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Basal subtribes of the Nymphidiini (Lepidoptera: Riodinidae): phylogeny and myrmecophily

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Abstract

Three cladistic analyses, based predominantly on adult morphology, are presented for myrmecophilous riodinid butterflies in the tribe Nymphidiini. The first is a species-level analysis of all 22 species recognized here in *Aricoris* (= *Audre* auctt.) using 27 characters. The second is a species-level analysis of all 24 species recognized here in *Synargis* using 53 characters. The third is a generic-level analysis of all six genera (*Aricoris*, *Ariconias* n. gen., *Lemonias*, *Thisbe*, *Juditha*, and *Synargis*) recognized here as belonging in the basal clades of the Nymphidiini (=Lemoniadinina auctt.) using 17 characters, with members of the Theopeina and Nymphidiina included with the ingroup to assess the monophyly of subtribes. Almost all characters are illustrated. The first analysis indicates that *Aricoris* consists of five monophyletic species groups, with the relationship ((*constantius* gr. + *colchis* gr.) + (*chilensis* gr. + (*aurinia* gr. + *epulus* gr.))), and contains the type species of *Eiseleia* and *Audre*, which are synonymized with *Aricoris* (n. syns.). The second analysis indicates that *Synargis* consists of four monophyletic species groups, with the relationship (*phliasus* gr. + (*regulus* gr. + (*pittheus* gr. + *abaris* gr.))), and contains the type species of *Ematurgina* and *Thysanota*, which are synonymized with *Synargis* (n. syns.). The third analysis indicates that the Lemoniadinina, or basal clades of the Nymphidiini, are paraphyletic with respect to the Theopeina and Nymphidiina, with the generic relationship ((*Aricoris* + *Ariconias*) + (((*Lemonias* + *Thisbe*) + (*Juditha* + *Synargis*)) + (Theopeina + Nymphidiina))). We therefore restrict the Lemoniadinina to include *Lemonias*, *Thisbe*, *Juditha*, and *Synargis* and provide the name *Aricorina* n. subtribe for *Aricoris* and *Ariconias*. All nymphidiine subtribes are characterized and a synonymic checklist for the *Aricorina* and *Lemoniadinina* is presented. A “supertree” composed of the species-level phylogenies derived here for *Aricoris* and *Synargis*, and those derived elsewhere for *Ariconias*, *Lemonias*, *Thisbe*, and *Juditha*, is used to map the distribution of larval host plant and attending ant taxa and the occurrence of aphytophagy. Observed patterns are discussed.

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The family Riodinidae is unique among Neotropical butterflies in being almost exclusively confined to that biogeographic region. It contains approximately 1300 described species and constitutes about 20% of the total Neotropical butterfly fauna (Heppner, 1991; Robbins, 1982, 1993; Robbins et al., 1996). The family is unique in several aspects of its adult behavior (Callaghan, 1983; Hall, 1999a) and early stage biology relating to myrmecophily (DeVries, 1988, 1990, 1991a,b,c, 1997; Fiedler, 1991; Harvey, 1987a; Ross, 1964, 1966), and it is conspicuous for its morphological (Stichel, 1910–1911) and phenotypic diversity (d’Abrera, 1994). However, the group has historically remained understudied, and the

first phylogenetic studies have only recently been completed (Hall, 1998, 1999b, 2002a,b; Hall and Harvey, 2001a,b, 2002; Harvey and Hall, 2002; Penz and DeVries, 1999, 2001).

The purpose of this paper is to present a comprehensive species-level phylogenetic hypothesis for the basal clades of the tribe Nymphidiini Bates, the largest of the nine tribes in the subfamily Riodininae (Hall, 1998, 1999a; Harvey, 1987a). We recognize 71 species in these clades, representing nearly one-quarter of the approximately 300 species currently estimated for the tribe (Hall, unpublished data). In the first modern higher classification of the Riodinidae, Harvey (1987a) treated these butterflies in the tribe Lemoniadini Kirby (as Lemoniini; see Hall and Heppner, 1999), defining it by its members possessing “bifurcate rami” or a bifurcate eighth male abdominal sternite. He placed the

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Table 1

Dissections examined for *Aricoris*, *Ariconias*, and *Synargis* taxa included in the phylogenetic analyses; those for *Lemonias*, *Thisbe*, and *Juditha* are given in Hall and Harvey (2001a)

| Taxon | Dissections examined |
|---|--|
| <i>Ariconias albinus</i> (C. & R. Felder, 1861) | 1♂, Panama (USNM); 1♂, Venezuela, Mérida, Lagunillas (USNM); 1♀, Panama, Panamá, Cerro Campana (USNM) |
| <i>A. glaphyra</i> (Westwood, [1851]) | 1♂, Brazil, Mato Grosso, Diamantino, Alto Rio Arinos (USNM); 1♂, 1♀, Paraguay, Paraguari, Sapucay (USNM) |
| <i>Aricoris terias</i> (Godman, 1903) | 1♂, Paraguay (USNM); 1♀, Argentina, Salta, Pichanal (USNM) |
| <i>A. constantius</i> (Fabricius, 1793) | 1♂, Brazil, Mato Grosso, Leitão (USNM); 1♂, Brazil, Santa Catarina, Curitiba (USNM); 1♀, No locality data (USNM) |
| <i>A. gauchoana</i> (Stichel, 1910) | 2♂, 1♀, Paraguay, Paraguari, Sapucay (USNM) |
| <i>A. colchis</i> (C. & R. Felder, 1865) | 1♂, Brazil, Mato Grosso do Sul, Nioaque (BMNH); 1♀, Brazil, Paraná, Castro (USNM) |
| <i>A. middletoni</i> (Sharpe, 1890) | 2♂, 1♀, Brazil, Mato Grosso, Diamantino (USNM); 1♂, 1♀, Brazil, Mato Grosso, Cuiabá (BMNH); 1♂, 1♀, Brazil, Goiás, Leopoldo de Bulhões (SMF); 1♂, Brazil, Paraná, Castro (USNM); 1♀, Brazil, Minas Gerais, Serra do Cipó (USNM); 1♂, No locality data (USNM) |
| <i>A. sp. n. 1</i> | 1♂, 1♀, Brazil, Paraná, Castro (ZMHU); 1♂, Paraguay, Paraguari, Sapucay (USNM) |
| <i>A. chilensis</i> (C. & R. Felder, 1865) | 2♂, 1♀, Argentina, La Rioja, La Rioja (USNM); 1♀ [HT <i>dovina</i>], Bolivia (USNM) |
| <i>A. notialis</i> (Stichel, 1910) | 1♂, 1♀, Argentina, Jujuy, Río Lozano, Morro de Alizari (USNM); 1♂ [ST <i>notialis</i>], Argentina, Córdoba, Cosquin (USNM); 1♀, Argentina, La Rioja, La Rioja (ZMHU) |
| <i>A. cinericia</i> (Stichel, 1910) | 1♂, Paraguay, Itapúa, Encarnación (BMNH); 1♀, Paraguay (USNM); 1♀, Argentina, Misiones, No specific locality (BMNH) |
| <i>A. domina</i> (Bates, 1868) | 1♂, Panama (FSCA); 1♂, 1♀, Panama, Canal Zone, La Pita (USNM) |
| <i>A. sp. n. 2</i> | 1♂, 1♀, Bolivia, Santa Cruz, Buena Vista (BMNH) |
| <i>A. montana</i> (Schneider, 1937) | 1♂, 1♀ [STs <i>montana</i>], Uruguay, Aiguá (SMF) |
| <i>A. incana</i> (Stichel, 1910) | 1♂, 1♀, Peru, San Martín, Tarapoto (SMF); 1♂, Peru, Junín, Chanchamayo (USNM); 1♀, Peru, Junín, Satipo (USNM) |
| <i>A. aurinia</i> (Hewitson, 1863) | 1♂, Brazil, Mato Grosso, Cuiabá (BMNH); 1♂, 1♀, Brazil, Pará, Santarém (BMNH); 1♀, Bolivia, Santa Cruz, Santa Cruz de la Sierra (BMNH) |
| <i>A. epulus</i> (Cramer, [1775]) | 1♂, 1♀, Brazil, Mato Grosso, Diamantino (USNM); 1♂, Brazil, Pará, Itaituba (USNM); 1♂, 1♀, Brazil, Piauí, Parnaíba (USNM); 1♂, 1♀, Brazil, Distrito Federal, Alto Rio Maranhão (USNM) |
| <i>A. propitia</i> (Stichel, 1910) | 1♂, Brazil, Mato Grosso, Diamantino (USNM); 1♀, Brazil, Minas Gerais, Serra do Cipó (USNM); 1♂, 1♀, Guyana, Cuyuni-Mazaruni, Takutu Mts. (USNM) |
| <i>A. signata</i> (Stichel, 1910) | 1♂, 2♀, Argentina, La Rioja, La Rioja (USNM); 1♀, Argentina, Buenos Aires, San Fernando (USNM); 1♂, Paraguay, Paraguari, Sapucay (USNM) |
| <i>A. indistincta</i> (Lathy, 1932) | 1♂, Argentina, Buenos Aires, San Fernando (USNM); 1♀, Brazil, Paraná, Iguazu (BMNH) |
| <i>A. hubrichi</i> (Stichel, 1926) | 1♂, Brazil, Mato Grosso, São Vicente, 90 km. E. of Cuiabá (USNM); 1♂, Brazil, Minas Gerais, Serra do Cipó (USNM); 2♀, Brazil, Paraná, Castro (USNM) |
| <i>A. caracensis</i> (Callaghan, 2001) | 2♂, Brazil, Distrito Federal, Brasília Country Club (USNM); 1♂, 1♀, Brazil, Minas Gerais, Leitão (USNM) |
| <i>A. erostratus</i> (Westwood, [1851]) | 2♂, 1♀, Venezuela, Esparta, Isla Margarita (USNM); 1♀, Panama, Canal Zone, Paraiso (USNM) |
| <i>A. campestris</i> (Bates, 1868) | 1♂, 1♀, Brazil, Paraíba, João Pessoa (USNM); 1♀, Brazil, Minas Gerais, Serra do Cipó (USNM) |
| <i>Synargis fenestrella</i> (Lathy, 1932) | 1♂, Ecuador, Morona-Santiago, Taisha (JHKW); 1♂, French Guiana, Cayenne, Galion (USNM); 1♀, Peru, Madre de Dios, Puerto Maldonado (USNM) |
| <i>S. phliasus</i> (Clerk, 1764) | 1♂, Panama, San Blas, Río Armila (USNM); 1♀, Panama, Canal Zone, Piña (USNM); 1♂, 1♀, Trinidad (USNM) |
| <i>S. victrix</i> (Rebel, 1901) | 1♂, Brazil, Rio de Janeiro, Tijuca (USNM); 1♀, Brazil, Rio de Janeiro, Rio de Janeiro (USNM) |
| <i>S. paulistina</i> (Stichel, 1910) | 1♂, Ecuador, Napo, Pano (JHKW); 1♂, 1♀, Brazil, Rio de Janeiro, Nova Friburgo (USNM); 1♂, Brazil, Paraná, Castro (USNM); 1♀, Brazil, Paraná, Guarapuava (USNM) |
| <i>S. sylvarum</i> (Bates, 1867) | 1♂, Peru, San Martín, Chambirayacu, Yurimaguas (BMNH); 1♀, Brazil (BMNH) |
| <i>S. regulus</i> (Fabricius, 1793) | 1♂, 1♀, Brazil, Espírito Santo (BMNH); 1♂, Brazil, Rio de Janeiro, Nova Friburgo (USNM); 1♀, Brazil, Rio de Janeiro, Rio de Janeiro (USNM); 1♂, French Guiana, Cayenne, Galion (USNM); 1♀, French Guiana, Cayenne, Cayenne (USNM) |
| <i>S. bifasciata</i> (Mengel, 1902) | 3♂, 2♀, Paraguay, Paraguari, Sapucay (USNM) |
| <i>S. axenus</i> (Hewitson, 1876) | 2♂, Brazil, Mato Grosso, Diamantino (USNM); 1♂, 1♀, Brazil, Mato Grosso, Colegio Buriti, Chapada dos Guimaraes (USNM); 2♂, 1♀, Paraguay, Paraguari, Sapucay (USNM) |
| <i>S. chaonia</i> (Hewitson, [1853]) | 1♂, Ecuador, Napo, Pimpilala (JHKW); 1♂, French Guiana, Cayenne, Route de L'est (USNM); 1♀, French Guiana, Cayenne, Galion (USNM) |
| <i>S. pittheus</i> (Hoffmannsegg, 1818) | 1♂, 1♀, Venezuela, Bolívar, Suapure (USNM); 1♂, Brazil, Pará, km. 1270 Cuiabá-Santarém highway (USNM); 1♀, No locality data (ZMHU) |
| <i>S. agle</i> (Hewitson, [1853]) | 1♂, Ecuador, Zamora-Chinchipe, Zamora (JHKW); 1♀, Ecuador, Napo, Chichicorrumi (JHKW); 1♂, Brazil, Pará, Bragança (USNM); 1♂, 1♀, French Guiana, Cayenne, Matoury (USNM) |
| <i>S. ochra</i> (Bates, 1868) | 1♂, Ecuador, Napo, Pimpilala (JHKW); 1♀, Ecuador, Pastaza, Sarayacu (USNM); 1♂, Peru, Huánuco, Tingo Maria (USNM); 1♀, Peru, Madre de Dios, Puerto Maldonado (USNM) |

Table 1 (continued)

| Taxon | Dissections examined |
|---|---|
| <i>S. dirca</i> (Stichel, 1911) | 2♂, 1♀, Guatemala, Retalhuleu, San Sebastián (USNM); 1♂, 1♀, Panama, Canal Zone, Cocoli (USNM); 1♂, Ecuador, Los Ríos, Vinces (USNM) |
| <i>S. galena</i> (Bates, 1868) | 1♂, 1♀, Venezuela, Amazonas, San Carlos (USNM); 1♂, Brazil, Rondônia, Cacauplândia (FSCA); 1♂, 1♀, Brazil, Mato Grosso, Diamantino (USNM) |
| <i>S. palaeste</i> (Hewitson, 1870) | 2♂, 2♀, Panama, Canal Zone, Gatun (USNM) |
| <i>S. ethelinda</i> (Hewitson, 1870) | 1♂, Brazil, Paraná, Iguazu (AME); 1♀, Brazil, São Paulo, Casa Branca (ZMHU) |
| <i>S. nymphidioides</i> (Butler, 1872) | 1♂, 1♀, Mexico, Veracruz, Paso San Juan (USNM); 1♂, Costa Rica, Guanacaste, Cañas (USNM); 1♀, Costa Rica, Alajuela, San Mateo (USNM) |
| <i>S. gela</i> (Hewitson, [1853]) | 1♂, Colombia, Caquetá, Montañita (USNM); 3♂, 1♀, Brazil, Mato Grosso, Diamantino (USNM); 2♂, Brazil, Mato Grosso, Cuiabá (BMNH); 1♂, Brazil, Paraíba, João Pessoa (USNM); 1♂, 1♀, French Guiana, Cayenne, Cayenne (USNM); 1♀, French Guiana, Cayenne, Vidal (USNM) |
| <i>S. calyce</i> (C. & R. Felder, 1862) | 1♂, Venezuela, Esparta, Isla Margarita (USNM); 1♂, Brazil, Rondônia, Cacauplândia (USNM); 1♂, Brazil, Mato Grosso, Diamantino (USNM); 2♂, 1♀, Brazil, Paraíba, João Pessoa (USNM); 1♂, Brazil, Minas Gerais, Serra do Cipó (USNM); 1♂, Brazil, Rio de Janeiro, Teresópolis (USNM); 1♂, 1♀, French Guiana, Cayenne, Montravel (USNM) |
| <i>S. mycone</i> (Hewitson, 1865) | 1♂, 1♀, Guatemala, Retalhuleu, San Sebastián (USNM); 1♂, 1♀, Panama, Canal Zone, Gatun (USNM) |
| <i>S. tytia</i> (Cramer, 1777) | 1♂, 1♀, Venezuela, Amazonas, San Carlos (USNM); 1♂, Ecuador, Napo, Pimpilala (JHKW); 1♂, 1♀, Brazil, Rondônia, Cacauplândia (USNM) |
| <i>S. abaris</i> (Cramer, 1776) | 1♂, Colombia, Meta, Río Negro (USNM); 1♀, Colombia, Caquetá, Florencia (USNM); 1♂, 1♀, French Guiana, Saint Laurent du Maroni, Saint Jean du Maroni (USNM); 1♂, French Guiana, Cayenne, Matoury (USNM) |
| <i>S. orestessa</i> Hübner, [1819] | 1♂, French Guiana, Saint Laurent du Maroni, Saint Jean du Maroni (USNM); 1♀, French Guiana, Cayenne, Belizon (USNM); 1♀, Brazil, Rondônia, Cacauplândia (USNM) |
| <i>S. soranus</i> (Stoll, [1781]) | 1♂, Venezuela, Amazonas, San Carlos (USNM); 1♂, French Guiana, Cayenne, Sinnamary (USNM); 1♂, French Guiana, Cayenne, Galion (USNM); 1♀, French Guiana (USNM); 1♀, Brazil, Rondônia, Cacauplândia (USNM) |

Lemoniadini as the sister group to the Nymphidiini on the basis of two shared characters of the larvae related to myrmecophily, namely, the possession of a ventral spiracle on abdominal segment 1 and rod-like vibratory papillae on the first thoracic segment (Bruch, 1926; Ross, 1964). However, concerns were subsequently raised about the monophyly of the Lemoniadini and, based on independent preliminary studies, this group was downgraded to a subtribe of the Nymphidiini by Hall (1999a) and synonymized with the Nymphidiini by Penz and DeVries (1999). The remaining subtribes of the Nymphidiini, the Nymphidiina and Theopeina Clench (*sensu* Hall, 1999a), have together been characterized by the ventral position of the spiracle on abdominal segment 3 in larvae and adults (Harvey, 1987a). The subtribal arrangement of Hall (1999a) for the Nymphidiini was followed in the most recent catalog of Neotropical rioidinid butterflies, by Callaghan and Lamas (in press).

The Nymphidiini contains the majority of myrmecophilous rioidinid species, with the remainder belonging to the small tribe Eurybiini Illiger, and ecological and evolutionary studies on them have contributed significantly to our understanding of myrmecophily in the butterflies (Bourquin, 1953; Bruch, 1926; DeVries, 1988, 1990, 1991a,b,c, 1997; DeVries et al., 1994; Fiedler, 1991; Harvey, 1987a; Pierce, 1995; Ross, 1964, 1966; Schremmer, 1978). Therefore, in addition to using the phylogenetic hypothesis derived here for the basal

nymphidiine clades to create a new generic and subtribal classification for the group, we also use it to examine patterns of host-plant use and the distribution and evolution of certain myrmecophilous traits.

