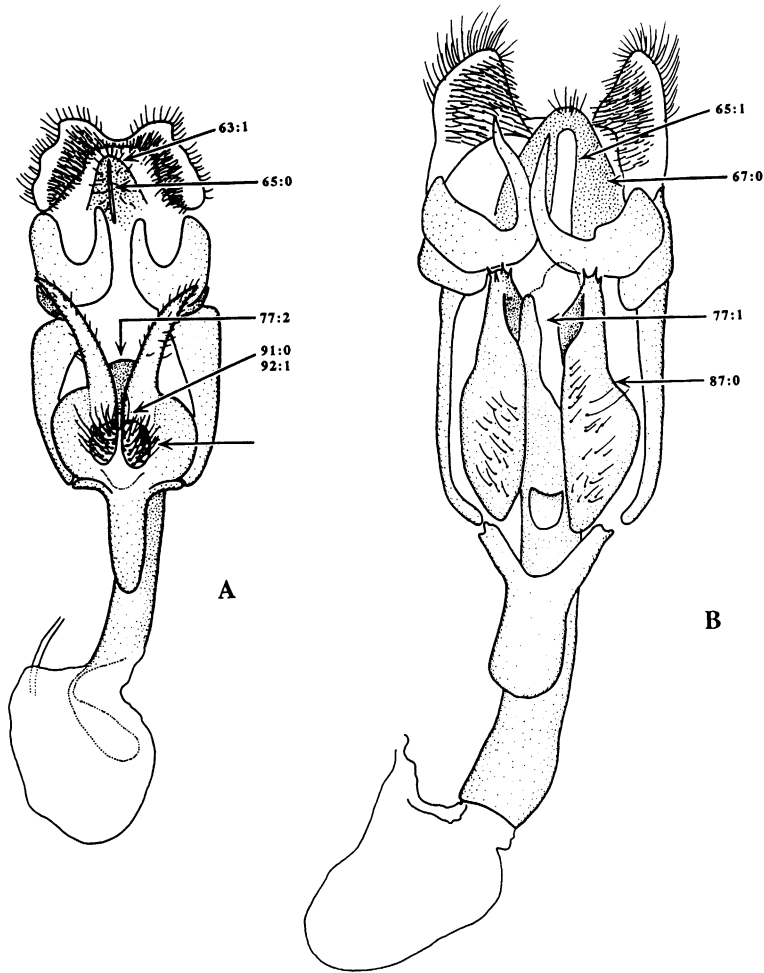


Fig. 15. Male genitalia in ventral view: **A**, *Thysanota galena* (arrow lacking a character number represents a patch of setae similar to character 93:0); **B**, *Audre domina*.

1998). Of potential interest is that for male notodontid moths in the Josiini, the posterior margin of the eighth sternite is excavated (Miller, 1996), a pattern that parallels that of certain Lemoniini and Nymphidiini. Our analysis suggests that abdominal projections were ancestral to Lemoniini plus Nymphidiini, and that they were subsequently modified or lost in various taxa (fig. 6), thus obfuscating the distinction between these tribes. Therefore, both our morphological and phylogenetic analyses seriously weaken bifurcated rami as a character that defines Lemoniini, and such analyses argue against maintaining Lemoniini and Nymphidiini as separate taxa.

THIRD ABDOMINAL SPIRACLE POSITION AND NYMPHIDIINI

Harvey (1987) justified the monophyly of Nymphidiini by the ventral position of the third abdominal spiracle in adults. This character was found in all sampled Nymphidiini, completely corroborating Harvey's observations (fig. 6). However, the grouping of *Nymphidium* and *Theope* with *Synargis* and *Thysanota* and not with *Adelotypa*, *Setabis* and *Calospila* (fig. 6) suggests that the ventral position of the third abdominal spiracle is homoplasious. Morphological analyses showed that the position of this spiracle was not uniform within all Lemoniini. Spiracles

