FORUM

From the Phylogeny of the Satyrinae Butterflies to the Systematics of Euptychiina (Lepidoptera: Nymphalidae): History, Progress and Prospects

MA MARÍN¹, C PEÑA², AVL FREITAS³, N WAHLBERG⁴, SI URIBE¹

¹Grupo de Investigación en Sistemática Molecular, Univ Nacional de Colombia, Medellín, Colombia
²Museo de Historia Natural, Univ Nacional Mayor de San Marcos, Lima, Peru
³Depto de Biología Animal e Museu de Zoologia, Instituto de Biología, Univ Estadual de Campinas, Campinas, SP, Brasil
⁴Lab of Genetics, Dept of Biology, Univ of Turku, Turku, Finland

Keywords
Brassolinae, Morphinae, Neotropics, rapid radiation, Satyrini

Abstract
We review the various proposals of evolutionary and classification schemes for Satyrinae and particularly Euptychiina butterflies, assessing progress and prospects of research for the group. Among the highlights is the proposal to include Morphini, Brassolini and Amathusiini as part of Satyrinae. Although it is clear that this hypothesis requires further investigation, phylogenetic studies recently conducted recover this clade as part of Satyrinae with high support. The phylogenetic analyses for Euptychiina carried out to date recover the monophyly of the group and have identified a variety of genera as non-monophyletic. Further work is necessary to resolve the position of the subtribe and the evolutionary relationships of several genera.

Introduction

The classification of organisms is an important endeavour in our attempt to understand the diversity of life on this planet (Wilson 2000). A desirable property of classification is that it reflects the evolutionary relationships of the organisms involved, such that names of taxa above the species level define monophyletic groups. This increases the information content of a name and places taxa in an evolutionary context. The advent of molecular systematics has over the past two decades allowed the testing of previous classifications with new forms of data, and indeed has allowed new classifications to be proposed for highly diverse groups of organisms that have previously defied stable classification (e.g., Zahiri et al. 2011). Here we review the latest studies on the diverse clade of butterflies, Satyrinae, and discuss their implications on the classification of the group, which has been very labile over the past 250 years.

The subfamily Satyrinae, with about 2,500 described species, is one of the most diverse groups of butterflies (Peña & Wahlberg 2008), comprising over a third of the Nymphalidae diversity and found on all continents except Antarctica (Ackery et al. 1999, DeVries 2000). The group is particularly diverse in the Neotropics, with approximately 1,200 species in 137 genera (Lamas et al. 2004a), occurring in all habitats with vegetation from sea level to the highlands of the Andes (DeVries 1987).

The host plants of Satyrinae are mostly monocots, with certain eudicot families such as Fabaceae and Menispermaceae being used as well, and some species have been recorded feeding on Lycopodiophyta (Selaginellaceae), Bryophyta (Neckeraceae) and gymnosperms (Cycadaceae) (Singer et al. 1971, Singer & Mallet 1986, Ackery 1988, Beccaloni et al. 2008). In general, Satyrinae consume plants that lack secondary chemical compounds, which partly explains the low specificity for their hosts (Murray 2001a). A consequence
of this is that they are mostly palatable organisms (DeVries 1987, but see Rothschild 2001) and are likely to rely mainly on crypsis to avoid predation.

The estimated age of origin of Satyrinae is from 60 to 65 million years (Ma), and their diversification is thought to be influenced by their host plant use (Peña & Wahlberg 2008, Wahlberg et al 2009, Peña et al 2011). The first Satyrinae evolved in an environment where forests covered most of the land surface and were dominated by dicotyledonous plants (Willis & McElwain 2002). Available monocots were present in the understory, represented by families Arecales, Liliales, Zingiberales and some Poales (Bromeliaceae) (Janssen & Bremer 2004, Linder & Rudall 2005). Diversification of the most species-rich tribe of Satyrinae, Satyrini, is linked to the radiation of the Poaceae (36-23 Ma), which was a determinant factor of the diversity of the tribe (Peña & Wahlberg 2008). Subtribes such as Euptychiina and Pronophilina, which together include more than 1,000 described species (Lamas 2004a, Lamas et al 2004b), are a good example of the impact that the Poaceae radiation had on the Satyrini diversification, where the majority of plant species used as hosts are found (DeVries 1987, Murray 2001ab, Viloria 2003).

The adults of most Satyrinae species are diurnal with low dispersal abilities, flying near the ground, preferably in shaded areas of the forest (understory), feeding on fruits in various stages of decomposition and associated fungi (DeVries 1987, Kremen 1994, Viloria 1998, Murray 2001a). Due to their biology, diversity and distribution, Satyrinae is a dominant group in most communities of butterflies (DeVries 1994, DeVries et al 1997, Brown & Freitas 2000, 2002, Pyrcz & Wojtusiak 2002, Tobar et al 2002, Ribeiro et al 2008, Vu 2009). The subfamily has species that exhibit special affinity for certain types of vegetation as open areas, primary or secondary forest (DeVries et al 1997), being considered useful indicators of ecosystem characteristics (Kremen 1992, 1994, Uehara-Prado et al 2007) and used in population studies (Vila & Björklund 2004, Schmitt et al 2005, Besold et al 2008) and conservation biology (Dennis & Eales 1997, Bergman 1999).

The great diversity of Satyrinae, both in species richness as well as morphology, has meant that there has been great uncertainty and taxonomic difficulties in classifying these butterflies. Until recently, there was no consensus regarding their phylogeny and classification (Viloria 1998, 2003, Lamas et al 2004a, Peña et al 2006, 2011). Thus, priority areas of study required for advancing the knowledge of their biological and evolutionary aspects need to be identified. This work summarizes the recent evolutionary proposals for Satyrinae, particularly for the Euptychiina, reviewing evidence from various studies and providing guidance for the development of further investigations on the group.

**Satyrinae in Nymphalidae**

The most accepted classification of Nymphalidae was proposed by Ackery et al (1999), which is based mainly on the evolutionary relationships suggested by de Jong et al (1996) and the classification of Harvey (1991). In these, as in most other studies, the taxonomic status of Satyrinae remains stable, but their evolutionary relationships with other subfamilies are contested and only agree on the position of Satyrinae being closely related to Morphinae sensu Ackery et al (1999) (Ehrlich 1958, Ehrlich & Ehrlich 1967, Miller 1968, Ackery 1984, DeVries et al 1985, Scott 1985, Martin & Pashley 1992, Weller et al 1996).