Materials and methods

Morphology

Dissections were made using standard techniques, after abdomens were soaked in hot 10% potassium hydroxide solution for approximately 5 min, and subsequently stored in glycerol. A list of dissections examined for *Aricoris* Westwood (= *Audre* Hemming, auctt.; see below), *Ariconias* Hall & Harvey (described below), and *Synargis* Hübner species is given in Table 1. A list of those examined for *Lemonias* Hübner, *Thisbe* Hübner, and *Juditha* Hemming is given by Hall and Harvey (2001a). Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation closely follows Comstock and Needham (1918) and Smith and Vane-Wright (2001), with cells named for the veins above them. Material for scanning electron microscopy was prepared by air-drying and coating with gold palladium in a Hummer V sputter coater. Micrographs of early stages were taken with an ISI Super IIIA and those of adult heads with a Leica Stereoscan 440.

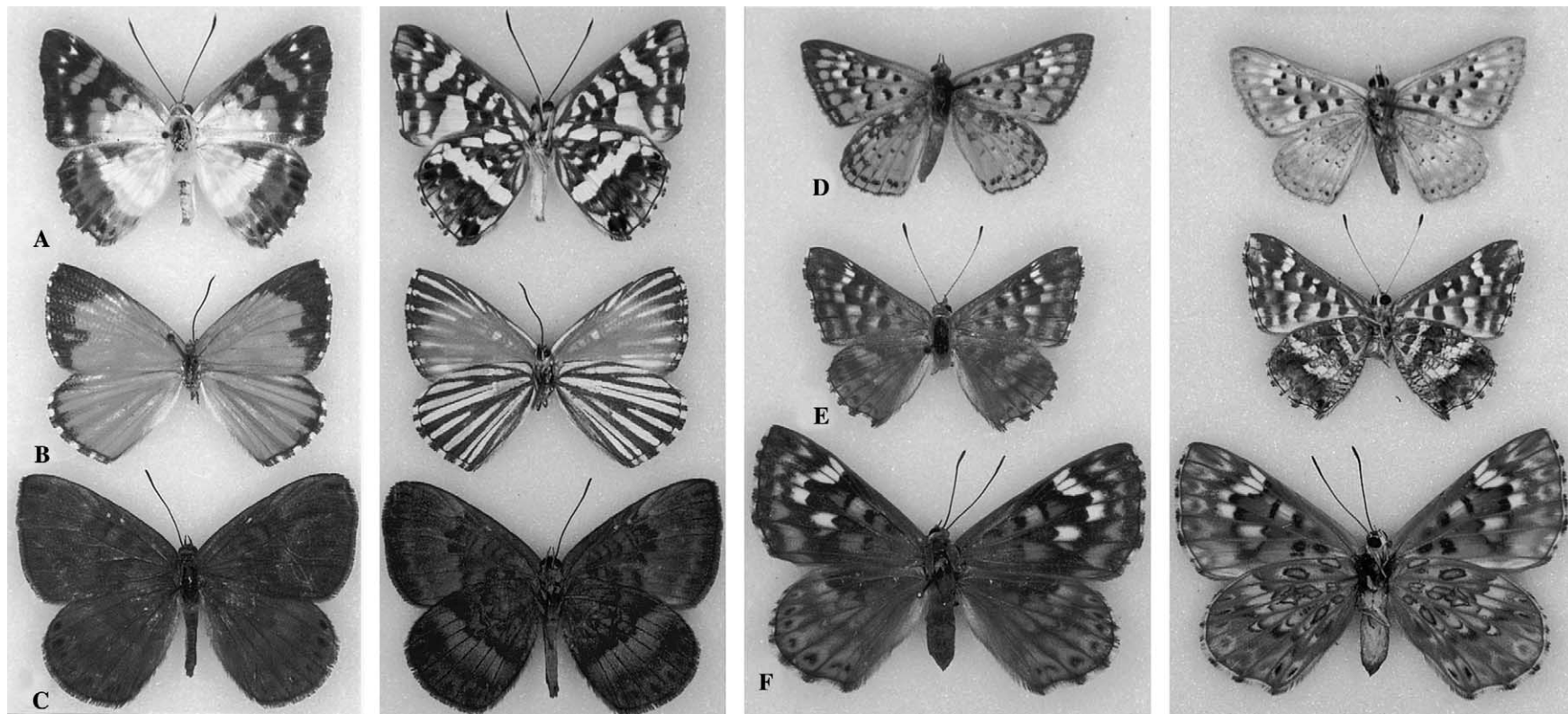


Fig. 1. *Ariconias*, *Aricoris*, and *Synargis* adults (males unless otherwise stated). (A) *Ariconias albinus*, Cocoli, Panama (USNM); (B) *Aricoris terias*, Paraguay (USNM); (C) *Aricoris constantius*, Joinville, Brazil [SC] (RPM); (D) *Aricoris gauchiana*, Sapucay, Paraguay (USNM); (E) *Aricoris chilensis*, La Rioja, Argentina (USNM); (F) *Aricoris incana*, female, Tarapoto, Peru (SMF); (G) *Aricoris epulus*, Takutu Mts., Guyana (USNM); (H) *Aricoris hubrichi*, Nova Lima, Brazil [MGe] (USNM); (I) *Aricoris erostratus*, Lagunillas, Venezuela (USNM); (J) *Synargis fenestrella*, Apuya, Ecuador (JHKW); (K) *Synargis regulus*, Joinville, Brazil [SC] (USNM); (L) *Synargis bifasciata*, Sapucay, Paraguay (USNM).

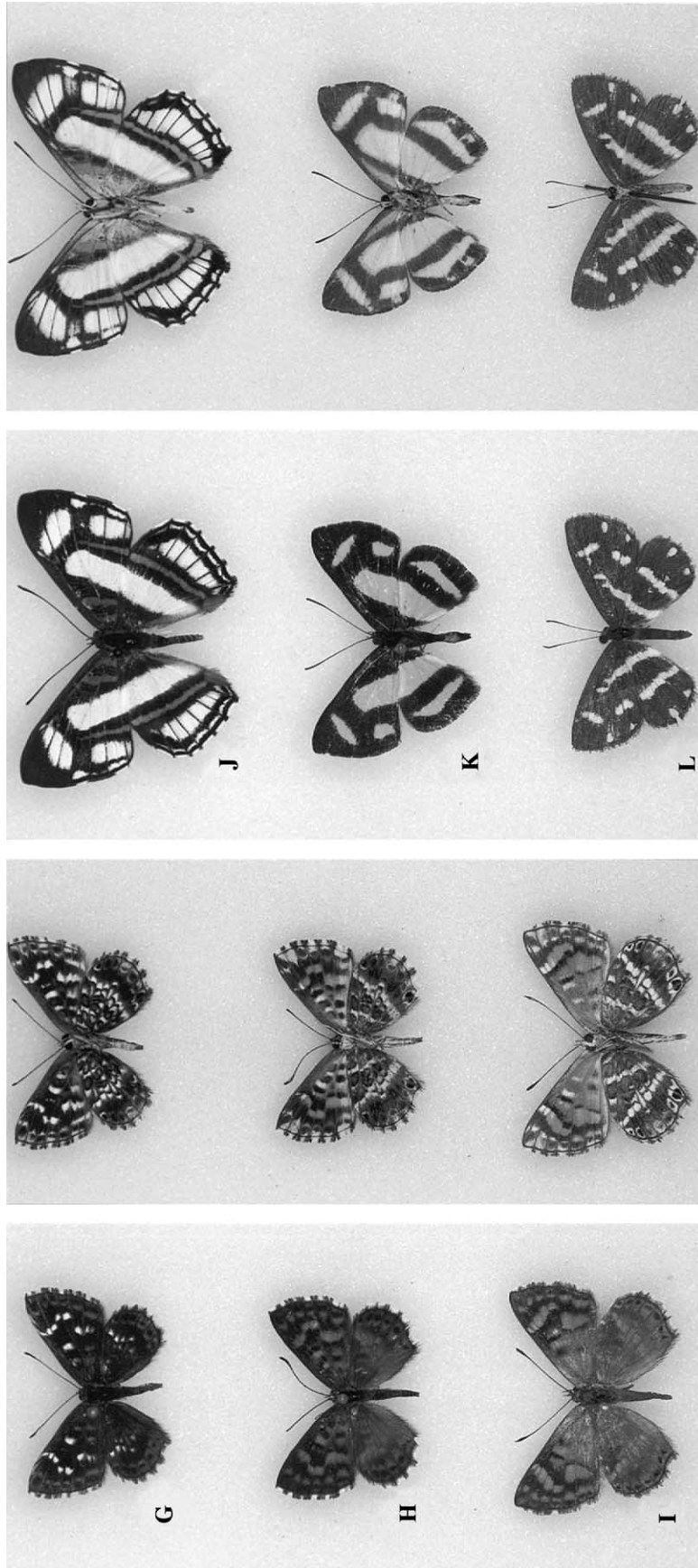


Fig. 1. (continued)

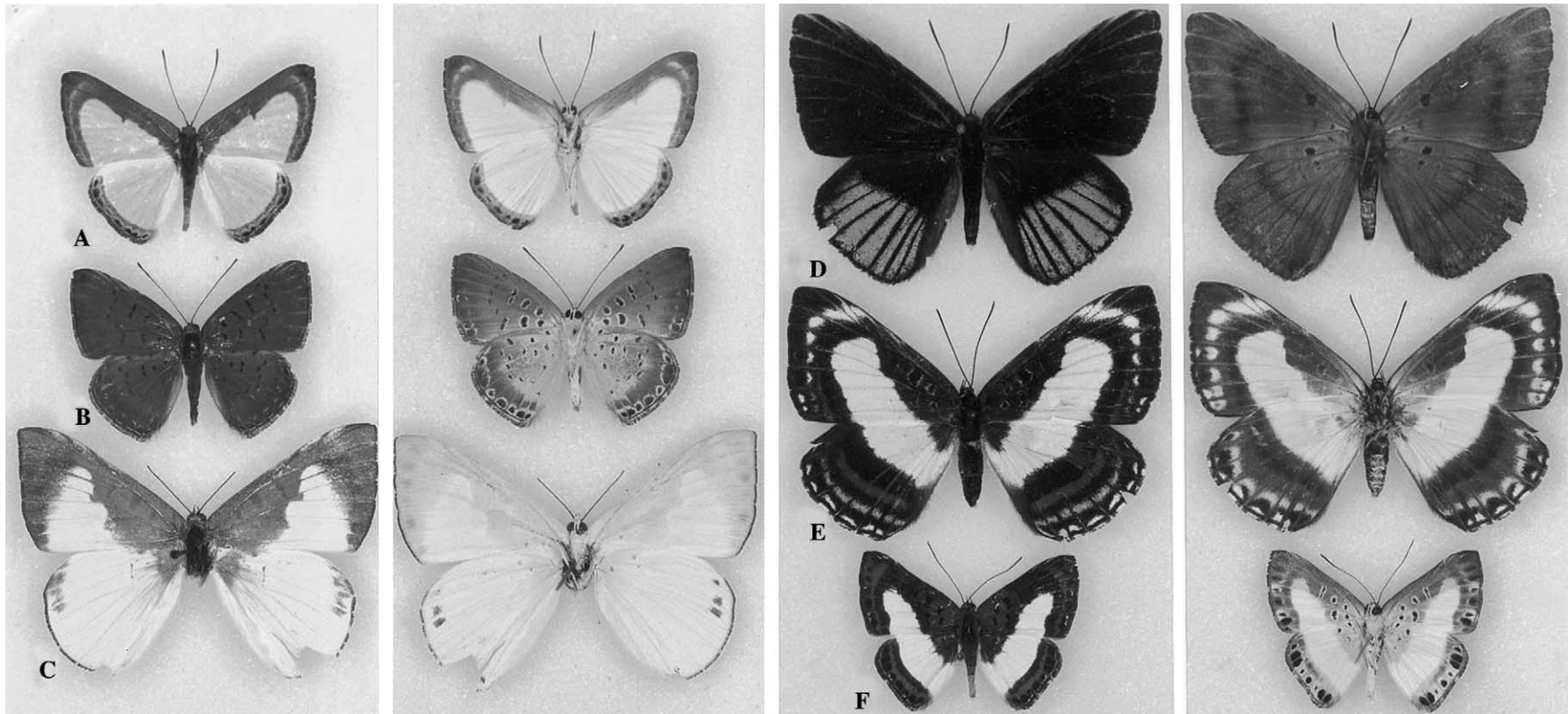


Fig. 2. *Synargis*, *Lemonias*, *Thisbe*, and *Juditha* adults (males unless otherwise stated). (A) *Synargis dirca*, San Sebastián, Guatemala (USNM); (B) *Synargis galena*, Colegio Buriti, Brazil [MGr] (USNM); (C) *Synargis nymphidioides*, Paso San Juan, Mexico (USNM); (D) *Synargis palaeste*, Piña, Panama (USNM); (E) *Synargis palaeste*, female, Gamboa, Panama (USNM); (F) *Synargis gela*, Recife, Brazil [Pe] (USNM); (G) *Synargis abaris*, Florencia, Colombia (USNM); (H) *Synargis abaris*, female, Río Bodoquero, Colombia (USNM); (I) *Synargis orestessa*, Saint Jean du Maroni, French Guiana (USNM); (J) *Synargis orestessa*, female, Geldersland, Surinam (USNM); (K) *Lemonias zygia*, Cacao, French Guiana (USNM); (L) *Thisbe molela*, Pimpilala, Ecuador (JHKW); (M) *Juditha odites*, La Punta, Ecuador (JHKW).

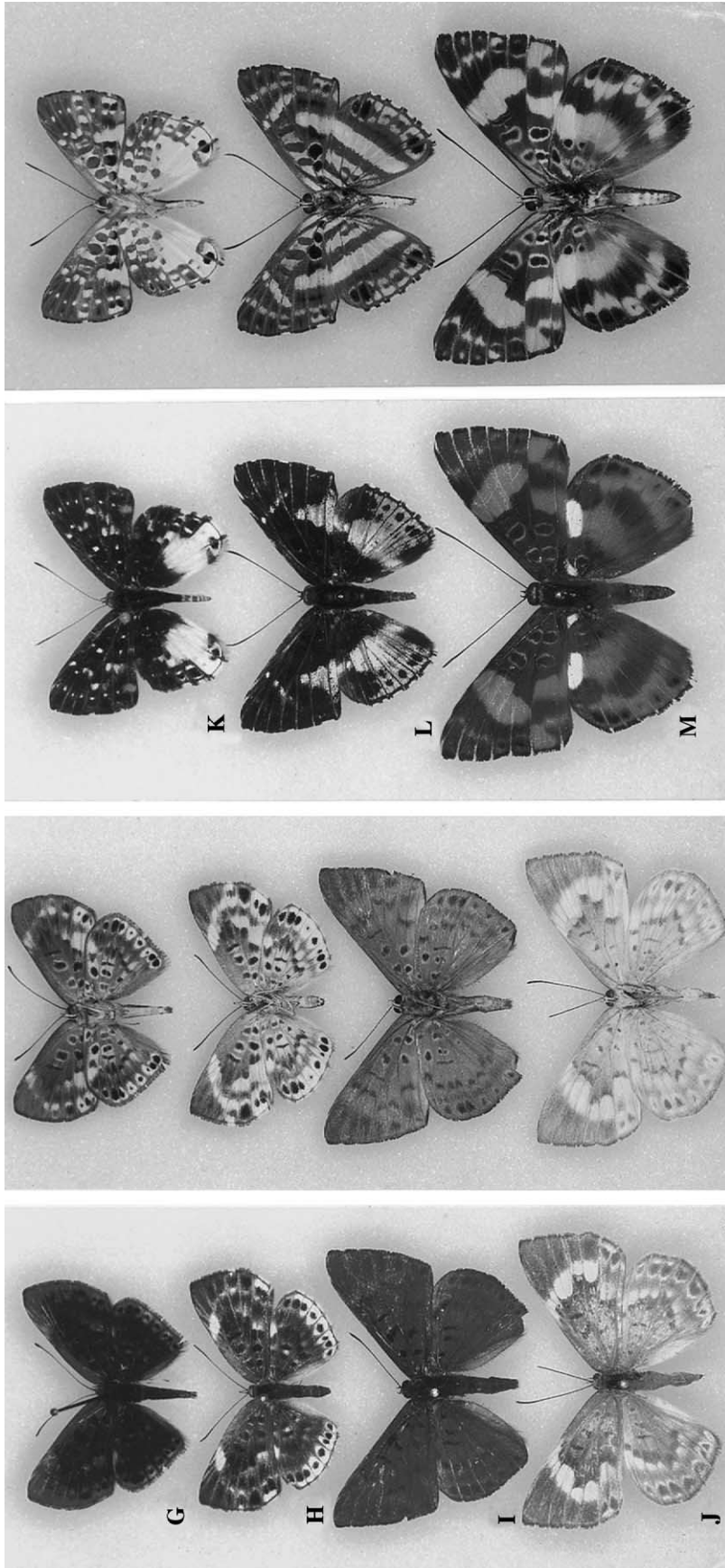


Fig. 2. (continued)

Taxa studied

Although Harvey (1987a) defined his Lemoniadini by its members possessing a bifurcate eighth male abdominal sternite, the character was acknowledged not to be present in all species, and the group is better circumscribed, within the context of the Nymphidiini, by its members possessing a spot at the base of ventral hindwing cell Sc + R₁. All nymphidiine species possessing this spot character were considered here as belonging to the basal clades of the tribe (71 species), except for 2 species of “*Adelotypa*,” 2 species of *Mender*, and 3 species of “*Calospila*,” which all possess genital morphology typical of the Nymphidiina, where they are currently placed, including a sclerotized transtilla joining the valve tips (Hall, 1999a,b, 2002a). The spot is not visible in a few members of the basal clades that have highly modified wing patterns, but it is clear from their genital morphology that their traditional placement in this group is correct. All those genera listed by Harvey (1987a) and Callaghan and Lamas (in press) as belonging in the Lemoniadina, namely *Aricoris*, *Eiseleia* Miller & Miller, *Audre*, *Lemonias*, *Thisbe* (= *Uraneis* Bates; Hall and Harvey, 2001a), *Juditha*, *Synargis*, *Thys anota* Stichel, and *Ematurgina* Röber, are treated here (Figs. 1 and 2), except for *Petrocerus* Callaghan, *Catocyclotis* Stichel, and *Mycastor* Callaghan. In addition to lacking the hindwing spot character, the genital morphology of these last three genera indicates that they belong elsewhere. *Petrocerus catiena* (Hewitson) has no morphological characters in common with the Nymphidiini and we return it to the four forewing radial-veined *incertae sedis* section of Harvey (1987a), near *Callistium* Stichel. Several intermediate morphological structures clearly indicate *Catocyclotis* to be sister to *Nymphidium* Fabricius (Nymphidiina), and *Mycastor* appears to be a polyphyletic assemblage of species that belong to *Catocyclotis* and *Nymphidium* (Hall, unpublished data).