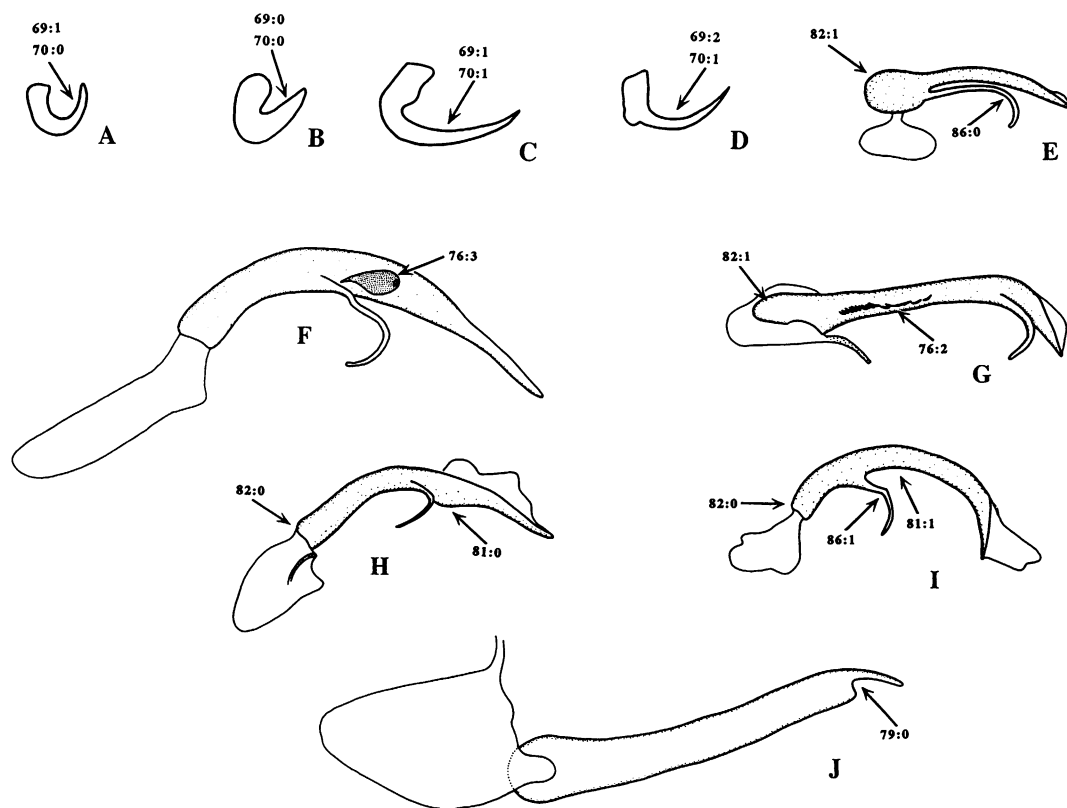


Fig. 16. Gnathos of **A**, *Juditha molpe*; **B**, *Synargis abaris*; **C**, *Audre domina*; and **D**, *Aricoris tutana*. Aedeagus in lateral view (except as indicated): **E**, *Nymphidium cachrus*; **F**, *Audre erostratus*; **G**, *Thisbe irenea*; **H**, *Uraneis hyalina*; **I**, *Juditha molpe*; **J**, *Lemonias caliginea* (in ventral view; juxta was omitted).

were located either closer to the tergite than to the sternite (40:2, fig. 10C) or at midline on the pleural membrane (40:1, fig. 10B), and intrageneric variation occurred in *Thisbe*, *Lemonias*, *Synargis* and *Audre* (fig. 6, Appendix 2). These observations in concert with those on abdominal projections (see above), argue for uniting Lemoniini and Nymphidiini under a single taxonomic category.

CHARACTER VARIABILITY

This study demonstrated high levels of morphological variation in riodinid butterflies. Despite including the most extensive character sampling and taxon saturation for any riodinid tribe thus far studied, our analyses did not provide a strongly supported phylogeny. Weak support to deep nodes of the tree (fig. 6) and unstable positions of

some taxa (fig. 7) indicated that recurrent patterns of character variation within both Lemoniini and Nymphidiini had a large effect on phylogeny reconstruction. Although excluding problem taxa can improve accuracy and resolution in certain cases (e.g., Mason-Gamer and Kellog, 1996; Campbell, 1998), deletion of one or more Lemoniini taxa had either a negative or no effect in the level of resolution of consensus trees (results not shown).

Of particular interest with respect to character variability, Campbell (1998) found faster rates of molecular evolution in riodinids than in other butterfly groups, and when analyzed separately, three sequenced genes produced different topologies that varied in level of resolution. If the riodinids have undergone rapid rates of character evolution, then comprehensive character and taxon sampling are

essential for phylogenetic analyses within this group (see Archie, 1996; Sanderson, 1996; Graybeal, 1998; Hillis, 1998). Given that high rates of character evolution have been suggested to benefit phylogenetic analysis if a tree is densely sampled (Hillis 1998; see also Graybeal 1998), increased taxon sampling within Lemoniini and Nymphidiini may yield more robust results than those given here. We further suggest that additional sources of characters, especially from early stages, may be useful for increasing deep node support (see Appendix 3 for character justification of subterminal nodes).

PROPOSED REVISION OF RIODINID CLASSIFICATION

Following chronological priority, we propose the amalgamation of the tribes Lemoniini and Nymphidiini under the name Nymphidiini (Bates, 1868). Justification for uniting these two riodinid tribes under a single taxon is based on our findings that the presence of bifurcated rami is a weak character to define Lemoniini, and that our phylogenetic analyses indicate that neither Lemoniini nor Nymphidiini is monophyletic. The tribe Nymphidiini as defined here therefore includes all taxa previously classified by Harvey (1987) and subsequent authors in the Lemoniini and Nymphidiini.

