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THE PRONOPHILINA: SYNOPSIS OF THEIR BIOLOGY AND SYSTEMATICS (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.– A summary of the current knowledge on the satyrine butterflies of the Neotropical subtribe Pronophilina is presented, with an emphasis on their larval host-plant relationships, the possible mimetic resemblances between these and other montane butterflies, and their conservation. The systematics of the group is re-assessed and the tribe re-defined on the basis of a minimum combination of morphological characters.

RESUMEN. – Se presenta una compilación del conocimiento disponible sobre las mariposas satirinas de la subtribu Pronophilina, con énfasis en, la relación de sus larvas con las plantas hospederas, las posibles semejanzas miméticas entre las mariposas pronofilinas y otras mariposas neotropicales de montaña, y su conservación. Se reevalúa la sistemática del grupo, quedando redefinida la tribu en base a una mínima combinación de caracteres morfológicos.

KEY WORDS.– *Altopedaliodes*, Andes, *Antopedaliodes*, *Arhuaco*, bamboos, *Bia*, Biina, *Calisto*, *Cheimas*, cloud forest, conservation, *Corades*, *Daedalma*, *Dangond*, *Diaphanos*, *Dioriste*, Diptera, *Drucina*, *Elina*, Erebiina, *Eretris*, *Eteona*, *Foetterleia*, Fuego-Patagonian, Gramineae, higher classification, host plants, Hypocystina, *Junea*, *Lasiophila*, *Lymanopoda*, *Manerebia*, mimicry, morphology, *Mygona*, Neotropical, *Oxeoschistus*, *Panyapedaliodes*, *Paramo*, paramo, *Parapedaliodes*, parasitism, *Pedaliodes*, *Pherepedaliodes*, *Physcopedaliodes*, Poaceae, *Praepedaliodes*, *Pronophila*, *Protopedaliodes*, *Pseudomaniola*, *Punapedaliodes*, *Redonda*, seasonality, sedentarism, *Sierrasteroma*, South America, *Steremnia*, *Steroma*, *Steromapedaliodes*, *Tamania*, *Thiemeia*, West Indies.

Among the nymphalid butterflies of the subfamily Satyrinae, the members of the subtribe Pronophilina are conspicuously represented at middle to high elevations in virtually all mountain systems of the Neotropical region. As redefined herein, they form a plausibly monophyletic group of 39 genera, represented by ca. 530 recognised species (Lamas *et al.*, 2004). The tribe is structurally cohesive, although morphologically diverse. Adult sizes range from small to relatively large. Wing patterns are generally dominated by tones of brown and dark grey, but they are also rather rich in colorful variations from white to iridescent blue. The range of colors exhibited is unusually wide for the Satyrinae.

The highest proportion of pronophiline species inhabits very humid cloud forests where poaceous plants (bamboos), known or supposed to be their larval host plants, are particularly abundant. Adults have low vagility and spend most of their lives within delimited areas of those forests. They rarely feed on flower nectar (only few cases are so far known), but mostly on other organic matter, specially animal excreta and rotting vegetal tissues.

Much of what is known about the adult biology of the pronophiline butterflies has already been presented by Adams and Bernard (1977, 1979, 1981), DeVries (1980, 1987), Adams (1983, 1985, 1986), Pyrcz and Wojtusiak (1999), Pyrcz *et al.* (1999), and Pyrcz (2004b). The reader is referred to these publications for behavioral aspects and details of the unique pattern of distribution of many members of the subtribe. Additional studies and discussions on the taxonomy and biogeography of the most speciose sections of the Pronophilina, the genus *Lymanopoda* Westwood and the *Pedaliodes* generic complex, are currently in preparation by Tomasz Pyrcz, of the Jagiellonian University (Krakow, Poland), and the author of this paper.

HOSTPLANTS AND EARLY STAGES

The only available records indicate that cloud forest pronophiline butterflies oviposite singly on the tip of bamboo leaves (DeVries, 1980, 1987; Pyrcz *et al.*, 1999). This is also true for most *Calisto* (Sourakov, 1996). In contrast, high elevation species of *Altopedaliodes* Forster and *Redonda* Adams & Bernard broadcast moderate to large numbers of eggs that are devoid of adhesive substances, and do not glue them in place (Apolinar, 1914; Viloria, 1994; Viloria *et al.*, 2003; Viloria and Pyrcz, MS). The latter is also the case for a number of species of *Calisto* Hübner (Wetherbee, 1992; Sourakov, 1996) and *Parapedaliodes* Forster (Pelz, 1996), which are commonly found in pasture land. Such a difference in oviposition strategy may be explained in the second case by the use of superabundant and homogeneously distributed host plants like páramo or savanna grasses instead of woody bamboos (Viloria *et al.*, 2003).

In the high altitude (oreal) zone of the Andes, pronophiline butterflies are found in association with tussock grasses (see *e.g.*, Lamas, 1999: 30). Some of these grasses have been confirmed as food plants (Brown, 1941: 436; Viloria *et al.*, 2003; Viloria and Pyrcz, MS), but the majority have just been inferred as potential hosts. Non-bambusoid grasses seem to be the more generalized food plant source for low elevation species of the Antillean endemic genus *Calisto* (Smith *et al.*, 1994; Sourakov and Emmel, 1995; Sourakov, 1996). However, several *Calisto* species have been recorded on the climbing bamboo *Arthrostylidium* Ruprecht (Wetherbee, 1992; Smith *et al.*, 1994).

Observations of strong associations of adult pronophiline butterflies to cloud forest bamboos have progressively accumulated (Müller, 1886: 611; Apolinar, 1914: 75; Schultze, 1930: 157-165; Adams and Bernard, 1977, 1979, 1981; Adams, 1983: 474-475, 1984: 94, 1985: 37; 1986: 237,1987: 36; DeVries, 1986, 1987; Miller, 1986: 193; Drummond, 1988; Londoño, 1990; Viloria, [1991]; Wetherbee, 1992: 2-28, 83; Maes, 1997: 6; Viloria

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and Camacho, 1999: 176, 179, 182; Pyrcz and Wojtusiak, 1999: 205; Pyrcz *et al.*, 1999: 498; Heredia and Viloria, 2004:81), but few of these records correspond to actual oviposition or larval host records. In my experience, it is as difficult to investigate oviposition sites or larval feeding on Neotropical bamboos as it is to determine the bamboo species themselves, in particular those of *Chusquea* Kunth, the world's most diverse genus of the Bambusoideae (Soderstrom *et al.*, 1988).