However, even within the aforementioned nine genera that truly belong in the Lemoniadina as currently conceived, several species are misplaced in the catalog of Callaghan and Lamas (in press) at the subtribal and tribal levels. The species *guttata* Stichel, currently placed in *Audre*, lacks all the characteristics of the Nymphidiini and has a wing pattern and genital morphology very similar to those of “*Emesis*” *xanthosa* Stichel. We therefore preliminarily transfer *guttata* to *Emesis* (**n. comb.**), in the four forewing radial-veined *incertae sedis* section of Harvey (1987a), with the caveat that neither species appears to belong there and a new genus will probably be required for them (Hall and Harvey, 2002). The taxa *leucotopus* Stichel, *nivosa* Stichel, *albovata* Stichel, *watkinsi* d’Abrera, and *nycteus* Godman & Salvin all possess the morphological characteristics of the Nymphidiina, and we transfer the first four species from

Ematurgina to *Zelotaea* Bates, and the last from *Synargis* to *Calociasma* Stichel (**n. combs.**). Although the “*leucotopus* group” almost certainly requires a new generic name (Hall, in preparation), we prefer to at least place the species in a related genus in the correct subtribe for the moment.

It was necessary to utilize specimens from the following museums to complete this study: (AME) Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL; (BMNH) The Natural History Museum, London, England; (FSCA) Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL; (JHKW) Collection of Jason P. W. Hall and K. R. Willmott, Washington, DC; (RPM) Reading Public Museum, Reading, PA; (SMF) Senckenberg Museum, Frankfurt, Germany; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, DC; and (ZMHU) Zoologisches Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

Cladistic analyses

Instead of analyzing a single data matrix for all 71 species, the data were partitioned and three analyses conducted (see Tables 2–4). This is done in part because a fully resolved phylogenetic hypothesis has already been generated for approximately one-third of the group (Hall and Harvey, 2001a) and in part because of the problems associated with analyzing large morphological data sets. Thus far, the analysis of large molecular data sets and the reduction in time needed to analyze them have received the most attention (e.g., Goloboff, 1999; Moncalvo et al., 2000; Nixon, 1999; Rice et al., 1997; Soltis and Soltis, 1997; Ronquist, 1998), but there are several problems specific to the analysis of large morphological data sets that have prompted considerably less discussion. The definition of “large” should also be different for molecular and morphological data sets, with that for the latter having a lower threshold in terms of taxa and characters. The problems center around the fact that at least as many characters (or character states if large multistate characters are employed) as taxa are needed to produce a fully resolved tree. But, from experience (Hall, 1999b, unpublished data), we have anecdotally found that as the number of taxa increases, although there is initially an increase in the number of codable morphological characters, as the number of taxa increases further the ratio of codable characters to taxa starts to decline. We would therefore expect a single analysis of all 71 species to produce a suboptimally resolved cladogram, with the use of partitioned analyses maximizing cladogram resolution. The reasons for the former scenario include the merging together of at first apparently discrete potential character states and thus the inability to code those characters, the increasing homoplasy of many characters (particularly wing pattern) (e.g., see Sanderson and

Table 2

List of characters used in the first species-level phylogenetic analysis for 22 ingroup species of *Aricoris* and outgroup *Ariconias albinus*

| Wing shape and pattern | |
|---|--|
| 1. <i>Marked indent in margin of forewing cell M₃</i> : (0) absent (e.g., Fig. 1D); (1) present (Fig. 1E). CI = 1; RI = 1 | |
| 2. <i>Marked indent in margin of hindwing cell Cu₂</i> : (0) present (e.g., Fig. 1F); (1) absent (e.g., Fig. 1C). CI = 1; RI = 1 | |
| 3. <i>Postdiscal markings between cells M₁ and R₂ of DFW</i> : (0) form approximately straight line (e.g., Fig. 1G); (1) contain distally displaced central spot (Fig. 1D). CI = 1; RI = 1 | |
| 4. <i>A straight inwardly semicircular line in DFW cells Cu₂ and Cu₁ narrowly dividing anal portion of postdiscal band from basal elements</i> : (0) absent (e.g., Fig. 1H); (1) present (Fig. 1I). CI = 1; RI = 1 | |
| 5. <i>Inner margin of postdiscal spot in DFW cell Cu₁</i> : (0) approximately straight (e.g., Fig. 1E); (1) markedly indented (at an angle of approximately 90°) (Fig. 1F). CI = 1; RI = 1 | |
| 6. <i>Postdiscal spot in DFW cell Cu₂</i> : (0) extends from vein Cu ₂ to 2A (e.g., Fig. 1E); (1) restricted to diagonal line in upper half of cell (Fig. 1F). CI = 1; RI = 1 | |
| In some species for which state (0) is typical the occasional specimen may lack this spot altogether. The taxon <i>terias</i> is coded with a “?” because this spot is not visible | |
| 7. <i>Well-contrasted and noncontiguous black spots immediately proximal to postdiscal band of pale spots on VFW</i> : (0) absent (e.g., Fig. 1E); (1) present (Fig. 1D). CI = 1; RI = 1 | |
| 8. <i>Elements of medial portion of postdiscal band on VHW distally displaced</i> : (0) those in cells M ₃ and M ₂ (e.g., Fig. 1D); (1) that in cell M ₃ only (e.g., Fig. 1F). CI = 1; RI = 1 | |
| The taxon <i>terias</i> is coded with a “?” because this band is not visible | |
| 9. <i>White markings around medial distal disjunction of VHW postdiscal band</i> : (0) disjunct (e.g., Fig. 1G); (1) continuous (Fig. 1E). CI = 1; RI = 1 | |
| The taxa <i>gauchoana</i> , <i>terias</i> , and <i>constantius</i> are coded with a “?” because no white is present | |
| Male abdomen | |
| 10. <i>Projections of eighth abdominal sternite beyond pleural membrane</i> : (0) absent (e.g., Fig. 3B); (1) present (e.g., Fig. 3F) (1). CI = 1; RI = 1 | |
| 11. <i>Eighth abdominal sternite</i> : (0) approximately evenly sclerotized; (1) heavily sclerotized and blackened toward tip. CI = 1; RI = 1 | |
| Male genitalia | |
| 12. <i>Small dorsal bump above lateral window of uncus</i> : (0) absent (e.g., Fig. 3B); (1) present (Fig. 3C). CI = 1; RI = 1 | |
| 13. <i>Large “U”-shaped dorsal excavation in uncus that reaches posterior margin of tegumen</i> : (0) absent (e.g., Fig. 6B); (1) present (Fig. 3D). CI = 1; RI = 0 | |
| 14. <i>Small, medial, dorsally notched posteriorly and inwardly curved projection on either side of vinculum</i> : (0) absent (e.g., Fig. 3E); (1) present (Fig. 3C). CI = 1; RI = 1 | |
| 15. <i>Aedeagal cornutus</i> (0) absent; (1) consists of a small flat plate (Fig. 3B); (2) consists of an elongate and contorted plate with a prominent dorsal “n-shaped” kink medially (Fig. 3D). CI = 0.67; RI = 0.5 | |
| Note that the medial section in the structure described in state (2) is very narrow and the distal portion is readily broken off, leaving only a small stalk to betray its prior presence. The broken portion is often found in the ductus or corpus bursae of the female genitalia | |
| 16. <i>Valve shape</i> : (0) narrow and elongate with asymmetrical upturned tips (Fig. 3A); (1) rectangular with prominent angular keel at lower posterior corner and elongate projection of equal width at upper posterior corner (Fig. 3D); (2) triangular with dorsal concavity toward tip (e.g., Fig. 3C); (3) rectangular with broadly rounded tip and undulating ventral margin (e.g., Fig. 3E). CI = 0.75; RI = 0.86 | |
| 17. <i>Spines at tip of valvae</i> : (0) absent (Fig. 3A); (1) present (e.g., Fig. 3B). CI = 1; RI = 0 | |
| 18. <i>Spines at tip of valvae relative to valve size</i> : (0) small (e.g., Fig. 3F); (1) large (e.g., Fig. 3C). CI = 1; RI = 1 | |
| The outgroup taxon <i>albinus</i> is coded with a “?” as it has no spines at the valve tips | |
| 19. <i>Spines at tip of valvae</i> : (0) few (2–7) (e.g., Fig. 3C); (1) many (8–10) (Fig. 3E). CI = 1; RI = 1 | |
| The outgroup taxon <i>albinus</i> is coded with a “?” as it has no spines at the valve tips | |
| Female genitalia | |
| 20. <i>Signa</i> : (0) approximately same length (e.g., Fig. 4F); (1) markedly asymmetrical in length (Fig. 4E). CI = 1; RI = 1 | |
| 21. <i>Posterior tip of signa</i> : (0) approximately straight (e.g., Fig. 4A); (1) twisted inward to reveal apex of invagination in lateral view (Fig. 4C). CI = 1; RI = 1 | |
| 22. <i>Signa</i> : (0) with a long anterior invaginated spine (e.g., Fig. 4D); (1) an elongate triangle at wall of corpus bursae (Fig. 4B). CI = 1; RI = 1 | |
| 23. <i>Anterior tip of signal invagination</i> : (0) pointed in both signa (e.g., Fig. 4C); (1) bluntly angular in at least one signum (Fig. 4E). CI = 1; RI = 1 | |
| 24. <i>Unsclerotized portion of ductus bursae exits sclerotized portion</i> : (0) in a straight line (e.g., Fig. 4C); (1) at an angle above 45° (e.g., Fig. 4E). CI = 1; RI = 1 | |
| 25. <i>Sclerotized portion of ductus bursae</i> : (0) relatively strongly sclerotized (e.g., Fig. 4A); (1) relatively weakly sclerotized with medial desclerotized region (the entire section can be folded in two with forceps) (e.g., Fig. 4F). CI = 1; RI = 1 | |
| 26. <i>Invaginated pocket between ostium bursae and papillae anales</i> : (0) present (e.g., Fig. 4B); (1) absent (e.g., Fig. 4E). CI = 1; RI = 1 | |
| 27. <i>If invaginated pocket between ostium bursae and papillae anales present (26:0), sclerotization restricted to pocket only</i> : (0) absent (e.g., Fig. 4A); (1) present (Fig. 4D). CI = 1; RI = 1 | |

Donoghue, 1989) that then fail to produce a meaningful phylogenetic signal (especially after successive weighting), and the presence of related but slightly differing character systems in different parts of the data set (e.g., the very different wing pattern elements visible in the two

large genera analyzed here) that make the creation of broadly inclusive characters and states very difficult, if not impossible.

Partitioned analyses can be justified only when there is a clear *a priori* indication that the subsets of taxa are

Table 3

List of characters used in the second species-level phylogenetic analysis for 24 ingroup species of *Synargis* and outgroup *Juditha odites*

Wing shape and pattern

1. *Elongation of hindwing tornus into small pointed tail*: (0) absent (e.g., Fig. 2B); (1) present (Fig. 1J). CI = 1; RI = 1
2. *Red squares contrasting with ground color in and below discal cell of DFW* (0) absent (e.g., Fig. 2B); (1) present (Fig. 1J). CI = 1; RI = 1
3. *Black spots in discal cell of DFW*: (0) present (e.g., Fig. 2B); (1) absent (e.g., Fig. 1K). CI = 0.5; RI = 0.75
4. *Broad pale DFW postdiscal band in males*: (0) present (e.g., Fig. 2C); (1) absent (e.g., Fig. 2B). CI = 0.33; RI = 0.71
5. *If broad pale DFW postdiscal band in males present (4:0), band*: (0) does not medially enter discal cell (e.g., Fig. 2C); (1) does medially enter discal cell (Fig. 2A). CI = 1; RI = 1
6. *Position of DFW postdiscal band*: (0) distal to discal cell end (e.g., Fig. 2C); (1) entirely proximal to and terminating at discal cell end (e.g., Fig. 1K). CI = 1; RI = 1
7. *Broad pale DHW postdiscal band in males*: (0) present (e.g., Fig. 2A); (1) absent (e.g., Fig. 2B). CI = 0.5; RI = 0.8
8. *Postdiscal band of DHW in males*: (0) does not extend to distal margin (e.g., Fig. 2A); (1) does extend to distal margin (e.g., Fig. 2C). CI = 1; RI = 1
9. *If postdiscal band of DHW in males does extend to distal margin (8:1), band consists of*: (1) uniform cream (Fig. 2C); (2) gray-blue rays (Fig. 2D). CI = 1; RI = 1
10. *Postdiscal band on DFW in females*: (0) extends from anal margin to beyond discal cell end (Fig. 2E); (1) absent; (2) restricted to a few spots in middle of forewing (e.g., Fig. 2H). CI = 1; RI = 1
11. *Two large orange or yellow markings surrounding discal cell end of DFW*: (0) absent (e.g., Fig. 1K); (1) present (Fig. 1L). CI = 1; RI = 1
12. *Prominent transverse red band between postdiscal and submarginal markings extending from tornus to costa on both wings*: (0) absent (e.g., Fig. 1K); (1) present (Fig. 1J). CI = 1; RI = 1
13. *Submarginal band of DFW consists of*: (0) two elements (inner and outer) (e.g., Fig. 1L); (1) one element (inner only) (Fig. 1K). CI = 0.33; RI = 0
14. *Inner and outer elements of DFW submarginal band*: (0) fused for at least part of their length (e.g., Fig. 2A); (1) entirely separate (e.g., Fig. 1L). CI = 0.5; RI = 0.5
The taxa *chaonia*, *sylvarum* and *regulus* are coded with a “?” since they only possess a single element
15. *Inner element of DFW submarginal band consists of a line that is*: (0) approximately continuous (e.g., Fig. 2A); (1) cleanly divided into a tornal and apical section (Fig. 1K). CI = 0.33; RI = 0.6
16. *Prominent pale unicolorous scaling surrounding all submarginal spots on DHW of males*: (0) absent (e.g., Fig. 2G); (1) present (Fig. 2A). CI = 0.25; RI = 0.5
17. *Inner element of DFW submarginal band in females with pale band at costa that extends as far as cell R₁*: (0) absent (Fig. 2E); (1) present (e.g., Fig. 2H) (1). CI = 1; RI = 1
18. *If inner element of DFW submarginal band in females has pale band at costa that extends as far as cell R₁ (17:1), band extends from costa to vein*: (1) M₁ (Fig. 2H); (2) M₃ (Fig. 2J). CI = 1; RI = 1
19. *Forewing fringe of males*: (0) entirely brown (e.g., Fig. 2G); (1) with some white elements (e.g., Fig. 1K). CI = 0.2; RI = 0.5
Hindwing fringe element patterns exhibit the same distribution as the forewing and are thus not coded again
20. *Forewing fringe of females*: (0) with some white elements (e.g., Fig. 2H); (1) entirely brown (Fig. 2J). CI = 0.33; RI = 0.5
Hindwing fringe element patterns exhibit the same distribution as the forewing and are thus not coded again.
21. *Three prominent dark brown spots encircled with paler scaling in discal cell of VFW*: (0) absent (e.g., Fig. 1K); (1) present (e.g., Fig. 2B). CI = 0.5; RI = 0.86
22. *Submarginal spots on VHW*: (0) of approximately equal size (e.g., Fig. 2B); (1) prominently enlarged in apex and tornus (e.g., Fig. 2I). CI = 0.5; RI = 0.88
The taxon *nymphidioides* is coded with a “?” since these submarginal spots cannot all be seen
23. *Submarginal spots on VHW*: (0) most broader proximally than laterally (e.g., Fig. 2G); (1) most broader laterally than proximally (e.g., Fig. 1J). CI = 0.5; RI = 0.89

Male abdomen

24. *Eighth abdominal sternite*: (0) sclerotized at base (e.g., Fig. 6A); (1) medially divided by unsclerotized tissue at base (e.g., Fig. 6D). CI = 1; RI = 1
25. *If eighth abdominal sternite sclerotized at base (24:0), base*: (0) entirely sclerotized (e.g., Fig. 6A); (1) sclerotized in anterior portion only with unsclerotized tissue posteriorly (Fig. 6C). CI = 1; RI = 1
26. *Elongate projections of eighth abdominal sternite with tips covered in fine spines*: (0) absent; (1) present (e.g., Fig. 6B). CI = 1; RI = 0
27. *Width of eighth abdominal sternite base*: (0) approximately same as length of posterior projections beyond membrane (e.g., Fig. 6B); (1) significantly shorter than length of posterior projections beyond membrane (e.g., Fig. 6D). CI = 1; RI = 1
28. *Lateral base of eighth abdominal sternite*: (0) approximately straight (e.g., Fig. 6B); (1) markedly concave (e.g., Fig. 6E). CI = 1; RI = 1
29. *Bulbous tip to projections of eighth abdominal sternite*: (0) absent (e.g., Fig. 6E); (1) present (Fig. 6D). CI = 0.5; RI = 0
30. *Outwardly turned tips to projections of eighth abdominal sternite*: (0) absent (e.g., Fig. 6E); (1) present (Fig. 6A). CI = 1; RI = 1
31. *Distal portions of eighth abdominal sternite projections*: (0) straight to divergent (e.g., Fig. 6C); (1) convergent (e.g., Fig. 6D). CI = 1; RI = 1
32. *Setae on eighth abdominal sternite*: (0) absent or short; (1) long. CI = 1; RI = 1

Male genitalia

33. *Distal margin of uncus*: (0) simple and entire (Fig. 6A); (1) modified into a variety of posteriorly projecting shapes (e.g., Fig. 6D). CI = 1; RI = 1
34. *If distal margin of uncus modified (33:1), upper portion of uncus*: (1) relatively unmodified (e.g., Fig. 6B); (2) modified into two small downwardly pointed spines (Fig. 6F); (3) modified into two elongate rounded projections (Fig. 6G); (4) modified into two moderately elongate pointed projections (Fig. 6D). CI = 0.67; RI = 0.78
35. *If distal margin of uncus modified (33:1), lower portion of uncus modified into*: (1) two bluntly pointed triangular projections (Fig. 6F); (2) two triangular projections with a downwardly pointed tip (e.g., Fig. 6D); (3) two short rounded projections (Fig. 6C). CI = 0.6; RI = 0.82