CONCLUSIONS

To assess the higher level phylogeny of the riodinid tribe Lemoniini, this study examined 97 adult characters from representatives of all described Lemoniini genera, with particular emphasis on characters that justify apparently monophyletic taxa within this tribe. This preliminary study constitutes the first assessment of the monophyly of Lemoniini genera, and represents the most extensive analysis of morphological characters for any riodinid tribe. Our results indicated that some genera (*Thisbe*, *Lemonias*, and *Audre*) are not monophyletic, thus providing a strong impetus for future revisionary work. During our investigation, it also became evident that the Lemoniini could not be considered outside the context of Nymphidiini. Our comparison of bifurcated rami and abdominal projections showed that these apparently ho-

mogeneous characters are present in members of both Lemoniini and Nymphidiini, and that the morphology of abdominal projections varied in a continuum between these tribes. We therefore concluded that the presence of bifurcated rami sensu Harvey is insufficient to define Lemoniini. Furthermore, our analytical results did not support the monophyly of either Lemoniini or Nymphidiini, thus warranting classification of taxa currently placed in Lemoniini and Nymphidiini into a single tribe, Nymphidiini.

The strong morphological convergence across taxa found in this study needs to be considered in future phylogenetic analyses. Although high levels of homoplasy can reduce the accuracy of phylogeny reconstruction (e.g., Sanderson and Donoghue, 1996), increased taxon sampling has been suggested as a means of overcoming this problem by breaking long branches (e.g., Graybeal, 1998) and utilizing character variation more efficiently (e.g., Hillis, 1998). If such is the case, we expect that better resolution of the Nymphidiini as defined here will be gained through increased taxon sampling.

Our grasp of riodinid myrmecophily depends on future comparative ecological, behavioral and morphological studies of caterpillars and adults, as well as on the availability of a robust phylogeny. Current evidence suggests that riodinid myrmecophily evolved independently in the tribes Nymphidiini (as defined here) and Eurybiini (e.g., Harvey, 1987; DeVries, 1991c, 1997; Campbell, 1998). Although caterpillars in both Nymphidiini and Eurybiini possess presumably homologous tentacle nectary organs, they differ in mechanisms of call production, release of semiochemicals, and in some cases, the identity of ant symbionts (DeVries, 1991a, 1991b, 1997). However, the evolution of riodinid myrmecophily is not well understood because the systematic relationships between these and other riodinid tribes are unresolved. The present study represents a first step toward filling this gap by providing morphological evidence for grouping certain riodinid genera and by questioning previous classifications of Lemoniini and Nymphidiini. A major thrust of phylogenetic systematics is to provide a framework for understanding the evolutionary history of biolog-

ical organisms, and we hope that our study stimulates both systematic and ecological research on the importance of symbiotic associations for diversification among riodinids.

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APPENDIX 1

Characters Included in This Study
(Abbreviations are listed in text under
Characters and Terminology)

External morphology

1. Prob of equal width in males and females (0); male Prob enlarged at base (1). Figure 8A; character 60 in Harvey (1987). See Harvey (1987) and DeVries (1997) for comments on possible functional significance of the enlargement of the proboscis.
2. Setae on Cha: as dark as cuticle (0); of lighter color than cuticle (1).
3. Base of tegula: bright orange or red, clearly contrasting with thorax (0); devoid of such a pattern (1).
4. Forewing R4: meets wing margin slightly anterior to apex or at apex (0); posterior to apex (1). Figure 8B, C.
5. Hindwing A2: produced to form a tail in at least one sex (0); not produced (1). Figure 8D; adapted from Harvey (1987) and DeJong et al. (1996).

Female forelegs

6. Spurs on Tsm of female L1: absent (0); present on Tsm2–3 (1); present on Tsm2–4 (2); present on Tsm2–5 (3). Figures 8E, H.
7. In lateral view of female L1, spur on Tsm2: approaches the length of Tsm1 (0); *ca.* one half of the length of Tsm1 (1). Figures 8F, H.
8. Distribution of sensilla on Tsm1 of female L1: along the distal four-fifths (0); along the distal two-thirds (1); along the distal half (2); distributed over less than one-half of the length of Tsm1 (3). Figures 8E–H; no measurements were taken, and character states were determined arbitrarily based on observed patterns. Adapted from Penz's (1999) character number 80.

