Systematic position of *Apodemia paucipuncta* (Riodinidae),
and a critical evaluation of the nymphidiine transtilla

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Abstract

Early stage and adult characters (morphology and behavior) indicated that the riodinid *Apodemia paucipuncta* had been erroneously placed in the genus *Apodemia* (Incertae Sedis, previously in tribe Emesini). To infer the systematic position of *paucipuncta*, we performed a cladistic analysis using 72 male morphology characters for 36 species placed in six genera. Our results show that (1) *Apodemia paucipuncta* is the sister species of *Adelotypa eudocia* and together they constitute a new genus in the tribe Nymphidiini, *Hallonympha*, new genus; (2) species of *Adelotypa* closely related to *Catocyclotis* and *Nymphidium* also constitute a new genus, *Harveyope*, new genus; and (3) sampled species of the Nymphidiini genera *Adelotypa* and *Calospila* do not form monophyletic groups, indicating that these genera are in need of revision. This study furthers our understanding of character definition and homology of the male valva and transtilla within the Nymphidiini, and provides a baseline for future work on riodinid systematics.

Key words: *Adelotypa*, *Calospila*, transtilla, genitalia, *Hallonympha*, *Harveyope*, Nymphidiini

Introduction

Caterpillars of *Apodemia paucipuncta* Spitz (Riodinidae) possess four sets of ant-organs — structures that are involved in interactions with ants (DeVries et al. 2004). Three of these appear to be homologous with those found in the tribe Nymphidiini: vibratory papillae (unique to Nymphidiini), tentacle nectary organs (also in Eurybiini), and balloon setae (also in Helicopini, Charitini and Insertae Sedis; for illustrations see DeVries et al. 2004). In addition, the caterpillars of *A. paucipuncta* possess a novel myrmecophilous cervical gland previously unknown in Lepidoptera (DeVries et al. 2004). Although larval structures indicate that *A. paucipuncta* should be placed in Nymphidiini, they were insufficient to establish a generic placement for this species. The purpose of this investigation is to determine the generic placement of *A. paucipuncta* by using a phylogenetic analysis of adult morphology.

This study uses cladistic analysis to infer the systematic position of *A. paucipuncta* within the Nymphidiini. To this end we examined 72 characters derived from male morphology for 36 representative species. Our results form the phylogenetic basis for describing a new genus for *A. paucipuncta* and its closest relative, *Adelotypa eudocia* (Godman & Salvin). In addition, we describe a second new genus to accommodate five species of *Adelotypa* Warren closely related to *Catocyclotis* Stichel. An important component of our study was the reassessment of homologies in male genitalia, with particular regard to the nymphidiine transtilla.

Material and methods

Preparation of material and terminology

All structures were examined using an optical stereomicroscope with light and dark
field and magnification up to 130 X. Abdomens were prepared using a 10% solution of potassium hydroxide, and subsequently stored in glycerol. Pinned adults were used to examine head, thorax and wings. Nomenclature for genitalia follows Klots (1970), except for the term ‘aedeagus’ (= phallus) that follows the usage by Penz & DeVries (1999) for consistency.

Character sampling

This analysis focused on males because their genitalia usually constitute a richer source of characters than those of females (e.g., Penz & DeVries 1999, 2001, Hall & Harvey 2001, Hall & Harvey 2002, Kristensen 2003), and because male specimens are more readily available in collections it ensures a more complete data matrix. We recognize, however, that female characters provide important information for phylogeny reconstruction (e.g., Penz 1999), and such characters can eventually be incorporated when females of all species become available. For the present analysis, male morphology yielded 72 characters (181 character states). To gather character data, we performed a detailed comparative study of male genitalia (including species previously studied by us; e.g., Penz & DeVries 1999). This comparative study resulted in significant changes in the interpretation of valva morphology within Nymphidiini, which is detailed in the Results section and incorporated into the character list.

Appendix 1 contains 62 characters of the male genitalia, including the eighth sternite (Stn8) (43 binary, 19 multistate), seven wing pattern characters (five binary, two multistate), and three characters from the head (two binary, one multistate). Some of these characters were used in their original formulation whereas others were re-evaluated from previous nymphidiine studies (Harvey 1987, Penz & DeVries 1999, Hall & Harvey 2002). The character matrix used in the analysis is in Appendix 2.

Taxon sampling

We examined males of 36 species among six genera selected on the basis of their taxonomic, phylogenetic or morphological affinities to A. paucipuncta (Table 1, Fig. 1). We did not sample taxa considered distantly related or too divergent from A. paucipuncta based on previous studies (Stichel 1910, 1930, Harvey 1987, DeVries 1997, Hall & Harvey 2002) and our interpretation of morphology. We used Callaghan & Lamas (2004) to estimate the total number of species in the six included genera. Criteria for taxon sampling were as follows:

Outgroups: The Emesini was previously considered an ideal outgroup for analyses focusing on Nymphidiini because it is external yet closely related to this tribe (Hall & Harvey 2002). However, recently the tribal name “Emesini” was abandoned, and genera included in this tribe are now considered Incertae Sedis (Callaghan & Lamas 2004). Within Incertae Sedis we sampled three species of Apodemia C. Felder & R. Felder (paucipuncta was originally classified in Apodemia) and two of Calydna (caterpillars of C. sturnula (Geyer) possess balloon setae; Hall et al. 2004, PJD and CMP pers. obs.).
<table>
<thead>
<tr>
<th>Genus and species</th>
<th>Locality data</th>
<th>source</th>
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<tbody>
<tr>
<td><strong>Apodemia C. Felder &amp; R. Felder</strong></td>
<td></td>
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<tr>
<td><em>mormo</em> (C. Felder &amp; R. Felder)</td>
<td>1 m, USA, California, San Diego, 11.Mar.1908*; 1 f USA, California, no date*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>palmerii</em> (Edwards)</td>
<td>1 m, USA, Arizona, no date*; 1 f, USA, California, San Diego, 9.Sep.1959*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>cythera</em> (Edwards)</td>
<td>1 m, USA, Colorado, Larimer, 19, Jul.1954*</td>
<td></td>
</tr>
<tr>
<td><strong>Calydna Doubleday</strong></td>
<td></td>
<td></td>
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<tr>
<td><em>thersander</em> (Stoll)</td>
<td>1 m, Brazil, Pará, Obidos, no date*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>sturnula</em> (Geyer)</td>
<td>1 m, Mexico, Yucatán, 9.Sep.1957*</td>
<td>MPM</td>
</tr>
<tr>
<td><strong>Adelotypa Warren</strong></td>
<td></td>
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<tr>
<td><em>bolina</em> (Butler)</td>
<td>1 m, no data*</td>
<td>MPM</td>
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<tr>
<td><em>penthea</em> (Cramer)</td>
<td>1 m, Brazil São Paulo?, Jun.1928*; 1 f, Brazil, Manicoré, Rio Madeira, no date*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>zerna</em> (Hewitson)</td>
<td>1 m Brazil, Rio de Janeiro, Petropolis, Independencia, 2.Aug.1939*; 1 m, Brazil, Rio de Janeiro, Guapy, 20.Sep.1940; 1 f, Brazil, Rio de Janeiro, Gávea, 21.Feb.1954*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>glaucia</em> (Godman &amp; Salvin)</td>
<td>1 m, 1 f, Costa Rica, Puntarenas, Las Alturas, 5.Sep.1990* and 26.Dec.1990*</td>
<td>PJD</td>
</tr>
<tr>
<td><em>sejuncta</em> (Stichel)</td>
<td>1 m, Brazil, Santa Catarina, Nova Teutônia, Dec.1937*; 1 m, Brazil, Santa Catarina, 8.Aug.1935; Brazil, [Santa Catarina] Palmital (label writing unclear) 1936*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>tinea</em> (Bates)</td>
<td>1 m, Brazil, probably Santa Catarina, 1.May*; 1 m, Brazil, Rio de Janeiro, Independência, 17.Nov.1936</td>
<td>MPM</td>
</tr>
<tr>
<td><em>eudocia</em></td>
<td>2 m, 1 f, Mexico, Sonora, Hwy 16, 20 mi east of Rio Yaqui, “Pine Barrena” 5.Aug.1986**</td>
<td>LACM</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Genus and species</th>
<th>Locality data</th>
<th>source</th>
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<tbody>
<tr>
<td>huebneri (Butler)</td>
<td>1 m, 1 f, Ecuador, Sucumbios, Garza Cocha, 7.May.1993* and 24.May.1993*</td>
<td>PJD</td>
</tr>
<tr>
<td>amasis (Hewitson)</td>
<td>1 m, 1 f, Ecuador, Sucumbios, Garza Cocha, 18.Feb.1995* and 24.May.1993*</td>
<td>PJD</td>
</tr>
<tr>
<td>leucophaea (Hübner)</td>
<td>1 m, 1 f, Ecuador, Sucumbios, Garza Cocha, 9. Nov.1996* and 10.Nov.1996*; 1 m Brazil, Amazonas, São Paulo Olivença, no date*; 1 f, Brazil, Pará, Santarém, no date</td>
<td>PJD</td>
</tr>
<tr>
<td>balista (Hewitson)</td>
<td>1 m, Colombia, Amazonas, Rio Tacana, 26-31.Oct.1946*; 1 m, Northeastern Peru, no date</td>
<td>AMNH</td>
</tr>
<tr>
<td>Catocyclotis Stichel</td>
<td>1 m, Brazil, Barrera, 18.Oct.1955*; 1 m Brazil, Rio de Janeiro, Petrópolis, 4.Feb.1962*; 1 f, Brazil, Rio de Janeiro, Mundo Novo, 15.May.1940*</td>
<td>MPM</td>
</tr>
<tr>
<td>adelina (Butler)</td>
<td>1 m, Peru, Iquitos, Oct.1959*</td>
<td>MPM</td>
</tr>
<tr>
<td>apotheta (Bates)</td>
<td>1 m, Brazil, Rio de Janeiro, 20.Jun.1941*</td>
<td>MPM</td>
</tr>
<tr>
<td>rhodope (Hewitson)</td>
<td>1 m, Peru Iquitos, Nov.1959*</td>
<td>MPM</td>
</tr>
<tr>
<td>pirene (Godman)</td>
<td>1 m, Peru Iquitos, Nov.1959*</td>
<td>MPM</td>
</tr>
<tr>
<td>irene (Westwood)</td>
<td>1 m, label data not legible*</td>
<td>MPM</td>
</tr>
<tr>
<td>latona (Hewitson)</td>
<td>1 m, Brazil, São Luiz Teffé, Jun.1927*</td>
<td>MPM</td>
</tr>
<tr>
<td>emylius (Cramer)</td>
<td>1 m, 1 f, Ecuador, Sucumbios, Garza Cocha, 16 May.1994* and 5 Oct.1993*; 1 m Brazil Amazonas, São Paulo Olivença, no date</td>
<td>PJD</td>
</tr>
<tr>
<td>lucianus (Fabricius)</td>
<td>1 m, Brazil, Obidos, Aug.1928*; 1 f, Amazonas, Monte Cristo, Oct.1911*</td>
<td>MPM</td>
</tr>
</tbody>
</table>
**FIGURE 1.** Sample of studied species: *Adelotypa bolena* (type species), *Adelotypa amasis*, *Adelotypa sejuncta*, *Adelotypa eudocia*, *Adelotypa leucophaea*, *Adelotypa glauca*, *Calospila parthaon* (type species), *Catocyclotis adelina*, *Apodemia mormo*.