We cannot be certain whether character state 3 represents the upper or lower portion of the uncus

Table 3 (continued)

| | |
|--|--|
| 36. <i>Vinculum joined to anterior portion of tegumen</i> : (0) only at a narrow point medially with desclerotized tissue visible on either side (Fig. 6B); (1) broadly (Fig. 6D). CI = 0.5; RI = 0.89 | |
| 37. <i>Prominent constriction near junction of vinculum and saccus</i> : (0) absent (e.g., Fig. 6B); (1) present (Fig. 6C). CI = 0.5; RI = 0.9 | |
| 38. <i>Saccus</i> : (0) long (longer than wide) (e.g., Fig. 6D); (1) short (not longer than wide) (Fig. 6A). CI = 1; RI = 1 | |
| 39. <i>Pediceal extends</i> : (0) immediately posteriorly from join with aedeagus (i.e., <45°) (e.g., Fig. 6D); (1) immediately ventrally from join with aedeagus (i.e., >45°) (Fig. 6C). CI = 1; RI = 1 | |
| 40. <i>Valvae</i> : (0) narrowly rectangular with a bifurcate tip (see illustration in Hall and Harvey, 2001a); (1) triangular with a dorsal notch before short upwardly pointed tip (Fig. 6A); (2) rectangular with variably prominent ventral medial notch and elongate upwardly and outwardly projecting tip (Fig. 6B); (3) triangular with a ventral notch before short straight pointed tip (Fig. 6C); (4) rectangular with short upwardly directed tip (e.g., Fig. 6D). CI = 1; RI = 1 | |
| 41. <i>If valvae rectangular with short upwardly directed tip (40:4), valve tips</i> : (1) rounded (Fig. 6D); (2) pointed (Fig. 6E). CI = 1; RI = 1 | |
| Female genitalia | |
| 42. <i>Anterior invagination of signa compressed</i> : (0) dorsoventrally (e.g., Fig. 7C); (1) laterally (e.g., Fig. 7D) (1). CI = 1; RI = 1 The lateral compression of the signa correlates with a flat instead of slightly concave opening of the signa at the corpus wall | |
| 43. <i>Anterior invagination of signa</i> : (0) forms well-defined spine (e.g., Fig. 7A); (1) extends directly to posterior tip creating triangular signa (Fig. 7B). CI = 1; RI = 1 | |
| 44. <i>Anterior invagination of signa</i> : (0) straight (e.g., Fig. 7C); (1) inwardly curved (e.g., Fig. 7A). CI = 0.33; RI = 0.67 | |
| 45. <i>Anterior invagination of signa directed</i> : (0) directly inwards (e.g., Fig. 7E); (1) slightly off to one side (Fig. 7D). CI = 0.5; RI = 0.67 | |
| 46. <i>Sclerotized invagination at posterior as well as anterior tip of signa</i> : (0) absent (e.g., Fig. 7E); (1) present (Fig. 7D). CI = 0.33; RI = 0.71 | |
| 47. <i>Anterior opening of signa at wall of corpus bursae</i> : (0) centrally positioned (Fig. 7C); (1) asymmetrically displaced to one side (e.g., Fig. 7D). CI = 0.5; RI = 0.88 | |
| 48. <i>Sclerotization encircling posterior section of ductus bursae</i> : (0) absent (e.g., Fig. 7A); (1) present (e.g., Fig. 7D). CI = 0.5; RI = 0.83 Note that some species have ventral sclerotization only (e.g., <i>S. ochra</i> in Fig. 7C) | |
| 49. <i>If sclerotization encircling posterior section of ductus bursae present (48:1), sclerotized section</i> : (1) short (not significantly longer than wide) (Fig. 7E); (2) long (significantly longer than wide) (Fig. 7D) (1). CI = 0.67; RI = 0.80 | |
| 50. <i>A well-sclerotized central plate with a continuous sclerotized invaginated pocket between ostium bursae and papillae anales</i> : (0) absent (e.g., Fig. 7A); (1) present (e.g., Fig. 7B). CI = 0.33; RI = 0.78 | |
| 51. <i>A narrow sclerotized invaginated pocket anterior to papillae anales</i> : (0) absent (e.g., Fig. 7C); (1) present (Fig. 7A). CI = 1; RI = 1 | |
| 52. <i>Increased lateral sclerotization at posterior margin of eighth abdominal tergite with relatively weakly sclerotized dorsal region</i> : (0) absent; (1) present (e.g., Fig. 7F). CI = 1; RI = 0 | |
| 53. <i>If increased lateral sclerotization at posterior margin of eighth abdominal tergite present (52:1), sclerotized area</i> : (1) relatively weakly sclerotized, poorly demarcated, and flat (Fig. 7F); (2) relatively well-sclerotized, well-demarcated, and concave (Figs. 7G and H). CI = 0.67; RI = 0.5 | |

monophyletic. In other words, such partitioned subsets of taxa must be supported by at least one, and preferably more, “strong” synapomorphies, such as unique complex structures. Preliminary morphological study clearly indicated that, once the few misplaced species highlighted above in the Taxa studied section were excluded, *Audre* (22 species) would be monophyletic with the inclusion of *Aricoris* and *Eiseleia*, necessitating a name change from *Audre* to the older name *Aricoris*, and that *Synargis* (24 species) would be monophyletic with the inclusion of *Thysanota* and *Ematurgina*.

The list of apomorphies used a priori to predict the monophyly of *Aricoris* and *Synargis*, which form the subject of the first two comprehensive species-level analyses, is given in Table 5. The third analysis was a generic-level one for all six basal genera in the tribe Nymphidiini. In addition to *Aricoris* and *Synargis*, this analysis included *Juditha*, *Lemonias*, *Thisbe*, and *Ariconias* (named here), for which a species-level phylogenetic hypothesis was proposed by Hall and Harvey (2001a). Two members from each of the subtribes Nymphidiina and Theopeina were also included to assess the monophyly of higher-level groups. Because the majority of characters in the generic-level analysis were based on adults, the hypothesized most basal species of each

genus, as determined by the species-level analyses in this paper and in Hall and Harvey (2001a), was used to represent it in the data matrix, but characters of the early stages were coded using the available reared representatives for each genus (i.e., not necessarily the species shown in the matrix). Species from 12 nymphidiine genera have been reared, namely, *Aricoris**, *Lemonias*, *Thisbe**, *Juditha**, *Synargis**, *Zabuella** Stichel, *Nymphidium**, “*Calospila*”*, *Menander**, *Setabis* Westwood, *Protonymphidia* Hall and *Theope**, and representative alcohol preserved material was examined for all the asterisked genera in this list.

Ariconias albinus (C. & R. Felder) and *Juditha odites* (Cramer) were used as outgroups for the analyses of *Aricoris* and *Synargis*, respectively, as basal members of the putatively most closely related genera (Hall and Harvey, 2001a; this study). *Calydna* Doubleday was chosen as the outgroup for the generic-level analysis from all genera in the four forewing radial-veined *incertae sedis* section of Harvey (1987a) (i.e., all those genera that have yet to be placed in a tribe), because its larvae are known to possess prothoracic balloon setae (Hall, 2002b; Janzen and Hallwachs, 2001), a rare character trait shared with several nymphidiine genera (Harvey, 1987a).

Table 4

List of characters used in the generic-level phylogenetic analysis, with all six genera of the Aricorina and Lemoniadina (*Aricoris*, *Ariconias*, *Lemonias*, *Thisbe*, *Juditha*, and *Synargis*), two representatives from each of the Theopeina (*Behemothia* Hall and *Theope* Doubleday) and Nymphidiina (“*Calospila*” Geyer and *Menander* Hemming), and outgroup *Calydna caieta* Hewitson (a basal species in that genus; Hall, 2002b)

Appendages

1. *Sexual dimorphism in size of proboscis*: (0) absent; (1) prominently present (Figs. 10A–D). CI = 1; RI = 1

Character state (1) is present in all species of *Aricoris* and one of the two *Ariconias* species (*albinus*). It is also prominently present in *Synargis galena* and less prominently so in *Synargis axenus*.

Wing pattern

2. *Spots in discal cell of DFW*: (0) plain (e.g., Fig. 1F); (1) ringed with paler scaling (e.g., Fig. 2M). CI = 1; RI = 1

Character state (1) is present in all species of *Juditha* (Hall and Harvey, 2001a) and about half the species of *Synargis*, including the most basal “*phliasus* group”

3. *Spot at base of VHW cell Sc + R₁*: (0) present (e.g., Fig. 1F); (1) absent. CI = 1; RI = 1

Character state (0) applies to the majority of species in the genera indicated, but in many derived species, particularly in *Synargis*, the spotting pattern in this section of the wing is obscured. Character state (1) applies to all species in the Theopeina and all in the Nymphidiina except two species of “*Adelotypa*,” two species of *Menander* and three species of “*Calospila*” (Hall, unpublished data) (see Materials and methods, Taxa studied section)

4. *Spot at base of VHW cell Rs*: (0) present (e.g., Fig. 1F); (1) absent (e.g., Fig. 2M). CI = 1; RI = 1

Character state (1) applies to all species in *Lemonias*, *Thisbe*, *Juditha*, and *Synargis* in which the costal part of the VHW is not obscured, all species in the Theopeina, and all species in the Nymphidiina except those of *Catocyclotis* and “*Adelotypa annulifera* (Godman) (Hall, unpublished data)

Male abdomen

5. *Two long and narrow posterior projections from eighth abdominal sternite*: (0) absent; (1) present (e.g., Fig. 3E). CI = 0.5; RI = 0.5

Character state (1) is present in all species of *Aricoris*, *Ariconias*, and *Synargis* (and also the more derived *Juditha* species, Hall and Harvey, 2001a). However, the structures in each genus are slightly different and are believed to have been multiply derived (see text)

6. *Lateral margins of eighth abdominal sternite*: (0) approximately parallel (e.g., Fig. 3C); (1) converge to small bifurcate tip (see illustration in Hall and Harvey, 2001a). CI = 1; RI = 1

Character state (1) is present in all species of *Lemonias*, except the three members of the “*ochracea* group,” and only the most basal species of *Thisbe*, namely *molela* (Hall and Harvey, 2001a)

7. *Spiracle on third abdominal segment*: (0) dorsal; (1) ventral. CI = 1; RI = 1

Both character states are illustrated by Harvey (1987a) and Hall (2002a). Character state (1) is present in all species of the Theopeina except the most basal member *Protonymphidia senta* (Hewitson) (Hall, 1999b, 2002a) and all genera of the Nymphidiina except *Catocyclotis* and *Zabuella* (Hall, unpublished data). In these cases the spiracle is in an intermediate medial position

Male genitalia

8. *Large dorsal indentation of uncus*: (0) absent; (1) present (Fig. 3C). CI = 1; RI = 1

Character state (1) is present in all species of *Aricoris* (as a large “U-shaped” indentation that reaches the posterior margin of the tegumen) and both species of *Ariconias* (as a shallower indentation that does not reach the posterior margin of the tegumen). This state is present nowhere else in the Lemoniadina or Theopeina but present to the degree found in *Ariconias* in a couple of species of the Nymphidiina (Hall, unpublished data)

9. *Vinculum at anterior margin of tegumen*: (0) a continuous band or variably merged with tegumen (e.g., Fig. 6D); (1) incomplete and ending dorsolaterally (see illustrations in Hall, 1999b, 2002a). CI = 1; RI = 1

Character state (1) is present in all species of the Theopeina except the most basal member *Protonymphidia senta* (Hall, 1999b, 2000, 2002a) and also in the Nymphidiina genera *Nymphidium* and *Catocyclotis* (Hall, unpublished data)

10. *Well-sclerotized transtilla joining tips of valvae*: (0) absent; (1) present (see illustration in Stichel, 1910–1911, for *Nymphidium*). CI = 1; RI = 1

Character state (1) is present in all species of the Nymphidiina and absent elsewhere in the Nymphidiini (Hall, unpublished data)

11. *Setae between base of valvae and pedicel*: (0) absent (e.g., Fig. 6A); (1) present (see illustrations in Hall and Harvey, 2001a). CI = 1; RI = 1

Character state (1) is present as very long setae (as long as the valvae) derived from a well-defined pad (except in *odites*) in all species of *Juditha* (Hall and Harvey, 2001a) and present as short sparse setae in most species of *Synargis*, including members of the most basal “*phliasus* group”

12. *Saccus*: (0) present (e.g., Fig. 6B); (1) absent (see illustrations in Hall, 1999a, b, 2002a). CI = 1; RI = 1

Character state (1) applies to all genera of the Theopeina except *Calicosama* Hall and Harvey (Hall, 1999a, b; Hall and Harvey, 2001c) and a handful of species in the Nymphidiina (Hall, unpublished data)

Female genitalia

13. *Position of posterior tip of signa at wall of corpus bursae*: (0) symmetrical (e.g., Fig. 7A); (1) asymmetrical (e.g., Fig. 4E). CI = 1; RI = 1

Character state (1) is present in all species of *Aricoris* and *Ariconias*, but not universally present in any of the remaining genera in the Nymphidiini (Hall, unpublished data). Species of the derived *Aricoris epulus* group additionally exhibit asymmetry in the length of the signa.

Early stages

14. *Single pair of projections from prothorax of late instar larva with length longer than width*: (0) absent (Fig. 10I); (1) present (Figs. 10E and F). CI = 1; RI = 1

15. *If single pair of projections from prothorax of late-instar larva with length longer than width present (14:1), length*: (1) less than twice width (see illustration in DeVries, 1997, for *Thisbe irenea*); (2) more than twice width (Figs. 10E and F). CI = 1; RI = 1

16. *Vibratory papillae on prothorax of larvae*: (0) absent; (1) present (Figs. 10F–I). CI = 1; RI = 0

17. *Spiracle on larval abdominal segment one*: (0) dorsal (but below level of spiracle on abdominal segment two) (Fig. 10H); (1) ventral (below lateral fringe of setae) (Fig. 10I). CI = 1; RI = 0

Table 5
List of synapomorphies for genera in the subtribes Aricorina and Lemoniadina

| Taxon | Synapomorphies |
|---------------------------------------|--|
| <i>Ariconias</i> Hall and Harvey [2] | <ul style="list-style-type: none"> • Hindwing tornus produced into a point at vein Cu₂ (Hall and Harvey, 2001a) • Posterior portion of ductus bursae immediately anterior to ostium bursae strongly bent to left (Hall and Harvey, 2001a) |
| <i>Aricoris</i> Westwood, [1851] [22] | <ul style="list-style-type: none"> • Deep “U-shaped” dorsal indentation in uncus that reaches posterior margin of tegumen [1: 15:1] (Fig. 3D) • Prominent socketed spines at tip of valvae [1: 20:1] (Figs. 3B–F) (derived <i>Thisbe</i> species have serrate valve tips but not socketed spines) |
| <i>Lemonias</i> Hübner, [1807] [8] | <ul style="list-style-type: none"> • Eighth abdominal male sternite with an abruptly narrowed and slightly bifurcate tip (Hall and Harvey, 2001a) (not present in <i>ochracea</i>, <i>theodora</i>, and <i>albofasciata</i>; also present in <i>T. molela</i>) • Posterior portion of ductus bursae, shortly before ostium bursae, markedly laterally compressed (Hall and Harvey, 2001a) |
| <i>Thisbe</i> Hübner, [1819] [7] | <ul style="list-style-type: none"> • Dorsal coloration overlying brown/black background white with blue iridescence (Hall and Harvey, 2001a) (not present in <i>lycorias</i>) • Eighth abdominal male sternite a plain rectangle with a variably shallowly indented posterior margin (Hall and Harvey, 2001a) (not present in <i>molela</i>; also present in <i>J. odites</i>) |
| <i>Juditha</i> Hemming, 1964 [8] | <ul style="list-style-type: none"> • Eighth male sternite with two long, triangular posterior projections with prominent spines along inner margin (Hall and Harvey, 2001a) (not present in <i>odites</i>) • Long setae on membranous region between pedicel and base of valvae (Hall and Harvey, 2001a) • Everted vesica of aedeagus with a small, roughened, yellowish, semisclerotized patch composed of very small spines (Hall and Harvey, 2001a) • Posterior tips of signa positioned at least length of opening of signa away from entrance of ductus bursae (Hall and Harvey, 2001a) |
| <i>Synargis</i> Hübner, [1807] [24] | <ul style="list-style-type: none"> • Eighth male sternite with two long, narrow posterior projections with finely serrate tips [2: 26:1] (Figs. 6A–E) • Eighth female tergite with well sclerotized lateral margins and desclerotized dorsal region [2: 52:1] (Figs. 7F–H) |

Note. These synapomorphies are universal within the particular genus unless otherwise stated. The numbers in brackets after each generic taxon represent the number of species it contains, and those after apomorphies refer to the first (*Aricoris*; Table 2) or second (*Synargis*; Table 3) phylogenetic analysis in this paper followed by the character number and state.

All analyses were based on morphological characters derived from the adult wings, appendages (generic-level analysis only), male and female genitalia, and early stages (generic-level analysis only). Generic-level autapomorphies were included in the first two analyses, with species-level autapomorphies always excluded, and subtribal autapomorphies were included in the third analysis. The analyses, based on maximum parsimony, were performed using heuristic searches with 500 random addition sequence TBR replicates (both species-level analyses) or an exhaustive search (generic-level analysis) in PAUP Version 4.0b4a (Swofford, 2000). All characters were equally weighted and unordered, therefore making no a priori assumptions about their relative importance or the transformation series of their component states. The strength of branch support was estimated by means of 1000 bootstrap replicates (Felsenstein, 1985) in PAUP and by calculating decay indices (Bremer, 1988, 1994) using the program AUTODECAY 4.0 (Eriksson, 1998) in combination with PAUP. Character evolution was studied using MacClade Version 3.05 (Maddison and Maddison, 1995), and when the optimization of characters on cladograms was ambiguous, the most plausible evolutionary scenario was adopted instead of universally applying the deltran or acctran options.

