

## INTRODUCTION TO THE CHECKLIST OF EUMAEINI (LYCAENIDAE)

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The purpose of this preface is to give the rationale for the taxonomic arrangement of the checklist of Eumaeini, followed by discussions of how the checklist was organized, how decisions were made, and what was learned. I address the discussions successively at the specific, generic, and tribal levels. A concluding author's note explains why some previous taxonomic results were not used.

The Atlas of Neotropical Lepidoptera (ANL) Checklist classification of 1,058 Neotropical eumaeine species partitioned into 83 genera and 15 "sections" (following the scheme in Eliot, 1973) is the first comprehensive taxonomic arrangement of these butterflies since Draudt (1919-20). A primary reason for this long interval is that most eumaeines are extraordinarily rare in collections. For example, about 20% of the species recognized in this checklist were not represented in major museum collections 25 years ago, and many eumaeine species, including some described two centuries ago, are still known from less than five individuals. A second reason for the long interval has been the lack of a higher classification (discussed briefly below). For example, *Janthecla* Robbins & Venables was distinguished from the entire Eumaeini because the genera that are closely related to *Janthecla* were unknown (Robbins and Venables, 1991). Although it may be somewhat unorthodox to introduce a new taxonomic arrangement in a checklist, there is no comprehensive alternative classification, and it is my hope that this arrangement will provide the framework necessary to stimulate further research.

The checklist includes 1,871 specific names attributable to the Neotropical Eumaeini (cf. Robbins and Lamas, 2002, for some recent changes), plus 26 *nomina nuda* and 15 misspellings for completeness. For those interested in Neotropical butterfly diversity, 274 undescribed species are systematically placed. A few of these species are undescribed due to misidentifications, but most, as noted, are extremely rare in museum collections and their geographical and seasonal variation is poorly documented. Subspecies are not used in the checklist following the compelling reasons in Wilson and Brown (1953), but those names that were proposed as subspecies are indicated for the convenience of those who wish to use them.

The species order in the checklist is intended to be phylogenetic, which is reasonably straightforward for those genera for which phylogenetic analyses have been done, such as *Rekoa* Kaye (Robbins, 1991) and *Cyanophrys* Clench (Robbins and Duarte, in prep.), or that possess conspicuous character states that appear to be phylogenetically consistent, such as *Arawacus* Kaye, *Atlides* Hübner, *Eumaeus* Hübner, *Ignata* Johnson, *Laothus* Johnson, Kruse & Kroenlein, and *Nesiostrymon* Clench. For those genera, such as *Nicolaea* Johnson and *Theritas* Hübner, for which a number of characters are homoplastic or difficult to interpret, I have endeavored to place closely related species next to each other.

I have had the good fortune to collaborate with Gerardo Lamas on nomenclature, and many outstanding problems have been corrected (Robbins, 2002; Robbins and Lamas, 2002). A recently discovered problem is that the forewings of the holotype of *Penaincisalia planuma* K. Johnson have four radial veins while eumaeines have three radial veins (Eliot, 1973). This name is transferred to the Polyommatinae, where it is a *nomen dubium*. All original eumaeine descriptions and virtually all extant types, or pictures of them, were seen. In a few cases where types were not found, such as *Thecla sylvana* Jörgensen, identification is based on named specimens that the describer sent to other museums. Occasionally, a generally recognized species and its type specimen were not the same (most notably, *Papilio cleon* Fabricius, *Thecla ira* Hewitson, *Thecla gadira* Hewitson, *Thecla nippia* Dyar, and *Thecla punctum* Herrich-Schäffer), and I correct the nomenclature for these names, which have not been widely used outside of technical publications and faunal or nomenclatural lists. There are still a number of old names, such as *Papilio lisus* Stoll, which are not definitively recognizable from the original description and which lack extant types. In these cases, I follow the prevailing usage over the past century, including that in the "agricultural pest" literature (e.g., Silva *et al.*, 1968), and would hope that others would continue this common-sense action.