**Ingroup:** Larval biology and morphology demonstrated that *A. paucipuncta* should be classified in the Nymphidiini (DeVries et al. 2004). Because *A. paucipuncta* lacks

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**TABLE 1 (continued).**

<table>
<thead>
<tr>
<th>Genus and species</th>
<th>Locality data</th>
<th>source</th>
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<tbody>
<tr>
<td><em>Nymphidium</em> Fabricius</td>
<td></td>
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</tr>
<tr>
<td><em>azanoides</em> Butler</td>
<td>1 m, Panama, Darién, Cerro Pirre; 1 m, Costa Rica, Heredia, La Selva*; 1 f, Costa Rica, Heredia, La Selva*</td>
<td>PJD</td>
</tr>
<tr>
<td><em>mantus</em> (Cramer)</td>
<td>1 m, Ecuador, Sucumbios, Garza Cocha*; 1 m, Panama, Darién, Cerro Pirre*; 1 m, Panama, Panama, Barro Colorado Island*; 1 f, Panama, Panama, Pipeline Road*</td>
<td>PJD</td>
</tr>
<tr>
<td><em>cachrus</em> (Fabricius)</td>
<td>1 m, Peru, Satipo, no date*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>leucosia</em> (Hübner)</td>
<td>1 m, Brazil, Tapajós, Taperinha, no date*; 1 f, Brazil (?), Itinga, 7.Sep.1924*</td>
<td>MPM</td>
</tr>
<tr>
<td><em>balbinus</em> Staudinger</td>
<td>1 m, Colombia, Antioquia, Feb.1977*</td>
<td>PJD</td>
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</tbody>
</table>
diagnostic characters of the subtribes Aricorina, Lemoniadiina, and Theopina *sensu* Hall & Harvey (2002), we limited our sampling to their Nymphidiina (but see Discussion). (1) Fourteen of 29 *Adelotypa* species were sampled because the wing color pattern of some species closely resembles that of *A. paucipuncta* (e.g., *A. eudocia, A. tinea* (Bates); Fig. 1). At present, there are no published accounts on the larval biology of *Adelotypa* species. (2) Nine of 33 *Calospila* Geyer species were sampled because this genus has been considered closely related to *Adelotypa* (Stichel 1930). (3) Five of 35 *Nymphidium* Fabricius species were sampled because the known caterpillars of *Nymphidium* appear superficially similar to *A. paucipuncta* and possess balloon setae (DeVries et al. 2004 and references therein). (4) Two species of *Catocyclotis* were sampled because *C. adelina* caterpillars possess balloon setae and body spiracles in the same position as *paucipuncta* (DeVries et al. 2004, K. Nishida pers. com. and in prep.).

**Phylogenetic analysis**

For parsimony analysis we used PAUP 4.0b10 (Swofford 1998) with the following settings: all characters weighted equally, multistate characters unordered, and polymorphic characters treated as uncertain. Heuristic searches used a stepwise-addition routine with 300 tree-bissection-reconnection replicates starting from random trees. Bootstrap (Felsenstein 1985; 1000 replicates) and Bremer support indices (Bremer 1994) were calculated.

To select from equally parsimonious trees produced by the initial analysis, we used successive approximation weighting (SAW; Farris 1969) with characters re-weighted based on the maximum value of their rescaled consistency index (listed in Appendix 1). We used MacClade 4 (Maddison & Maddison 2000) to trace distribution of character state changes and the presence or absence of larval balloon setae. The complete list of character state changes is in Appendix 3.

**Results**

**Generic placement of Apodemia paucipuncta**

Parsimony analysis yielded six equally parsimonious trees. Figure 2 presents the strict consensus of these trees, and current generic classification for the 36 included species. The strict consensus tree shows that species fell into two groups. Successive approximation weighting (SAW) selected one of six initial trees (Fig. 3), which was used to trace character state changes (Farris 1969, 1983, Carpenter 1988).

Adult male characters grouped *A. paucipuncta* with Nymphidiini species, not with *Apodemia* or *Calydna* (Incertae Sedis), confirming findings based on early stages (DeVries et al. 2004). *Apodemia paucipuncta* and *Adelotypa eudocia* constitute sister taxa based on three character state changes (Fig. 3, Table 2 A), one of which is unique to these two species (in lateral view, uncus arched upward; 10:1). Four character state changes join the
paucipuncta-group with Nymphidium + Catocyclotis + zerna-group of Adelotypa, one of which is unique and universal (ventral process extended at base to form a sclerotized bridge, 48:0; Table 2 B). Of five character state changes that set the Nymphidium + Catocyclotis + zerna-group apart from the paucipuncta-group, one is unique and universal (lateral margins of tegumen thickened at edges of lateral fenestra to form ribs, 13:0; Table 2 C). These groups are also represented in the strict consensus tree (Fig. 2) with bootstrap and Bremer support values ranging from moderate to high (Fig. 3).

FIGURE 2. Strict consensus of six equally parsimonious trees from the analysis of 72 male characters (tree length=295, CI=0.3716, RI=0.7207, RC=0.2678, times hit=260 of 300). Generic classification prior to our analysis is indicated on the right. The position of A. cythera close to A. palmerii is of tangential interest inasmuch as this taxon is considered a subspecies of A. mormo (Callaghan & Lamas 2004).
FIGURE 3. One of six equally parsimonious trees, selected by successive approximation weighting and used to trace character state changes. Numbers above and below branches correspond to bootstrap and Bremer support values respectively. Letters correspond to groups listed in Table 2 and in the text.

**Status of Adelotypa**

The 14 representative species of *Adelotypa* sorted into four separate lineages (Fig. 3). *Adelotypa eudocia* paired with *Apodemia paucipuncta* (see above), *A. zerna* (Hewitson) and relatives constituted the sister group of *Catocyclotis*, and two other groups emerged within *Calospila*. Characters supporting these relationships are found in Table 2.
**TABLE 2.** Character state changes assigned to groups A–I in Figure 3. Abbreviations follow terminology in MacClade (Maddison & Maddison 2000): ho, homoplasious outside; hao, homoplasious above and outside; u, unique, changing above; uu, unique, unchanged above. Unique character state changes are in bold. Groups A and E refer to *Hallonympha* and *Harveyope*, respectively.

<table>
<thead>
<tr>
<th>group</th>
<th>character</th>
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</table>
| A     | 10:1 (uu): In lateral view, uncus arched upward  
29:6 (ho) Cornuti: multiple spines, short, thick, heavily sclerotized  
70:1 (ho) Second segment of labial palpus, long, erect hair-like scales projecting ventrally beyond the flattened scales present |
| B     | 27:1 (hao) Sculpturing of the vesica present  
42:1 (ha) Dorsal processes of valva, when separated, not extended to form a sclerotized bridge  
48:0 (uu) When dorsal process separated, ventral process of valva extended at base to form a sclerotized bridge  
59:1 (ho) Ventral bracing of valvae forming a bridge between the valvae |
| C     | 1:1 (ha) Location of 3rd abdominal spiracle: at midline  
3:0 (ho) Stn8 with terminal projection extending beyond edge of pleural membrane  
13:0 (uu) Lateral margins of tegumen thickened at edges of lateral fenestra to form ribs  
64:1 (hao) Number of spots in ventral hindwing cell Rs: 1  
66:1 (hao) Dorsal forewing, two marginal lines present (continuous or broken) |
| D     | 11:1 (ho) In lateral view, dorsal outline of tegumen completely straight  
20:0 (hao) Cuticular sculpturing prominent around subscaphium  
43:1 (hao) Dorsal process of valva more sclerotized distally  
60:1 (ho) In ventral view, anterior edge of valva projected  
69:1 (hao) Ventral hindwing of much lighter color than ventral forewing |
| E     | 18:1 (ha) Sclerotized plate of the subscaphium uniformly broad  
19:1 (ho) Sclerotized plate of the subscaphium extends to the end of subscaphium lobe  
26:2 (ho) In ventrolateral view, vinculum laterally widened below tegumen to form a blade that maintains its width towards saccus  
28:2 (u) Sculpturing of the vesica: enlarged spines  
29:1 (hao) Cornuti: a simple plate  
54:1 (hao) In ventrolateral view, proximal region of ventral process slightly raised, rounded  
70:1 (ho) Second segment of labial palpus, long, erect hair-like scales projecting ventrally beyond the flattened scales present |
| F     | 29:5 (ha) Cornuti: two spines  
40:1 (u) Ventral process of valva extends posteriorly beyond dorsal process  
62:0 (hao) In rear view, shape of the outline of the genital capsule (as formed by the tegumen + vinculum + saccus): []  
64:3 (ha) Number of spots in ventral hindwing cell Rs: 3 |
| G     | 14:1 (ho) Notch in the anterior margin of tegumen present  
15:0 (ho) Posterior end of subscaphium: one narrow lobe  
29:3 (ho) Cornuti: a plate with two terminal spines of uneven size |
Species in the *zerna*-group constitute the sister lineage to *Catocyclotis* based on five character state changes (Table 2 D), but seven changes set them apart from *Catocyclotis*, one of which is unique (sculpturing of the vesica: enlarged spines, 28:2; Table 2 E). *Adelotypa zerna* and close relatives can therefore be considered a well-defined species group within a larger assemblage including two other Nymphidiini genera. Bremer support for this group is moderate (Fig. 3). These results demonstrate the monophyly of the *zerna*-group outside of the remaining *Adelotypa*.