To examine the evolution of host-plant use and certain myrmecophilous traits in the basal clades of the

Nymphidiini, a “supertree” (*sensu* Sanderson et al., 1998) was compiled using the species-level phylogenetic hypotheses for *Aricoris* and *Synargis* from this study and those for *Ariconias*, *Lemonias*, *Thisbe*, and *Juditha* from Hall and Harvey (2001a). Because a comprehensive generic-level phylogenetic hypothesis was generated in this study to form the phylogenetic “map” necessary to place the species-level cladograms, matrix representation with parsimony methods (Baum, 1992; Ragan, 1992) were not needed to combine the topologies of the source cladograms. The previous species-level analysis by Hall and Harvey (2001a) used in the construction of the supertree utilized *Aricoris* as the outgroup, based on results of an earlier preliminary study by Penz and DeVries (1999), instead of the apparently more closely related genus *Synargis*, as determined here. Therefore, to test whether a more optimal outgroup would have altered the relationships hypothesized by Hall and Harvey (2001a), that data set was reanalyzed using *Synargis* as the outgroup.

Results and discussion

Aricoris

Twenty-seven characters were identified (Table 2) from the wing shape and pattern (nine), male abdomen

(two), male genitalia (eight), and female genitalia (eight) (Figs. 1, 3, and 4) (see Appendix A for character matrix). No characters were found to be codable in the appendages or external markings of the thorax and abdomen. The heuristic searches generated a single most-parsimonious cladogram (MPC) with length 32 steps, CI 0.94, and RI 0.98 (Fig. 5). Although the morphology of *Aricoris* is rather homogeneous, resulting in relatively few codable characters for the number of taxa, homoplasy in the data was very low. Characters and their states are marked on the cladogram in Fig. 5B. We

propose five species groups for *Aricoris*, which all have fair to good branch support given the relatively small number of characters, although atypically, the strongest branch support is for the deeper nodes uniting the “*constantius*” and “*colchis*” groups, the “*chilensis*,” “*aurinia*,” and “*epulus*” groups, and the “*aurinia*” and “*epulus*” groups.

Aricoris appears to be monophyletic as preconceived here to include *Eiseleia* and *Audre* (synapomorphies for the genus are given in Table 5), and these genera are formally synonymized with *Aricoris* (**n. syns.**). Members

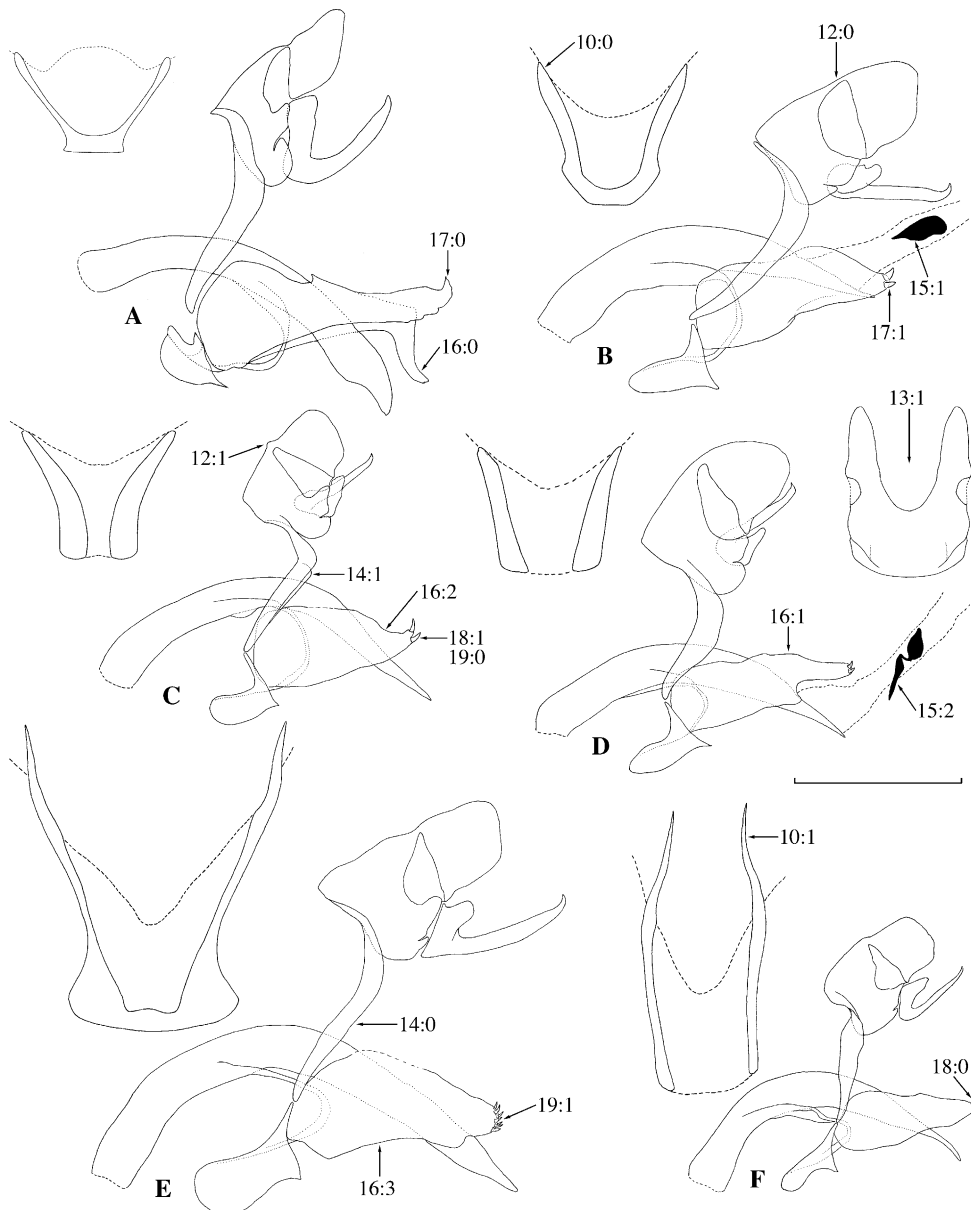


Fig. 3. Male terminalia for *Ariconias* and *Aricoris*. Lateral view of genitalia and ventral view of eighth sternite at upper left unless otherwise stated. The everted vesica is omitted from A (no cornuti present), C, E, and F (same cornutal arrangement as D). Characters and their states for the phylogenetic analysis are given where relevant (character list in Table 2 and data matrix in Appendix A). Scale bar is 1 mm. (A) *Ariconias albinus*, Lagunillas, Venezuela (USNM); (B) *Aricoris constantius*, Leitão, Brazil [MGe] (USNM); (C) *Aricoris middletoni*, Diamantino, Brazil [MGr] (USNM); (D) *A. chilensis*, La Rioja, Argentina (USNM), plus dorsal view of uncus; (E) *Aricoris domina*, La Pita, Panama (USNM); (F) *Aricoris epulus*, Diamantino, Brazil [MGr] (USNM).

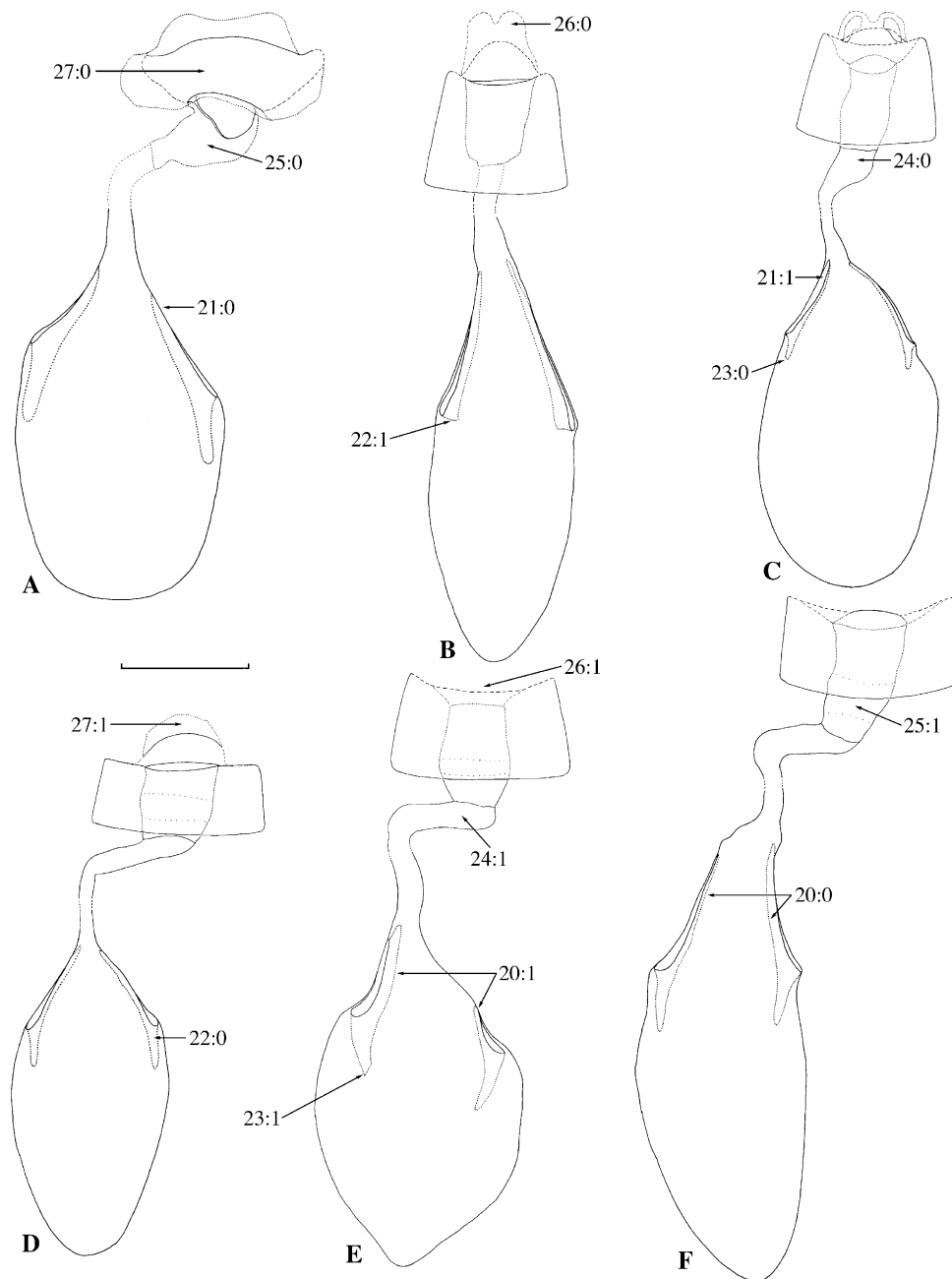


Fig. 4. Female genitalia in ventral view for *Ariconias* and *Aricoris*. Characters and their states for the phylogenetic analysis are given where relevant (character list in Table 2 and data matrix in Appendix A). Scale bar is 1 mm. (A) *Ariconias albinus*, Cerro Campana, Panama (USNM); (B) *Aricoris constantius*, no locality data (USNM); (C) *Aricoris middletoni*, Diamantino, Brazil [MGr] (USNM); (D) *Aricoris chilensis*, La Rioja, Argentina (USNM); (E) *Aricoris campestris*, João Pessoa, Brazil [Pe] (USNM); (F) *Aricoris montana*, Aiguá, Uruguay (SMF).

of the “*colchis*,” “*chilensis*,” “*aurinia*,” and “*epulus*” species groups, as defined in Fig. 5, were long inappropriately known under the name *Hamearis* Hübner (e.g., Stichel, 1910–1911, 1930–1931), a small genus of Palearctic riodinids. Hemming (1934) eventually corrected this mistaken practice and provided the new name *Audre*, with *epulus* Cramer as its type species. This apparently paraphyletic genus has been maintained ever since (Bridges, 1994; Callaghan and Lamas, in press), and never regarded as congeneric with *Aricoris*, the older

potential name, because the single species of that genus, *constantius* Fabricius (= *tutana* Godart auctt. and *monotona* Sichel; see Appendix D), has such a highly modified wing pattern (see Fig. 1). The genus *Eiseleia* was also based on a single externally highly modified species, *terias* Godman (= *pichanalensis* Miller & Miller, see Appendix D), without reference to *Aricoris* or *Audre* (Miller and Miller, 1972). Fig. 5 indicates that the two species of *Aricoris* and *Eiseleia*, as previously conceived, together form the basal *constantius* group. All three

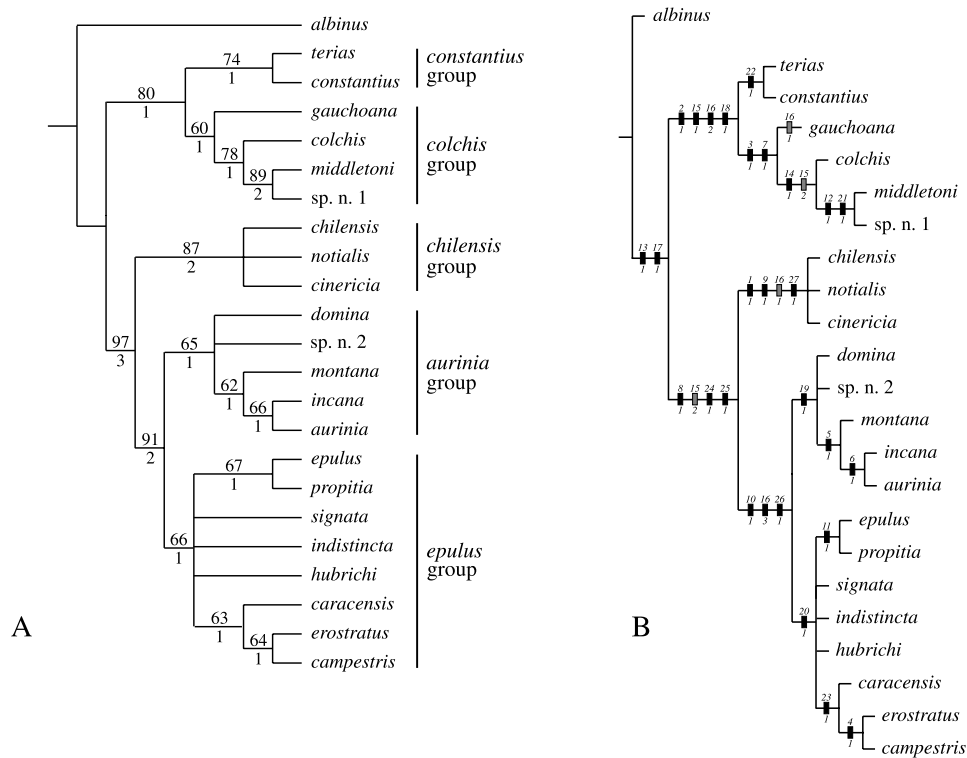


Fig. 5. The single most-parsimonious cladogram resulting from the heuristic analysis of 27 characters for all 22 species of *Aricoris* (= *Audre* and *Eiseleia*). (A) Cladogram showing estimates of branch support, with bootstrap values above branches and decay indices below branches, and limits of species groups. (B) Cladogram illustrating distribution of character states; black bars indicate unique apomorphies, shaded bars indicate homoplasious apomorphies, and white bars indicate reversals.

genera, *Aricoris*, *Eiseleia*, and *Audre*, could be preserved as monophyletic entities if a genus were described for the “*colchis*” group. However, given the morphological homogeneity of the whole, we believe it most biologically meaningful to treat all five species groups in an expanded *Aricoris*.

Synargis

Fifty-three characters were identified (Table 3) from the wing shape and pattern (23), male abdomen (9), male genitalia (9), and female genitalia (12) (Figs. 1, 2, 6, and 7) (see Appendix B for character matrix). No characters were found to be codable in the appendages or external markings of the thorax and abdomen. The heuristic searches generated a single MPC with length 106 steps, CI 0.63, and RI 0.85 (Figs. 8 and 9). Characters and their states are marked on the cladogram in Fig. 9.

Synargis appears to be monophyletic as preconceived here to include *Ematurgina* and *Thysanota* (synapomorphies for the genus are given in Table 5), and these genera are formally synonymized with *Synargis* (**n. syns.**). We propose four species groups for *Synargis*, as defined in Fig. 8, of which the “*phliasus*” and “*abaris*” groups have the strongest branch support. The two species previously treated in *Ematurgina*, *axenus* Hewitson and *bifasciata* Mengel, are shown to be the most

derived members of the “*regulus*” group, and the single species of *Thysanota*, *galena* Bates, to be the most basal member of the large and most derived “*abaris*” group. *Synargis fenestrella* (Lathy), recently transferred from *Thisbe* to *Synargis* by Hall and Harvey (2001a) (and Penz and DeVries, 2001), is shown to belong to the most basal “*phliasus*” group. All groups are reasonably homogeneous except the “*pittheus*” group, whose basal member, *chaonia* Hewitson, shares several symplesiomorphic characters with the “*regulus*” group.