Vegetative parts of *Chusquea* bamboo species exhibit high phenotypic plasticity in response to ecological conditions (Widmer, 1997a), therefore it is unreliable (if not impossible) to identify species simply by observation of their vegetative parts. Finding and collecting bamboo reproductive structures (flowers) for taxonomic study is difficult and unpredictable, as these plants often have very lengthy flowering cycles (Janzen, 1976). For example, Widmer (1997b) reckoned that *Chusquea abietifolia* Grisebach in Jamaica has a flowering period of 31-33 years. Although bamboo systematics in the Neotropics has received considerable attention by taxonomists in recent decades (*e. g.*, McClure, 1966, 1973; Calderón and Soderstrom, 1980; Clark, 1989, 1990, 1995), it still lags behind taxonomic studies of many other groups of plants. This is very largely due to insufficient or inadequate (flowering) material in herbaria.

Plant taxonomy is not the only limitation to study the biology of butterflies associated to bamboos in remote tropical montane areas. Research on the early stages of the members of the subtribe Pronophilina is further complicated by the need to pursue any study *in situ*, because immature insects often die very quickly from physical stress during transportation to lower elevations (especially if, as usual, their geographical range is not accessible by modern means of transportation). Additionally, most of the known larvae of the Pronophilina are active nocturnally (Adams, 1984, and pers. comm.; Wetherbee, 1992), resting in extremely cryptic positions during the day. This is a rather intriguing behavior for an invertebrate group that dwells mainly in temperate and cold montane habitats of the Neotropics, and in particular for those species adapted to páramo, jalca, and puna where nocturnal temperatures usually decrease to frost (Díaz *et al.*, 1997). It is noteworthy that not only other poikilotherm animals, in particular micro-vertebrates (such as lizards and all frogs), but also almost every animal form, are diurnally active in high elevation tropical environments.

Apolinar (1914) had already complained about the difficulties of finding larvae of *Altopedaliodes nebris* (Thieme) in the Páramo de Choachí in the Cordillera Oriental of Colombia, while I and several collaborators have spent more than a decade of intense field work in the Andes of Venezuela without succeeding in finding diurnally active larvae of satyrine butterflies in the páramos (although we have investigated a number of possible hosts). During the day, larvae of *Redonda*, for example, hide inactively at the base of bunch of grasses in the páramo, or beneath loose, small-sized rocks high up in the periglacial zone, always more or less close to grassland.

Searching for larvae at night in the cloud forest bamboos has yielded satisfactory and interesting results for other workers (M. J. Adams, pers. comm.), and it appears to be a good alternative left for future work in this field.

Table 1 contains all host plant records so far known for larvae of the Pronophilina. This information has been compiled from published and unpublished sources during the recent elaboration of a catalogue of host plants for the larvae of Neotropical butterflies (Beccaloni *et al.*, in press).

PARASITISM

During juvenile stages, high rates of mortality among several species of Colombian pronophilines are certainly due to the incidence of parasitoids (M. D. Heredia, pers. comm.), but it is unknown whether parasitoids in these cases are host-specific. No formal study has so far been undertaken to investigate which taxa are involved in these butterfly-parasitoid relationships, nor are their consequences known on the dynamics of the butterfly populations. This phenomenon could play an important role in the spatial distribution of parapatric taxa.

A preliminary note on the occurrence of ectoparasitic Diptera (probably Ceratopogonidae) attached to the wing veins of several butterfly species in Venezuela (Lichy, 1946) is the only study available about such interesting relationships within Neotropical montane satyrines. The species of the Pronophilina known to be heavily and frequently parasitized by Diptera are: *Corades enyo enyo* Hewitson, *Lasiophila zapatoza zapatoza* (Westwood), *Lymanopoda obsoleta* (Westwood), *Mygona irmina* (Doubleday), *Pedaliodes piletha* (Hewitson), *P. plotina* (Hewitson), and *P. prytanis* (Hewitson).

ADULT DISPERSAL ABILITY

Lichy (1946), Adams (1983, 1985), De Marmels *et al.* (1996), and Viloria *et al.* (2001a), have emphasized the fact that adult pronophiline butterflies are very sedentary and heavily dependent on certain microhabitats where bamboo plants are dominant vegetation elements. High elevation species have not only very low relative vagility, but in some cases females show varying degrees of flight loss (Adams and Bernard, 1981; Viloria *et al.*, 2003).

Adams (1986) has suggested that the low level cloud forest species *Pedaliodes pisonia* (Hewitson) could have migratory habits. However, this possibility is now regarded as unlikely (Viloria *et al.*, 2001a). Beebe's records of some alleged migratory species of Pronophilina in northern Venezuela (Beebe, 1951) are misinterpretations of local individual displacements, and should no longer be accepted (see Viloria *et al.*, 2001a). In general, the marked sedentary habits of this group are rather extreme, and may be considered very important for understanding its biogeography (Viloria, 1998).

MIMICRY

Early studies on the Pronophilina were accomplished in museums chiefly based on specimens of uncertain provenance. It was then virtually impossible to elucidate any biological feature of these butterflies, other than (often incorrect) systematic relationships. Modern research has greatly increased our knowledge of the actual distribution and biology of Neotropical butterflies, including those inhabiting remote mountain ranges. In the last three decades, the advent of taxonomists who are also competent field workers has revealed coexisting montane butterfly species that exhibit similar color and/or behavioral patterns. Possible mimetic associations among satyrine butterflies of the subtribe Pronophilina, and between them and representatives of other Neotropical butterfly families found in high elevations, were unknown to early students of the phenomenon of mimicry, who dealt mainly with brightly colored taxa of the warm tropical zones.