*Adelotypa bolena* (Butler) (type species of *Adelotypa*), *borsippa* (Hewitson) and *penthea* (Cramer) grouped with six species of *Calospila*, including *parthaon* (Dalman) (type species of *Calospila*). This grouping is supported by four character state changes, one of which is unique (ventral process of valva extends posteriorly beyond dorsal process, 40:1; Table 2 F). Bootstrap and Bremer support values for this group are low (Fig. 3).

The *amasis*-group is strongly supported by ten character state changes, one unique and universal (tip of aedeagus acutely pointed and short, 31:0; Table 2 G), and bootstrap and Bremer support values for this group are high (Fig. 3). The association of the *amasis*-group with *Calospila emylius* (Cramer) + *cilissa* (Hewitson) is supported by a single character state change (Table 2 H), and bootstrap and Bremer support values for this group are low (Fig. 3), underscoring the need for a phylogenetic reassessment of these groups.
Status of Calospila

The nine species representing Calospila appear to be paraphyletic with respect to two lineages of Adelotypa. These relationships are strongly supported by eight character state changes, including two that are unique (distal edges of vinculum fused to anterior edge of tegumen, remainder of vinculum connected to tegumen by weakly sclerotized tissue, 25:1; distal portion of ventral process of valva bent upward, 52:3; Table 2 I). Bootstrap and Bremer support values are moderately high (Fig. 3). This group is not fully resolved in the strict consensus tree because of the uncertain position of Calospila apotheta (Bates) (Fig. 2). In five of six equally parsimonious trees C. apotheta appeared as sister species to the amasis-group, but in one tree it was basal to the group including Calospila parthaon and Adelotypa bolena (trees not illustrated). Successive approximation weighting favored the latter topology (Fig. 3), but instability in tree topology points to the need for further examination of C. apotheta in the context of increased taxon and character sampling.

Descriptions of new genera

Our analysis demonstrated that paucipuncta and eudocia together constitute a monophyletic group well separated from the remaining Adelotypa. Placing the paucipuncta-group as a sister clade to any of the three Adelotypa clades in Fig. 3 produces a considerable increase in tree length (bolena + borsippa + penthea: 21 steps; amasis-group: 16 steps; zerna-group: seven steps). Based on the shortest, most parsimonious tree, we describe a new genus for eudocia and paucipuncta. Furthermore, subsuming the paucipuncta-group into any of the existing genera studied here (e.g., Nymphidium) would require an unwieldy number of generic changes.

Our results showed that the zerna-group is monophyletic, and that it does not group with other lineages of Adelotypa (Fig. 3). Placing the zerna-group as a sister lineage to bolena + borsippa + penthea or the amasis-group increases tree length by 30 and 18 steps, respectively. The zerna-group differs substantially from Catocyclotis in color pattern; in the former the forewing and hindwing are similar in dorsal coloration, whereas in the latter they differ (see character 68 in Appendices 1 and 2, and Figs. 1 and 5). Based on the shortest, most parsimonious tree and differences in color pattern, we describe a new genus for the zerna-group. Differences in wing coloration make the new genus easily recognizable from Catocyclotis.

Hallonympha Penz & DeVries, NEW GENUS

Type species: Apodemia paucipuncta Spitz, 1930
Description (Fig. 4)

Character state changes from our analysis are indicated by numbers in parentheses. **Head**: predominantly brown. Frons brown, bordered in white and covered mostly with long hair-like scales projecting anteriorly. Head apex with long scales projecting anteriorly. Second segment of labial palpus laterally white (*paucipuncta*) to brown + white (*eudocia*), with long hair-like scales projecting ventrally (character 70:1); first and third segments brown. Antenna brown with white rings, club orange at tip. **Body**: dorsal body scales brown, ventral body and leg scales silvery beige (*paucipuncta*) to brown (*eudocia*). **Wings**: FW length 10–11 mm (n=7). Sexes similar. See Fig. 4 for wing shape, venation, and location of spots. **Dorsal wing color pattern**: brown with darker brown spots contained inside cells, and a band across the distal edge of both FW and HW discal cells. Dark brown spots with neighboring bright white spots (*paucipuncta*), or lacking such white spots (*eudocia*). FW and HW similar in color and pattern. **Ventral wing color pattern**: slightly paler than dorsal surface. Brown spots with neighboring bright white spots (*paucipuncta*), or bordered dirty white (*eudocia*). **Male terminalia**: Sternite 8 not extended posteriorly beyond the pleural membrane. Genitalic capsule short and compact. Uncus arched dorsally (character 10:1), small central indentation vestigial or absent. Sclerotized plate of subscaphium broad, diamond-shaped. Gnathos sickle-shaped with a blunt tip. Vinculum not continuous through anterior edge of tegumen. Aedeagus (=phallus) with a long, acute tip. Coecum penis small. Cornuti comprising multiple short, thick and heavily sclerotized spines (character 29:6). Valvae clearly divided into two processes; dorsal processes separated laterally, ventral processes forming a bridge above aedeagus. Tip of ventral process reduced and fused to bridge (*paucipuncta*), or reduced and not visible (*eudocia*). Lateral, rounded extension of ventral process protruding outward to form a small flap.

Remarks on female genitalia

We observed the following female genitalic characters in *paucipuncta* (Fig. 4) and *eudocia*: (1) antrum broad and well-sclerotized; (2) ductus bursa with a mildly sclerotized, internally spined enlargement anterior to corpus bursa in *paucipuncta*, ductus bursa simple in *eudocia*; (3) corpus bursa moderately elongated; (4) *paucipuncta* with signa symmetrically placed in corpus bursa, asymmetrically positioned in *eudocia*. Differences in female genitalic morphology between *paucipuncta* and *eudocia* appear to be comparable to those found between *Catocyclotis aemulius* (Fabricius) and *adelina* (Butler) (see illustrations in Penz & DeVries 2004).

Natural history

*Hallonympha paucipuncta* is an ant-associated, polyphagous species endemic to the Brazilian cerrado (DeVries et al. 2004 and references therein). The larvae have balloon setae, vibratory papillae, and tentacle nectary organs similar to other Nymphidiini
(DeVries et al. 2004), but are unique within Riodinidae by possessing a cervical gland used in myrmecophily. The A3–7 spiracles of *paucipuncta* are located dorsally, a character state that is also present in *Catocyclotis adelina*.

**FIGURE 4.** *Hallonympha paucipuncta*: adult male in dorsal and ventral views; wing scheme showing venation and location of dark (heavy stippling) and white markings (open); male genitalia in lateral and ventral views; male sternum 8 (note extended membranous area with a small, ventrolateral cluster of setae); female genitalia (inset: ventral view of ostium bursa). Scale bars: 1 mm.
The relationships between *eudocia* and *paucipuncta* suggest that the larva of *eudocia* (currently unknown) may also possess balloon setae, dorsal spiracles and a cervical gland. In Mexico, *eudocia* inhabits a habitat similar to that of *paucipuncta* (A. Warren pers. com.). Natural history studies of this species will be of much interest.

**Etymology**

We name this new genus after J. P. W. Hall in recognition for his contribution to riodinid systematics.

**Species in the genus**

Based on our phylogenetic analysis (Fig. 3) and generic definition (above), we place the following species in *Hallonympha*:

- *Hallonympha paucipuncta* (Spitz, 1930) [type species], **new combination**
- *Hallonympha eudocia* (Godman & Salvin, 1897), **new combination**

**Harveyope Penz & DeVries, NEW GENUS**

Type species: *Lemonias zerna* Hewitson, 1872

**Description (Fig. 5)**

Character state changes from our analysis are indicated by numbers in parentheses.