Female genitalia

9. Female Stn7: elongated posteriorly to cover Ob (0); devoid of such a pattern (1). Figure 9B.
10. Female Ob: associated with a heavily sclerotized genital plate (*sensu* Pierce, 1909 *in* Klots, 1970) (0); surrounded by weakly sclerotized tissue or membrane (1). Figures 8I, 8L, 9D.
11. Genital plate: equally well developed anteriorly and posteriorly (0); more developed posteriorly than anteriorly (1); more developed anteriorly than posteriorly (2). Figures 8I, 8J, 8L, 8M.
12. Genital plate composed of a single unit (0); two units (1); three units (2). Figures 8J, 8K, 8L, 8M, 8N.
13. Genital plate: relatively broad (0); thin, arched rim (1). Figures 8I, 8L, 8N.
14. Genital plate: with one or more transverse ribs (0); devoid of ribs (1). Figures 8I–K, 8M, 9A, 9B.
15. Genital plate: concave (0); flat or convex (1). Figures 8I–K, 8M, 8N, 9C.
16. Paired pockets located posteriorly to Ob: absent (0); present (1). Figure 9D; these were considered independent structures from the genital plate, as they occurred in species that did not have a sclerotized genital plate.
17. Antr: uniformly sclerotized along its length from Ob to Du.sml (0); weakly sclerotized near Ob, with a sclerotized portion near Du.sml (1); well sclerotized near Ob and Du.sml, with a weakly sclerotized central region (2); completely membranous (3). Figures 9E, 9F.
18. Antr: well sclerotized both dorsally and ventrally (0); dorsal portion weakly sclerotized (1); ventral portion weakly sclerotized (2).
19. Antr: narrow (0); broad (1). Figures 9E, 9F; no measurements were taken, and character states were determined from a comparison between the widths of the antrum, ductus bursa, and seventh sternite. Adapted from Penz's (1999) character number 137.
20. Antr: much shorter than Stn7 (0); similar in length to Stn7 (1); longer than Stn7 (2). No measurements were taken, and character states were determined arbitrarily based on observed patterns. Adapted from Penz's (1999) character number 137.
21. Portion of Du.bu bordering Antr: well sclerotized (0); membranous (1).
22. Connection of Du.bu with Crp.bu: narrow (0); broad (1). Figures 9I, 9K.
23. Spiny sculpturing on Du.bu: present along entire length (0); vestigial or absent at mid-length (1).
24. Du.bu: adorned with longitudinal ribs (0); adorned with ribs forming a honeycomb pattern (1); devoid of ribs (2).
25. Du.bu: longer than abdomen (0), shorter than abdomen (1).
26. Crp.bu: rounded (0); elongated (1). Figures 9G, 9I, 9J, 9L.
27. Spiny sculpturing on Crp.bu: absent (0); present (1).
28. Spiny sculpturing of Crp.bu composed of single spines (0); groups of spines organized in rows (1); groups of spines organized in clusters (2).
29. Spines that compose the sculpturing of Crp.bu: small (0); large (1).
30. Sig: absent (0); present (1). Figures 9H, 9I; variation in the presence of the signum was

mentioned by Harvey (1987), but was not included in his character list. This character was also used by Emsley (1963).

31. Sig shape: shallow invagination (0); well-developed, spine-shaped invagination (1). Figures 9H, 9I, 9K.
32. Base of Sig: small (0); elongated (1). Figures 9G, 9H, 9K, 9L.
33. Sig: with two spine-shaped invaginations located at opposite ends (0); adorned with a single spine (1). Figures 9H, 9K, 9L.
34. Sig: compressed longitudinally (0); compressed transversely (1); not compressed (2). Figures 9G, 9H, 9J, 9L; species for which the signum appears as a shallow invagination were not given a score for this character.
35. Sig: with spiny sculpturing in its entirety (0); spiny sculpturing restricted to base (1); lacking sculpturing (2).
36. Spiny sculpturing of Sig: large (0); small (1). No measurements were taken, and character states were determined arbitrarily based on observed patterns.
37. Lateral portion of Pap.a: adorned with minute setae (0); devoid of setae (1).
38. Posterior abdominal tufts of scales absent (0); present (1). Figure 8I; character 63 in Harvey (1987).

Male Genitalia

39. Number of male abdominal Stn: eight (0); reduced, seven (1). See Figures 10H and 10I for anterior displacement of terminal stenite resulting from a reduction in number of abdominal sterna.
40. Third abdominal Spr: located closer to Stn3 than to Tg3 (0); at midline (1); closer to Tg3 than to Stn3 (2). Figures 10A–C; character 61 in Harvey (1987). This character was scored in males because female pleural membranes could be expanded by egg load.
41. Male Tg8: similar in length to Tg7 (0); about 1.5 times as long as Tg7 (1); about twice as long as Tg7 (2). No measurements were taken, and character states were determined arbitrarily based on observed patterns.
42. Posterolateral margin of male Tg8: adorned with projections (0); devoid of such projections (1). Figures 10H–J.
43. Genital capsule attached dorsally to male Tg8: by a membranous region (0); by a sclerotized plate (1).
44. Male Stn8 with terminal abdominal projection extending beyond edge of pleural membrane (0); devoid of such a pattern (1). Figures 10D, 10L, 11A, 11E, 11L, 11N, 11O.
45. Abdominal projection on male Stn8: simple (0); bifurcated (= bifurcated rami sensu Harvey, 1987) (1). Figures 10E–H, 10J, 10L, 10M, 11I; character number 59 in Harvey (1987). Although the pattern displayed by *Nymphidium cachrus* (fig. 10F) could be considered “bifurcated,” this species was scored in a conservative manner (appendix 2).
46. Abdominal projection on male Stn8: asymmetrical (0); symmetrical (1). Figures 10F, 10L, 11K; asymmetry in the abdominal projection of *Nymphidium* was mentioned by Harvey (1987), but was not included in his character list.
47. Bifurcated abdominal projection on male Stn8: separated at base (0); fused at base (1). Figures 11B, 11C, 11K.
48. Abdominal projection on male Stn8: well sclerotized in its external portion, membranous along entire length of its internal portion (0); well sclerotized both externally and internally (1).
49. Tip of bifurcated abdominal projection on male Stn8: adorned with spines (0); devoid of such a pattern (1). Figure 11I.
50. Posteromedial margin of male Stn8: with a conspicuous V-shaped notch that is markedly deeper than edges of pleural membrane (0); devoid of such a pattern (1). Figures 11H, 11I, 11K, 11O.
51. Posteromedial margin of male Stn8: well sclerotized (0); weakly sclerotized (1). Figures 10D, 11I, 11K; mentioned by Harvey (1987), although not included in his character list. Harvey (1987) regarded the presence of “two sclerotized bands” on the terminal sternite as evidence of secondary loss of bifurcated rami in certain Lemoniini taxa, whereas we considered the presence of such sclerotized bands to result from the desclerotization of the central portion of the terminal sternite.
52. Weakly sclerotized posteromedial margin of male Stn8: extending to reach anterior edge of Stn8 (0); anterior edge of Stn8 well sclerotized (1). Figures 11E, 11I, 11K.
53. Ventrolateral sclerotized cuticular bars: flattened (0); forming an internal rib (1). The ribs described by character state “1” are internal to the male eight sternite and are somewhat difficult to observe, although they can be detected by running forceps laterally in the internal portion of the male terminal sternite.
54. Un: entire (0); split (1). Figures 12C–E.
55. Anterior margin of Un: with a semicircular, smooth area (0); devoid of such a pattern (1). Figure 12D; this was considered a separate character from 60 due to the sclerotized band separating the assumed posterior edge of the tegumen from the uncus (fig. 12D).
56. Posterior margin of Un: adorned with spiny