Phylogenetic relationships among Satyrinae and Morphinae sensu Ackery et al (1999) are reviewed by recent studies that improved our understanding of the group’s position. These studies have used both morphological (Freitas & Brown 2004) and molecular characters (Brower 2000, Wahlberg et al 2003, Peña et al 2006) to find further support for clades, and more recently employing a total evidence approach in order to obtain more consistent and coherent hypotheses (Wahlberg et al 2005, 2009, Peña & Wahlberg 2008). These studies yielded similar results with morphological characters of adults and immatures (Freitas & Brown 2004) and with DNA sequences of mitochondrial (COI) and nuclear (EF-1α and wingless) (Brower 2000, Wahlberg et al 2003) genes, finding a “satyroid” clade made up of Charaxinae, Calinaginae, Satyrinae and Morphinae. Also, combining morphological characters of adults and molecular data provides further support for this clade (Wahlberg et al 2005), but its relationship to the rest of Nymphalidae remains unresolved.

The lack of resolution within the “satyroid” clade can be attributed to taxonomic sampling, i.e., due to not including a number of taxa in proportion to the diversity of the clade, causing long branch attraction artifacts that affect the resulting topology and stability of the nodes (Poe 1998, Hedtke et al 2006, Heath et al 2008a). This problem is compounded by the presence of variations in rates of speciation and extinction among taxa, producing unbalanced topologies, where limited taxonomic sampling causes a greater loss of balance in the resulting tree (Heath et al 2008b). This situation occurs due to the diversification of Satyrinae (Satyrini in particular), which is linked to the radiation of Poaceae (36-23 Ma) (Peña & Wahlberg 2008, Peña et al 2011), and probably has higher speciation rates than the rest of Nymphalidae.

Seeking to reduce the effect of attraction of long branches and with the aim of obtaining a more robust phylogenetic proposal, Peña et al (2006) conducted a sampling of 191 taxa using characters of the mitochondrial gene COI and the nuclear genes EF-1α and wingless. These authors assessed mainly the monophyly of Satyrinae and relations among their tribes and subtribes, finding...
a solid support for the clade comprised of Satyrinae and Morphinae (Morphini, Brassolini and Amathusiini). The Satyrinae, as conceived by the traditional classification (Ackery et al. 1999), appeared as a paraphyletic assemblage also including Morphinae tribes, suggesting that these tribes should be placed within Satyrinae.

These results are also supported by Peña & Wahlberg (2008) and Wahlberg et al. (2009). The latter study used a combination of 235 morphological characters and 10 nuclear and mitochondrial genes in 400 genera of Nymphalidae (75% of the total generic diversity). The results establish a “satyroid” clade made up of Calinaginae, Charaxinae and Satyrinae, where Calinaginae is the sister group of Charaxinae + Satyrinae. Morphinae sensu Ackery et al. (1999) emerges as an unnatural group, with the tribes Morphini, Brassolini and Amathusiini grouped within Satyrinae (Fig 1). Thus, with this delineation of Satyrinae, the subfamily is recovered as a monophyletic group and its taxonomic position and evolutionary relationships with other subfamilies of the group are clear.

Evolutionary Relationships within Satyrinae

Satyrinae has complex relations among its groups, some being cohesive (tribes and subtribes), structured and others poorly defined. According to the schemes proposed by Peña et al. (2006, 2011), Peña & Wahlberg (2008) and Wahlberg et al. (2009) (Fig 1), the subfamily includes four well defined groups: 1) the two Neotropical clades (Morphini + Brassolini), 2) the clade [Elymnini + Amathusiini + Zetherini + (Dirini + Melanitini)], 3) the clade including the Neotropical Haeterini, and 4) the speciose Satyrini. Taking into account these clades, Satyrinae could include nine tribes and 16 subtribes (Table 1), although several of these groups have received little attention, and do not have clear and more definitive studies to assess their position and taxonomic status.

The Morphini + Brassolini clade was initially recognized by Ehrlich (1958) and Ehrlich & Ehrlich (1967) and treated as the subfamily Morphinae, until Miller (1968) included most of its members [Brassolini and Antirrhina (Morphini)] within Satyrinae. Later studies resurrected Morphini + Brassolini (including Biina) (DeVries et al. 1985, Ackery et al. 1999, Vane-Wright & Boppré 2004) and the clade is currently considered as one of the most stable within Satyrinae, being supported by molecular and morphological characters (Peña et al. 2006, Peña & Wahlberg 2008, Wahlberg et al. 2009).

The clade composed by Melanitini, Dirini, Amathusiini, Zetherini and Elymnini, of almost exclusively Paleotropical distribution, has been recovered by various studies, but the deeper relationships remain unresolved. The most stable group is composed by the Old World Melanitini + Dirini, which is recovered in all studies (Peña et al. 2006, Peña & Wahlberg 2008, Wahlberg et al. 2009, Price et al. 2010), with both tribes being well-defined.
From the Phylogeny of the Satyrinae Butterflies to the Systematics of Euptychiina

Marín et al.

Table 1 Different classification proposals for Satyrinae.

| Satyrinae | Satyrinae | Satyrinae |
|-----------|-----------|-----------|
| Miller (1968) | Harvey (1991) | Recent results¹ |
| Satyrinae | Satyrinae | Satyrinae |
| Haeterinae | Haeterini | Morphini |
| Haterini | Biini | Antirrhinea |
| Brassolinae | Melanitii | Morphina |
| Brassolini | Biiti | Brassolini |
| Biinae | Eriti | Biina |
| Melanitini | Ragadiini | Brassolina |
| Antirrhini | Elymiini | Naropina |
| Blini | Elymiini | Elymiini |
| Elymiinae | Lethini | Amathusiini |
| Elymiini | Mycalesi | Zetherini |
| Lethini | Zethertii | Dirini |
| Mycalesini | Satyrini | Melanitini |
| Zetherini | Hypocystini | Haeterini |
| Eritinae | Ypthimiti | Satyrini |
| Eritini | Euptychiti | Parargina |
| Ragadiinae | Coenonymphiti | Lethina |
| Ragadini | Manioliti | Mycalesina |
| Satyrinae | Erebiiti | Coenonymphina |
| Hypocystini | Pronophiliti | Eritina |
| Ypthimini | Melanargiti | Ragadiina |
| Euptychini | Satyriti | Euptychina |
| Coenonymphini | Ypthimina | Ypthimina |
| Manioloni | Melanargina | Maniolina |
| Erebiini | Pronophili | Pronophili |
| Pronophili | Eribeina | Eribeina |
| Melanargiini | Satyrina |

¹Consensus resulting from Kodandaramaiah et al (2010a), Peñz (2007), Peña et al (2006), Peña & Wahlberg (2008), Peña et al (2011) and Wahlberg et al (2009).