Several studies have indicated possibly mimetic, specific pairs or trios of pronophiline and other Andean butterflies (Adams and Bernard, 1979, 1981; Adams, 1986; Torres-N. *et al.*, 1996), but

TABLE 1

Genus	Species	Hostplant (and source)
Altopedaliodes Forster	*A. nebris* (Thieme)	Poaceae (Schultze, 1930)
Calisto Hübner	*C. archebates* Ménétriès	*Isachne rigidifolia* Urb.[association], reared on *Stenotaphrum secundatum* (Walt) Kuntze (Sourakov, 1996)
	C. batesi Michener	reared on *Cynodon dactylon* Pers., *Stenotaphrum secundatum* (Sourakov, 1996)
	C. chrysaoros M. Bates	*Arthrostylidium* sp. (Smith *et al.*, 1994)
	C. confusa Lathy	reared on *Cynodon dactylon, Stenotaphrum secundatum* (Sourakov, 1996)
	C. crypta Gali	*Leptochloopsis virgata* (Poir.) Yates (Wetherbee, 1988), *Uniola virgata* Bartr. ex Schut. (Sourakov, 2001)
	C. galii Schwartz	*Arthrostylidium* sp. (Sourakov, 1997)
	C. grannus grannus M. Bates	reared on *Poa pratensis* L. (Sourakov and Emmel, 1995)
	C. grannus dilemma González	*Panicum xalapense* H. B. & K., reared on *C. dactylon* and *S. secundatum* (Sourakov, 1996)
	C. herophile Hübner	low grasses (Alayo and Hernández, 1987), *Saccharum officinarum* L., *Zea mays* L. (Dethier, 1940; Riley, 1975; Smith *et al.*, 1994), reared on wire grass (Sourakov, unpubl., pers. comm.)
	C. hysius (Godart)	reared on *C. dactylon* and *S. secundatum* (Sourakov, 1996)
	C. nubila	reared on rye grass and others (Sourakov, 2001)
	C. obscura Michener	*Bothriochloa pertusa* (Billd.) Maire, *Solphio japonica* [?] (Wetherbee, 1996)
	C. pulchella Lathy	*S. officinarum* [secondary host] (Riley, 1975; Schwartz, 1989; Smith *et al.*, 1994; Sourakov, 1996, 2001)
	C. sibylla smintheus M. Bates	Poaceae (Alayo and Hernández, 1987)
	C. sommeri Schwartz & Gali	reared on *C. dactylon* and *S. secundatum* (Sourakov, 1996)
	C. tasajera Gozález, Schwartz & Wetherbee	*Danthonia domingensis* Hackel & Pilger (Sourakov, 2001)
	C. zangis (Fabricius)	grasses (Riley, 1975), *Axonopus compressus* Beauv. (Brown & Heineman, 1972; Smith *et al.*, 1994), *C. dactylon* (Brown & Heineman, 1972; Riley, 1975; Smith *et al.*, 1994)
Corades Doubleday	*C. chelonis chelonis* Hewitson	*Chusquea* aff. *scandens* Kunth (Heredia *in* Beccaloni *et al.*, in press)
	C. enyo almo Thieme	*Chusquea* sp. (Salazar *in* Beccaloni *et al.*, in press)
	C. pannonia ploas Thieme	*Chusquea* aff. *scandens* Kunth (Heredia *in* Beccaloni *et al.*, in press)
	Corades sp. (Colombia)	bamboo species (Drummond, 1988)

Dangond Adams & Bernard	*D. dangondi* Adams & Bernard	*Chusquea (Swallenochloa)* sp. (Viloria, [1991])
Drucina Butler	*D. leonata* Butler	*Pennisetum purpureum* Schum. (Haber *in* Beccaloni *et al.*, in press)
Eretris Thieme	*E. ocellifera* (C. & R. Felder)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
	E. porphyria ssp.	*Chusquea* aff. scandens (Heredia *in* Beccaloni *et al.*, in press)
	E. suzannae DeVries	*Chusquea* sp. (DeVries, 1980, 1987), *Chusquea longifolia* Swallen (Haber *in* Beccaloni *et al.*, in press)
Eteona Doubleday	*E. tisiphone* (Boisduval)	Taguara (Hoffmann, 1937), bamboo spp. (Brown, 1992), *Chusquea* sp. (Freitas *in* Beccaloni *et al.*, in press)
Junea Hemming	*J. doraete* (Hewitson)	*Chusquea* sp. (Schultze, 1930)
Lasiophila C. & R. Felder	*L. zapatoza* (Westwood)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
Lymanopoda Westwood	*L. obsoleta* (Westwood)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
	L. panacea (Hewitson)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
	L. paramera Adams & Bernard	*Chusquea (Swallenochloa)* sp. (Viloria, [1991])
	L. samius Westwood	'wild sugar cane' (Weymer, 1912), *Chusquea* sp. (Schultze, 1930; Acosta, 1999)
Mygona Thieme	*M. irmina* (Doubleday)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
Oxeoschistus Butler	*O. cothon* Salvin	*Chusquea* sp. (DeVries, 1987; Santin, 1998)
	O. cothonides Grose-Smith	*Chusquea* sp. (DeVries, 1986, 1987; Santin, 1998)
	O. puerta simplex Butler	grasses (Heredia *in* Beccaloni *et al.*, in press), *Chusquea* sp. (Vélez & Salazar, 1991; Salazar *in* Beccaloni *et al.*, in press)
	O. puerta submaculatus Butler & Druce	*Chusquea longifolia*, *Olyra caudata* Trinius (Cubero, 1985)
Parapedaliodes Forster	*P. parepa parepa* (Hewitson)	*Poa annua* L. [substitution host] (Pelz, 1997)
Pedaliodes Butler	*P. cremera* Godman & Salvin	*Chusquea* sp. (DeVries, 1986; Santin, 1998)
	P. dejecta (Bates)	*Chusquea* sp. (DeVries, 1987; Santin, 1998)
	P. phoenissa (Hewitson)	*Chusquea* sp. (Schultze, 1930)
	P. peucestas (Hewitson)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
	P. poesia (Hewitson)	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
	P. triaria Godman & Salvin	*Chusquea longifolia* (Haber *in* Beccaloni *et al.*, in press)
	P. zingara Heredia & Viloria	*Chusquea* spp. (Heredia and Viloria, 2004)
Praepedaliodes Forster	*P. amussis* (Thieme)	'bamboo' (Freitas *in* Beccaloni *et al.*, in press)
	P. phanias (Hewitson)	bamboo spp. (Müller, 1886; Weymer, 1912; Brown, 1992; Freitas *in* Beccaloni *et al.*, in press), *Bambusa vulgaris* Nees, *Chusquea meyeriana* Rupr. ex Doell, *Guadua riograndensis* Dutra (Biezanko, 1960; Silva *et al.*, 1968), *Bambusa* sp., *Chusquea* sp. (Hayward, 1969), *Bambusa arundinacea* (Retz.) Willd. (Biezanko *et al.*, 1974)