The only other (partial) cladogram generated for *Synargis* is that by Penz and DeVries (2001). They recovered only the “*phliasus*” group as monophyletic, but as a derived subset of a paraphyletic “*abaris*” group instead of the most basal group in the genus, as determined here. There are multiple reasons for the disparity in cladogram structure. First, Penz and DeVries (2001) did not use the closest relative as an outgroup, using *Aricoris* instead of *Juditha*. Second, their taxon sampling was insufficient, with only 11 of the 23 terminal taxa included, 4 of which were misidentified, encompassing members of only the “*phliasus*” and “*abaris*” groups. Third, only male genital characters were used, thus omitting phylogenetically informative wing pattern and female genital characters. However, even our male genital character set alone retrieved all species groups as monophyletic except the “*regulus*” group, and in the same phylogenetic order

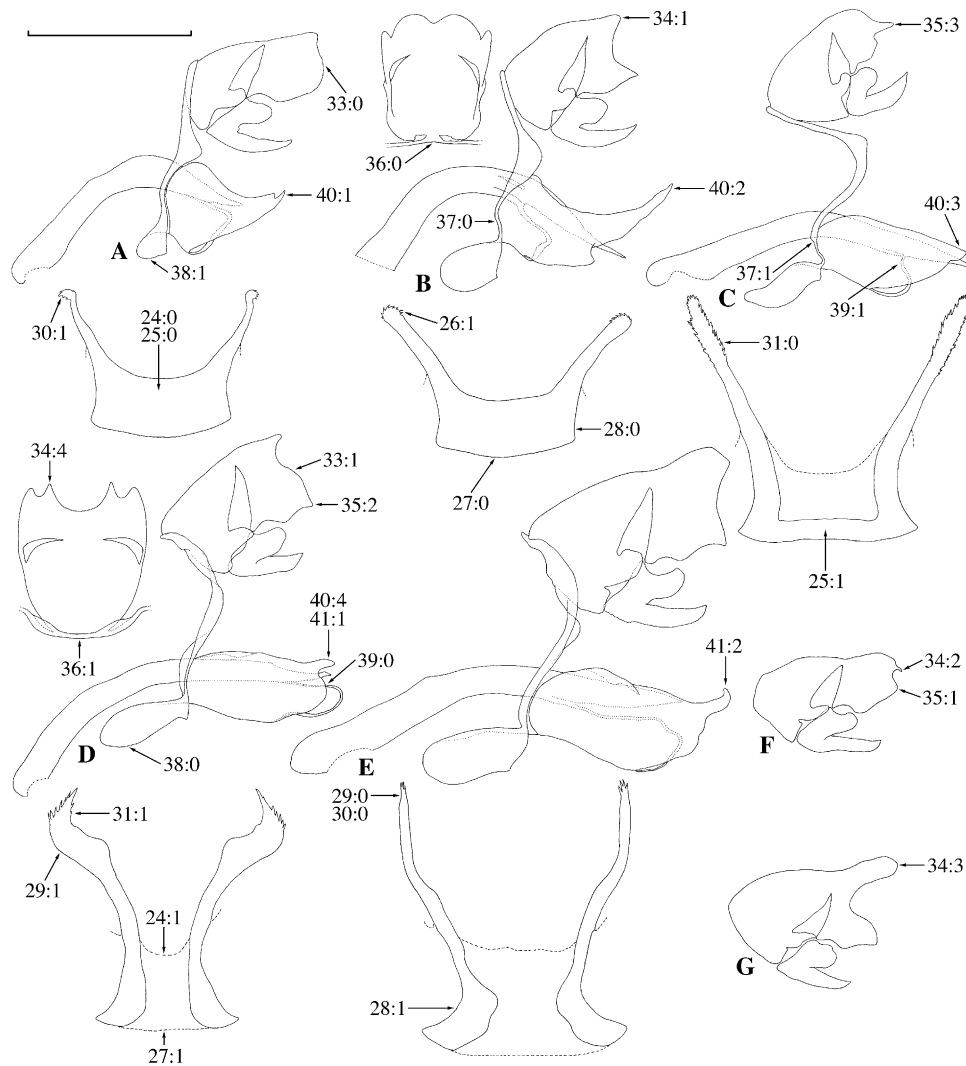


Fig. 6. Male terminalia for *Synargis*. Lateral view of genitalia above and ventral view of eighth sternite below unless otherwise stated. Characters and their states for the phylogenetic analysis are given where relevant (character list in Table 3 and data matrix in Appendix B). Scale bar is 1 mm. (A) *Synargis fenestrella*, Galion, French Guiana (USNM); (B) *S. axenus*, Diamantino, Brazil [MGr] (USNM), plus dorsal view of uncus; (C) *S. ochra*, Tingo Maria, Peru (USNM); (D) *S. abaris*, Matoury, French Guiana (USNM), plus dorsal view of uncus; (E) *S. orestessa*, Saint Jean du Maroni, French Guiana (USNM); (F) *S. galena*, lateral view of uncus only, Diamantino, Brazil [MGr] (USNM); (G) *S. tytia*, lateral view of uncus only, Cacaúlândia, Brazil [Ro] (USNM).

as they were in the complete character analysis. So finally, although their data set was limited in taxa and characters, it also included several characters that were ultimately uninformative, when viewed in the context of the variation known to be present across all terminal taxa, and inaccurately coded. For example, their character 3, asymmetry in the eighth sternite for certain “*phliasus*” group species, was apparently an artifact due to not flattening the structure properly.

Generic analysis

Seventeen characters were identified (Table 4) from the appendages (one), wing shape and pattern (three), male abdomen (three), male genitalia (five), female

genitalia (one) and early stages (four) (Figs. 1, 2, and 10) (see Appendix C for character matrix). The exhaustive search generated a single MPC with length 19 steps, CI 0.95, and RI 0.96 (Fig. 11). Characters and their states are marked on the cladogram in Fig. 11B.

The subtribe Lemoniadina, comprising a group of six monophyletic genera (Hall and Harvey, 2001a, this study) treated here as the “basal clades of the Nymphidiini,” is shown to be paraphyletic with respect to the remaining sister subtribes, Theopeina and Nymphidiina. We therefore restrict the Lemoniadina to contain only *Lemonias*, *Thisbe*, *Juditha*, and *Synargis*, and describe a new subtribe, Aricorina Hall & Harvey, to contain *Aricoris* and the new genus *Ariconias*. Aricorina and *Ariconias* are described in Appendix E. The Aricorina

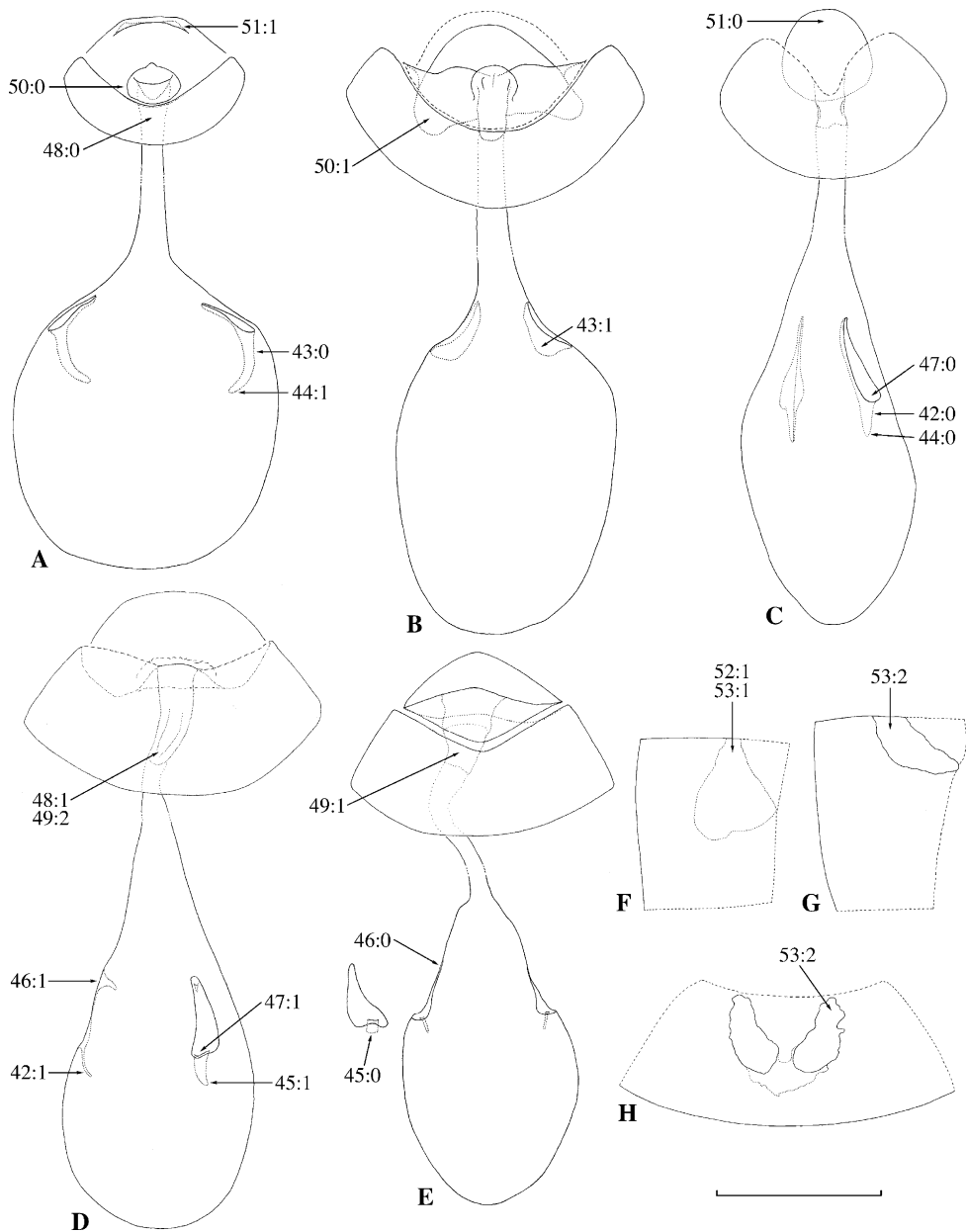


Fig. 7. Female genitalia in ventral view for *Synargis*. (A–E) ventral view of genitalia; (F–H) lateral (F, G) and dorsal views (H) of eighth abdominal sternite. Characters and their states for the phylogenetic analysis are given where relevant (character list in Table 3 and data matrix in Appendix B). Scale bar is 1 mm. (A) *Synargis fenestrella*, 50 km WSW Puerto Maldonado, Peru (USNM); (B) *S. axemus*, Colegio Buriti, Brazil [MGr] (USNM); (C) *S. ochra*, 10 km N Puerto Maldonado, Peru (USNM); (D) *S. tytia*, Cacaulândia, Brazil [Ro] (USNM); (E) *S. orestessa*, Cacaulândia, Brazil [Ro] (USNM); (F) *S. ochra*, Puerto Maldonado, Peru (USNM); (G, H) *S. mycone*, Montraval, French Guiana (USNM).

represents the “*Audre* section” of Harvey’s (1987a) Lemoniadini without *Ematurgina*, which is a synonym of *Synargis*, the *Lemonias* + *Thisbe* sister pair of our Lemoniadina represents the “*Lemonias* section” of Harvey, and the *Juditha* + *Synargis* sister pair of our Lemoniadina represents the “*Synargis* section” of Harvey without *Catocyclotis*, which as discussed earlier belongs to the Nymphidiina. The cladogram in Fig. 11 finally allows us to examine the distribution and evolution of “bifurcate rami,” used by Harvey (1987a) to define his Lemoniadini. While several genera in the

Theopeina and Nymphidiina possess posterior modifications to the eighth male abdominal sternite (Hall, 1999a, unpublished data; Hall and Harvey, 2001c; Stichel, 1910–1911), none compares in length and shape to those found in the Aricorina and Lemoniadina. However, the bifurcate rami of these latter groups differ in each major clade and appear to have evolved multiple times: at least once in *Ariconias* and *Aricoris* (Fig. 3), again in *Synargis* (Fig. 6), again in *Lemonias* and basal *Thisbe* species, and again in *Juditha* (see illustrations of both types in Hall and Harvey, 2001a), in the last case

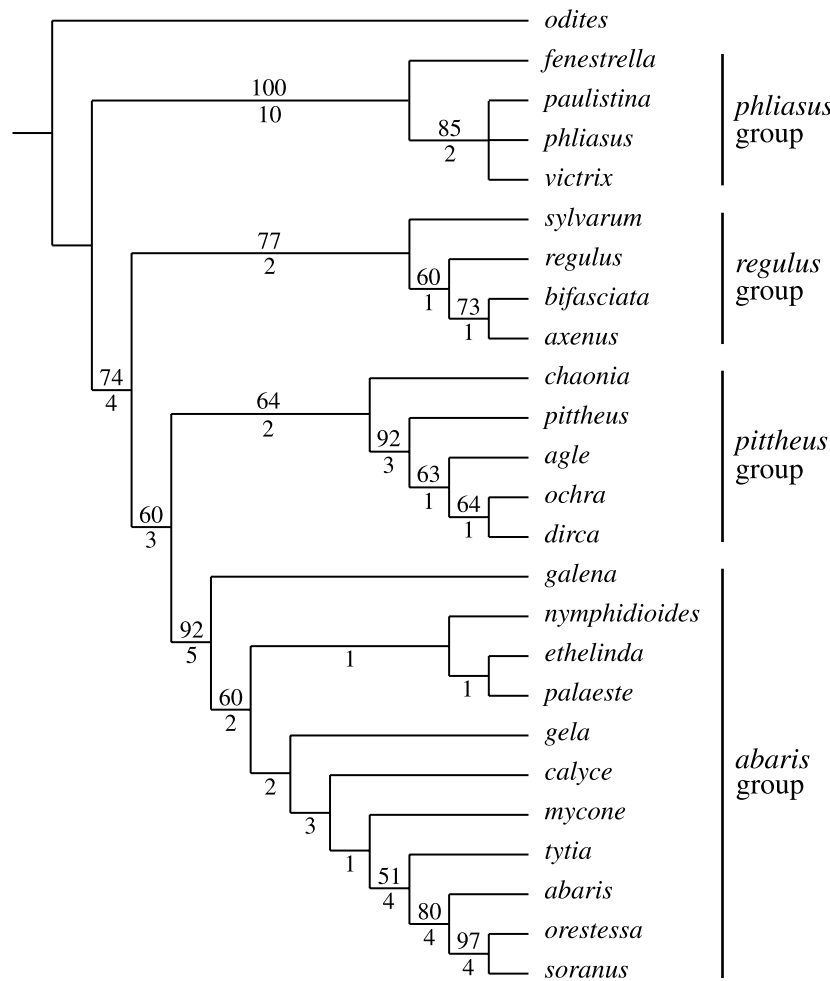


Fig. 8. The single most-parsimonious cladogram resulting from the heuristic analysis of 53 characters for all 24 species of *Synargis* (= *Ematurgina* and *Thysanota*). Estimates of branch support are given in the form of bootstrap values above branches and decay indices below branches.

apparently from an *odites*-like ancestor with an unmodified eighth sternite, assuming this condition is not secondarily derived in that species. It is most parsimonious to assume that the intermediate state between a plain and fully bifurcate eighth sternite, exhibited by the three most basal species groups of *Aricoris*, was a precursor to the fully developed condition rather than a case of secondary loss, as initially tentatively hypothesized by Harvey (1987a).

There is strong character support for the Aricorina, Theopeina, and Nymphidiina (see Table 6), although the small number of evident morphological characters at this taxonomic level translates into only moderate branch support for the Nymphidiina, but support for the Lemoniadina is currently relatively weak. No synapomorphies of adult morphology were found, and the grouping is based on all genera possessing a pair of long projections from the prothorax of late-instar larvae (character 14:1 in Table 4). Additionally, our examination of early stage characters and their interpretation must be regarded as very preliminary for the moment, given the few

species that have been reared to date and the dearth of adequately preserved material available for study.

The only other phylogenetic hypothesis proposed to date for the Nymphidiini, using representatives from each subtribe, is that by Penz and DeVries (1999, 2001). Using about one-quarter of the taxa treated here in the Aricorina and Lemoniadina (their ingroup), a handful of species from the Theopeina and Nymphidiina, and (unwittingly) two species (*guttata* and *agave* Godman & Salvin) from outside the Nymphidiini (Hall and Harvey, 2001a, 2002), Penz and DeVries (1999) reported the tribe Nymphidiini of Harvey (1987a) (Theopeina + Nymphidiina) to be paraphyletic with respect to his Lemoniadini (Aricorina + Lemoniadina). However, when three “problematic taxa” were subsequently removed, including both species listed above that do not belong to the Nymphidiini, and the same data set was reanalyzed with the addition of “*Thisbe*” *fenestrella* and “*Uraneis*” *incubus* Hall, Lamas & Willmott (as *zamuro* Thieme), their strict consensus cladogram became an unresolved octochotomy (Penz and DeVries, 2001). Although not

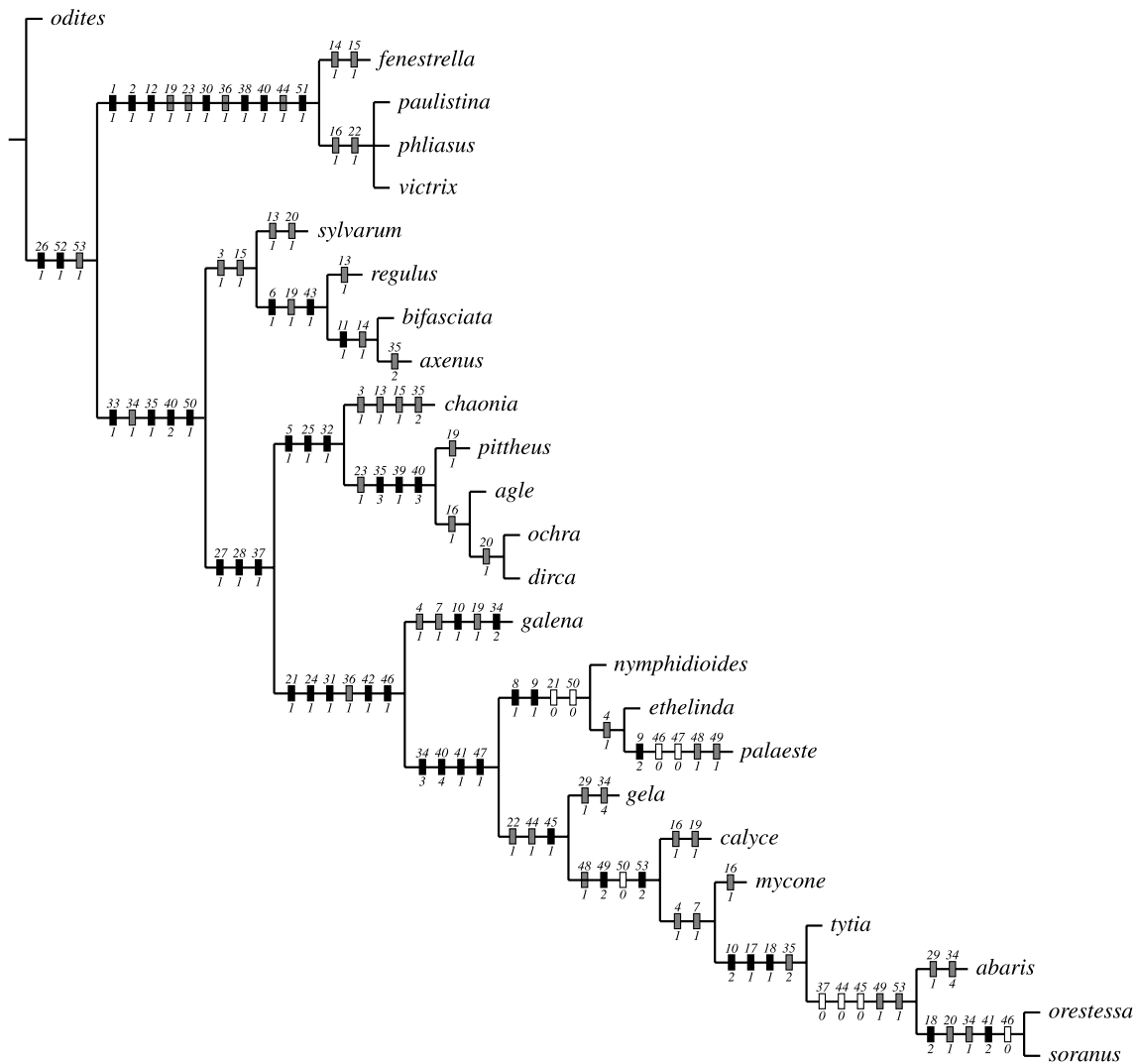


Fig. 9. The single most-parsimonious cladogram for *Synargis* illustrating the distribution of character states. Black bars indicate unique apomorphies, shaded bars indicate homoplasious apomorphies, and white bars indicate reversals.

discussed in that second paper, this fact invalidates the main systematic conclusion of their first paper. Penz and DeVries (1999, 2001) failed to recover any of the intergeneric relationships generated here. Again, as mentioned above for *Synargis*, this is presumably because they did not use a logical close relative as an outgroup (their outgroup, *Stalactis* Hübner, is a highly derived genus with unknown affinities to the rest of the subfamily), their taxon sampling was inadequate, their character matrix was limited to adult morphology (i.e., excluding wing pattern and the morphology of early stages), and they failed to find many of the important synapomorphic characters found to define genera and species groups in this study.