The evolutionary relationships of Amathusiini, Zetherini and Elymiini within the clade are not yet resolved. The tribes Amathusiini (without Hyantis and Xanthotaenia) and Zetherini appear well supported, but Elymiini (comprising only Elymiias) is grouped with different tribes in different studies: with Haeterini (fig 7 in Peña et al 2006), Amathusiini (fig 1 in Peña & Wahlberg 2008, and Wahlberg et al 2009) and Melanitini + Dirini (fig 3s in Wahlberg et al 2009). The genus Xanthotaenia is sister to the tribe Zetherini with strong support, and should be transferred to that tribe. The position of Hyantis (and the putatively related Morphopsis), a genus traditionally placed in Amathusiini, seems uncertain as it is not supported as part of this tribe and in some cases appears to be related with Elymiini (fig 3s in Wahlberg et al 2009) or the clade Dirini + Melanitini (Peña & Wahlberg 2008). Clearly this clade of butterflies requires further work to resolve relationships of the taxa comprising it.

Haeterini is a small group of Neotropical distribution consisting of 21 species and five genera (Lamas 2004b). Although well supported, its phylogenetic position is ambiguous. Miller (1968) placed the Haeterini as the sister of all other Satyrinae. In recent studies, however, this group appeared as sister to Satyrini (Peña & Wahlberg 2008) or to the clade ((Melanitini + Dirini) + Amathusiini + Zetherini + Elymniini) (fig 3s in Wahlberg et al 2009).

The tribe Satyrini is the most diverse of the subfamily, comprising over 80% of the species, distributed in five continents. This clade is recovered in various phylogenetic studies (Peña et al 2006, 2011, Peña & Wahlberg 2008, Wahlberg et al 2009) with partially resolved relationships and only supported by molecular characters (Fig 2) [Peña et al 2006, 2011, Peña & Wahlberg 2008 (their fig 1), Wahlberg et al 2009 (their figs 1 and 3s), Kodandaramaiah et al 2010a].

The lack of resolution in the topology of Satyrini is
most likely due to the rapid radiation of the group (Peña & Wahlberg 2008, Peña et al 2011) that produces a combination of long and short branches causing branch attraction problems and creates an artifact between the outgroup and ingroup, making it difficult to recover the monophyly of the entire group (Shavit et al 2007, Whittlefield et al 2007).

This phenomenon occurs in most of the subtribes of Satyrini (Peña et al 2011) and has been recently reported in Coenonymphina (Kodandaramaiah et al 2010a), Euptychina (Peña et al 2010) and Mycalesina (Kodandaramaiah et al 2010b). Peña et al (2011) find that the initial selection of Haeterini as outgroup for Satyrini produces unstable trees where Euptychia (Euptychina) appears outside of Satyrini. This problem was solved with an improved taxonomic sampling in the outgroup level with the inclusion of several Morphini (rooting with Morpho) and Brassolini. This managed to break the branch attraction that Haterini produced with the long terminal branch of the ingroup (Euptychia) recovering Satyrina as a monophyletic group.

In a study on Coenonymphina, Kodandaramaiah et al (2010a) established that the in-group relationships can be affected by changes in sampling density in combination with the outgroup taxa selected, finding that the effect of the outgroup is more pronounced in the basal nodes (Kodandaramaiah et al 2010a, Peña et al 2011). Thus, proper selection of outgroups can reduce the traction between them and the genera near the basal nodes, allowing to recover the monophyly of the group.

Satyrini is divided into two major clades. One clade includes Coenonymphina + Ragadiina + Eritina + [Parargina + (Mycalesina + Lethina)], with Coenonymphina represented by the genera that Miller (1968) placed in his Coenonymphina, Hypocystina and the genus Oressinoma (Euptychini). The position of Ragadiina within the clade is complex, appearing polyphyletic, with Ragadia as the sister group of Eritina, while Acroptalmia forms a clade with Loxerebia and Coelites (Peña et al 2011), a result that requires further study as these genera are poorly represented in phylogenetic studies conducted to date.

The other clade is composed by the tribes Euptychiina + Ypthimina + (Melanargiina + Satyrina) + Maniolina + Pronophilina + Erebiina, with poorly resolved internal relationships. Ypthimina appears as a monophyletic group that includes the genera that Miller (1968) located in Ypthima-series and Melampias-series, however the genera belonging to the Callerebia-series seem not to belong to Ypthimina, sampled genera include Loxerebia, Callerebia and Paralasa, which are located in different parts of the phylogeny of Satyrini (Peña et al 2011).

The Neotropical Pronophilina is one of the most diverse groups of butterflies with complex phylogenetic relationships, reflected in the classification of Lamas & Viloria (2004a) and Lamas et al (2004b). In this classification, the genera that Miller (1968) grouped in Pronophilina are divided into three subtribes, Hypocystina (now Coenonymphina), Erebiina and Pronophilina. This proposal arose from the phylogenetic study by Viloria (1998, 2003, 2007), which was based on morphological characteristics of adults, and reported a close relationship of the Neotropical genera of Pronophilina with Australian Coenonymphina and Palearctic Erebiina.

The phylogeny proposed by Viloria (1998, 2003, 2007) recovered Pronophilina sensu Miller (1968) largely as a non-monophyletic group, with most of the genera organized in two clades largely agreeing with the classification proposed by Lamas et al (2004b). The first clade is composed mostly by what he called the “Neotropical Coenonymphina and Erebiina”, and the second clade corresponds to the Pronophilina sensu stricto. However, recent comprehensive studies (Peña et al 2006, 2011, Wahlberg et al 2009) recovered the two clades as sister groups which are not related to the Old World Coenonymphina and Erebiina. Thus, it appears that the classification proposed by Lamas et al (2004b) and Lamas & Viloria (2004a) should be reverted back to the one proposed by Miller (1968).

The phylogenetic relationships within Pronophilina continue to be a complex issue. The studies of Peña et al (2006, 2011) and Wahlberg et al (2009) did not recover the complete monophyly of the group, with Calisto and Eretris, two genera traditionally treated as part of Pronophilina, appearing outside this clade, probably as an artifact of long branch attraction (Peña et al 2011). There is a clear need for further phylogenetic studies that involve large taxonomic sampling and employing a large number of molecular and morphological characters. Assessing the monophyly of the subtribes of Satyrini is a priority in order to obtain more robust phylogenetic proposals for the group.