- projections (0); devoid of spiny projections (1). Figure 13D.
57. Posterior margin of Un: convex or straight (0); slightly concave (1); strongly concave, Un apparently four-lobed (2). Figures 12A–D.
 58. In ventral view, lateral margins of Un: widened (0); not widened (1).
 59. Posterior edge of Teg: completely fused to Un (0); not completely fused to Un (1).
 60. Posterior edge of Teg: with a depression resulting in a D.fen (0); smoothly rounded (1); with a prong that projects into anterior edge of Un (2). Figures 12B–D, 12F; see comments on character 55.
 61. Lateral margins of Teg: thickened at edges of L.fen to form ribs (0); devoid of such a pattern (1). Figures 13D, 14B.
 62. Posterior end of Ssca: forms a simple lobe (0); two contiguous lobes (1). Figure 13B.
 63. Posterior end of Ssca: forms a narrow lobe (0); forms a broad lobe (1). Figures 13A, 13B, 14A, 14C, 15A; the species that had two lobes was not given a score for this character.
 64. Setae in the posterior end of Ssca: thicker than setae in the ventral surface of Un (0); similar in thickness to (or thinner than) setae in the ventral surface of Un (1).
 65. Ssca: uniformly narrow (0); uniformly broad (1); broad posteriorly and narrowed anteriorly (2); broad anteriorly and narrowed posteriorly (3). Figures 13B, 13C, 14A, 14D, 15A, 15B.
 66. In lateral view, Ssca: depressed (0); flat (1); sharp, bladelike protrusion (2); rounded protrusion (3).
 67. Cuticular sculpturing: prominent around Ssca (0); restricted to posterior end of Ssca (1). Figures 14C, 15B.
 68. Long setae located laterally and anteriorly to Ssca: absent (0); present (1).
 69. Distal portion of Gn: wide (0); intermediate (1); narrow (2). Figures 16A–D; no measurements were taken, and character states were determined based on observed patterns.
 70. Distal and proximal portions of Gn: similar in length (0); distal portion about twice as long as proximal portion (1). Figures 16A–D; no measurements were taken, and character states were determined based on observed patterns.
 71. Vin: extends along entire anterior edge of Teg (0); extends along most of the anterior edge of Teg (1); restricted to dorsolateral edge of Teg (2). Figures 12B, 12C, 12E.
 72. Vin: completely fused to anterior edge of Teg (0); distal edge fused to anterior edge of Teg, remainder of Vin connected to Teg by weakly sclerotized tissue (1); connected to anterior edge of Teg entirely by weakly sclerotized tissue (2). Figures 12A, 12C, 12E.
 73. In ventrolateral view, Vin: laterally widened to form a blade (0); widened below Teg and sharply decreasing in width (1); narrow (2). Figures 14C, 14D.
 74. Tra: membranous (0); sclerotized (1). Figures 13A, 13D.
 75. Ves: with conspicuous cuticular sculpturing (0); devoid of cuticular sculpturing (1). Figure 13D; the vesica was observed through the aedeagus wall (i.e., it was not extended); this character was scored under relatively low magnification (70×) and thus precision of the scores depends upon the equipment used.
 76. Crn: absent (0); composed of one or few large spines (1); many small spines (2); a broad thin plate (3). Figures 13B, 16F, 16G.
 77. Distal end of Ae: acute (0); intermediate (1); blunt (2). Figures 13C, 14A, 15A, 15B.
 78. Tapering tip of Ae: short (0); elongated (1). No measurements were taken, and character states were determined based on observed patterns.
 79. Tapering tip of Ae: abruptly notched (0); devoid of such a pattern (1). Figure 16J.
 80. Distal opening of Ae: dorsal (0); dorsolateral or lateral (1); ventral (2).
 81. Ae: with a ventral swelling immediately distal to Jx (0); devoid of such a pattern (1). Figure 16H, 16I; this character was used by Hanner (1997) in a study of *Eurybia* Illiger (*Eurybiini*).
 82. Coe: absent (0); present (1). Figures 16E, 16G–I.
 83. Coe: equal or slightly wider than the Ae shaft (0); much wider than the Ae shaft, bulb-shaped (1). Figures 13A, 13C, 14D.
 84. Coe: short (0); intermediate (1); long (2). Figures 13C, 14A, 14D; no measurements were taken, and character states were determined based on observed patterns.
 85. Ventral edge of Jx: straight (0); split (1); rounded (2). Figures 13A, 14A; adapted from Harvey's (1987) character number 50.
 86. Jx: forms a smooth curve (0); forms an angular curve (1); reduced in length, straight (2). Figures 16E, 16I.
 87. Va: well developed (0); reduced to a medial compact prong (1). Figures 13B, 15B; the medial prong observed in *Theope* was assumed to be a result of the reduction and fusion of the valvae.
 88. Sl: projected (0); devoid of such a pattern (1). Figure 14C.
 89. Sl: symmetrical (0); asymmetrical (1). Figure 14C. Species devoid of a projected sacculus were not scored for this character.