Praepronophila Forster	*P. perperna* (Hewitson)	*Rhipidocladum maxonii* (Hitchcock) McClure (DeVries, 1986; Santin, 1998)
	P. petronius kerrianna Miller	*Olyra standleyi* Hitchc. (Small *in* Miller, 1986, as possible host-plant)
Pronophila Doubleday	*P. thelebe brennus* Thieme	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)
Pseudomaniola Röber	*P. phaselis rogersi* (Godman & Salvin)	*Chusquea* sp. (DeVries, 1987)
Punapedaliodes Forster	*P. albopunctata* (Weymer)	'gramíneas' (grasses) (Forno, 1991)
Steremnia Thieme	*S. rugilas* Thieme	bunch-grass (*Festuca*?) (Brown, 1941)
Steroma Westwood	*S. bega* Westwood	*Chusquea* aff. *scandens* (Heredia *in* Beccaloni *et al.*, in press)

these isolated observations have not been experimentally tested, and still remain highly conjectural. An interesting case of a replacing series of three altitudinally parapatric species of *Manerebia* Staudinger (recently tranferred to a different subtribe) found in association with three similarly patterned true pronophiline species belonging to three different genera in the Andes of Colombia and Venezuela (Serranía del Tamá), is shown in Fig. 1. Each pair co-exists at the same altitudinal level (see legend of figure). Other species of *Manerebia* in the northern Andes fly together with similarly colored pronophilines, individuals of *Manerebia* always being scarcer.

The following are possible mimetic associations found by the author and collaborators, or recorded in the literature:

Associations of resemblance between pronophiline species belonging to different genera:

1. *Cheimas opalinus* (Staudinger) and *Lymanopoda marianna* Staudinger (Adams and Bernard, 1981: 346, 358; Pyrcz *in* Torres-N. *et al.*, 1996: 85); Cordillera de Mérida, Venezuela, sympatric altitudinal range: 3000-3300m (Fig. 2).
2. *Lasiophila prosymna* (Hewitson) and *Pedaliodes peucestas* (Hewitson)/*P. pylas* (Hewitson) (Adams, 1986: 243, 262); Andes of Colombia (all three Cordilleras), sympatric altitudinal range: 2200-3000m and 2450-2700m (Fig. 3).
3. *'Pedaliodes' praxithea* (Hewitson) and *Panyapedaliodes phila* (Hewitson) (Adams, 1986: 243, 277); Cordilleras Central and Oriental, Colombia, sympatric altitudinal range: 2450-3500m (Fig. 4).

Associations of resemblance between pronophiline species and other satyrines:

1. *Eretris porphyria perija* Adams & Bernard and *Manerebia navarrae* (Adams & Bernard) [Erebiina] (Adams and Bernard, 1979: 97, 114-115); Sierra de Perijá, Colombia and Venezuela, sympatric altitudinal range: 2300m (Fig. 5).
2. *Eretris apuleja altamira* Adams & Bernard and *Manerebia quinterae* (Adams & Bernard) [Erebiina] (Adams and Bernard, 1979:97, 114-115); Sierra de Perijá, Colombia and Venezuela, sympatric altitudinal range: 2750-3050m (Fig. 5).
3. *Lymanopoda albocincta* Hewitson and *Manerebia franciscae* (Adams & Bernard) [Erebiina]; Cordillera de Mérida, Venezuela, sympatric altitudinal range: 2300-2500m (Fig. 6).
4. *Lymanopoda albocincta* Hewitson and *Manerebia leaena gonzalezi* Pyrcz and Viloria [Erebiina]; Serranía del Tamá, Colombia and Venezuela, sympatric altitudinal range: 1850-2600m (Fig.1).
5. *Lymanopoda albocincta* Hewitson and *Manerebia inderena* (Adams) [Erebiina]; Cordillera Central, Colombia, sympatric altitudinal range: 2450-3000m (Fig. 6).
6. *Lymanopoda albocincta* Hewitson and *Manerebia leaena leaeana* (Hewitson); Andes from Colombia to Peru, sympatric altitudinal range: approx. 2500-3000m.
7. *Pedaliodes reyi* Viloria & Pyrcz (2007) and *Manerebia pluviosa* Viloria [Erebiina]; Serranía del Tamá, Colombia and Venezuela, sympatric altitudinal range: 2800-2850m (Fig. 1).
8. *Altopedaliodes tamaensis* Viloria & Pyrcz (2007) and *Manerebia pervaga* Pyrcz & Viloria [Erebiina]; Serranía del Tamá, Colombia and Venezuela, sympatric altitudinal range: 3100-3350m (Fig. 1).

Associations of resemblance between pronophiline species and butterfly species of other families:

1. *Lymanopoda hazelana* Brown and *Podanotum clarissimus* Hall, Willmott & Johnson [Lycaenidae: Eumaeini] (Torres-N. *et al.*, 1996: 81-86); Cerro Palma, Loja, Ecuador, sympatric altitudinal range: 3000m.
2. *Lymanopoda samius* Westwood and *Podanotum metallicus* Torres-N. & Johnson [Lycaenidae: Eumaeini] (Torres-N. e*t al.*, 1996:81-86); Cordillera Oriental, Colombia, sympatric altitudinal range: 2970m.
3. *Lymanopoda acraeida* Butler and *Actinote* spp. [Nymphalidae: Acraeinae] (Pyrcz *in* Torres-N. *et al.*, 1996:85); Equatorial Andes.
4. *Lymanopoda paramera* Adams & Bernard and *Tatochila* sp. [Pieridae] (Pyrcz *in* Torres-N. *et al.*, 1996:85); Sierra de Perijá, Colombia and Venezuela, sympatric altitudinal range: 3400-3660m.
5. *Lymanopoda paramera* and *Dalla* sp. nov. [Hesperiidae]; Sierra de Perijá, Colombia and Venezuela, sympatric altitudinal range: 3100-3660m (Fig. 7).
6. *Lymanopoda nevada* Krüger and *Tatochila* sp. [Pieridae] (Pyrcz *in* Torres-N. *et al.*, 1996:85) [?]; Sierra Nevada de Santa Marta, Colombia, sympatric altitudinal range: approx. 3000-3500m.
7. *Lymanopoda viventieni* (Apolinar) and *Tatochila* sp. [Pieridae] (Pyrcz *in* Torres-N. *et al.*, 1996:85); Cordillera Oriental, Colombia, sympatric altitudinal range: 2900-3350m.