To deal with the species-level taxonomy of the Eumaeini, I (1) amassed a collection of 64,000+ pinned eumaeines at the Smithsonian Institution, supplemented extensively by specimens borrowed from the world's major museum and private collections; (2) examined the wing pattern, androconia, genitalia, legs, antennae, wing venation, and other structures of the vast majority of the world's Eumaeini; and (3) quantified intra- and interspecific eumaeine variation when appropriate (e.g., Robbins, 1990, 1991). Despite these efforts, it is yet difficult to assess variation for much of the fauna because of insufficient collections. On the other hand, the annual

rate at which previously unknown species are being collected is down to about 1% (almost entirely from the Andes), and I have seen no previously uncollected species from Central America in about a decade. It likely will yet be a decade or more before the species-level taxonomy of Neotropical eumaeines stabilizes.

The checklist treatment of species pairs from Central America and the Amazon Basin is generally reflective of the way in which I dealt with geographical variation. In some cases, such as *Strephonota proba* (Godman & Salvin) and *S. sphinx* (Fabricius) (= *dindymus* Cramer), wing pattern appears to completely intergrade in central Venezuela. In others, such as *Lamprospilus collucia* (Hewitson) and *L. orcidia* (Hewitson), the wing patterns of both sexes differ without any evidence of intergradation where their distributions meet (these taxa were confused in Draudt, 1919-20, and both species were misidentified in D'Abrera, 1995). Finally, some species pairs, such as *Paiwarria antinous* (C. Felder & R. Felder) and *P. telemus* (Cramer), have nearly identical wing patterns, but their genitalia differ substantially without evidence of intergradation. In cases like the first, the taxa are synonymized while in those like the latter two, they are treated as distinct species. I generally treat montane taxa with geographically variable wing patterns, such as *Penaincisalia loxurina* (C. Felder & R. Felder), as one geographically variable species unless it has been shown that this arrangement is incorrect.

Associating males and females is sometimes problematic, either because the sexes are very different, such as *Trichonis* Hewitson and some lineages of *Erora* Scudder and *Lamprospilus* Geyer, or because wing pattern hardly varies among species, such as some lineages of *Calycopis* Scudder and *Oenomaus* Hübner. In the absence of better information, I relied on distribution, habitat, and systematic placement to associate sexes in these genera. I am satisfied with the results in *Trichonis* (Robbins, 1987) and *Lamprospilus*, which includes many new pairings of males and females, but there is yet much work to be done in *Calycopis* and *Erora*, as I am only too well aware. The best ways to make progress with genera where males and females are not easily associated is by rearing and by describing new species only from males, which usually have more taxonomic characters because of their androconia and brush organs (*sensu* Eliot, 1973, = coremata in Clench, 1964).

In the first "modern" eumaeine generic revision, Nicolay (1971a) wrote, ". . . the genitalia of all species in *Arcas* are very similar. Furthermore, the genitalia of both sexes show considerable individual variation within a single species. It would indeed be difficult to separate species in this genus on the basis of the genitalia alone." My experience with many eumaeine genera corroborates this finding. Indeed, the richest source of traits for distinguishing eumaeine species is wing pattern, followed by androconia and only then by genitalia, including brush organs. Of course, this rank order is not a "hard and fast" rule. In *Oenomaus*, for example, male genitalic characters distinguish some species better than wing pattern. In *Cyanophrys*, identification is complex, with a combination of androconia, brush organs, frons color, wing pattern and venation, and genitalia each providing some distinguishing characters (Robbins and Duarte, in prep.). Although genitalic structures often cannot be used to identify species, they appear to be the richest source of characters for distinguishing eumaeine genera, followed in order by brush organs and associated structures, androconia, wing pattern and venation, and legs. Despite many exceptions, these rank orders appear to be good working "rules of thumb."

The checklist includes 230 generic names — including 15 that are described in the Appendix to this work — plus four misspellings. In Draudt (1919-20) the vast majority of Eumaeini were lumped in *Thecla* Fabricius, a name that technically refers to a small Palearctic genus in the Theclini (Eliot, 1973). All Neotropical eumaeines are now placed in genera that are nomenclaturally valid in the Eumaeini. Additionally, the list of generic names is complete for the world because all eumaeine genera occur in the Neotropics as delimited in the *Atlas* series checklist. As in the case with the order of species, I try to place genera that are closely related next to each other.

