FORUM

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

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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.
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 Euptuchiina 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 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 Euptuchiina, 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) 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 Antirrheina (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 Elymnii, 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.
The evolutionary relationships of Amathusiini, Zetherini and Elymniini within the clade are not yet resolved. The tribes Amathusiini (without Hyantis and Xanthotaenia) and Zetherini appear well supported, but Elymniini (comprising only Elymnias) 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 Elymnini (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), Wahlberg et al 2009 (their figs 1 and 3s), Kodandaramaiah et al 2010a)].

The lack of resolution in the topology of Satyrini is morphologically. The exception is Manataria, the only genus in the clade with a Neotropical distribution, which in some cases appears as sister to Melanitini and other times to Dirini.

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The lack of resolution in the topology of Satyrini is

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**Table 1 Different classification proposals for Satyrinae.**

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<td>Satyrini</td>
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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), Euptychiina (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 (Euptychiina) 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 ingroup 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, Hypocystini and the genus Oressinoma (Euptychiini). 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 Palaearctic 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.

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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, Cytb and ND1) and nuclear genes (EF-1a, 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 Amphidecta and Palaeonympha, are now included in Euptychiina, and Oressinoma, a genus traditionally recognized as a member of Euptychiina, is more closely related to Coenonymphina (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 \{[Megisto + (Hermeuptychia + [(Pareuptychia + Taygetis + Splendeuptychia)])] (Peña et al 2010), with some well defined groups and others that appear to be unnatural taxonomic units (Murray 2001a, Murray & Prowell 2005, 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., Euptychoides castrensiais (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 cloi (Weymer) + (Amphidecta calliomma (C. Felder & R. Felder) + Euptychia 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 Euphytica by Peña et al (2006).

The Taygetis clade is the most stable group within Euphytica, being recovered in all known studies (Murray & Prowell 2005, Peña et al 2006, 2010, Marin et al 2009). Two main groups can be recognized in this clade, the first composed by Forsterinaria + Harjesia blanda (Möscher) + 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 Satyrotaygetis satyrina (H. W. Bates), Neonympha aerolatus (Smith), Taydebis peculiaris (Butler), Splendeuptychia doxes (Godart), Splendeuptychia furina (Hewitson) and of the genera Pareuptychia, Megeuptychia and Erichthodes (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 Caereluptychia, 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 (Cercyeuptychia + Godartiana) + [Chloreuptychia catharina (Staudinger) + Pindis] and a clade consisting of Zischkaia, Phareuptychia inofficentia (C. Felder & R. Felder), Splendeuptychia boliviensis and S. itonis (Peña et al 2010). More data will be required to elucidate the phylogenetic relationships of these taxa.

To summarize, several Euphyctica 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 Euptyochoiades, Cissia, Splendeuptychia, Chloroptychia, 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 Euphyctica 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 more stable 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 Euphyctica 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 Euphyctica 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, Taygetis, 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.

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