IN SEARCH FOR POSSIBLE EXPLANATIONS OF WING PATTERN CONVERGENCES

According to Adams and Bernard (1979, 1981) and Adams (1986), except for a few individuals that showed evidence of having been attacked by birds but not eaten (beak-marked specimens), there is no direct evidence that species of pronophilines are unpalatable, and therefore models for classical Batesian mimicry. Butterflies in general can be protected chemically either by assimilating secondary compounds (or their precursors) from their larval hosplants, or by synthesizing them independently (see Vane-Wright, 1991). For the first case it is notable that many bamboos contain potentially poisonous flavonoids (L. G. Clark, comm. pers.), and cyanogenesis occurs in young shoots (and more rarely in the leaves) of a significant proportion of bambusoid species. Tests to detect cyanogenic activity in several species of

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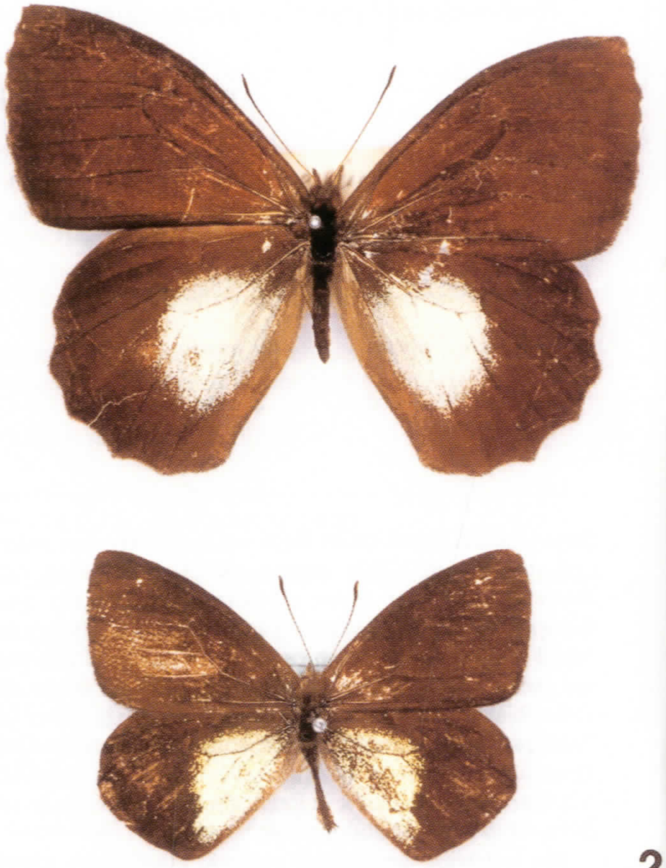

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Fig. 1-2. **1.** Associations of resemblance in an altitudinal gradient between three species of *Manerebia* Staudinger (Erebiini) and three pronophiline species from the Serranía del Tamá, Colombia and Venezuela. Upper pair (3100-3350 m):*Manerebia pervaga* Pyrcz & Viloria and *Altopedaliodes tamaensis* Viloria & Pyrcz; middle pair (2800-2850m): *Manerebia pluviosa* Pyrcz & Viloria and *Pedaliodes reyi* Viloria & Pyrcz; lower pair (1850-2600m):*Manerebia leaena gonzalezi* Pyrcz & Viloria and *Lymanopoda albocincta* Hewitson; **2.** Mimetic association between *Cheimas opalinus* (Staudinger) (above) and *Lymanopoda marianna* Staudinger (below), both endemic to the Cordillera de Mérida in Venezuela (3000-3300m).

Chusquea yielded negative results, but other Neotropical bamboos, like *Anomochloa* Brongniart, *Bambusa* Retzius corr. Schreber, and *Guadua* Kunth, appear to be cyanogenic (Guala, 1993). The phenomenon of cyanogenesis has also been detected in grasses (*e. g.*, genus *Cortaderia* Stapf., Tjon Sie Fat, 1979).

Since evidence is either absent or negative, Batesian or Müllerian mimicry may not offer an appropriate explanation for wing pattern resemblances between Pronophilina and other montane butterflies. On the other hand, arithmetic mimicry, or protection through confusion among many individuals (van Someren and Jackson, 1959; Vane-Wright, 1976), appears equally unlikely because individuals of the species involved in the cases of possible mimicry mentioned above do not occur or congregate in large numbers.

A more detailed exploration of the possible mimetic relationships of selected pronophiline butterflies is currently in progress (Pyrcz *et al.*, in prep.).

SEASONALITY

Among north Andean satyrines, *Diaphanos huberi* Adams & Bernard and *Manerebia franciscae* (from the Cordillera de Mérida) (Adams and Bernard, 1981:346; Adams, 1985:37; 1986: 305), as well as, *M. navarrae*, *M. quinterae* (from the Sierra de Perijá) (Adams and Bernard, 1979:114-115), and *Manerebia pluviosa* and *M. pervaga* (from the Serranía del Tamá) (see Pyrcz and Viloria, this issue) are reported to be seasonal. The high elevation (páramo) species of *Diaphanos* and *Manerebia* seem to be on the wing only during the dry season (corresponding to boreal winter), while the cloud forest species of the latter genus fly during the rainy season. These butterflies, as discussed in the following paper of this issue, are in my view not members of the subtribe Pronophilina. Their seasonality could perhaps be linked to the fact that they may have originated from a boreal clade (Viloria, 2007a).