My primary criteria for deciding generic limits are monophyly and stability (cf. Robbins and Henson, 1986), and secondary criteria are ease of identification, especially in the field, and biological homogeneity. In the absence of phylogenetic analyses, delimiting genera by character states that are complex, conspicuous, and easy to interpret increases the likelihood of monophyly and stability. Examples are the ductus seminalis arising from the middle of the ductus bursae in *Erora* (Field, 1941) and trichoid sensilla that are modified into anterior-pointing teeth on the valve-tips in *Strymon* Hübner (Clench, 1961, Robbins and Nicolay, 2002). Ease of identification contributed to the checklist concept of *Cyanophrys*, which is delimited by two hypothesized synapomorphies (Robbins and Duarte, in prep.) and also allows individuals to be immediately recognized by their wing pattern and shape as belonging to *Cyanophrys*. The checklist characterization of *Evenus* Hübner is an example in which biological homogeneity was a taxonomic factor. *Evenus* species have similar genitalia, unique androconial structures (discovered by Godman and Salvin, 1887, but androconia are lacking in a few species), and larvae, including those of the type species of the recently described *Cryptaenota* K. Johnson and *Ipoecia* Brévignon, that eat leaves of trees in the plant family Sapotaceae. This larval foodplant use is unique within the Eumaeini except for the unrelated *Paiwarria umbratus* (Geyer) (Jørgensen, 1934, 1935; Lima, 1936; Hoffmann, 1937; Schultze-Rhonhof, 1938; Zikán, 1956;

Silva *et al.*, 1968; Kendall, 1975; D. Murray, unpubl.; Robbins, unpubl.).

For those genera that occur widely in North America, I follow the generic classifications of Ziegler (1960) and Clench (1961, 1979) where they basically agreed, such as *Callophrys* Billberg, and use character information from both where they disagreed, such as *Satyrium* Scudder. I follow the generic characterizations in Nicolay's path-breaking revisions (Nicolay, 1971a,b, 1976, 1977, 1979, 1980, 1982) with only a few minor exceptions, such as *Panthiades* Hübner, which is probably not monophyletic unless *phaleros* (Linnaeus) is transferred to it from *Cycnus* Hübner.

Some genera, such as *Micandra* Schatz and *Nicolaea*, are provisionally delimited because of difficulties interpreting morphology or because the distribution of character states is phylogenetically inconsistent. For example, most characters of the wing pattern, male forewing venation, and female genitalia (except the signa) are consistent with the monophyly of *Micandra* as delimited in the checklist (Clench, 1971; Robbins, 1987), while most structures of the male genitalia and androconia are not. Phylogenetic analyses are required to put the monophyly of these genera on a more solid foundation. Despite these problems, I suspect that the vast majority of generic groupings proposed in the checklist will prove to be monophyletic. And since I have worked with the world's eumaeine fauna, I am optimistic that the generic level classification, unlike that at the species level, will be stable, at least among those for whom monophyly and stability are guiding precepts.

Many, if not most, of the generic placements proposed in the checklist are new and may occasionally seem "odd" to those who know these insects primarily by their wing patterns. In some cases, members of the same genus may be "different looking," such as *Thaeides theia* (Hewitson) and *T. muela* (Dyar), but in this case, they share "pincer-like" valve tips, a structure that is not found elsewhere. At the other extreme, some genera, such as *Atlides* and *Brangas* Hübner (Draudt, 1919-20), have traditionally been treated as congeners because of superficially similar wing patterns, but are otherwise structurally dissimilar. A few genera, such as *Ipidecla* Dyar, have easily recognizable wing patterns, and I have tried to keep them intact, but uncertainties remain. For example, *Ipidecla* is closely related to *Penaincisalia* Johnson (especially *P. balzapamba* Johnson), which may be paraphyletic in terms of *Ipidecla*. The generic placement of 33 names remains uncertain (these cases are noted with a question mark [?]), usually because of uncertain interpretation of the morphology.