Myrmecophily and patterns of host-plant use

Although the first report for immature stages and host plants in the Nymphidiini was given by Sepp (1829–

1852) over 150 years ago, it is only in recent years that more concerted and intensive searching for riodinid early stages has led to a significant number of further such discoveries (DeVries, 1997; DeVries et al., 1994; Harvey, 1987a). Although early stage information has been published for only 26 species in the basal nymphidiine clades (species highlighted in bold-face type in Fig. 12), this represents the highest percentage (37%) for any higher grouping in the Riodinidae. This information is still scanty in relative terms, and the fact that the majority of rearings are confined to relatively few clades does not allow many conclusions to be drawn concerning the detailed evolution of myrmecophilous traits, for example, between basal and derived clades of a single genus. However, certain meaningful patterns are nonetheless evident.

Larvae of basal members in the Nymphidiini are known to form symbiotic relationships with over 10 secretion-foraging ant genera (trophobionts) in the

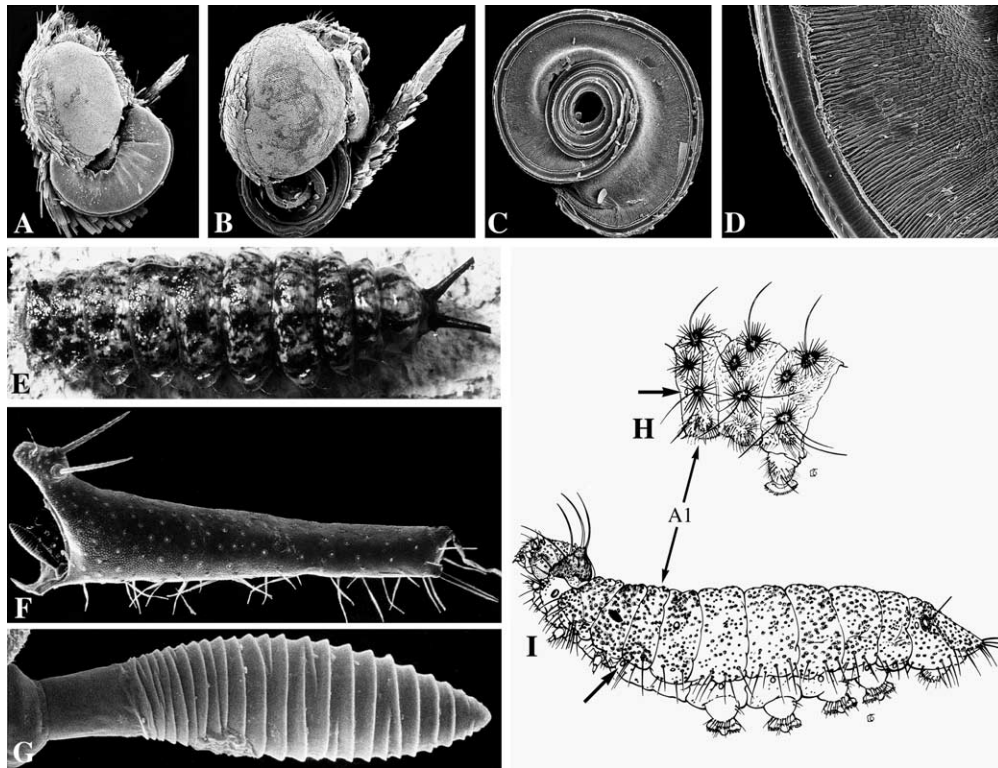


Fig. 10. Scanning electron micrographs (SEMs) and larval illustrations. (A–D) SEMs of adult heads and probosces; (E, H, I) late-instar larvae ((E) photograph by L. Gilbert; (H and I) reproduced from Harvey, 1987b; arrows in H and I indicate spiracle position); (F) SEM of prothoracic “horn” of late-instar larva; (G) SEM of vibratory papilla of late instar larva. (A, C, D) male *Aricoris middletoni*; (B) female *Aricoris middletoni*; (E–G) *Synargis palaeste*; (H) *Apodemia mormo*; (I) “*Calospila*” *cilissa*.

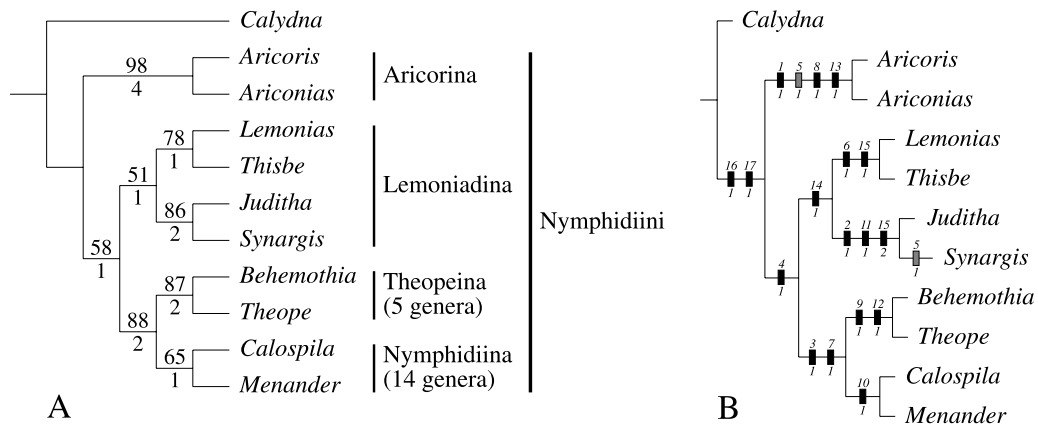


Fig. 11. The single most-parsimonious cladogram resulting from the heuristic analysis of 17 characters for all six genera in the subtribes Aricorina and Lemoniadina and representatives from the subtribes Theopeina and Nymphidiina (all tribes of the Nymphidiini). (A) Cladogram showing estimates of branch support, with bootstrap values above branches and decay indices below branches, and limits of subtribes. (B) Cladogram illustrating distribution of character states; black bars indicate unique apomorphies, shaded bars indicate homoplasious apomorphies, and white bars indicate reversals.

families Formicinae, Ponerinae, Myrmicinae, and Dolichoderinae. From Fig. 12 it can be seen that some taxa, such as *Thisbe irenea* (Stoll) and several derived members of the *Synargis abaris* group, form associa-

tions with many genera of ants. However, although most species have been reared only once, and further rearings will undoubtedly highlight associations with additional ant genera, multiple rearings for *Juditha*

Table 6
List of synapomorphies for subtribes in the Nymphidiini

| Taxon | Synapomorphies |
|------------------------------|---|
| Aricorina Hall & Harvey [2] | <ul style="list-style-type: none"> • Pronounced sexual dimorphism in size of proboscis, with proboscis laterally enlarged in males (Harvey, 1987a) [3: 1:1] (Figs. 10A–D) (not in <i>Aricorinis glaphsa</i>; also in <i>Synargis galena</i> and to a lesser degree in <i>Synargis axenus</i>) • Large dorsal indentation of uncus [3: 8:1] (Fig. 3D) • Signa asymmetrically positioned at wall of corpus bursae [3: 13:1] (Figs. 4A–F) |
| Lemoniada Kirby, 1871 [4] | <ul style="list-style-type: none"> • A pair of projections from prothorax of late-instar larvae with length longer than width [3: 14:1] (Figs. 10E and F) |
| Theopeina Clench, 1955 [5] | <ul style="list-style-type: none"> • Vinculum at anterior margin of tegumen incomplete (Hall, 1999a, b, 2000, 2002a) (not present in <i>Proxonymphidia senta</i>; also in <i>Nymphidium</i> and <i>Catocyclotis</i>) [3: 9:1] • Saccus absent [3: 12:1] (Hall, 1999a, b, 2002a) (present in <i>Calicosama</i> and also absent in a few Nymphidiina species) |
| Nymphidiina Bates, 1859 [14] | <ul style="list-style-type: none"> • Well-sclerotized transtilla joining tips of valvae (Hall, 2000, 2002a) [3: 10:1] |

Note. These synapomorphies are universal within each subtribe unless otherwise stated. The numbers in brackets after each taxon represent the number of recognized described genera it contains (for the Nymphidiina this is based on unpublished data of the first author, and approximately 10 more genera require description), and those after apomorphies refer to the third generic-level phylogenetic analysis (Table 4) in this paper, followed by the character number and state.

species suggest that their larvae form associations with only one ant genus, *Dolichoderus* (Hall and Harvey, 2001a). The phenomenon of larvae, such as those of *Juditha caucana* (Stichel), utilizing a remarkably broad range of unrelated host plants has been attributed to their obligate associations with specific ant taxa, in which the symbiotic relationship is so strong that females tend to use the presence of these ants instead of the plant as an oviposition stimulus (DeVries, 1997; Fiedler, 1991; Pierce, 1983). Elsewhere in Fig. 12, the only ant symbionts recorded for *Lemonias* are *Camponotus* species, while *Camponotus* (the most common), *Ectatomma*, and *Solenopsis* species are known to tend *Aricoris* larvae.

Ninety-nine percent of reared Lepidoptera are known to be phytophagous (Strong et al., 1984) and the rare condition of aphytophagy is believed to have evolved in Rhopalocera only within myrmecophilous lineages (Cottrell, 1984; Ehrlich and Raven, 1965; Pierce, 1995). Although aphytophagy is well known in the lycaenid subfamilies Liphyrinae, Polyommatainae, and Miletinae (e.g., Ackery, 1990; Akino et al., 1999; Cottrell, 1984; Maschwitz et al., 1988; Pierce, 1995), it has been unequivocally documented for only two riordinid species, *Alesa amesis* (Cramer) (Eurybiini) (DeVries and Penz, 2000), and *Setabis lagus* (Cramer) (Nymphidiini: Nymphidiina) (DeVries et al., 1994; Kaye, 1921). However, if a broader definition of aphytophagy is used, to include larvae that have been found within ant nests or those that refuse to eat the plant material upon which the eggs were deposited, then the phenomenon can be said to be rather better known. Aphytophagy in riordinids is used here to imply feeding on ants themselves or their regurgitations or on homopterans and their secretions. Such information is mapped onto the cladogram in Fig. 12 as “aphytophagy indicated.” DeVries and Penz (2000) have suggested that unusually

long thoracic legs in larvae, which are used for prey handling, are a good indicator for aphytophagy, but the suggestion that greasy wings in adults indicate aphytophagy (DeVries, 1997; Hall and Willmott, 1995) potentially allows the distribution and evolution of the phenomenon to be considerably better understood. The presence of greasy wings is widespread in the basal nymphidiine clades and distributed nonrandomly. The condition is widespread in the basal *constantius*, *colchis*, and *aurinia* groups of *Aricoris* and the derived *abaris* group of *Synargis*, present in only the most basal species of *Juditha*, and notably absent from the *Lemonias* + *Thisbe* clade. Since the presence of greasy wings correlates with aphytophagy indicated in five of the six cases given in Fig. 12, the former would seem to be a good indicator of the latter. If the presence of greasy wings is assumed to be a reliable indicator of aphytophagy, then that phenomenon is prevalent in at least 19 of the 71 basal nymphidiine species, or 27%, and has apparently evolved multiple times in these clades alone. It is clear from Fig. 12 that most of the species remaining to be reared are either rare (e.g., *Synargis regulus* and *pittheus* groups) or possess larvae believed to be aphytophagous (e.g., *Aricoris constantius* and *colchis* groups).

Larvae of basal nymphidiine species are known to utilize over 10 host-plant families and, whereas some species, such as *Juditha caucana* and derived members of the *Synargis abaris* group, are highly polyphagous, others, such as the species of *Lemonias*, appear to be monophagous, in this case on *Croton* (Euphorbiaceae). Since this food plant is also used by the most basal of the reared *Thisbe* species, this condition was probably ancestral in the *Lemonias* + *Thisbe* clade. The subsequent shift in the derived *Thisbe* species (formerly *Uraneis*) from *Croton* to toxic mistletoes (*Phoradendron*) mirrors that to a modified aposematic and presumably

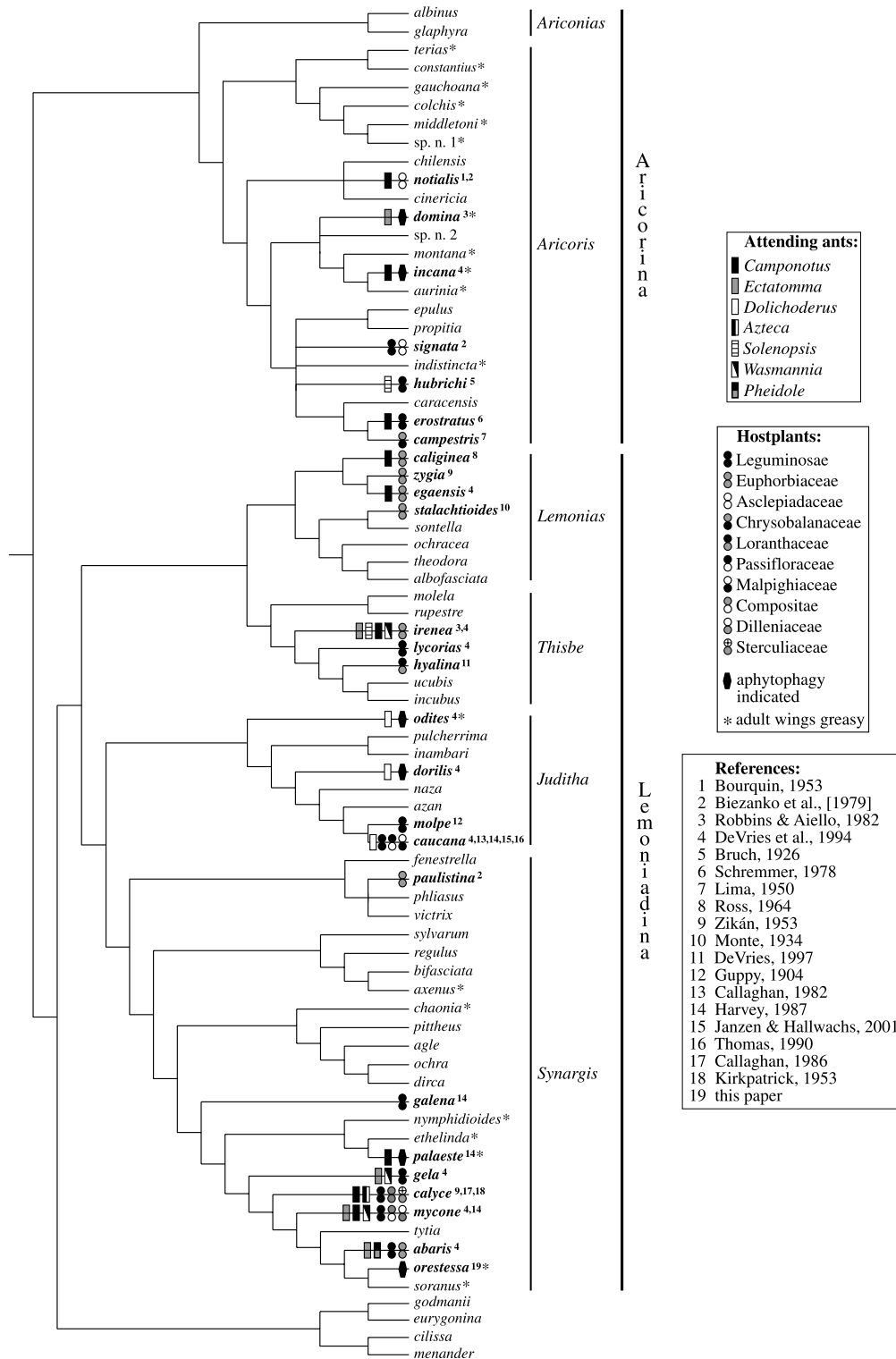


Fig. 12. A supertree for all 71 species of the basal nymphidiine subtribes Aricorina and Lemoniadina, compiled using the generic-level phylogenetic hypothesis of this study, the species-level phylogenies for *Aricoris* and *Synargis* from this study, and those for *Ariconias*, *Lemonias*, *Thisbe*, and *Juditha* from Hall and Harvey (2001a). Note that the reanalysis of this last data set using *Synargis* instead of *Aricoris* as the outgroup produced the same topology, and that although the recently described *Thisbe rupestre* was not included in the cladogram of Hall and Harvey (2001a), reanalysis of that data set using the limited morphological information available in Callaghan (2001) indicated it to be the sister to *Thisbe molela*, as suggested by Hall and Harvey (2001a). Reared species are indicated in bold-face type with the relevant references as superscript numbers. Attending ant genera, host-plant families (*sensu* Gentry, 1993), and the suggested presence of aphytophagy and greasy wings in the adults are mapped onto the cladogram. Only the most common ant symbionts are given for *Thisbe irenea* and *Synargis mycone* and the most common hostplants for *Juditha caucana* and *Synargis mycone*. Note that the host-plant record of *Cassia* for *Thisbe lycorias* (DeVries et al., 1994) requires confirmation, as the larval description (DeVries, 1997) reads like that of a *Juditha* or *Synargis* species and there is no adult voucher.

mimetic wing pattern (Hall and Harvey, 2001a). Overall, the most frequently used host plants for basal nymphidiine species are those in the Leguminosae and Euphorbiaceae.