**Phylogenetic Relationships and Classification of Euptychiina**

Euptychiina is a very diverse group of Satyrinae, with over 400 recognized species (Lamas 2004a) in 44 genera (Table 2, Fig 3) (Peña et al 2010). The group is distributed mainly in the Neotropical region, with the presence of some species in the Nearctic region and one in Southeast Asia. They are found from sea level to 3,500 m.a.s.l, although the largest species richness occurs in the lowlands (DeVries 1994, DeVries et al 1997, Brown & Freitas 2002, Tobar et al 2002, Ribeiro et al 2008).

The taxonomy of the group is among the most poorly known of all Neotropical butterflies because of their high diversity and the morphological homogeneity of its members (Peña & Lamas 2005). There is a large number of species to be described (e.g. in Caeruleuptychia,
## Table 2 Different proposed classifications of Euptychiina.

| Miller (1968)               | Lamas (2004b)                      | Peña et al (2010)                        |
|-----------------------------|-----------------------------------|-----------------------------------------|
| Archeuptychia Forster       | Archeuptychia Forster             | Amphidecta Butler                       |
| Caeruleuptychia Forster     | Caenoptychia Le, Cerf             | Archeuptychia Forster                   |
| Capronnieria Forster        | Caeruleuptychia Forster           | Caenoptychia Le, Cerf                   |
| Cepheuptychia Forster       | Capronnieria Forster              | Cepheuptychia Forster                   |
| Chloreuptychia Forster      | Cepheuptychia Forster             | Capronnieria Forster                    |
| Cissia Doubleday            | Cercyeuptychia Miller & Emmel     | Cepheuptychia Forster                   |
| Coeruleotaygetis Forster   | Chloreuptychia Forster            | Cercyeuptychia Miller & Emmel           |
| Cyllopsis Felder            | Cissia Doubleday                  | Chloreuptychia Forster                  |
| Erichthodes Forster         | Coeruleotaygetis Forster          | Cissia Doubleday                        |
| Euptychia Hübner            | Cyllopsis Felder                  | Coeruleotaygetis Forster                |
| Euptychoides Forster        | Erichthodes Forster               | Cyllopsis Felder                        |
| Godartiana Forster          | Euptychia Hübner                  | Euptychoides Forster                    |
| Harjesia Forster            | Euptychoides Forster              | Euptychia Hübner                        |
| Haywardiana Forster         | Forsterinaria Gray                | Euptychoides Forster                    |
| Hermeuptychia Forster       | Godartiana Forster                | Forsterinaria Gray                      |
| Magneuptychia Forster       | Harjesia Forster                  | Godartiana Forster                      |
| Megeuptychia Forster        | Hermeuptychia Forster             | Guianaza Freitas & Peña                 |
| Megisto Hübner              | Magneuptychia Forster             | Harjesia Forster                        |
| Moneuptychia Forster        | Magneuptychia Forster             | Hermeuptychia Forster                   |
| Neonympha Hübner            | Megisto Hübner                    | Magneuptychia Forster                   |
| Oressinoma Doubleday        | Moneuptychia Forster              | Megeuptychia Forster                    |
| Paramacera Butler           | Oressinoma Doubleday              | Megisto Hübner                          |
| Parataygetis Forster        | Paramacera Butler                 | Moneuptychia Forster                    |
| Pareuptychia Forster        | Parataygetis Forster              | Neonympha Hübner                        |
| Paryphthimoides Forster     | Paryphthimoides Forster           | Palaeonympha Butler                     |
| Pharneuptychia Forster      | Paryphthimoides Forster           | Paramacera Butler                       |
| Pindis Felder               | Pharneuptychia Forster            | Parataygetis Forster                    |
| Posttaygetis Forster        | Pindis Felder                     | Pareuptychia Forster                    |
| Praefaunula Forster         | Posttaygetis Forster              | Paryphthimoides Forster                 |
| Pseudoptychia Forster       | Praefaunula Forster               | Pharneuptychia Forster                  |
| Pseudodebis Forster         | Pseudoptychia Forster             | Pindis Felder                           |
| Rareuptychia Forster        | Pseudodebis Forster               | Posttaygetis Forster                    |
| Satyrotaygetis Forster      | Rareuptychia Forster              | Praefaunula Forster                     |
| Splendeuptychia Forster     | Satyrotaygetis Forster            | Pseudoptychia Forster                   |
| Taygetina Forster           | Splendeuptychia Forster           | Pseudodebis Forster                     |
| Taygetis Forster            | Taydebis Freitas                  | Rareuptychia Forster                    |
| Vareuptychia Forster        | Taygetina Forster                 | Satyrotaygetis Forster                  |
| Weymerana Forster           | Taygetis Hübner                   | Splendeuptychia Forster                 |
| Yphtimoides Forster         | Taygetomorpha Miller              | Taydebis Freitas                        |
| Zischkaia Forster           | Yphtimoides Forster               | Taygetina Forster                       |
|                            | Zischkaia Forster                 | Taygetis Hübner                         |
|                            |                                   | Taygetomorpha Miller                    |
|                            |                                   | Yphtimoides Forster                     |
|                            |                                   | Zischkaia Forster                       |
Fig 3 A pout-pourri of Euptychiina diversity (all in ventral view): 1) *Cepheuptychia cephus*, 2) *Chloreuptychia arnaca*, 3) *Cissia similis*, 4) *Euptychoides gripe*, 5) *Euptychia enyo*, 6) *Forsterinaria boliviana*, 7) *Hermeuptychia pompilia*, 8) *Magneuptychia tricolor*, 9) *Megisto cymela*, 10) *Moneuptychia paeon*, 11) *Paramacera xicaque*, 12) *Splendeuptychia boliviensis*, 13) *Pareuptychia hesionides*, 14) *Palaeonympha opalina*, 15) *Taygetis thamyra*, 16) *Taygetomorpha celia*, 17) *Yphthimoides* sp., 18) *Zischkaia pacarua*. 
Euptychia, Magneuptychia and Splendeuptychia), making clear the importance of detailed taxonomic work in the group.