Eliot (1973) distinguished the Eumaeini from its close relatives, the Deudorigini and the Tomarini, primarily by three forewing radial veins and a stubby-tipped male foretarsus. Although neither trait is unique within the Theclinae (Clench, 1955; Eliot, 1973), this concept of the Eumaeini is likely to be stable because other characters are phylogenetically consistent with it (based on an examination of representative species from the 18 other thecline tribes; Robbins, in prep.). Within the Eumaeini, however, a well-supported higher classification is lacking. Eliot (1973) preliminarily divided the Eumaeini in two on the basis of male foretarsus structure, but these sections do not appear to be monophyletic (Robbins, 1987). Clench (1964) also divided the Eumaeini in two, with *Eumaeus* in its own tribe, presumably because it lacks tibial spurs and has "subquadrate" valves (Clench, 1961). Clench's classification is not used because four of the six *Eumaeus* species possess tibial spurs and three have "conical" valves (Robbins, unpubl.). However, other characters discovered by Clench delimit sections (see the following) and are an integral part of the developing higher classification of the Eumaeini.

With the goal of providing information on inter-generic relationships, the 83 eumaeine genera are arranged in 15 "sections." Some sections have conspicuous characterizing traits, which I hypothesize to be synapomorphies. Examples include: the brush organs (when present) that surround (or nearly surround in *Paiwarria* Kaye) the genital capsule of the *Eumaeus* Section (Robbins, unpubl.); the anal lobe cleft of the *Atlides* Section (modified from Godman and Salvin, 1887); the flattened valve tips lacking setae of the *Callophrys* Section (modified from Clench, 1961; Robbins and Duarte, in prep.); the structures supporting the brush organs in the *Thereus* Section (Robbins, 1991); the serrate ventral keel of the penis and the microtrichia on the distal valve tips of the penis of the *Satyrium* Section (Clench, 1961, 1970); the sclerotized, inwardly curved, lateral edge of the female 8<sup>th</sup> abdominal tergum and the fan-shaped signa in the *Lamprospilus* Section (Duarte and Robbins, in prep.); and the modification of the valve tips in the *Strymon* Section (Robbins and Nicolay, 2002). Some of these characterizing traits may be modified or lacking in some species and may occur elsewhere. As an example, a ventral keel of the penis has apparently been "lost" three times in *Satyrium* (Kons and Robbins, in prep.) and also occurs in (presumably) analogous form in *Podanotum* Torres & K. Johnson. Despite these instances of apparent homoplasy, these characters are a reasonable starting point for a higher classification, especially since there is no alternative classification. However, I have had a difficult time determining the systematic position of some genera, such as *Bistonina* Robbins and *Celmia* Johnson and relatives, and it is yet premature to erect formal subtribes.

I try to place closely related sections next to each other, as determined by the distribution of character states that do not occur in the hairstreak tribes related to the Eumaeini (Eliot, 1973). For example, all species with a

"thick vinculum" (Robbins, 1987) belong to the *Panthiades*, *Hypostrymon*, and *Erora* Sections; all species whose males have blue scaling on the ventral forewing belong to the *Eumaeus*, *Brangas*, *Atlides*, and *Micandra* Sections (a few species in other sections may have a blue sheen on the ventral forewings); and all species (with two exceptions) whose ventral postmedian line is basally bordered with red scales belong to the last six sections (*Lamprospilus* to *Erora* Sections).

Although the tribe Eumaeini is Holarctic and Neotropical (Eliot, 1973), it is primarily a South American group, a situation akin to the Riodinidae. Eighty of the 83 eumaeine genera in the checklist occur in South America (the exceptions are the primarily Holarctic *Callophrys*, *Satyrium*, and *Phaeostrymon* Clench), and no eumaeine genus is strictly endemic to Central America (including Mexico) or to the Palearctic. Of the approximately 1,130 currently recognized eumaeine species in the world, about 80% (910 species) occur in South America, of which 238 are undescribed. The faunas of Colombia, Ecuador, Peru, and Brazil are the world's richest and most poorly known (500 or more species in each country). Considering the rate of newly collected species over the past decade, I estimate that eventually 1,250-1,300 eumaeine species will be recognized worldwide, of which almost 95% will be Neotropical in whole or part.