Head: predominantly brown. Frons varying from brown (*zerna*) to mostly white (*glauca* (Godman & Salvin)); white marking at center ranging from small (e.g., *zerna*) to prominent (*glauca*), bordered in white or dull yellow (*densemaculata* (Hewitson)). Frons mostly covered with long hair-like scales projecting anteriorly. Head apex with long scales projecting anteriorly. Second segment of labial palpus laterally white or dull yellow (*densemaculata*), with long hair-like scales projecting ventrally; first and third segments brown. Antenna brown with white rings, club orange at tip. Body: dorsal body scales brown, ventral body and leg scales vary from white (*glauca*) to light brown (*densemaculata*). Wings: FW length 11–15 mm (n=15). Sexes similar. See Fig. 5 for wing shape, venation, and location of spots and stripes. Dorsal wing color pattern: brown with darker brown spots ranging from conspicuous (*sejuncta* (Stichel), *tinea*) to faded (e.g., *zerna*), to nearly completely obliterated by colored scales (*glauca*). Green, blue or yellow lines crossing cell boundaries ranging from broad (*glauca*), to thin (*zerna, densemaculata*), or absent (*sejuncta, tinea*). Ventral wing color pattern: FW slightly paler than dorsal surface, brown spots always conspicuous, bordered or encircled with white to dull yellow scales. HW varies from being similar in color to ventral FW (*tinea, densemaculata*) to predominantly white with brown spots (*zerna, glauca*). Male terminalia: Sternite 8 extending posteriorly beyond the pleural membrane to form symmetrical, rounded, pointed or squared projections. Genitalic capsule varies from

Remarks on female genitalia

The single female of the type species available to us had a broken abdomen, preventing examination of the genitalia. From examination of the female genitalia of glauca (Fig. 5) and tinea, we note the following: (1) antrum narrow and sclerotized in both species (but less sclerotized in tinea), long in glauca and short in tinea; (2) in glauca ductus bursa with a lightly sclerotized, internally spined enlargement before corpus bursa that seems identical to that found in Hallonympha paucipuncta (this structure is absent in tinea); (3) corpus bursa highly elongated; (4) four signa in glauca, two in tinea. Differences in female genitalic morphology between glauca and tinea appear to be comparable to that in Hallonympha (this study) and Catocyclotis (Penz & DeVries 2004).

Natural history

Collectively, species in this genus range from Nicaragua south to Costa Rica, and in South America from Venezuela, Colombia, Peru and Brazil. Early stages of Harveyope species are unknown or undescribed. DeVries (1997) reported natural history observations for glauca and densemaculata.

Etymology

We name this new genus for D. J. Harvey in recognition for his contribution to riodinid systematics.

Species in the genus

Based on our phylogenetic analysis (Fig. 3) and generic definition (above), we transfer the following species from Adelotypa to Harveyope:

Harveyope zerna (Hewiston, 1872) [type species], **new combination**
Harveyope glauca (Godman & Salvin, 1886), **new combination**
Harveyope densemaculata (Hewitson, 1870), **new combination**
Harveyope sejuncta (Stichel, 1910), **new combination**
Harveyope tinea (Bates, 1868), **new combination**
FIGURE 5. *Harveyope zerna*: adult male in dorsal and ventral views; wing scheme showing venation and location of dark (heavy stippling), faint (light stippling) and iridescent markings (open); male genitalia in lateral and ventral views, male sternum 8 (note projections). *Harveyope glauca*: female genitalia (inset: ventral view of ostium bursa). Scale bars: 1 mm.

*Other species possibly included in Harveyope*

We did not examine *Adelotypa curulis* (Hewitson, 1874) or *Adelotypa argiella* (Bates, 1868). The male holotype of *curulis* (in the Natural History Museum, London; illustrated in D’Abrera 1994) appears similar to *H. glauca*. The specimen illustrated in D’Abrera
(1994) as argiella resembles H. tinea. The possible phylogenetic relatedness among these taxa should be verified by future work.

**Comparative morphology of the nymphidiine valva and transtilla**

*Regions of the valva*

Based on the dytrisian groundplan (Kristensen 2004 and references therein), we interpret the valva of species in our ingroup as having two recognizable regions that slightly twist around each other: (1) an outer region curved downward and extended towards the ventral portion of the valva, and (2) an inner region curved upward and extended towards the dorsal portion of the valva (Fig. 6). Both ventral and dorsal regions bear a row of setae that can be used to help recognize their spatial orientation and degree of morphological modification. In the ingroup these regions are not sclerotized in their entirety, and a fissure is visible laterally on the valva. The valva regions can diverge from each other and give rise to distinguishable ventral and dorsal processes (e.g., *Calospila lucianus* (Fabricius) and *Harveyope zerna*, Fig. 6), or can merge to produce a simple tube (e.g., *Adelotypa bolena*, Fig. 6). The ventral and dorsal processes vary in length, width, degree of sclerotization, spatial orientation, and ornamentation. Illustrations in Fig. 6 will facilitate their identification and comparison. We stress that only through unequivocal identification of the valva processes as a frame of reference can meaningful comparisons across species be made. The following subsection illustrates this particularly well.

*Fusion of the valvae and the nymphidiine transtilla*

In Nymphidiini, the fusion of the valvae can be described as pertaining to two general categories of morphological modifications: (1) the longitudinal fusion of the valvae, or (2) the development of an outgrowth that forms a bridge between the valvae.

Either the dorsal or the ventral processes of the valva can be fused along their length, and produce unambiguously distinct morphological patterns. For example, the valvae of *Calospila parthaon* and *Adelotypa bolena* (Fig. 6, 18) are fused dorsally along a large portion of their length by cuticle that is less sclerotized than the remainder of the valvae. In contrast, in species of *Synargis* (e.g., see *S. abaris* illustrated in Penz & DeVries 1999) the valvae are heavily fused ventrally along most of their length. Lateral movement of the valvae is compromised in both cases, and the dorsal or ventral fusions of the valvae likely have distinct effects on the mechanics of copulation. The difference in topological origin suggests that the dorsal and ventral fusions of the valvae evolved independently within Nymphidiini.

When the entire valvae are sufficiently separated from each other laterally, either the dorsal or the ventral processes may produce an outgrowth that bridges the two valvae above the aedeagus. Here the resulting morphological patterns can be misleadingly similar. A case in point is to compare the bridge formed by the dorsal process of the valva
FIGURE 6. Male genitalia in ventrolateral view. Outlines of the genitalic capsules are provided to show the tilting angle (approximately the same for all species). The dorsal process of the valva is shaded in gray to facilitate comparison across species. Note that sclerotized bridges between the valvae have different origins: they arise from the dorsal process in *lucianus* but from the ventral process in *paucipuncta* and *zerna*. The bridge is absent in *bolena* and *parthaon*, where the valvae are in close proximity to each other dorsally.
in *Calospila lucianus* with that formed by the ventral process in *Harveyope zerna* (Fig. 6). Consideration of the different topological origin of these bridges suggests that they are not homologous (see Discussion). For this reason we used separate characters (42 and 48) to address the ‘dorsal’ and ‘ventral’ bridges identified in this study (Appendix 1).

In sum, within Nymphidiini we identified four distinct morphological modifications that limit the lateral movement of the valvae. From direct, comparative observation and careful consideration of published studies (e.g., Hall & Harvey 2002), we concluded that three of these modifications have been collectively called transtilla: the dorsal fusion of the valvae, plus the two different sclerotized bridges between the valvae described above. We therefore recommend that the term transtilla be replaced by language that precisely defines the structures found within Nymphidiini (e.g., characters 41, 42 and 48; Appendix 1). In this way information potentially useful for phylogeny reconstruction can be more rigorously assessed.

Discussion

*Monophyly of Adelotypa and Calospila*

Our initial quest for the generic position of *Hallonympha paucipuncta* became a broader venture than anticipated. Our preliminary intuition suggested that *paucipuncta* was a member of *Adelotypa*. However, we found that neither *Adelotypa* nor its relative *Calospila* were monophyletic. Although the purpose of our analysis was to provide a generic placement for *paucipuncta*, we also found it necessary to re-define male characters relevant to phylogenetic studies of Nymphidiini and to describe two new genera.

In the most recent attempt to sort *Adelotypa* into species groups, Stichel (1930) divided the genus (as *Echenais*) into four groups (Table 3): aristiformes (15 species), densemaculatiformes (5 species), pentheiformes (4 species), and sentiformes (5 species). Our analysis (Figure 3) does not fully confirm Stichel’s classification, as noted below:

1. **aristiformes**: we found that this does not constitute a natural group, but includes members of at least four lineages — the *amasis*-group, part of *Harveyope, Hallonympha eudocia*, and the notably divergent *lampros* that seems misplaced in *Adelotypa* and almost certainly represents a distinct genus;

2. **densemaculatiformes**: this group contains three species in *Harveyope*, plus *curulis* and *melitta* (not examined by us). Stichel’s densemaculatiformes is therefore paraphyletic with respect to *sejuncta* and *tinea*;

3. **penthiformes**: *Adelotypa penthea* was the only species within pentheiformes sampled here, and it grouped with *bolena* and *borsippa*. Judging by the large number of character state changes accumulated by *penthea* (Appendix 3), this species seems problematic and warrants further study;

4. **sentiformes**: the type species of *Adelotypa (bolena)* plus *borsippa* were included by Stichel in the sentiformes, and in our analysis *bolena* and *borsippa* emerged as sister
taxa, confirming Stichel’s grouping. The nominate species of this group, *senta*, was placed in the genus *Protonymphidia* (*Nymphidiini:Theopeina*) by Hall (2000). In agreement with Penz & DeVries (2004), *elpinice* Godman was moved to *Catocyclotis* by Callaghan & Lamas (2004).

Although our analysis did not include the whole of *Adelotypa*, it confirmed the suggestion that the genus is polyphyletic (Hall 2000), thus establishing a framework for future studies.

The genus *Calospila* is thought to include 33 species (Callaghan & Lamas 2004), and acknowledged to be in need of revision (DeVries 1997). We examined a small fraction of *Calospila*, but all species grouped with various *Adelotypa* in our trees (Fig. 2 and 3). While our sample size is insufficient to justify taxonomic changes, our study provides evidence that *Calospila* is not monophyletic. Finally, based on our analysis it is evident that *Adelotypa* and *Calospila* have intertwined evolutionary histories and that future phylogenetic studies should examine species representing both genera.