Most Euptychiina genera were described by Forster (1964), based on specimens from Bolivia. In that work, Forster described a total of 33 genera, although he did not provide detailed descriptions or diagnostic characteristics for them, and also did not include many species from other regions of the Neotropics. Forster’s results were taken into account by Miller (1968) in his proposal for the classification of Euptychiina (Table 2), but it has been ignored by many authors, who have preferred to use Euptychia in a broad sense or just considered the genera described prior to the work of Forster (DeVries 1987, D’Abrera 1988). Recently, Lamas (2004a), following the classification of Miller (1968), retained most of the genera proposed by Forster (1964) and included several additional genera (Cercyeuptychia, Caenoptychia, Taydebis and Taygetomorpha) (Table 2). Although this scheme is still lacking evolutionary support, it is now widely accepted and is taken as a baseline for conducting further studies in this group.

Investigations conducted so far that have looked at phylogenetic relationships in Euptychiina used DNA sequences of mitochondrial (COI, Cyb and ND1) and nuclear genes (EF-1α, wingless, GAPDH and RpS5) (Murray & Prowell 2005, Peña et al 2006, 2010, Marín et al 2009), as well as characters of immature morphology (Murray 2001a). Although the results of Murray (2001a) have not been formally published, they provide important information on immature stages for further investigations on the group.

The proposed phylogenies of Murray & Prowell (2005) and Peña et al (2006, 2010) show that Euptychiina sensu Lamas (2004a) is not a monophyletic taxon. Some genera previously regarded as incertae sedis, such as Amphipecta and Palaeonympha, are now included in Euptychiina, and Oressinoma, a genus traditionally recognized as a member of Euptychiina, is more closely related to Coenonympha (Peña et al 2006).

The research on Euptychiina has struggled to show the monophyly of the group (Murray & Prowell 2005, Peña et al 2010). Again, it is believed that this is caused by problems of long branch attraction, particularly in Euptychia (Peña et al 2011), which is recognized as the sister group of the remaining members of the subtribe (Peña et al 2006, 2010). For this genus, it is established that, after diverging from the original lineage, species underwent rapid evolutionary changes, resulting in spurious grouping with other long branches of Satyrini (Peña et al 2011).

Within the subtribe, the evolutionary reconstruction proposed shows three (Murray & Prowell 2005) to five clades (Peña et al 2010). The Megisto group proposed by Peña et al (2010) was not recovered in previous studies, probably due to a lower taxonomic sampling, although similar groups were recovered (Murray & Prowell 2005, Peña et al 2006). This group is found to be sister to the rest of Euptychiina and consists of the genera (Palaeonympha + Megisto + Cissia + Moneuptychia + Yphthimoides). The first two genera are of North America and Southeast Asia distribution, Cissia is widely distributed in the Neotropical region and is particularly diverse in Central America and Northern Andes and appears as the sister group of Yphthimoides + Moneuptychia, both highly diversified in Southeast Brazil.

Recent results suggest a North American origin of Palaeonympha, a genus that shares several morphological characters with Megisto (Miller 1968), giving support to the proposed biogeographic scenario of Peña et al (2010), in which Palaeonympha ancestors crossed the Asian continent by the Bering Strait and settled in Southeast Asia.

Cissia is always recovered as a polyphyletic group, with their members spread in the clades Splendeuptychia and Megisto (Murray & Prowell 2005, Peña et al 2010). In the group Yphthimoides + Moneuptychia (Peña et al 2010), Yphthimoides is recovered as monophyletic, even though taxonomic sampling is still unsatisfactory and has not included the type species, Y. yphthima (C. Felder & R Felder). For Moneuptychia, the species are split into two clades, one composed by M. paeon (Godart) and M. griseldis (Weymer) and related to Yphthimoides, and a second composed by M. itapeva Freitas, Pharneuptychia sp., Euptcyoides castrensis (Shaus), M. giffordi Freitas et al and M. soter (Butler), the latter being the type species of the genus (Freitas 2007, Freitas et al 2010, Peña et al 2010).

The Hermeuptychia clade consists of Hermeuptychia and several taxa that were previously considered incertae sedis. It is the most widely distributed group of Euptychiina, found from northern Argentina to southern United States, occurring from sea level to about 3,000 meters above sea level (DeVries 1987). This clade is recovered as monophyletic in all published studies so far (Murray & Prowell 2005, Marín et al 2009, Peña et al 2010). However, Hermeuptychia includes a complex of cryptic species of undefined phylogenetic relationships (Marín et al 2009).

Peña et al (2010), with increased taxonomic sampling, found the sister group of Hermeuptychia to be the clade formed by [Rareuptychia clia (Weymer) + (Amphidecta calliomma (C. Felder & R. Felder) + Euptcyoides ordinata (Weymer)]], the latter two species treated as incertae sedis by Lamas (2004b). The genus Amphidecta, previously
treated as part of Pronophilina (Miller 1968) and as *incertae sedis* by Lamas & Viloria (2004b), has been finally included in Euptychina by Peña et al. (2006).

The *Taygetis* clade is the most stable group within Euptychina, being recovered in all known studies (Murray & Prowell 2005, Peña et al. 2006, 2010, Marín et al. 2009). Two main groups can be recognized in this clade, the first composed by *Forsterinaria* + *Harjesia blanda* (Möslicher) + *Parataygetis* + *Guaianaza* + *Posttaygetis*, and the second composed by *Pseudodebis* + *Taygetis* + *Taygetomorpha* + *Harjesia oreba* (Butler). In the first group, *Forsterinaria* is paraphyletic in relation to *Guaianaza*, and the validity of the former genus should be revised. In the second group, *Taygetis* appears, as a non-monophyletic taxon, in two separate clades, showing that there is a need for a revision of this genus.

The *Pareuptychia* clade consists of *Satyrotauggetis satyrina* (H. W. Bates), *Neonympha aerolatus* (Smith), *Taydebis peculiaris* (Butler), *Splendeuptychia doxes* (Godart), *Splendeuptychia furina* (Hewitson) and of the genera *Pareuptychia*, *Mgeuptychia* and *Eriichthodes* (Murray & Prowell 2005, Peña et al. 2010). The sister group of the *Pareuptychia* clade is formed by *Chloreuptychia* + *Cepheuptychia cephus* (Fabricius) + *Archeuptychia*. Although this is a clade with high support, its internal phylogenetic relationships are poorly defined. The genus *Chloreuptychia* is clearly polyphyletic, with their members divided into two distinct clades, and by including *Archeuptychia* and *Cepheuptychia* within it.