Although the Eumaeini and Riodinidae are primarily South American taxa, they are otherwise a "study of contrasts." While most Riodinidae occur in wet lowlands — with much smaller faunas in cloud forest and xeric areas — the Eumaeini occur in a wide variety of habitats from rain forest to desert and from lowlands to Andean grasslands above tree line. The vast majority of species that were first collected in the last five years occur in the Andes above 1800 m, where very few Riodinidae occur. While the Riodinidae exhibit an amazing diversity of wing shapes and patterns, the Eumaeini tend to have a basic pattern (despite obvious exceptions), which is perhaps one reason why they were mostly placed in "*Thecla*" for such a long time (Draudt, 1919-20). Finally, while males of about 25% of riodinid species have androconia (Hall and Harvey, 2002), males of more than 95% of the Eumaeini have androconia or brush organs.

**Author's Note.** Kurt Johnson is the most prolific describer of eumaeine taxa. He and his co-authors have proposed 433 Neotropical eumaeine species names (in "second place," Hewitson described 331) and 96 generic names (Hübner described 20). Even a casual reader will note a huge discrepancy between their published taxonomy and this checklist. I briefly note four reasons why I largely disagree with the results of Johnson and co-authors.

(1) Evidence suggests that Johnson and colleagues do not recognize and assess intraspecific variation. Brown (1983) illustrated greater genitalic differences within species than Johnson (1976, 1978) had reported between these same species. I quantified differences that Johnson (1986) had proposed to distinguish two species, showed that they are unimodally distributed, and calculated 95% confidence limits (about four standard deviations), but found that Johnson had distinguished his species on the basis of about one standard deviation of difference (Robbins, 1990). As a result, Johnson and co-authors repeatedly describe the same species. For example, they described five synonyms of *Ministrymon una* (Hewitson) from the adjoining Brazilian states of Rio de Janeiro and Espírito Santo (Bálint *et al.*, 1999).

(2) Evidence indicates that Johnson and colleagues overlook or ignore published character evidence. **Example 1:** Godman and Salvin (1887) described *Theclopsis* for hairstreaks whose male forelegs have a clawed pretarsus and 5-segmented tarsus. Although this trait characterizes a monophyletic lineage within *Theclopsis* as delimited in the checklist, Johnson (1991) and Johnson and Le Crom (1997) described *Asymbiopsis* (a synonym of *Theclopsis*) and four *Theclopsis* species with this trait (*Uzzia splendor*, *Asymbiopsis velezi*, *A. designarus*, and *A. remolinensis*), but mentioned neither Godman and Salvin nor the foreleg structure. **Example 2:** *Strymon* is characterized by a complex and conspicuous modification of its valves (Clench, 1961; Robbins and Nicolay, 2002), as noted above, but Johnson and co-authors have not mentioned this trait. They described six species in *Strymon* that lack this modification and that were transferred to five other genera (Robbins and Nicolay, 2002). Conversely, Johnson *et al.* (1992) stated that *Thecla tegea* Hewitson does not belong in *Strymon*, but Robbins and Nicolay (2002) placed it in *Strymon* because it possesses the valve modification. **Example 3:** Clench (1970) characterized *Ocaria* primarily by a penis with a "terminal triangular keel" and "two apical multidentate cornuti" (clearly illustrated with a third subapical cornutus in Clench's description). Although the conspicuous and unusually-shaped apical cornuti actually appear to be a complex single cornutus that is medially unsclerotized (wholly unsclerotized in some individuals of one species), Johnson (1992) described four genera (*Galba*, *Lamasa*, *Arases*, *Variiegatta*) whose type species have both of the distinguishing genitalic characters of *Ocaria*, but neither mentioned Clench's paper nor used these distinguishing traits in the generic diagnoses. **Example 4:** *Thecla eunus* Godman & Salvin and relatives were characterized by a "raised boss" on the dorsal forewing (associated with androconia on the ventral forewings) and by an area on the dorsal hindwing costa that is devoid of scales (Godman and Salvin, 1887;

Robbins, 1987, dubiously suggested that the scales might be fused). Johnson, Kruse and Kroenlein (1997) made a species with both characters the type of *Enos*, and Johnson, Austin, Le Crom and Salazar (1997) made another with both characters the type of *Falerinota* without referring to these characters or to the previous literature.