**TABLE 3.** Species groups proposed by Stichel (1910) for the genus *Adelotypa* (as *Echenais*), including the author and year of description and type locality of each species. A revised group is proposed after our analysis, and an inferred group is suggested for some species not available for examination based on published illustrations. Dissection and examination of *A. lampros* (Bates) demonstrated that this species is highly divergent from other *Adelotypa*, and it was therefore excluded from our analysis (unpublished obs.; a forthcoming manuscript will address this issue). Note that Callaghan & Lamas (2004) synonymized *torquata* Stichel with *annulifera* (Godman) and also provided an updated name for *alector* (Butler), now *violacea*.

<table>
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<th>Type locality</th>
<th>Revised group</th>
<th>Inferred group</th>
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<td><em>amasis</em>-group</td>
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<td><em>alector</em> Butler, 1867 (now <em>violacea</em>)</td>
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<td><em>amasis</em>-group</td>
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<td><em>amasis</em> Hewitson, 1870</td>
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<td><em>amasis</em>-group</td>
<td></td>
</tr>
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<td><em>leucocyana</em> Geyer, 1837</td>
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<td></td>
<td><em>amasis</em>-group</td>
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<td><em>amasis</em>-group</td>
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<td>Harveyope</td>
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<td><em>sejuncta</em> Stichel, 1910</td>
<td>Nova Friburgo, Brazil</td>
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<td><em>maclea</em> Schaus, 1902</td>
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.....continued
TABLE 3 (continued).

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<th>Inferred group</th>
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<td>tinea Bates, 1868</td>
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<td>carulis Hewitson, 1874</td>
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<td>zerna Hewitson, 1872</td>
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<td>“Calospila” b</td>
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<td>petronia Schaus, 1913</td>
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<td>torquata Stichel, 1916</td>
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<td></td>
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<tr>
<td>borsippa Hewitson, 1863</td>
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<td>“Calospila” b</td>
<td></td>
</tr>
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<td>borsippina Butler, 1867</td>
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<tr>
<td>elpinice Godman, 1903 c</td>
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<tr>
<td>bolenia Butler, 1867</td>
<td>Brasilia (=Brazil)</td>
<td>“Calospila” b</td>
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</tbody>
</table>

a currently in the genus Protonymphidia (Hall 2000).
b based strictly on our analysis. Additional Nymphidiini genera are needed to verify these suggestions.
c currently in the genus Catocyclotis (Penz & DeVries 2004, Callaghan & Lamas 2004).

Tracing characters of special interest

Here we illustrate characters of special interest traced onto the SAW tree (Fig. 3). A complete list of character state changes for all branches of this tree is provided in Appendix 3. The aim of the discussion below is to complement the characters listed in Table 2 that define Hallonympha and Harveyope, and to summarize our viewpoint on particular characters currently used in the systematics of Nymphidiini.

Character 1 (Fig. 7). Location of 3rd abdominal spiracle [in male adult]: above midline (0), at midline (1), below midline (2).

The original formulation of this character (Harvey 1987) included two character states: dorsal (closer to tergite than sternite), and ventral (closer to sternite than tergite).
FIGURE 7. Changes for character 1 traced onto the SAW tree.
The latter character state was considered diagnostic of, and universal to Nymphidiini (as defined by Harvey 1987), and correlated with the ventral position of larval spiracles on A3–7.

We found scoring the position of the 3rd abdominal spiracle was not completely straightforward. Our measurements indicated that it is located clearly above or below the midline in some species, but in others it is located at midline (Fig. 7). In our sample most of the variation in this character was confined to the group including *Nymphidium*, *Catocyclotis* and *Harveyope*, and the A3 spiracle is dorsal in *Hallonympha* and three of five species of *Harveyope*. Of further interest is that in the larva of *Catocyclotis adelina* the A3–7 spiracles are dorsal (DeVries et al. 2004), yet the adult A3 spiracle position does not seem to correspond with that of the larva. In sum, the variation in spiracle position strongly suggests that comparative measurements of many more species are needed to improve our understanding of this character and its ontogenetic correlates.

**Character 3** (Fig. 8). Stn8 with terminal projection extending beyond edge of pleural membrane (0), devoid of such projection (1); and

**Character 4** (Fig. 8). Stn8: simple, not divided (0), divided into two symmetrical projections (1), divided into asymmetrical projections (2).

Harvey (1987) defined his Lemoniini based on the presence of ‘bifurcated rami.’ Due to its highly diverse morphology and clear possession by several taxa of Harvey’s Nymphidiini, this structure was reinterpreted by Penz & DeVries (1999) who used ten characters to describe the range of variation in 15 genera. Subsequently Hall & Harvey (2002) used two characters to describe variation in the ‘bifurcated rami’ in an analysis including 11 species in 11 genera, and suggested that this structure probably evolved multiple times within Nymphidiini.

Our observations suggest that abdominal projections seem to be extraordinarily plastic (Penz & DeVries 1999, this study). In the context of out- and ingroups analyzed here, abdominal projections have been lost in *apotheta* and *lucianus* (Fig. 8), while both simple projections in *bolena + borsippa* and the *amasis*-group, and the asymmetrical projections of *Nymphidium* appear to be derived from ancestral divided, symmetrical projections (i.e., bifurcated rami *sensu* Harvey). These patterns suggest that these structures might evolve in any given direction. Even with our limited taxon sampling it seems evident that morphological divergence is unevenly distributed on the tree, and that some groups (e.g., *amasis*-group) are less variable than others (e.g., *Catocyclotis*, see illustrations in Penz & DeVries 2004). Although the projections of the last abdominal sternite may be useful for species level associations, marked differences in morphology, in concert with apparently uneven rates of divergence, may limit their utility in higher-level classification (Penz & DeVries 1999, Hall & Harvey 2001, 2002).
FIGURE 8. Changes for characters 3 and 4 traced onto the SAW tree.

Character 24 (Fig. 9). Vinculum: continuous through entire anterior edge of tegumen (0), not continuous through entire anterior edge of tegumen (1).

This character was first defined by Penz & DeVries (1999) and used to group Nymphidium and Theope. Hall & Harvey (2002) later termed it ‘incomplete vinculum’ and used it to define their Theopeina, with the caveat that Nymphidium and Catocyclotis (in their Nymphidiina) also possess an incomplete vinculum. Here we show that character state 24:1 is a synapomorphy for Hallonympha + Nymphidium + Catocyclotis + Harveyope and it also appears in the distant Apodemia mormo (C. Felder & R. Felder), A. palmerii (Edwards) and A. cythera (Edwards) (plus A. walkeri Godman & Salvin and A. nais (Edwards), not included in our analysis). This character state is therefore more
ubiquitous than recognized previously, and its value for subtribal classification requires reassessment through analysis of a broader range of taxa than presently available.
Character 29 (Fig. 9). Cornuti: absent (0); a simple plate (1); a plate with one terminal spine (2); a plate with two terminal spines of uneven size (3); a plate with multiple terminal spines of approximately even size (4); two spines (5); multiple spines, short, thick, heavily sclerotized (6); multiple spines, long, thin, lightly sclerotized (7).

Cornuti were highly variable within the species sampled here; we identified seven character states. Tracing these onto the tree illustrates that while it is conserved in certain taxa (e.g., amasis-group, lucianus and emylius + cylissa) it can be variable within others (e.g., Harveyope, Catocyclotis). Furthermore, except for Harveyope where a ‘plate with
multiple spines’ seems to have arisen from a ‘spineless plate,’ none of the other character state changes represent intuitive morphological transitions. In sum, although the cornuti can provide phylogenetic information useful for some species-level groupings, high plasticity may limit their utility for higher-level groupings within Nymphidiini.

**Character 39** (Fig. 10). Valva: inner and outer regions forming dorsal and ventral processes that are visibly separated (0); inner and outer regions merging to form a single piece (1); and

**Character 40** (Fig. 10). Dorsal process of valva extends posteriorly beyond ventral process (0), ventral process extends posteriorly beyond dorsal process (1).

When considered together, characters 39 and 40 can be used to propose a hypothesis about the evolution of valva morphology in *Adelotypa bolena* and *borsippa* and *Calospila penthea* and *pirene* (Godman). The valva of these species can be described as a laterally compressed tube that terminates in a single terminal point. Both rows of setae that serve as landmarks of the dorsal and ventral processes converge toward this point (39:1 above; Fig. 20).

However, due to the tube-like configuration found in *bolena, borsippa, penthea* and *pirene*, it was not possible for us to determine a priori if the valva point originated from the dorsal (40:0) or the ventral process (40:1). These species were thus scored ‘uncertain’ (‘?’) for character 40 (Appendix 2).

Despite being scored as ‘uncertain’ for character 40, *bolena, borsippa, penthea* and *pirene* fell within a species group where the ventral process of the valva extends posteriorly beyond the dorsal process (40:1; Fig. 10). Thus, we hypothesize that the dorsal process is reduced in these species, and that the terminal point of their valva corresponds to the ventral process. The combined information from characters 39 and 40 appear to provide a means for understanding morphological evolution within one species lineage in this paper.

**Character 41** (Fig. 11). Valva: dorsal processes closely adjacent to each other, fused or nearly so (0); separated (1); and

**Character 48** (Fig. 11). Valva, when dorsal process separated: ventral process extended to form a sclerotized bridge (i.e., ventral bridge) (0); not extended to form a sclerotized bridge (1).

In some riodinid species where the entire valvae are sufficiently separated laterally (41:1), sclerotized bridges may join them above the aedeagus (48:0). Character state 48:0 clearly groups the new genera *Hallonympha* and *Harveyope* with *Catocyclotis* and *Nymphidium*, and the ‘ventral’ bridge present in species of these genera should not be confused with that produced by the dorsal process of the valva (42:0, state changes not illustrated), or with the dorsal fusion of the valvae (41:0).
Character 58 (Fig. 12). In ventral view, rounded extension of the outer region of the valva: protruding outward to form a ‘flap’ (0), not protruding outward (1).