- 90. Am: split (0); devoid of such a pattern (1). Figure 13C.
- 91. Va: fused ventrally (0); devoid of such a pattern (1). Figures 14D, 15A; species of *Theope* were not given a score for this character (see comments on character 87).
- 92. Va: fused ventrally for more than half of their length (0); fused ventrally for less than one half of their length (1). Figures 14D, 15A.
- 93. Inner base of Va: adorned with patches of setae that are almost as long as Va itself (0); devoid of such a pattern (1). Figure 14C; patches of setae in similar position were found in *Theope publius* and *Thysanota galena* (indicated by arrows in figs. 13B and 15A, respectively) but were arbitrarily considered independent from those described here.
- 94. Inner base of Va: with thickened cuticular bracing (0); devoid of such a pattern (1). Figure 13A.
- 95. Sa: absent (0); present (1). Figure 13B; see comments on character 87.
- 96. Posterolateral ends of Sa: elongated to connect with anterior portion of Vin (0); shortened, Vin extends to surround anterior portion of Sa partially or entirely (1).
- 97. In lateral view, anterior end of Sa: widened dorsoventrally (0); not widened dorsoventrally (1).

APPENDIX 2
Data Matrix

	10	20	30	40	50
<i>Stalactis euterpe</i>	0111101010	1001100100	0102111101	1012000102	0101?????1
<i>Adelotypa alector</i>	0110121111	?????00102	1111011101	1010011000	010001?011
<i>Setabis lagus</i>	0110120210	1011000100	1111111011	1112011000	010001?011
<i>Calospila emylius</i>	0110121210	1011010100	1000111010	???????1000	110001?011
<i>Nymphidium azanoides</i>	0010121210	1001001101	1111101011	1110111000	111000?111
<i>Nymphidium cachrus</i>	0010111110	1001001101	1001101001	1010111000	211000?111
<i>Nymphidium mantus</i>	0110120210	1011003?00	1111101001	1110111000	211000?111
<i>Theope publius</i>	0110131210	0001003?01	0111101101	1110011010	100001?011
<i>Theope virgilius</i>	0110131210	2001003?00	1112101011	1110001010	200001?011
<i>Thisbe irenea</i>	0010 (01) 31210	1001000100	0012001001	00???001002	2100110011
<i>Thisbe lycorias</i>	0000020110	1201000100	0011101200	???????1001	1101?????1
<i>Thisbe molela</i>	0010030310	0001000100	0011101201	10100001002	1100110011
<i>Uraneis hyalina</i>	0001031110	1101000100	1011101200	???????1002	0101?????1
<i>Uraneis ucubis</i>	0001031110	1101010100	1011101201	00???011002	0101?????1
<i>Catocyclotis aemulius</i>	0010110210	1001000102	1100111101	1010001002	0100110011
<i>Lemonias agave</i>	0110131300	0001000210	1110111201	1012001002	0101?????1
<i>Lemonias caliginea</i>	0110120300	0000000010	0110111101	1110011001	0100111011
<i>Lemonias zygia</i>	0010120200	0000000010	0111111101	1110011002	0100111111
<i>Juditha azan</i>	0110120300	0000000011	1110111101	1010111002	0100110011
<i>Juditha molpe</i>	0110120300	0000000012	1110111101	1010111002	0100110011
<i>Synargis abaris</i>	0110110211	?????03?00	0110111101	1101111002	1100110101
<i>Synargis mycone</i>	0110120310	1001100000	0100111001	11012?1001	2100110101
<i>Synargis orestes</i>	0110131211	?????00000	0110111101	1111111002	2100110101
<i>Synargis palaeste</i>	0110131310	1001100000	0100111001	111011002	1100110111
<i>Thysanota galena</i>	111013?200	0001000000	1100111101	1101011002	2100110101
<i>Audre domina</i>	1110130211	?????02111	1111110??1	1110011002	0100110110
<i>Audre erostratus</i>	1110130111	?????12011	1?????????	???????1001	1100110110
<i>Audre guttata</i>	0010131111	?00???10100	1102111001	1010011002	0101?????1
<i>Audre sp.</i>	1110130210	1001002011	1110110??1	1110011001	1101?????0
<i>Aricoris tutana</i>	11101?????	???????????	???????????	???????02	0101?????0
<i>Ematurgina nr. leucotopus</i>	01101?????	???????????	???????????	?????????0?	0100110110
<i>Eiseleia pinchanalensis</i>	1110120311	?????10011	1110111101	11102?1002	0101?????0