Finally, the *Splendeuptychia* clade is a group composed of several poorly defined genera, with the exception of *Caerulepuytichia*, which is recovered as a monophyletic group. Currently, *Splendeuptychia*, *Magneuptychia* and *Cissia* are recovered as polyphyletic or paraphyletic groups, being indicative of the complex taxonomic problems of this group (Murray & Prowell 2005, Peña et al. 2010).

In addition to the clades discussed above, there are a number of taxa that do not form clearly defined groups, and whose phylogenetic position remains unclear. Among these taxa we can highlight (*Cercuyeptichia + Godartiana*) + (*Chloreuptychia catharina* (Staudinger) *+ Pindis*) and a clade consisting of *Zischkaia*, *Pharmeuptychia innocenta* (C. Felder & R. Felder), *Splendeuptychia bolivienis* and *S. itonis* (Peña et al. 2010). More data will be required to elucidate the phylogenetic relationships of these taxa.

To summarize, several Euptychiina genera are polyphyletic, with species being recovered scattered in different lineages as inferred by different phylogenetic proposals of the subtribe (Murray & Prowell 2005, Peña et al. 2010). This is the situation of *Euptychoides*, *Cissia*, *Splendeuptychia*, *Chloreuptychia*, *Harjesia* and *Paryphthimoides*, which are thus of possible artificial composition and need to be revised. In addition, several genera are paraphyletic, such as *Taygetis*, *Pseudodebis*, *Forsterinaria*, *Magneuptychia* and *Moneuptychia*. These results show that Euptychina is a group with taxonomic problems with some incorrectly defined genera of paraphyletic or polyphyletic composition and presence of complex species, making identification difficult at this level.

**Are Stable Classifications Attainable?**

The use of molecular characters has been crucial to the resolution of phylogenetic relationships in the subfamily Satyrinae. Certain clades, such as Morphini and Haeterini, have long been well characterized by morphological characters, yet their positions within Satyrinae, or indeed Nymphalidae, have been controversial as previously discussed. Molecular characters have the advantage that their numbers can be increased almost without limit, and phylogenetic hypotheses derived using them can be informative about the evolution of morphological characters. Morphological characters on the other hand are still very necessary to visually categorize specimens in the field and in museum collections. Molecular means of identifying specimens to species or higher taxa will never replace visual inspection of them, and can be seen as a complementary method to the traditional methods (see discussion in Silva-Brandão et al. 2009).

As our review of the studies of Satyrinae has shown, molecular methods have allowed robust testing of proposed classifications of the group. Many proposed classifications can be rejected based on the results and new, unexpected, relationships have been uncovered. The amount of data used (up to 10 gene regions) or taxa sequenced (up to 90% of all extant species for some higher taxa) has cleared many questions, but has also left many questions unanswered, as well as raised new questions. Clearly much more work is necessary to arrive at a stable classification for all species in Satyrinae, yet the work so far has suggested a stable higher classification for the subfamily.

An advantage of the Linnean hierarchical system is that all clades do not need to be named, and thus unstable clades need not be placed in a formal classification. Our review on Satyrinae is a case in point, as we are able to place almost all species in higher taxa, such as subfamily, tribe and subtribe, which are stable and robust to the addition of data, even though the relationships of some taxa are not stable. For example, the position of Euptychina within Satyrini is not stable, but it is without question within the larger clade Satyrini, and not e.g. in Morphini. The classification thus remains stable, even if the position of Euptychiina changes within Satyrini. It is the search for such stable clades that should drive the studies on the higher classification of life. Such thoughts are not entirely relevant to the species level, as different
processes are acting on populations and the course of evolutionary history is still in the running, whereas in higher taxonomic groups, one can consider that what happened, happened and we are simply trying to uncover that history.

Conclusions

The phylogenetic proposals of Peña et al. (2006), and especially those of Wahlberg et al. (2009), give light on the situation and phylogenetic position of Satyrinae, solving in part the evolutionary relationships of this subfamily and its tribes. Likewise, these studies done with molecular and morphological characters for obtaining stronger evolutionary hypothesis. These studies leave the door open for future research on each of the tribes of Satyrinae and show the need of a biogeographic analysis to evaluate the hypothesis proposed by Miller (1968). The latter seems to be corroborated in part by current assumptions.

In Euptychina, it is necessary to conduct phylogenetic studies that employ ecological or morphological characters to complement the work done with molecular and morphological characters of immature stages (Murray & Prowell 2005, Peña et al. 2006, 2010, Marín et al. 2009). This work has helped to resolve the monophyly of the group, but still has problems and ambiguities. The inclusion of other characters can bring information to the solution of these problems. It will be possible to identify morphological synapomorphies that define genera and other clades, which is needed to properly classify the new species that still remain to be described.

Within the subtribe, it is necessary to perform phylogenetic studies focused on clades that have some support (Megisto, Hermeuptychia, Tagetis, Pareuptychia and Splendeuptychia), allowing more detailed analyses, particularly of the most diverse genera. This work should continue with the revision of various Euptychina genera, giving priority to Splendeuptychia, Paryphthimoides, Euptychoides, Euptychia, Magneuptychia, Cissia and Chloreuptychia, which are paraphyletic or polyphyletic, covering much of the diversity of the tribe.

Acknowledgments

The first author is grateful to Ana Maria Velez, who gave valuable feedback on earlier drafts of this paper, Angel Viloria, who collaborated with valuable information for the discussion, and DIME (90202038) for financial support. AVLF acknowledges FAPESP (grants no. 00/01484-1 and no. 04/05269-9), CNPq (fellowship no. 300282/2008-7) and the National Science Foundation (DEB grant no. 0527441). NW acknowledges the Academy of Finland for financial support.

References

Ackery PR (1984) Systematic and faunistic studies on butterflies, p.9-21. In Vane-Wright RL Ackery PR (eds) The biology of butterflies. Symposium of the Royal Entomological Society of London, Number 11. Academic Press, London.

Ackery PR (1988) Hostplants and classification: a review of nymphalid butterflies. Biol J Linn Soc 33: 95-203. doi: 10.1111/j.1095-8312.1988.tb00446.x

Ackery PR, de Jong R, Vane-Wright RI (1999) The butterflies: Hedyloidea, Hesperoidea and Papilionoidea. In Kristensen NP (ed) Lepidoptera: moths and butterflies. I. Evolution systematics and biogeography. Handbook of zoology. Vol IV Arthropoda: Insecta. Part 35. Walter de Gruyter, Berlin, 491p.