Excepting eudocia, this ‘flap’ (Fig. 20) was present in all other species of Hallonympha, Nymphidium, Catocyclotis and Harveyope examined here. Because it is easily recognized and scored, and seems consistent within this group of genera (additional Nymphidium species need to be examined for confirmation), we believe this character may be useful and highly informative for phylogenetic studies of Nymphidiini.

Character 60 (Fig. 12). In ventral view, anterior edge of valvae straight (0), projected (1).
FIGURE 12. Changes for characters 58 and 60 traced onto the SAW tree.

This is one of the characters setting Harveyope and Catocyclotis (60:1, Fig. 20) apart from Hallonympha and other genera (60:0). In our analysis, although highly consistent within the ingroup, this character also occurs in the more distantly related outgroups, illustrating the difficulty in finding unique, universal characters to support genus-level relationships within Riodinidae.

Character 63 (Fig. 13). Number of spots in ventral hindwing cell Sc+R1: none (0), 1 (1), 2 (2), 3 (3); and

Character 64 (Fig. 13). Number of spots in ventral hindwing cell Rs: none (0), 1 (1), 2 (2), 3 (3).
Characters 63 and 64 were adapted from Hall & Harvey (2002). Excepting _Nymphidium_, the number of spots in the ventral hindwing cell Sc+R1 appeared consistent across species (plesiomorphic in 2 of our taxa) and their position inside the cell varied among taxa. In contrast, the pattern of spots in the neighboring cell Rs was much more variable both in number and position (not illustrated). Based on the study by Hall & Harvey (2002) and tracing patterns of characters 63 and 64 (Fig. 13), we speculate that the ‘presence of wing spots’ may constitute an ancestral condition within Nymphidiini. In a way similar to Schwanwitsch’s nymphalid groundplan (see Nijhout 1991), it is possible that a ‘spotted’ configuration may contribute the pattern elements from which others have arisen.
FIGURE 14. Changes for characters 70 and 71 traced onto the SAW tree.

**Character 70** (Fig. 14). *Second segment of labial palpus, long, erect hair-like scales projecting ventrally beyond the flattened scales: absent (0), present (1); and*

**Character 71** (Fig. 14). *Frons scales: mixed broad and thin, converging from sides to midline (0); thin scales more prominent and long, erect (1).*

The presence of projected hair-like scales in the palpi (70:1, homoplasious in our tree), and the long, projected scales on the frons (71:1, plesiomorphic in our tree) are shared by *Hallonympha* and *Harveyope*. Although other characters provided evidence for separating these two genera (Table 2), we note that head morphology provides potential evidence to group them. In the context of our taxon sampling regime, placing *Hallonympha* as sister to *Harveyope* increases tree length by six steps. Nonetheless, the usefulness of characters 70
and 71 should be revisited in the context of a more comprehensive study.

The transtilla and the classification of Nymphidiini

The term transtilla has been used to represent structures present in several groups of Lepidoptera that clearly have multiple origins, such as a transverse bar originating from the diaphragma or basal extensions of the valvae (Klots 1970, Kristensen 2004). Kristensen (2004) noted that this structure constitutes a functional unit that is not part of the Lepidoptera genitalic groundplan, which explains the evolution of multiple “transtillas” within the order. Within Nymphidiini we find that there are three recognizable “transtillas” that are neither part of the diaphragma, nor do they arise from the base of the valva (see Results and Fig. 6).

We believe previous studies of Nymphiniini have employed an overly inclusive character definition for the transtilla (e.g., Penz & DeVries 1999, Hall & Harvey 2001, 2002). This study assessed morphological variation at a finer level than was done previously. For example, a comparison between C. lucianus and H. zerna clearly demonstrates that sclerotized bridges in these species arise from separate regions of the valva (Fig. 6), thus failing the test of topographical correspondence required for homology (e.g., Wiley 1981, DePinna 1991, Rieppel & Kearny 2002). Furthermore, in the context of our taxon sampling and tree (Fig. 3) the ventral bridges are congruent but the dorsal bridges are not; they are homoplasious (ibid.).

The dorsal fusion of the valvae (e.g., A. bolena) and the development of a dorsal bridge (e.g., C. lucianus; Fig. 6) involve the same part of the valva. In the former the dorsal processes of the valvae merge extensively toward each other, whereas in the latter the valvae are separated. Because dorsal fusion requires a spatial rearrangement of the valvae but the dorsal bridge does not, we treat these structures separately (characters 41 and 42, Appendix 1), and hypothesize that they have independent evolutionary origins. Perhaps future work can provide a rigorous homology assessment of these structures through comprehensive studies of riodinid valvae and a test of congruence (e.g., Rieppel & Kearney 2002). However, the present study serves to point out the distinct variation in these structures.

According to principles of phylogenetics, only homologous modifications can be used as synapomorphies to support species groups. Hall & Harvey (2002:pp. 550, 560) use the presence of a sclerotized transtilla as the single character defining the subtribe Nymphidiina, and state that this structure is “present in all species of Nymphidiina and absent elsewhere in the Nymphidiini (Hall, unpublished data).” However, in light of our discussion above, the amalgamation of three distinct structures (dorsal and ventral bridges, and dorsal fusion of the valvae) into one character (sclerotized transtilla) should not be used to justify the monophyly of this subtribe. This suggests the status of the Nymphidiina needs reevaluation.
FIGURE 15. Character state changes reconstructed for the presence/absence of balloon setae (not used in the analysis). Character states were assigned for each species based on published and unpublished life history accounts (DeVries et al. 1994, DeVries 1997 and pers. obs.; K. Nishida pers. com.).
Balloon setae and myrmecophily

Myrmecophily is an aspect of caterpillar biology that is undeniably important in the history of riodinid evolution, and key for caterpillar survival (DeVries 1988, 1991a, b, c). Thus, the possession of caterpillar ant-organs has played a significant role in developing riodinid classification and how we view their evolution (e.g., Harvey 1987, DeVries 1991c). In fact, the discovery that *H. paucipuncta* is myrmecophilous formed the *raison d'être* for the present phylogenetic study.

Despite incomplete life history records we traced the presence of balloon setae onto the tree yielded by our analysis. The pattern shown in Fig. 15 leads to the prediction that caterpillars of *C. aemulius* and species of *Harveyope*, for which immatures are currently unknown, will have balloon setae. It is also possible that caterpillars of *C. elpinice* and *Mycastor* possess balloon setae (not included in our analysis, but see Table 3, Callaghan 1983 and Penz & DeVries 2004). Furthermore, Fig. 15 can be used to hypothesize that balloon setae are homologous within Nymphidiini, and will be found to define a monophyletic group within this tribe. If correct, it will underscore the importance of larval biology and morphology for inferring classification and phylogeny in riodinid butterflies.

Field observations of ants manipulating caterpillar balloon setae suggest that these structures are involved in myrmecophily, with the caveat that they also occur in some non-ant-associated riodinids (DeVries 1997 and references therein). Based on the argument that nature is economical, Hall et al. (2004) cast doubt on this proposal — caterpillars should not have two organs that perform the same function (i.e., ATOs and balloon setae). Field observations on caterpillars and ants bring forth an alternative perspective. Caterpillars of *Nymphidium*, *Theope* Doubleday (PJD pers. obs. and L. Kaminski pers. com.), *Catocyclotis* (K. Nishida pers. com. and PJD pers. obs.), and *H. paucipuncta* (DeVries et al. 2004) have not been observed to extrude anterior tentacle organs (ATOs) when interacting with their ant symbionts. Caterpillars of *H. paucipuncta* lack ATOs, while preserved caterpillars of *Nymphidium*, *Theope* and *Catocyclotis* examined by us seem to possess a small slit in the cuticle on T3 corresponding to the position of ATOs. In contrast, ATOs are frequently extruded and easily observed in caterpillars of *Thisbe* Hübner, *Synargis* Hübner, and *Juditha* Hemming (PJD pers. obs.). These observations show a clear difference in behavior — caterpillars that possess balloon setae have not been observed to extrude ATOs, suggesting that ATOs might not be fully functional in these species.

Histological examination will be required to confirm this. Because the type of chemicals being released by either balloon setae or ATOs is unknown, the hypothesis by Hall et al. (2004) that these two structures cannot have an analogous function remains to be verified. It seems to us that while nature is often economical, the presence of both balloon setae plus a prominent cervical gland in *H. paucipuncta* suggests that it may also be generous.
Conclusions

The discovery that *H. paucipuncta* caterpillars associate with ants, and possess ant-organs characteristic of Nymphidiini provided undisputable evidence regarding the tribal placement of this species (DeVries et al. 2004). We were then left with a deceptively simple question: to what genus does *paucipuncta* belong? The present analysis sought a solution for this quandary, and pointed to three main conclusions:

1. based on the phylogenetic analysis of 72 characters for 36 species, a new genus *Hallonympha* was described for *paucipuncta* and *eudocia* (previously in *Apodemia* and *Adelotypa*, respectively);
2. *Hallonympha* is closely related to *Nymphidium*, *Catocyclotis* and the new genus *Harveyope* (which also includes species previously in *Adelotypa*);
3. our analysis confirmed previous suggestions that neither *Adelotypa* nor *Calospila* constitute monophyletic taxa.

Finally, the detailed comparative study of the valva reported here allowed us to clarify previous misconceptions regarding the nymphidiine transtilla.

Acknowledgments

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Literature cited


science: New York.
Appendix 1

— Illustrated character List including 72 characters of male morphology. See Penz & DeVries (1999) for additional illustrations. Rescaled Consistency Indices (RC) given for each character were used for successive approximation weighting (rounded here, not in the analysis).

1. Location of 3rd abdominal spiracle: above midline (0), at midline (1), below midline (2). RC:0.244. Adapted from character 61 in Harvey (1987) by adding state ‘1’. Character 40 in Penz & DeVries (1999). Character 7 in Hall & Harvey (2002:550). Measurements used to determine spiracle position were taken by pressing the open abdominal shell under a microscope cover slide, lining the measuring grid with the center of the spiracle and then measuring the pleural membrane above and below it (data not shown).