APPENDIX 2
Continued

	60	70	80	90	
<i>Stalactis euterpe</i>	0??0110111	0001121021	00211111112	10??200001	1?10100
<i>Adelotya alector</i>	0??0110102	1001021000	0000131110	10??2001?0	1?11111
<i>Setabis lagus</i>	0??1110102	1001020110	0001101110	10??001?0	1?10111
<i>Calospila emylius</i>	0??0110102	1011020010	1100121111	10??001?0	1?10111
<i>Nymphidium azanoides</i>	0??0112002	0010200021	2201101010	1111200001	1?10100
<i>Nymphidium cachrus</i>	0??0112012	00?0100010	2201000010	1111200001	1?10110
<i>Nymphidium mantus</i>	0??0112002	01?1021021	2201031010	1112200001	1?10110
<i>Theope publius</i>	0??0111011	0010210000	2211011012	1100221??1	??100??
<i>Theope virgilius</i>	0??0111011	0000010000	2201001011	10??221??1	??1?0??
<i>Thisbe irenea</i>	0??0110101	1011020000	1110120011	01011001?1	1?10111
<i>Thisbe lycorias</i>	0??0110101	1001020010	1120101111	00??2101?1	1?10111
<i>Thisbe molela</i>	0??0110101	1011020000	1110121011	11001101?1	1?10111
<i>Uraneis hyalina</i>	0??0110101	1011020010	1120101111	01001101?1	1?10111
<i>Uraneis ucubis</i>	0??0110101	1011020010	1120101110	00??1101?1	1?10111
<i>Catocyclotis aemulius</i>	0??0100110	0010200010	1101000010	11012001?0	1?10111
<i>Lemonias agave</i>	11?0110101	1011210010	1120100001	10??(12)10001	1?10110
<i>Lemonias caliginea</i>	0??0110101	1001021010	1110120001	11001101?1	1?10110
<i>Lemonias zygia</i>	0??0110101	1001020010	1110120001	10??1101?1	1?10110
<i>Juditha azan</i>	1101111102	1001021010	1220100011	10??10011	1?01101
<i>Juditha molpe</i>	1101110102	1001021010	1220100011	10??210011	1?01101
<i>Synargis abaris</i>	1010011001	0011311000	0100102011	1102?001?0	0011100
<i>Synargis mycone</i>	1010112001	1011311000	1100102011	1102?101?1	0011100
<i>Synargis orestes</i>	1010011001	0011321000	0100102011	1102?101?1	0011100
<i>Synargis palaeste</i>	1000111011	0011301000	0100102011	1102?101?0	0011100
<i>Thysanota galena</i>	1010001101	0011010000	0100102010	1102?101?1	0111110
<i>Audre domina</i>	11011100?1	1011130011	1120101111	10??2001?0	1?11100
<i>Audre erostratus</i>	11011101?1	1011030021	1120131111	10??0101?1	1?11100
<i>Audre guttata</i>	1100111101	1011100010	0120001011	10??201?1	0011111
<i>Audre sp.</i>	10011100?1	1011130011	1120131111	11001001?0	1?11100
<i>Aricoris tutana</i>	10011100?1	1011030021	0120131111	10??1101?1	1?11100
<i>Ematurgina</i> nr. <i>leucotopus</i>	0?00110002	1011210011	2020131010	10??2001?1	1?11100
<i>Eiseleia pinchanalensis</i>	1101?100?1	1011010021	1220131111	10??001?1	1?11100

APPENDIX 3

Nymphidiini Characters with Little Variation

Although our analyses demonstrate high levels of overall character variation, some characters showed little variation, and these define many of our study taxa. As an aid to future studies on Nymphidiini, these characters are summarized here (taxa that they support are indicated in parentheses).