No true Pronophilina is known to be seasonal, as the Fuego-Patagonian species of satyrines, certainly adapted to seasonal regimes in their life cycles, also belong to different tribes (Viloria, 2007a).

SYSTEMATIC PROFILE OF THE SUBTRIBE PRONOPHILINA

Previous tribal and subtribal definitions

Reuter (1896) studied in some detail the comparative morphology of the labial palpi of 13 adult species belonging to ten distinctive genera of South American satyrid butterflies, which he first denominated the *Pronophila*-group (Reuter, 1896: 138-142), apparently on the basis of general external similarity and shared geographical origin. Analyses of the proportions of the palpal segments, their hairiness, and even chitinization and color, enabled Reuter to conclude that the *Pronophila*-group was actually a natural one for which he erected the tribal entity Pronophilidi (Reuter, 1896:371-374). In his work, there is some discussion about the possible relationship between the genera *Steroma* Westwood and *Elina* Blanchard which have unusually long palpi

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Fig. 3-4. **3.** Trio of white-banded pronophiline species with possible mimetic resemblances (Cordillera Oriental, Colombia, 2450-2700m): *Lasiophila prosymna* (Hewitson) (above), *Pedaliodes peucestas* (Hewitson) (middle), and *P. pylas* (Hewitson) (below); **4.** Mimicry between '*Pedaliodes*' *praxithea* (Hewitson) and *Panyapedaliodes phila* (Hewitson) from Sillutincara (3000-3500m) Bolivia. The pair occurs sympatrically and synchronously from Colombia to Bolivia (with several subspecies).

(therefore, presenting problems for Reuter's classification). Although Reuter (1896) did consider some other characters to support the uniformity of the tribe (such as venation and hairiness of the body), he defined it using just palpal characters: palpi very long, basal segment short and as broad as long, middle segment at least three times as long as the basal one (often longer), distal segment nearly as long as the basal one, although slightly longer (very short in *Steroma*), in most cases pointing forwards. It is interesting to note that later Miller (1968: 8) and Pyrcz (1995: 522) mentioned that the palpi of the Pronophilina have the longest distal segment of any subtribe of the Satyrinae. Such an assertion directly contradicts not only Reuter's accurate observations, which I have corroborated for many taxa of the Pronophilina, Erebiina, Euptychiina, and Hypocystina, but also several of the illustrations of labial palpi throughout Miller's publication: *e. g.*, distal segment appears relatively longer in some Ypthimina (p. 84, fig. 172), Coenonymphina (p. 97, fig. 214), Erebiina (p. 103, fig. 245), Diriina (p. 107, fig. 250).

Reuter's (1896) boundaries for his tribe Pronophilidi seem paradoxically insufficient and not narrow enough. The tribe initially embraced a very poor representation of the genera that should be considered, and included the genus *Elina*, which does not fit the diagnostic characters on which the subtribe has been re-defined in this work (accordingly, it has had to be transferred to another subtribe (Viloria, 2006a)). On the other hand, it may be the case that the shared palpal configuration defined by Reuter does naturally group the Pronophilina (at least for the *Pedaliodes* generic complex), but the characters are not exclusive to this tribe, being found widely in several others (see Miller, 1968). Within the enormous taxic diversity of the Pronophilina, palpal characters are obviously not sufficient, and perhaps not homogeneous enough to provide tribal or subtribal definition for a group that contains, among others, the most speciose butterfly genus in the world.

Clark (1947) gave subfamily rank to the group (Pronophilinae), wrongly including within it the basically North-American genus *Gyrocheilus* Butler (which has a particular forewing venation, glabrous eyes and a very unusual genitalic configuration, pers. observ.) (Clark, 1948). Neither of these decisions is justified, not only because there is not explanation in Clark's papers of the criteria he used (other than consultation with colleagues), but also because there is no reference to the works of many scientists who had previously discussed higher classification systems for the butterflies. Clark did not even mention Reuter, although it seems evident that his satyrid subfamilies were roughly the same as Reuter's tribes.

The work of Miller (1968: 108-118) continues to be the major — and perhaps only — modern contribution towards a morphological conception of the subtribe Pronophilina. However, it lacks a concise definition. Some morphometric characters used by Miller in his analyses appear confusing, and neither very useful nor conclusive for tribal discrimination within the Satyrinae. This is particularly true for standarized measures of legs. In some cases his assignment of a genus to a certain tribe appears to be intuitive rather than based on character congruence; therefore, it sometimes shows contradictions, and a fair number of overlapping characters, making tribal separation difficult.

Pyrcz (1995) attempted to discuss the diagnosis of the tribe

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Fig. 5-7. **5.** Example of resemblance involving parapatric pairs of Pronophilina (left) / Erebiina (right) in the Sierra de Perijá, Colombia and Venezuela: *Eretris apuleja altamira* Adams & Bernard and *Manerebia quinterae* (Adams & Bernard) (range: 2750-3050m) (above); *Eretris porphyria perija* Adams & Bernard and *Manerebia navarrae* (Adams & Bernard) (range: 2300m) (below); **6.** Two cases of erebiine 'mimics' of *Lymanopoda albocincta* Hewitson (above): *Manerebia inderena* (Adams) (Colombia, Cordillera Oriental) (below, left), *Manerebia franciscae* (Adams & Bernard) (Venezuela, Cordillera de Mérida) (below, right); **7.** Upperside (above) and underside (below) mimetic resemblances between *Lymanopoda paramera* Adams & Bernard and a species of *Dalla* (Hesperiidae), sympatric and synchronous species in the paramos of the Sierra de Perijá (3100 -3660m, Venezuela and Colombia). A much scarcer species of *Tatochila* (Pieridae) also seems to partake in this resemblance complex.

Pronophilini by recalling and citing Miller's (1968) approach. In this work, repetition of Miller's diagnostic features are alternated with ambiguous interpretations, often leading to contradictory conclusions (the genus *Tamania* Pyrcz itself, therein erected as a new member of the Pronophilini does not fit within the tribe). Furthermore, the emmendation of Miller's main diagnostic feature of the hindwing venation of the Pronophilini "crossvein m1-m3 produced distad at M2" (Miller, 1968:110) makes no sense (Pyrcz, 1995: 522). For these reasons and other obvious inconsistencies in the observations and comments regarding *Tamania jacquelinae* Pyrcz (a species belonging to a different tribe, and not associated to bamboo habitats in the cloud forest at all, as stressed), this work remains misleading.