(3) Evidence suggests that most "infratribes" and genera described by Johnson and colleagues are not monophyletic. "Infratribe" *Macusiina* (listed in Johnson, Kruse and Kroenlein, 1997) includes some species of *Evenus* as characterized in the checklist and not others. "Infratribe" *Strephonina* (listed in Johnson, Austin, Le Crom and Salazar, 1997) contains some species of *Enos* as characterized in Robbins (1987) and not others. "Infratribe" *Thecloxurina* (listed in Johnson, 1992; Johnson and Kroenlein, 1993) contains some species of *Ocaria* as characterized by Clench (1970) and not others. "Infratribes" *Thecloxurina* and *Thereusina* (listed in Johnson and Kroenlein, 1993) both contain species of *Thereus* Hübner as characterized in Robbins (1991). There are 29 cases in which species described in one genus by Johnson and co-authors are placed in the checklist in two or more different genera. For example, the four species, which they described in *Radissima* Johnson, are placed in the checklist in four genera belonging to four different sections. Conversely, Johnson and colleagues have described synonyms of the same species in different genera 31 times. For example, both *Contrafacia mexicana* Johnson and *Orcya supra* Johnson are synonyms of *C. imma* (Prittwitz) (Robbins, 1991).

(4) Evidence indicates that Johnson and co-authors are not careful. The illustrated adult holotype of *Strymon andrewi* Johnson & Matusik is a female, but its illustrated genitalia are male of a different species (Robbins and Nicolay, 1999). Johnson labeled the holotype and paratype of *S. rhaptos* from Argentina, but the species is otherwise known only from the Dominican Republic and an adjoining island (Robbins and Nicolay, 1999). Johnson (1992: 206) transferred *Theritas mavors* Hübner to *Cryptaenota* Johnson even though *T. mavors* has been the type species of *Theritas* Hübner for almost two centuries. Salazar, Vélez and Johnson described *Trochusinus elizabetha* (in Johnson, Salazar and Vélez, 1997) from a female holotype (male unknown) with a partial illustration of her genitalia, but the illustrated holotype adult is correctly identified as a male in their figure legend (Robbins and Lamas, 2002). Johnson (1992) named *Ignata illepada* from a female holotype (male unknown) from Bolivia with a partial illustration of her genitalia, but the figured holotype is a male with androconia (also figured in D'Abrera, 1995: 1144, as the male type of *Thecla levis* Druce even though it is not the type of this species). This type is in poor condition, but appears to be a male of *Satyrium saepium* (Boisduval), a widespread species from western North America (Robbins and Lamas, 2002). The forewings of both types of *Tmolus victoria* Johnson & Matusik are *Ministrymon albimicus* (Johnson) or a close relative, and the hindwings of both are *Celmia celmus* (Cramer) (Robbins and Lamas, 2002). Neither species occurs in the Dominican Republic type locality or elsewhere in the Antilles. Robbins and Lamas (2002) corrected yet other examples of these kinds of problems.

The evidence above is representative of the difficulties I encountered when dealing with the publications of Johnson and colleagues. In the current checklist, over 80% of the genera and recognizable species that Johnson and co-authors have proposed are synonymized. Their proposed "infratribes" are not used. The differences between the two classifications cannot be attributed solely to different species concepts or to different philosophies of splitting and lumping, as is clear from the examples in reason #3 above. Put bluntly, it is not possible for both classifications to be reasonable estimates of phylogenetic relationships among the Eumaeini. Future generations of systematists will determine which classification is better supported by evidence.

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