- (1:1) Male Prob enlarged at base (*Audre* [excepting *A. guttata*], *Aricoris*, *Eiseleia*, and *Ematurgina*; also in *Thysanota galena*).
- (5:0) Hindwing A2 produced to form a tail at least in one sex (*Thisbe* plus *Uraneis*).
- (9:0) Female Stn7 elongated posteriorly to

cover Ob (*Lemonias* plus *Juditha*; also in *Thysanota galena*).

- (13:1) Genital plate thin, arched rim (*Adelotya*, *Setabis*, and *Calospila*; also in *Nymphidium mantus*).
- (14:0) Genital plate with one or more transverse ribs (*Lemonias caliginea*, *L. zygia*, *Juditha azan*, and *J. molpe*).
- (19:1) Antr broad (*Audre* [excepting *A. guttata*], *Aricoris*, and *Eiseleia*; also in *Lemonias* plus *Juditha*).
- (22:0) Connection of Du.bu with Crp.bu narrow (*Thisbe* plus *Uraneis*; also in *Calospila emylius* and *Nymphidium cachrus*).
- (26:0) Crp.bu rounded (*Thisbe* plus *Uraneis*; also in *Nymphidium* plus *Theope*).
- (28:2) Spiny sculpturing of Crp.bu composed of groups of spines organized in clusters

- (*Thisbe* [excepting *Thisbe irenea*] plus *Uraneis*; also in *Lemonias agave*).
- (34:1) Sig compressed transversely (*Synargis* plus *Thysanota*).
- (39:1) Number of male abdominal Stn reduced, seven (*Theope*).
- (40:0) Third abdominal Spr located closer to Stn3 than to Tg3 (*Adelotypa*, *Setabis*, and *Calospila*; also in *Nymphidium* plus *Theope*).
- (42:0) Posterolateral margin of male Tg8 adorned with projections (*Theope*).
- (43:1) Genitalic capsule attached dorsally to male Tg8 by a sclerotized plate (*Nymphidium*).
- (45:0) Abdominal projection on male Stn8 simple (*Adelotypa*, *Setabis*, and *Calospila*; also in *Nymphidium* plus *Theope*).
- (46:0) Abdominal projection on male Stn8 asymmetrical (*Nymphidium*).
- (47:1) Bifurcated abdominal projection on male Stn8 fused at base (*Lemonias*, excepting *L. agave*).
- (48:1) Abdominal projection on male Stn8 well sclerotized both externally and internally (*Nymphidium*, *Synargis*, *Thysanota*, *Audre* [excepting *A. guttata*], *Aricoris*, *Eiseleia*, and *Ematurgina*; also in *Lemonias zygia*).
- (49:0) Tip of bifurcated abdominal projection on male Stn8 adorned with spines (*Synargis* [excepting *S. palaeste*] plus *Thysanota*).
- (50:0) Posteromedial margin of male Stn8 with a conspicuous V-shaped notch that is markedly deeper than edges of pleural membrane (*Audre* [excepting *A. guttata*] plus *Aricoris*, *Eiseleia*, and *Ematurgina*).
- (52:0) Weakly sclerotized posteromedial margin of male Stn8 extending to reach anterior edge of Stn8 (*Synargis* plus *Thysanota*; also in *Audre* sp. and *Aricoris tutana*).
- (57:2) Posterior margin of Un strongly concave, Un apparently four-lobed (*Nymphidium*; also in *Synargis mycone*). See also 57:1 in appendix 2.
- (61:0) Lateral margins of Teg thickened at edges of L.fen to form ribs (*Nymphidium*, *Theope*, *Synargis* [excepting *S. mycone*], and *Thysanota*; also in *Catocyclotus*).
- (65:3) Ssca broad anteriorly and narrowed posteriorly (*Synargis*).
- (70:1) Distal portion of Gn about twice as long as proximal portion (*Audre* [excepting *A. guttata*] plus *Aricoris*, *Eiseleia* and *Ematurgina*; also in *Nymphidium azanoides* plus *N. mantus*).
- (71:2) Vin restricted to dorsolateral edge of Teg (*Nymphidium* plus *Theope*; also in *Ematurgina* nr. *leucotopus*).
- (74:1) Tra sclerotized (*Nymphidium* plus *Theope*; also in *Setabis lagus* and *Catocyclotus*).
- (77:2) Distal end of Ae blunt (*Synargis* plus *Thysanota*).
- (81:0) Ae with a ventral swelling immediately distal to Jx (*Thisbe* [excepting *T. molella*] plus *Uraneis*).
- (83:1) Coe much wider than Ae shaft, bulb-shaped (*Nymphidium*).
- (84:2) Coe long (*Synargis* plus *Thysanota* in which the Coe is bent, fig. 15D; also in *Nymphidium mantus*).
- (87:1) Va reduced to a medial compact prong (*Theope*).
- (89:1) Sl asymmetrical (*Juditha*).
- (91:0) Va fused ventrally (*Synargis* plus *Thysanota*; also in *Audre guttata*).
- (93:0) Inner base of Va adorned with patches of setae that are almost as long as Va itself (*Juditha*).
- (95:0) Sa absent (*Theope*).

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