In conclusion, it is clear that to answer more complex questions concerning the evolution of myrmecophilous traits, it is necessary to rear many more species. This study has highlighted those clades for which we have no early stage information, such as *Ariconias*, the *constantius* and *colchis* groups of *Aricoris*, the *ochracea* group of *Lemonias*, and the *regulus* and *pittheus* groups of *Synargis*, and predicted which species may be phytophagous or aphytrophagous. Thus far, it is mainly the more common phytophagous species that have been reared and the challenge for the future is to try and uncover the secretive lives of the rarer and often aphytrophagous species.

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Appendix A

Character matrix for the species-level phylogenetic analysis of Aricoris

| | 5 | | | | | 1 | | | | | 1 | | | | | 2 | | | | | 2 | | | | | | | | | |
|--------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | | | | | 0 | | | | | 5 | | | | | 0 | | | | | 5 | | | | | | | | | |
| <i>albinus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>terias</i> | 0 | 1 | 0 | 0 | 0 | ? | 0 | ? | ? | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>constantius</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>gauchoana</i> | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>colchis</i> | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>middletoni</i> | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| sp. n. 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>notialis</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>chilensis</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>cinericia</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>domina</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| sp. n. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>montana</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>incana</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>aurinia</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>epulus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>propitia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>signata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>indistincta</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>hubrichi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>caracensis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>erostratus</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |
| <i>campestris</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? |

Appendix B

Character matrix for the species-level phylogenetic analysis of Synargis

| | 5 | 1 0 | 1 5 | 2 0 | 2 5 | 3 0 | 3 5 | 4 0 | 4 5 | 5 0 |
|--------------------|---|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| <i>odites</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>fenestrella</i> | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>paulistina</i> | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>phliasus</i> | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>victrix</i> | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>sylvarum</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>regulus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>bifasciata</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>axenus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>chaonia</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>pittheus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>agle</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>ochra</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>dirca</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>galena</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 1 |
| <i>nymphidio-</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>ides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>ethelinda</i> | 0 | 0 | 0 | 1 | ? | 0 | 0 | 1 | 1 | 0 |
| <i>palaeste</i> | 0 | 0 | 0 | 1 | ? | 0 | 0 | 1 | 2 | 0 |
| <i>gela</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>calyce</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>mycone</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 0 |
| <i>tytia</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 2 |
| <i>abaris</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 2 |
| <i>orestessa</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 2 |
| <i>soramus</i> | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 2 |

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Appendix C

Character matrix for the generic-level phylogenetic analysis of the nymphidiine subtribes Aricorina and Lemoniadina

| | 5 | | | | | 0 | | | | | 1 | | | | | | | | | |
|----------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Calydna caieta</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Aricoris gauchoana</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>Ariconias albinus</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? |
| <i>Lemonias zygia</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| <i>Thisbe molela</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| <i>Juditha odites</i> | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 |
| <i>Synargis phliasis</i> | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 |
| <i>Behemothia godmanii</i> | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | ? | ? | ? | ? | ? |
| <i>Theope eurygonina</i> | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>“Calospila” cilissa</i> | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>Menander menander</i> | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |

Appendix D

To establish the correct names for all terminal taxa in the analyses, taxonomic revision of all genera in question and examination of types was necessary. Presented below is a synonymic checklist of the 71 species in the basal nymphidiine subtribes Aricorina and Lemoniadina prepared by the first author. Taxonomic changes are marked in bold-face type. Short dashes represent subspecies and long dashes synonyms. Numbers of species in each subtribe and genus are given in square brackets.

Nymphidiini Bates, 1859

Aricorina Hall & Harvey, n. subtribe [24]

Aricoris Westwood, [22] [1851]= *Lemonias* Hoffmannsegg, 1818, preocc.= *Melanope* Röber, 1892= *Audre* Hemming, 1934 n. syn.= *Eiseleia* L. & J. Miller, 1972 n. syn.*aurinia* (Hewitson, 1863) n. comb.*campestris* (Bates, 1868) n. comb.*caracensis* (Callaghan, 2001) n. comb.*chilensis* (C. & R. Felder, 1865) n. comb.– *affinis* (Schweizer & Kay, 1941) n. syn.– *catamarquense* (Hayward, 1968) n. syn.– *cisandrina* (Seitz, 1916) n. syn.– *cosquinia* (Giacomelli, 1928) n. syn.– *dovina* (Schaus, 1902) n. syn.– *umbrata* (Giacomelli, 1928) n. syn.*cinericia* (Stichel, 1910) n. comb.– *precaria* (Schweizer & Kay, 1941)– *similis* (Schweizer & Kay, 1941)*colchis* (C. & R. Felder, 1865) n. comb.*constantius* (Fabricius, 1793)– *bahiana* C. & R. Felder, 1865– *monotona* Stichel, 1910 n. syn.– *tisiphone* Westwood, [1851]– *tutana* (Godart, [1824])*domina* (Bates, 1868) n. comb.*epulus* (Cramer, [1775]) n. comb.– *albimaculata* (Lathy, 1932) n. syn.– *epula* (Hübner, [1821])– *epule* (Hübner, [1819])– *pasquita* (Stichel, 1910) n. syn.*erostratus* (Westwood, [1851]) n. comb.– *antaeus* (Seitz, 1916)– *insularis* (Lathy, 1932) n. syn.*gauchoana* (Stichel, 1910) n. comb.*hubrichi* (Stichel, 1926) n. comb.– *almironensis* (Schweizer & Kay, 1941)

n. syn.

incana (Stichel, 1910) n. comb. n. stat.– *drucei* (Giacomelli, 1914)*indistincta* (Lathy, 1932) n. comb.– *ina* (Schweizer & Kay, 1941)*middletoni* (Sharpe, 1890) n. comb.– *philene* (Stichel, 1916) (good species ?)– *diamantina* (Callaghan, 1999) n. syn.*montana* (Schneider, 1937) n. comb.– *erycina* (Schweizer & Kay, 1941) n. syn.– *nordensis* (Callaghan, 2001) n. syn.*notialis* (Stichel, 1910) n. comb.– *mesopotamica* (Hayward, 1968) n. syn.– *susanae* (Orfila, 1953) n. syn.*propitia* (Stichel, 1910) n. comb., n. stat.*signata* (Stichel, 1910) n. comb., n. stat.*terias* (Godman, 1903) n. comb.– *pichanalensis* (L. & J. Miller, 1972) n. syn.

sp. n. 1

sp. n. 2

Unplaced expected synonyms
(type material not examined):

Appendix D (continued)

- arenarum* (Schneider, 1937)
zachaeus (Fabricius, 1798)
 – *zachea* (Godart, [1824])
- Ariconias** Hall & Harvey, **n. gen.** [2]
albinus (C. & R. Felder, 1861) **n. comb.**
glaphyra (Westwood, [1851]) **n. comb.**
 – *campicola* (Seitz, 1916)
 – *modesta* (Mengel, 1902) **n. syn.**
- Lemoniadinina** Kirby, 1871 [47]
Lemonias Hübner, [1807] [8]
 = *Lemonias* Illiger, 1807, *suppr.*
 = *Anatole* Hübner, [1819]
albofasciata (Godman, 1903)
caliginea (Butler, 1867)
 – *rossi* (Clench, 1964)
egaensis (Butler, 1867)
 – *reducta* Brévignon, 1998 **n. syn.**
 – *restricta* (Talbot, 1928) **n. syn.**
 – *suffusa* (Lathy, 1932) **n. syn.**
ochracea (Mengel, 1902)
 – *phyciodes* (Hayward, 1949) **n. syn.**
sontella (Schaus, 1902)
stalactioides (Butler, 1867)
 – *canidia* (H. Druce, 1904)
 – *stellidia* (Schaus, 1902)
theodora (Godman, 1903)
zygia Hübner, [1807]
 – *baroptenosa* (Stichel, 1910) **n. syn.**
 – *caletor* (Dalman, 1823)
 – *epone* (Godart, [1824]) **n. syn.**
 – *chea* Hewitson, 1863 **n. stat.**
 – *peristera* (Stichel, 1910) **n. syn.**
- Thisbe** Hübner [1819] [7]
 = *Uraneis* Bates, 1868
 = *Esthemopheles* Röber, 1903
hyalina (Butler, 1867)
 – *zamuro* (Thieme, 1907)
incubus (Hall, Lamas & Willmott, 2001)
irenea (Stoll, [1780])
 – *atlantis* Stichel, 1910 **n. syn.**
 – *belides* Stichel, 1910 **n. syn.**
 – *belise* (Stoll, [1781])
 – *branca* Penz & DeVries, 2001 **n. syn.**
 – *interjecta* Talbot, 1928 **n. syn.**
 – *prodiga* Stichel, 1929 **n. syn.**
lycorias (Hewitson, [1853])
 – *adelphinum* (Godman & Salvin, 1878)
 – *germanus* (Godman & Salvin, 1886)
 – *incarum* Seitz, 1916 **n. syn.**
molela (Hewitson, 1865)
 – *palilis* Stichel, 1910
rupestre Callaghan, 2001
ucubis (Hewitson, 1870)

- Juditha** Hemming, 1964 [8]
 = *Pseudopeplia* Hemming, 1967
azan (Westwood, [1851])
 – *australis* (C. Felder, 1862)
 – *completa* (Lathy, 1904)
 – *majorina* Brévignon & Gallard, 1998
 – *lamis* (Stoll, [1780]), *preocc.*
caucana (Stichel, 1911)
dorilis (Bates, 1866)
 – *ipsea* (Godman & Salvin, 1886)
 – *licimias* (Staudinger, [1887])
inambari Hall & Harvey, 2001
molpe (Hübner, [1808])
 – *bahiana* (Stichel, 1929)
naza Hall & Harvey, 2001
odites (Cramer, 1775)
 – *apame* (Hewitson, 1865)
 – *laodamia* (Stichel, 1923)
 – *magnifica* (Stichel, 1911)
 – *oditis* (Hübner, [1819])
 – *orontes* (Stichel, 1923)
 – *phylacis* (Godart, [1824])
 – *phyllea* (Hübner, [1819])
 – *phylleus* (Cramer, 1775)
 – *praeclarum* (Bates, 1866)
pulcherrima (Butler, 1867)
 – *felicis* (Rebillard, 1958)
 – *comparata* (Stichel, 1911)
- Synargis** Hübner, [1819] [24]
 = *Nymula* Boisduval, 1836
 = *Acystipoda* Röber, 1892
 = *Ematurgina* Röber, 1903 **n. syn.**
 = *Thysanota* Stichel, 1910 **n. syn.**
abaris (Cramer, 1776)
 – *abarissa* (Hübner, 1819)
 – *sperthias* (C. & R. Felder, 1865)
 – *tenes* (Doubleday, 1847)
agle (Hewitson, 1853)
 – *furva* (Stichel, 1911)
 – *menalcidas* (Seitz, 1913)
axenus (Hewitson, 1876) **n. comb.**
 – *acervata* (Seitz, 1932)
 – *perrupta* (Seitz, 1932)
 – *roeberi* (Seitz, 1932)
 – *ochrophlegma* (Stichel, 1911) **n. stat.**
 – *dissimilis* (Hayward, 1949)
 – *distincta* (Hayward, 1949)
 – *leucomelaina* (Breyer, 1930)
bifasciata (Mengel, 1902) **n. comb.**
 – *mabildei* (Röber, 1903)
calyce (C. & R. Felder, 1862)
 – *brennus* (Stichel, 1910) **n. syn.**
 – *manius* (Stichel, 1910)
 – *mesoleucum* (Bates, 1868) **rev. syn.**
 – *pernambuco* Callaghan, 1999 **n. syn.**

Appendix D (continued)

- chaonia* (Hewitson, [1853])
 – *indivisa* Brévignon, 1998 **n. syn.**
dirca (Stichel, 1911)
ethelinda (Hewitson, 1870)
fenestrella (Lathy, 1932)
 – *cayennensis* (Brévignon & Gallard, 1992)
n. syn.
galena (Bates, 1868) **n. comb.**
gela (Hewitson, 1853)
 – *ferruginea* (Lathy, 1932) **n. syn.**
mycone (Hewitson, 1865) **stat. rev.**
nymphidioides (Butler, 1872)
 – *labdacus* (Godman and Salvin,
 1886) **rev. syn.**
ochra (Bates, 1868)
 – *sicyon* (Godman and Salvin, 1878)
n. syn.
orestessa Hübner [1819]
 – *arche* (Hewitson, 1865)
 – *cinerea* (Stichel, 1925)
 – *orestes* (Cramer, 1780)
 – *pseudomandana* (Röber, 1927)
palaeste (Hewitson, 1870)
 – *grande* (Godman, 1903)
 – *salvator* (Stichel, 1911) **n. syn.**
paulistina (Stichel, 1910) **n. stat.**
 – *enimanga* (Seitz, 1917) **n. syn.**
 – *pedronia* (Stichel, 1910) **n. syn.**
 – *velatum* (Stichel, 1914) **n. comb.,**
n. syn.
pittheus (Hoffmannsegg, 1818)
 – *cavifascia* (Butler, 1877)
 – *pelope* (Hübner, [1819])
 – *pelops* (Cramer, 1777)
 – *quinoni* (Weeks, 1906)
phliasus (Clerk, 1764)
 – *hewitsoni* (Rebel, 1901)
 – *phillone* (Godart, [1824])
 – *maravalica* (Seitz, 1913)
 – *velabrum* (Godman and
 Salvin, 1878)
regulus (Fabricius, [1793])
 – *atilius* (Stichel, 1925) **n. syn.**
 – *ingens* (Stichel, 1925)
soranus (Stoll, [1781])
sorane Hübner, [1819]
sylvarum (Bates, 1867)
tytia (Cramer, 1777)
 – *arctos* (Hewitson, [1853])
n. syn.
 – *ariadne* (Stichel, 1911) **n. syn.**
 – *eroe* (Hewitson, 1865)
 – *gnosis* (Boisduval, 1836)
victrix (Rebel, 1901)

Appendix E

Subtribal and generic descriptions

Aricorina Hall & Harvey, n. subtribe (Fig. 1A–I, 3A–F, and 4A and F)

Type genus. *Aricoris* Westwood [1851].

Diagnosis. Aricorina is described as the most basal subtribe within the Nymphidiini to contain the genera *Aricoris* and *Ariconias* (described below). Within the Nymphidiini, only these two genera exhibit the symplesiomorphic state of possessing a spot at the base of both ventral hindwing cells Sc + R₁ and Rs (both are subsequently lost in the more derived groups). The synapomorphies defining the subtribe are as follows: (1) pronounced sexual dimorphism in the size of the proboscis, which is laterally enlarged in males; (2) a large dorsal indentation of the male genital uncus; and (3) asymmetrically positioned signa at the wall of the corpus bursae in the female genitalia (see Table 6).

Ariconias Hall & Harvey, n. gen (Fig. 1A, 3A, and 4A)

Type species. *Lemonias albinus* C. & R. Felder, 1861.

Etymology. The name is formed from the first part of *Aricoris* and the last part of *Lemonias*, in reference to the external similarity of *Ariconias* species to the species of those genera (*albinus* was formerly placed in *Audre* (= *Aricoris*) and *glaphyra* in *Lemonias*).

Description. MALE: forewing length 17–21 mm. *Wing shape:* both wings compact; forewing somewhat pointed, costa convex, distal margin slightly concave in cell M₃; hindwing angular, tornus pointed, small tail at end of cell Cu₂. *Venation:* as in *Aricoris* (see Stichel, 1910–1911), four forewing radial veins. *Dorsal surface:* ground color of both wings brown; three large white or orange marks in discal cell of each wing (fused in *albinus*), distal marks often divided, blue or white scaling at base of each wing; on forewing broad white or orange postdiscal band consists of vertical band between anal margin and vein Cu₁ and outwardly diagonal and distally displaced band between vein Cu₁ and costa, on hindwing a continuous broad white band; submarginal bands reduced to separate white spots, outer set absent on forewing, extensive orange between spots on hindwing (and forewing in *glaphyra*); forewing fringe brown with white elements in cells Cu₂, M₃, M₁, and R₄₊₅, hindwing fringe brown with white elements in each cell space. *Ventral surface:* differs from dorsal surface in following ways: ground color of both wings brown and orange, three white spots beyond discal cell end and three white spots at base of cell Cu₂ on forewing, three white spots along basal half of costa on hindwing, postdiscal band on hindwing better defined, submarginal markings more prominent with outer elements present largely in alternating cell spaces on forewing, black pupils in spots of hindwing tornus and

apex. *Head*: labial palpi white on ventral surface, brown on dorsal surface, second and third segments elongate; proboscis enlarged with downwardly curved lateral margins (most prominent in *albinus*), eyes brown and bare, white scaling at margins; frons brown and white striped; antennal length approximately 70% of forewing length, segments brown with white scaling at base, nudum along inner ventral margin of shaft prominent and continuous and increasing in width toward clubs; clubs black, tips orange-brown. *Body*: thorax and abdomen whitish; eighth sternite medially desclerotized and produced into two posterior projections (extending substantially beyond pleural membrane in *glaphyra* only); all legs whitish, tarsus of foreleg unimerous, coxa of medium length for family, midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tibia and spines along inner margin of all tarsal segments. *Genitalia* (Fig. 3A): uncus rectangular with prominent indentation at middle of posterior dorsal margin, falces of average size and shape for family; vinculum a narrow and sinuate ribbon, slightly swollen medially, broadly desclerotized at junction with saccus, saccus short; aedeagus narrow and convex with pointed tip, opens broadly to right, cornutus absent (*albinus*) or a small sclerotized pad (*glaphyra*), simple strap-like pedicel joins aedeagus at midpoint; valvae elongate triangles with upturned and highly sclerotized tips (asymmetrical in *albinus*).

FEMALE: differs externally from male in the following ways: forewing length 19–23 mm; both wings more rounded; both wing surfaces paler, postdiscal bands broader and entirely white on forewing. *Head*: second and third palpal segments slightly more elongate; nudum extends broadly along entire inner ventral margin of antennae. *Body*: foreleg with spines at inner distal tip of tibia and tarsal segments 1–4. *Genitalia* (Fig. 4A): corpus bursae elongate, signa large spine-like invaginations with elongate extension along wall of corpus bursae, slightly asymmetrically positioned; ductus bursae sclerotized and laterally compressed in distal portion, membranous ductus seminalis exits ductus bursae dorsally within sclerotized region, central ostium bursae laterally compressed and well sclerotized, large sclerotized invagination between ostium and papillae anales with “hood” at posterior margin extending to connect with ostium.

Diagnosis. See Table 5 for list of generic synapomorphies.

Component species: See Appendix D for a synonymic checklist.

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