3. Stn8 with terminal projection extending beyond edge of pleural membrane (0), devoid of such projection (1). RC: 0.25. Fig. 16; character 44 in Penz & DeVries (1999), character 10 in Hall & Harvey (2002:547).

4. Stn8: simple, not divided (0), divided into two symmetrical projections (1), divided into asymmetrical projections (2). RC:0.611. Fig. 16; adapted from characters 59 in Harvey (1987), and from characters 45 and 46 in Penz & DeVries (1999) by re-defining character states to provide the best possible description of morphological variation in the ingroup considered here. See Hall & Harvey (2001) for alternative character state definitions.


FIGURE 16. Male eighth sternum, cornuti, coecum penis in lateral view, and tip of aedeagus in ventral view showing characters used in the analysis.
6. Tip of bifurcated projections: rounded (0), pointed (1), squared (2). RC:0.444. Fig. 16.

7. Posterior margin of uncus: completely smooth (0), with nubs (1), with spiny projections (2). RC:0.333. Fig. 17; adapted from character 56 in Penz & DeVries (1999) by adding state ‘1’ to provide the best possible description of morphological variation in the ingroup.

8. Posterior margin of uncus: rounded (0), straight (1), slightly concave (2), strongly concave, uncus apparently four-lobed (3). RC:0.343. Fig. 17; adapted from character 57 in Penz & DeVries (1999) by splitting one of the character states to provide the best possible description of morphological variation in the ingroup. Modified versions of this character were used by Hall & Harvey (2001, 2002).

9. Uncus lateral saw-toothed projection: absent (0), present (1). RC:0.4. Fig. 17.

10. In lateral view, uncus: straight (0), arched upward (1). RC:1. Fig. 18.

11. In lateral view, dorsal outline of tegumen: arched (0), completely straight (1). RC:0.083. Fig. 18.

12. In lateral view, posterior edge of tegumen: forming a hump before uncus (0), not forming a hump before uncus (1). RC:0.4. Fig. 18; character 12 in Hall & Harvey (2002:547).

13. Lateral margins of tegumen: thickened at edges of lateral fenestra to form ribs (0); not thickened at edges of lateral fenestra (1). RC:1. Fig. 18.

14. Notch in the anterior margin of tegumen: absent (0), present (1). RC:0.103. Fig. 17.

15. Posterior end of subscaphium: one narrow lobe (0), one broad lobe (1), two lobes (2), three lobes (3). RC:0.48. Adapted from character 63 in Penz & DeVries (1999) by adding character states to provide the best possible description of morphological variation in the ingroup. Illustrated in Penz & DeVries (1999).

16. Setae in the posterior end of subscaphium: thicker than setae in the ventral surface of uncus (0), similar in thickness to (or thinner than) setae in the ventral surface of uncus (1). RC:0.238. Character 64 in Penz & DeVries (1999).

17. Setae in the posterior end of subscaphium: concentrated at the end of subscaphium (0), some setae located more anteriorly (1). RC:0.037.

18. Sclerotized plate of the subscaphium: uniformly narrow (0), uniformly broad (1), broad posteriorly and narrow anteriorly (2), broad anteriorly and narrow posteriorly (3), diamond-shaped (4). RC:0.296. Adapted from character 65 in Penz & DeVries (1999) by adding character states to provide the best possible description of morphological variation in the ingroup. States 18:1 and 18:4 can be seen in Fig. 5 and 4 respectively.

19. Sclerotized plate of the subscaphium: ends before end of subscaphium lobe (0), extends to the end of subscaphium lobe (1). RC:0.091.


21. Gnathos: decreasing in width gradually, sickle-shaped (0); decreasing in width sharply, proximal and distal arms markedly distinct (1). RC:1. Fig. 17.

22. Gnathos: proximal and distal arms entirely in the same visual plane (0), proximal and distal arms not in the same visual plane, twisted (1). RC:0.4.

23. In ventrolateral view, distal end of gnathos: pointed (0), blunt (1). RC:0.133. Fig. 17; adapted from character 69 in Penz & DeVries (1999) by making character state definitions more clear and thus eliminating one character state. For best view of the tip and reliable scoring of character states it is necessary to tilt the genitalic capsule from a ventral to a lateral position.
24. Vinculum: continuous through entire anterior edge of tegumen (0), not continuous through entire anterior edge of tegumen (1). RC:0.469. Fig. 17 and 18; adapted from character 71 in Penz & DeVries (1999) by making character state definitions more clear and eliminating one character state. Character 9 in Hall & Harvey (2002:550).
25. **Vinculum**: completely fused to anterior edge of tegumen (0); distal edges fused to anterior edge of tegumen, remainder of vinculum connected to tegumen by weakly sclerotized tissue (1); connected to anterior edge of tegumen entirely by weakly sclerotized tissue (2). RC:0.622. Character 72 in Penz & DeVries (1999).

26. In ventrolateral view, vinculum: relatively narrow throughout its entire length, only mildly varying in width (0); with a localized bulge below the edge of tegumen that does not overlap with the valva edge, and decreases in width towards saccus (1); laterally widened below tegumen to form a blade that maintains its width towards saccus (2); with a localized bulge that overlaps with the valva edge (3). RC:0.238. Adapted from Character 73 in Penz & DeVries (1999) by adding character states that were not present in the previously studied species. A simplified version of this character was used by Hall & Harvey (2002:547 character 14).

27. Sculpturing of the vesica: absent (0), present (1). RC:0.111. Fig. 18; re-worded and reversed from character 75 in Penz & DeVries (1999).

28. Sculpturing of the vesica: small bumps or spines (0), intermediate bumps or spines (1), enlarged spines (2). RC:1.

29. **Cornuti**: absent (0); a simple plate (1); a plate with one terminal spine (2); a plate with two terminal spines of uneven size (3); a plate with multiple terminal spines of approximately even size (4); two spines (5); multiple spines, short, thick, heavily sclerotized (6); multiple spines, long, thin, lightly sclerotized (7). RC:0.392. Fig. 16; adapted and re-defined from character 76 in Penz & DeVries (1999) by adding character states and sharpening definitions. A different version of this character was used by Hall & Harvey (2002:547, character 15).

30. In dorsal view, distal end of aedeagus (=phallus): acute point (0), broad point (1). RC:1. Fig. 16; adapted from character 77 in Penz & DeVries (1999) by reducing the number of character states due to narrower morphological variation in the present ingroup than in previously studied species.

31. When acutely pointed, aedeagus tip: short (0), long (1). RC:1. Fig. 16; re-worded from character 78 in Penz & DeVries (1999).

32. Distal opening of aedeagus: dorsal (0), dorsolateral or lateral (1), ventrolateral or ventral (2). RC:0.15. Adapted from character 80 in Penz & DeVries (1999) by broadening the definition of state ‘2’.


35. Coecum penis flare: absent (0), present (1). RC:1. Fig. 16.

36. Ventral edge of juxta: straight (0), split (1), rounded (2). RC:0.156. Adapted from character 50 in Harvey (1987), character 85 in Penz & DeVries (1999).

37. Juxta: forms a smooth curve (0), angular curve (1). RC:0.333. Adapted from character 86 in Penz & DeVries (1999), by eliminating one character state that is not found in the present ingroup.

38. In lateral view, juxta arch: extending beyond edge of valvae (0), not extending beyond edge of valvae (1). RC:0.222. Fig. 18.

39. Valva: inner and outer regions forming dorsal and ventral processes that are visibly separated (0); inner and outer regions merging to form a single piece (1). RC:1. Fig. 18 and 20. See text for an explanation of male valva pertinent to characters 39–58.

40. Dorsal process of valva extends posteriorly beyond ventral process (0), ventral process extends posteriorly beyond dorsal process (1). RC:1. Fig. 18.
FIGURE 18. Male genitalia in lateral view showing characters used in the analysis.

41. Valva: dorsal processes closely adjacent to each other, fused or nearly so (0); separated (1). RC: 0.464. Fig. 18 and 20.

42. Valva, when dorsal processes separated: dorsal processes extended to form a sclerotized bridge (i.e., dorsal bridge) (0), not extended to form a sclerotized bridge (1). RC: 0.4. Fig. 6. The dorsal bridge described in 42:0 is likely not homologous to the ventral bridge described in character 48 (see Discussion).
FIGURE 19. Schematic of the valva tip in dorsal view showing the differences in spatial orientation of the dorsal process (shaded in gray).

FIGURE 20. Valvae in ventral view showing characters used in the analysis.