Because of some tribal misplacements for several genera in the classification proposed by Miller (1968), the Neotropical subtribes considered for the present study were not homogeneous. Overlapping characters among tribes have often been detected (see Holloway, 1974; Adams and Bernard, 1977; Craw, 1978). Thus, Harvey (1991) possibly felt inappropriate to retain Miller's classification, and downranked a number of satyrine tribes to sub-tribes (but also inevitably to accommodate Miller's system for Satyridae at the lower rank of subfamily). Harvey (1991:256) notes that the "Satyrinae and its component groups also need further study". Apparently the fundamental incongruences were beyond the comprehension of the author. It is evident that he was unable to study the satyrines, and his classification is basically just a re-working of Miller (1968) system. As a result, I am not able to detect morphological support to join Mycalesiti and Lethiti under a common tribal group; on the other hand, *Bia* Hübner (Biina) is probably not a member of the Satyrinae, but of the Morphinae: Brassolini (Vane-Wright and Boppré, 2005.). There are many other debatable issues, but these are beyond the scope of this work.

I have chosen to adopt Harvey's subtribe Pronophiliti (which should be called Pronophil*ina* instead), because it is obvious that it was used in the same sense of Miller's heterogeneous Pronophilini, for which much change is here proposed. Therefore, the group is herein treated as a subtribal taxon. There are few, but consistent morphological characters for clear-cut definition of the Pronophilina to separate it from similar satyrines. In the process of redefining the group I have retained Pronophilina *sensu novum* as a subtribe, and moved several genera into other tribes (Viloria, 2006a). A phylogenetic study of selected taxa, and the biogeographical aspects addressed in a recent study (Viloria, 1998), are consistent with this taxonomic hypothesis.

Restricted morphological diagnosis of subtribe Pronophilina Reuter (*sensu novum*)

Adult members of the Neotropical subtribe Pronophilina can be separated from other American satyrines by the exclusive combination of the following three superficial characters:

1. Eyes always densely hairy.
2. Hindwing cross vein m1-m2 always curved or angled basad into the discal cell (see Fig. 10-12).
3. Maximum length of hindwing discal cell equal to or longer than half total maximum length of hindwing (excluding tails) (Fig.10-12).

Genera belonging to the Subtribe Pronophilina Reuter (*sensu novum*)

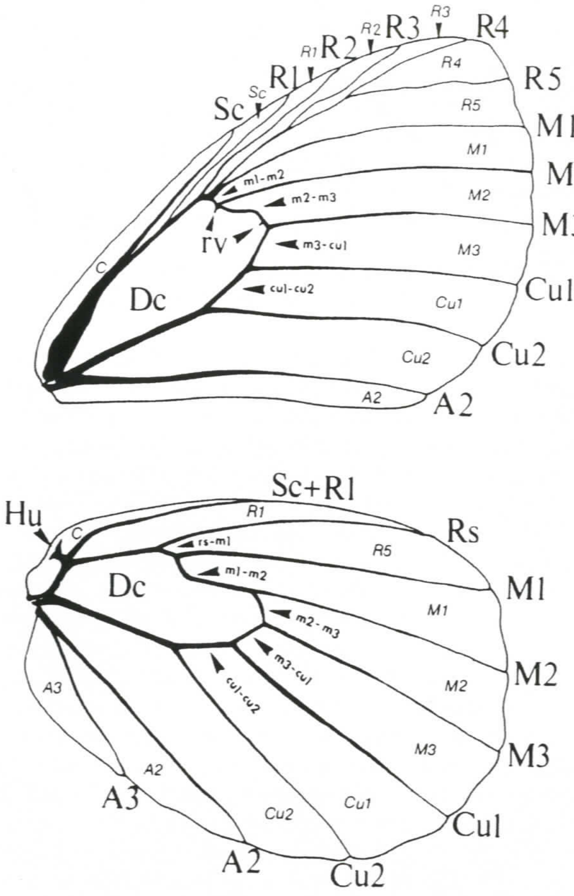
* Note: concise explanations for the genera with status revised are to be published elsewhere. However, Viloria (1998) presents preliminary discussions.