Becalona GW, Hall SK, Viloria AL, Robinson GS (2008) Catalogue of the hostplants of the neotropical butterflies / catálogo de las plantas huésped de las mariposas neotropicales. In m3m - Monografías tercer milenio, Vol. 8. S.E.A., RIBES-CYTED, The Natural History Museum, Instituto Venezolano de Investigaciones Científicas, Zaragoza, 536p.

Bergman K-O (1999) Habitat utilization by Lopinga achine (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biol Conserv 88: 69-74. doi: 10.1016/S0006-3207(98)00088-3

Bergsten J (2005) A review of long-branch attraction. Cladistics 21: 163-193. doi: 10.1111/j.1091-0312.2005.00059.x

Besold J, Huck S, Schmitt T (2008) Allozyme polymorphisms in the small heath, Coenonympha pamphilus: recent ecological selection or biogeographical signal? Ann Zool Fenn 45: 217-228.

Brower AVZ (2000) Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the wingless gene. Proc R Soc Biol Sci Ser B 267: 1201-1211. doi: 10.1098/rspb.2000.1129

Brown Jr KS, Freitas AVL (2000) Atlantic Forest butterflies: indicators for landscape conservation. Biotropica 32: 934-956. doi: 10.1111/j.1744-7429.2000.tb00631.x

Brown Jr KS, Freitas AVL (2002) Butterflies communities of urban forest in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. J Insect Conserv 6: 217-231. doi: 10.1023/A:1024462523826

D’Abera B (1988) Butterflies of the Neotropical Region, Part 5 Nymphalidae (conc.), Satyrinae. Fearny Creek, Hill House Publishers, 190p.

de Jong R, Vane-Wright RL Ackery PR (1996) The higher classification of butterflies (Lepidoptera): problems and prospects. Entomol Scand 27: 65-101.

Dennis RLH, Eales HT (1997) Patch occupancy in Coenonympha tullia (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. J Insect Conserv 1:
167-176. doi: 10.1023/A:1018455714879

DeVries PJ (1987) The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton, Princeton University Press, 327p.

DeVries PJ (1994) Patterns of butterfly diversity and promising topics in natural history and ecology, p. 187-194. In MacDade L, Bawa KS, Hartshorn G, Hespenheide H (eds) La Selva: ecology and natural history of a neotropical rainforest. Chicago, University of Chicago Press, 493p.

DeVries PJ (2000) Diversity of butterflies, p. 559-574. In Levin S (ed) Encyclopedia of biodiversity. San Diego, Academic Press, 4666p.

DeVries PJ, Kitching IJ, Vane-Wright RI (1985) The systematic classification of the butterflies (Lepidoptera: Papilionoidea). Univ Kansas Sci Bull 39: 305-370.

DeVries PJ, Murray D, Lande R (1997) Species diversity in vertical, horizontal and temporal dimensions of fruit-feeding butterfly community in an Ecuador rainforest. Biol J Linn Soc 62: 343-364.

Ehrlich PR (1958) The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). Univ Kansas Sci Bull 39: 305-370.

Ehrlich PR, Ehrlich AH (1967) The phenetic relationships of the butterflies I. Adult taxonomy and the nonspecificity hypothesis. Syst Zool 16: 301-317.

Forster W (1964) Beiträge zur Kenntnis der Insekten fauna Boliviens XIX Lepidoptera III. Satyridae. Veröffentlichungen der Staatssammlung München 8: 51-188, pls. 27-35.

Freitas AVL (2003) Description of a new genus for "Euptychia" peculiaris (Nymphalidae: Satyrinae): immature stages and systematic position. J Lepid Soc 57: 100-106.

Freitas AVL (2007) A new species of Moneuptychia Forster (Lepidoptera: Satyrinae: Euptychiina) from the highlands of Southeastern Brazil. Neotrop Entomol 36: 919-925. doi: 10.1590/S1519-566X2007000600014

Freitas AVL, Emery EO, Mielke OHH (2010) A new species of Moneuptychia Forster (Lepidoptera: Satyrinae: Euptychiina) from central Brazil. Neotrop Entomol 39: 83-90, doi: 10.1590/S1519-566X2010000100011

Harvey DJ (1991) Higher classification of the Nymphalidae, Appendix B, p. 255-268. In Nijhout HF (ed) The development and evolution of butterfly wing patterns. Washington, D.C., Smithsonian Institution Press, 318p.

Heath TA, Hedtke SM, Hillis DM (2008a) Taxon sampling and the accuracy of phylogenetic analyses. J Syst Evol 46: 239-257. doi: 10.3724/SJR.1002.2008.08016

Heath TA, Zwickl DJ, Kim J, Hillis DM (2008b) Taxon sampling affects inferences of macroevolutionary processes from phylogenetic trees. Syst Biol 57: 160-166. doi: 10.1080/10635150701884640.

Hedtke SM, Townsend TM, Hillis DM (2006) Resolution of phylogenetic conflict in large data sets by increased taxon sampling. Syst Biol 55: 522-529. doi: 10.1080/10635150600697358

Jansen T, Bremer K (2004) The age of major monotypic groups inferred from 800 rbcL sequences. Bot J Linn Soc 146: 385-398. doi: 10.1111/j.1095-8339.2004.00345.x

Kodandaramaiah U, Peña C, Braby MF, Grund R, Müller CJ, Nylin S, Wahlberg N (2010a) Phylogenetics of Coenonymphina (Nymphalidae: Satyrinae) and the problem of rooting rapid radiations. Mol Phylogenet Evol 54: 386-394. doi: 10.1016/j.ympev.2009.08.012

Kodandaramaiah U, Lees DC, Müller CJ, Torres E, Karanth KP, Wahlberg N (2010b) Phylogenetics and biogeography of a spectacular Old World radiation of butterflies: the subtribe Mycalesina (Lepidoptera: Nymphalidae: Satyrini). BMC Evol Biol 10: 317, doi: 10.1186/1471-2148-10-172

Kremen C (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. Ecol Appl 2: 203-217.

Kremen C (1994) Biological inventory using target taxa: a case study of the butterflies of Madagascar. Ecol Appl 4: 407-422.

Lamas G (2004a) Nymphalidae. Satyrinae. Euptychiina, p.217-223. Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner J B (ed) Atlas of the Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers, 439p.

Lamas G (2004b) Nymphalidae. Satyrinae. Haeterini, p.205-206. Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner J B (ed) Atlas of the Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers, 439p.