43. Dorsal process of valva: uniformly sclerotized (0), more sclerotized distally (1). RC:0.063. Fig. 20.

44. Distal portion of the dorsal process of valva: forming a point (0), not forming a point (1). RC:0.282. Fig. 20.
45. Distal portion of dorsal process of valva: straight (0), bent inward (1), bent outward (2). RC:1. Fig. 20.
46. Ridge of dorsal process of valva: runs exactly in parallel with long axis of valva (0), at an angle with long axis of valva (1), completely transversal to long axis of valva (2). RC:0.244. Fig. 19.
47. Spines of dorsal process of valva: absent (0), present (1). RC:1. Fig. 20; character 17 Hall & Harvey (2002:547), defined more precisely here.
48. Valva, when dorsal processes separated: ventral process extended to form a sclerotized bridge (i.e., ventral bridge) (0); not extended to form a sclerotized bridge (1). RC:1. Fig. 6 and 20. The ventral bridge described in 48:0 is likely not homologous to the dorsal bridge described in character 42 (see discussion).
49. When ventral process of valva forms a sclerotized ventral bridge, distal portion of ventral process somewhat reduced and fused to sclerotized ventral bridge (0), completely reduced, not distinguishable from ventral bridge (1). RC:0.063. Fig. 20.
50. Ventral process of valva: uniformly sclerotized (0), distal portion more sclerotized than proximal (1). RC:0.278. Fig. 20.
51. Distal portion of ventral process of valva: forming a point (0), not forming a point (1). RC:0.156. Fig. 20.
52. Distal portion of ventral process of valva: straight (0), bent inward (1), bent outward (2), bent upward (3). RC:1.
53. Pointed distal portion of ventral process of valva: one sharp point (0), two sharp points (1), squared (2) rounded (3). RC:0.375.
54. In ventrolateral view, proximal region of ventral process of valva: straight (0); slightly raised, rounded (1); bump with clear edges (2); large projections (3). RC:0.09.
55. In lateral view, base and upper edge of outer region of valva: cuticle thickened to form a brace (0), cuticle not thickened to form a brace (1). RC:1.
56. In lateral view, upper edge of outer region of valva: extended dorsally and posteriorly to form a structure separated from the remainder of the valva by a lateral fissure (0), lacking such a pattern (1). RC:1.
57. In ventrolateral view, lateral fissure of valva: transverse to long axis of valva (0); continuing itself along long axis of valva (1). RC:0.192.
58. In ventral view, rounded extension of the outer region of valva: protruding outward to form a ‘flap’ (0), not protruding outward (1). RC:0.458. Fig. 20.
59. Ventral bracing of valva: absent (0), forming a bridge between the valvae (1), limited to edges of valvae, not forming a bridge between them (2). RC:0.433. Fig. 20; adapted from character 94 in Penz & DeVries (1999) by adding detail to the description and definition of the bracing.
60. In ventral view, anterior edge of valvae straight (0), projected (1). RC:0.454. Fig. 20.
61. Vinculum costula surrounding saccus (0), not surrounding saccus (1). RC:0.182.
62. In rear view, shape of the outline of the genital capsule (as formed by the tegumen + vinculum + saccus): [] (0), \_\_ (1), ( ) (2), \_/ (3). RC:0.195.
64. Number of spots in ventral hindwing cell Rs: none (0), 1 (1), 2 (2), 3 (3). RC:0.118. Adapted from character 4 in Hall & Harvey (2002:550).
65. Dorsal forewing, dark brown spots: absent (0), present (1). RC:0.192. Some Apodemia
species were scored ‘?’ because their wing spots are white, not brown. In several species with brown wings (e.g. *paucipuncta*), darker brown spots can be seen relatively easily in fresh individuals, but with increased difficulty in warn or damaged specimens.

66. Dorsal forewing, marginal and submarginal lines: absent (0), present (continuous or broken) (1). RC:0.187.

67. Dorsal forewing, submarginal line: forming smooth arches in each cell (0), not forming arches in each cell (1). RC:1.

68. Dorsal forewing and dorsal hindwing: similar in their color pattern (0), different in their color pattern (1). RC:0.097.

69. Ventral hindwing similarly colored as ventral forewing (0), ventral hindwing of much lighter color than ventral forewing (1). RC:0.063.

70. Second segment of labial palpus, long, erect hair-like scales projecting ventrally beyond the flattened scales: absent (0), present (1). RC:0.417.

71. Frons scales: mixed broad and thin, converging from sides to midline (0); thin scales more prominent and long, erect (1). RC:0.278.

72. Color of the cuticle of the ventral mesothorax: orange (0), orange-brown (1), brown (2). RC:0.131.
### Appendix 2

— Character matrix.

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Appendix 3

— Character state changes for each tree branch as traced in the successive approximation weighting tree (Fig. 3). Abbreviations: ho, homoplasious outside; hao, homoplasious above and outside; u, unique, changing above; uu, unique unchanged above. Unique character state changes are in bold.

mormo 27:1 ho
palmerii 18:4 ho, 29:6 ho, 32:2 uu
cythera
thersander 8:2 ho, 68:1 ho
sturnula 16:0 ho, 17:1 ho, 36:0 ho, 42:1 ho, 65:0 ho
bolena
borsippa 17:0 ho, 36:0 ho, 62:1 ho
pirene 17:0 ho, 57:1 ho, 63:3 ho
irene
latona 11:0 ho
parthaon 14:1 ho, 29:3 ho, 38:0 ho, 54:1 ho
rhodope 33:1 ho, 64:1 ho
apotheta 7:1 ho, 15:0 ho, 18:0 ho, 32:1 ho
violacea 54:1 ho, 64:1 ho, 72:2 ho
huebneri
amasis 54:1 ho, 62:0 ho, 64:0 ho
leucophaea 66:1 ho
balista
emylius 17:1 ho, 32:1 ho
cilissa 41:1 ho
lucianus 22:1 ho, 43:1 ho
zerna
glauca
densemaculata 17:1 ho
sejuncta 1:1 ho
tinea 15:0 ho
aemulius 6:1 ho, 26:0 ho, 29:6 ho
adelina 28:1 uu, 54:2 ho, 64:0 ho

leucosia 15:3 uu, 63:0 ho, 69:1 ho, 72:1 ho
balbinus 20:0 ho, 44:1 ho, 46:1 ho, 54:2 ho, 68:1 ho
cachrus 19:1 ho, 43:1 ho, 63:0 ho
mantus 15:2 uu, 18:0 ho, 26:2 ho, 29:1 ho, 44:1 ho, 46:1 ho, 54:3 uu, 61:1 ho
eudocia 19:1 ho, 62:0 ho
paucipuncta 17:1 ho, 43:1 ho

(palmerii, cythera) 8:0 ho, 61:1 ho
(mormo(palmerii, cythera)) 11:1 ho, 26:3 uu, 29:4 hao, 36:1 ho, 63:1 ho
(thersander, sturnula) 30:1 uu, 33:0 ho, 51:1 ho
(bolena,borsippa) 4:0 ho, 18:0 ho, 26:0 ho
(((bolena,borsippa)penthea) 19:1 ho, 59:1 ho
(((bolena,borsippa)penthea)pirene) 15:1 ho, 39:1 uu
(irene,latona) 64:0 ho
(((bolena,borsippa)penthea)pirene)(irene,latona)) 26:1 hao, 46:1 ho
(parthaon,rhodope) 36:0 ho, 37:1 ho, 62:1 ho
(((bolena,borsippa)penthea)(irene,latona)) 19:1 ho, 59:1 ho
(((bolena,borsippa)penthea)(irene,latona)(parthaon,rhodope)) 17:1 hao, 57:0 hao, 72:0 hao
(((bolena,borsippa)penthea)(irene,latona)(parthaon,rhodope)apotheta) 29:5 ha, 40:1 u, 62:0 hao, 64:3 ha

(violacea,huebneri) 66:1 ho, 68:1 ho, 69:1 ho
(leucophaea,balista) 20:1 ho, 65:1 ho, 72:ho
(amasis(leucophaea,balista)) 18:0 ho
((violacea,huebneri)(amasis(leucophaea,balista))) 14:1 ho, 15:0 ho, 29:3 ho, 31:0 uu, 38:0 ho, 46:1 ho, 50:0 ho, 51:1 ho, 57:0 ho, 62:3 ha
(emylis,cilissa) 26:2 ho, 35:1 uu, 36:2 ho, 64:1 ho, 72:2 ho
(((violacea,huebneri)(amasis(leucophaea,balista))(emylis,cilissa)) 4:0 ho
(((bolena,borsippa)penthea)(irene,latona)(parthaon,rhodope)(apotheta))((violacea,huebneri)(amasis(leucophaea,balista))(emylis,cilissa))) 11:1 hao, 41:0 ha, 44:1 ho

(((bolena,borsippa)penthea)(irene,latona)(parthaon,rhodope)(apotheta))(((violacea,huebneri)(amasis(leucophaea,balista))(emylis,cilissa)))lucianus) 1:2 hao, 25:1 u, 26:0 hao, 29:7 ha, 52:3 u, 62:2 hao, 71:0 hao, 72:1 hao

(densemaculata(sejuncta,tinea)) 62:2 ho
(glaucadensemaculata(sejuncta,tinea)) 1:0 hao, 6:2 ha, 64:2 ho
(zerna(glaucadensemaculata(sejuncta,tinea))) 18:1 ha, 19:1 ho, 26:2 ho, 28:2 u, 29:1 hao, 54:1 hao, 70:1 ho
(aemulius,adelina) 17:1 ho, 36:0 ho, 62:2 ho, 68:1 ho
((zerna(glaucadensemaculata(sejuncta,tinea)))(aemulius,adelina)) 11:1 ho, 20:0 hao, 43:1 hao, 60:1 ho, 69:1 hao
(azanoides,leucosia) 26:2 ho, 32:1 ho
((azanoides,leucosia)balbinus) 1:2 ho, 50:0 ho
(((azanoides,leucosia)balbinus)cachrus) 27:0 ho, 62:0 hao, 64:0 ho
(((azanoides,leucosia)balbinus)cachrus)mantus) 2:1 uu, 4:2 uu, 8:3 uu, 9:1 ho, 21:1 uu, 22:1 ho, 34:1 uu, 57:0 ho, 65:0 ho, 67:0 uu, 71:0 ho
(eudocia,paucipuncta) 10:1 uu, 29:6 ho, 70:1 ho
(((zerna(glaucadensemaculata(sejuncta,tinea)))(aemulius,adelina))((azanoides,leucosia)balbinus)cachrus)mantus) 1:1 ha, 3:0 ho, 13:0 uu, 64:1 hao, 66:1 hao
(((zerna(glaucadensemaculata(sejuncta,tinea)))(aemulius,adelina))((azanoides,leucosia)balbinus)cachrus)mantus)(eudocia,paucipuncta) 27:1 hao 42:1 ha, 48:0 uu, 59:1 ho