Lamas G, Viloria AL (2004a) Nymphalidae. Satyrinae. Erebiina - Hypocystina, p.215-217. Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner J B (ed) Atlas of the Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers, 439p.

Lamas G, Viloria AL, Pyrcz TW (2004a) Nymphalidae. Satyrinae. Incertae sedis, p.224. Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner J B (ed) Atlas of the Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers, 439p.

Lamas G, Viloria AL, Pyrcz TW (2004b) Nymphalidae. Satyrinae. Pronophiliina, p.206-215. Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner J B (ed) Atlas of the Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers, 439p.
molecular de Euphychina (Lepidoptera: Satyrinae) del norte de la cordillera central de los Andes. Rev Colomb Entomol 35: 235-244.

Martin JA, Pashley DP (1992) Molecular systematic analysis of butterflies family and some subfamily relationships (Lepidoptera: Papilionoidea). Ann Entomol Soc Am 85: 127-139.

Miller LD (1968) The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). Mem Am Entomol Soc 24 [6] + iii + 174p.

Murray DL (2001a) Immature stages and biology of Taygetis Hübner (Lepidoptera: Nymphalidae). Proc Entomol Soc Wash 103: 932-945.

Murray DL (2001b) Systematics of Neotropical Satyrinae butterflies (Nymphalidae: Satyrinae: Euphychina) based on larval morphology and DNA sequence data and the evolution of life history traits. Ph.D. thesis. New Orleans, Louisiana State University, 380p.

Murray DL (2002) The vertical distribution of pronophiline butterflies (Lepidoptera, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. Glob Ecol Biogeogr 11: 211-221. doi: 10.1046/j.1466-822X.2002.00285.x

Ribeiro DB, Prado PI, Brown Jr KS, Freitas AVL (2008) Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. Divers Distrib 14: 961-968. doi: 10.1111/j.1472-4642.2008.00905.x

Rothschild M (2001) The Marbled White (Melanargia galathea) a toxic butterfly. Antenna, 25: 176-177.

Scott JA (1985) The phylogeny of butterflies (Papilionoidea and Hesperoidea). J Res Lepid 23: 241-181.

Singer MC, Ehrlich PR, Gilbert LE (1971) Butterfly feeding on lycopsid. Science 172: 1341-1342.

Shavit L, Penny D, Hendy MD, Holland BR (2007) The problem of rooting rapid radiations. Mol. Biol. Evol 24: 2400-2411. doi: 10.1093/molbev/msm178

Silva-Brandão KL, Lyra M L, Freitas AVL (2009) Barcoding Lepidoptera: current situation and perspectives on the usefulness of a contentious technique. Neotrop Entomol: 441-451. doi: 10.1590/S1519-566X2009000400001

Singer MC, Mallet J (1986) Moss feeding by satyrine butterfly. J Res Lepid 24: 392.

Tobar D, Rangel JO, Andrade MG (2002) Diversidad de mariposas (Lepidoptera: Rhopalocera) en la parte alta de la cuenca del roble (Quindio-Colombia). Caldasia 24: 393-409.

Uehara-Prado M, Brown Jr KS, Freitas AVL (2007) Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Glob Ecol Biogeogr 16: 43-54. doi: 10.1111/j.1466-8238.2006.00472.x

Vane-Wright RI, Boppré M (2004) Adult morphology and higher classification of Bia Hübner (Lepidoptera: Nymphalidae). Born Zool Beitr 53: 235-254.

Vila M, Björklund M (2004) Testing biennialism in the butterfly Erebia palarica (Nymphalidae: Satyrinae) by mtDNA sequencing. Insect Mol Biol 13: 213-217. doi: 10.1111/j.0962-1075.2004.00472.x

Viloria AL (1998a) Studies on the Systematics and Biogeography of some Montane Satyrid Butterflies (Lepidoptera). Ph.D. thesis. London, University of London, 493p.

Viloria AL (1998) Studies on the Systematics and Biogeography of some Montane Satyrid Butterflies (Lepidoptera). Ph.D. thesis. London, University of London, 493p.

Viloria AL (2003) Historical biogeography and the origins of the satyrine butterflies of the tropical Andes (Lepidoptera: Rhopalocera), p.247-261. In Morone M, Llorente J [eds] Una perspectiva latinoamericana de la biogeografía. Ciudad de Mexico, Universidad Autónoma de Mexico, 307p.

Viloria AL (2007) The Pronophilina: synopsis of their biology and systematics. Trop Lep 15: 1-17. 

From the Phylogeny of the Satyrinae Butterflies to the Systematics of Euphychina Marin et al.
Yu LV (2009) Diversity and similarity of butterfly communities in five different habitat types at Tam Dao National Park, Vietnam. J Zool 277: 15-22. doi: 10.1111/j.1469-7998.2008.00498.x

Wahlberg N, Braby MF, Brower AVZ, de Jong R, Lee M-M, Nylin S, Pierce N, Sperling FA, Vila R, Warren AD, Zakharov E (2005) Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. Proc R Soc Biol Sci Ser B 272: 1577-1586. doi: 10.1098/rspb.2005.3124

Wahlberg N, Leneveu J, Kodandaramaiah U, Peña C, Nylin S, Freitas AVL, Brower AVZ (2009) Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. Proc R Soc Biol Sci Ser B 276: 4295-4302. doi: 10.1098/rspb.2009.1303

Wahlberg N, Weingartner E, Nylin S (2003) Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). Mol Phylogenet Evol 28: 473-484. doi: 10.1016/S1055-7903(03)00052-6

Weller SJ, Pashley DP, Martin JA (1996) Reassessment of butterfly family relationships using independent genes and morphology. Ann Entomol Soc Am 89: 184-192.

Whitfield JB, Lockhart PJ (2007) Deciphering ancient rapid radiations. Trends Ecol Evol 22: 258-265. doi: 10.1016/j.tree.2007.01.012

Willis KJ, McElwain JC (2002) The evolution of plants. Oxford, Oxford University Press, 392p.

Wilson EO (2000) A global biodiversity map. Science 289: 2279.

Zahiri R, Kitching IJ, Lafontaine JD, Mutanen M, Kaila L, Holloway JD, Wahlberg N (2011) A new molecular phylogeny offers hope for a stable family-level classification of the Noctuoidea (Lepidoptera). Zool Scr 40, in press. doi: 10.1111/j.1463-6409.2010.00459.x