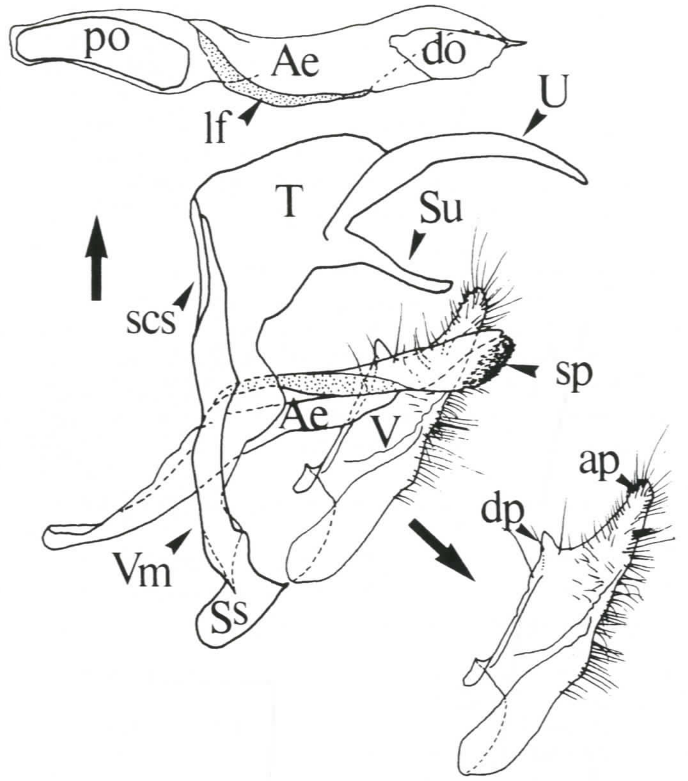
1. *Altopedaliodes* Forster, 1964
2. *Antopedaliodes* Forster, 1964
3. *Arhuaco* Adams & Bernard, 1977
4. *Calisto* Hübner, [1823]
5. *Cheimas* Thieme, 1907
6. *Corades* Hewitson, 1849
7. *Corderopedaliodes* Forster, 1964; **stat. rev.*** [Viloria & Lamas, in prep.]
8. *Daedalma* Hewitson, [1858]
9. *Dangond* Adams & Bernard, 1979
10. *Dioriste* Thieme (in Doubleday), 1907
11. *Drucina* Butler, 1872
12. *Apexacuta* Pyrcz, 2004a
13. *Eretris* Thieme, 1905
14. *Eteona* Doubleday, 1848
15. *Foetterleia*, gen. nov. Viloria, 2006b
16. *Junea* Hemming, 1964
17. *Lasiophila* C. & R. Felder, 1859
18. *Lymanopoda* Westwood, [1851]
19. *Mygona* Thieme, 1907
20. *Neopedaliodes* Viloria, L. D. Miller & J. Y. Miller, 2004
21. *Oxeoschistus* Butler, 1867
22. *Panyapedaliodes* Forster, 1964
23. *Paramo* Adams & Bernard, 1977
24. *Parapedaliodes* Forster, 1964
25. *Pedaliodes* Butler, 1867
26. *Pherepedaliodes* Forster, 1964
27. *Physcopedaliodes* Forster, 1964
28. *Praepedaliodes* Forster, 1964
29. *Praepronophila* Forster, 1964
30. *Pronophila* Doubleday, 1849 [Type genus of the tribe].
31. *Protopedaliodes* Viloria & Pyrcz, 1994
32. *Pseudomaniola* Röber, [1889]
33. *Punapedaliodes* Forster, 1964; **stat. rev.***, [Viloria and Lamas, in prep.]
34. *Redonda* Adams & Bernard, 1981
35. *Sierrasteroma* Adams & Bernard, 1977
36. *Steremnia* Thieme, 1905
37. *Steroma* Westwood, [1850]
38. *Steromapedaliodes* Forster, 1964
39. *Thiemeia* Weymer, 1912

THE PRONOPHILINA AND OTHER SATYRINE CLADES IN THE NEOTROPICS

The taxonomic conclusions of this article as well as those arrived to in Viloria (2007a,b) supported the arrangement of genera within satyrine subtribes for the butterfly catalog of the *Atlas of Neotropical Lepidoptera* (Lamas, 2004). They resulted from extensive morphological analysis during three years (October 1995 to November 1998), mainly in the collections of the Natural History Museum (London), but also in other institutions of Venezuela, the United States of America, Germany, and Poland. During that period, the author had the opportunity to examine in detail the morphology of representatives of all living genera of Neotropical Satyrinae so far known (ca. 120), and species of more than 20 genera from the Holarctic, African, Malagasy, and Australasian regions. Special care was taken in assessing traditional morphological characters (antennae, palpi, proboscis, eyes, sternites, legs, androconial systems and other secondary sexual characters, male genitalia, wing shape, venation, color pattern, and wing scale morphology) among all genera of the 'Pronophilini' (*sensu* Miller, 1968), establishing homologies for comparative purposes with other Neotropical clades (Euptychiini *sensu* Miller, for instance). This study ended up with 92 morphological characters considered informative. Using this character system the author generated a cladogram for 48 selected taxa (Viloria, 1998). This analysis has not been formally published yet, but it is currently under revision and will eventually be made available.

Thus, the combination of three simple diagnostic characters found to define what I call the Pronophilina, is universally shared by species of the 39 genera listed above, including *Pronophila*, the type genus of the taxon. In the same way, the morphological diagnoses for the 19 genera I propose to belong to the Hypocystina, and the 8 genera transferred to the Erebiina (Viloria, 2007a) are universally detectable in all of them, respectively, and mutually exclusive for the three subtribes involved. The minimal combination of three characters found to be diagnostic for the Neotropical Erebiina is also found in *Erebia*, the type genus of the subtribe. Whether they equally fit the diagnosis of other genera believed by other authors to be members of the Erebiina is a matter for separate discussions. On the other hand, it is necessary to make clear that the generic affinities within the Hypocystina (Hypocystini *sensu* Miller) of the Australian region were found to be totally inconsistent (see Holloway, 1974 and Craw, 1978), which indicates that the entire subtribe is in urgent need of a revision. However, as the putative hypocystine species endemic to New Zealand, Tasmania, and New Caledonia, share the same diagnostic characters of the Fuego-Patagonian species and genera I have examined in great detail, I have been inclined to group them all together, temporarily as Hypocystina. This might easily change, for example if found that *Hypocysta* Westwood (again, the type genus of the subtribe) does not exhibit the combination of the three diagnostic characters of *Argyrophorus* Blanchard and *Argyrophenga* Doubleday (two of the members of this amphipacific





Figs. 8-9. Morphological nomenclature as used in this contribution: **8.** Wing veins and cells in a pronophiline butterfly, *Punapedaliodes flavopunctata* (Staudinger) (following Miller, 1970): **A**: anal, **C**: costal, **Cu** (or **cu**): cubital, **Dc**: discal cell, **Hu**: humeral, **M** (or **m**): medial, **R**: radial, **rv**: recurrent veinlet, **Sc**: subcostal; **9.** Hypothetical male pronophiline genitalia: **Ae**: aedeagus, **ap**: apical process of valva, **do**: distal opening of aedeagus, **dp**: dorsal (ampullar) process of the valva, **lf**: longitudinal furrow of aedeagus, **po**: proximal opening of aedeagus, **scs**: semi-circular segment attached to vinculum, **sp**: spiny process of aedeagus, **Ss**: saccus, **Su**: subuncus, **T**: tegumen, **U**: uncus, **V**: valva, **Vm**: vinculum.

connection that additionally share an impressive number of homologous characters in male genitalia and wing pattern). The name of the clade is not as relevant as the meaning of the transpacific relationship, both for biogeography and phylogenetic history (Peña *et al.* (2006) call this clade Coenonymphina, without discussion of the nomenclatural priority).

Peña *et al.* (2006) have managed to produce the first extensive molecular phylogeny for the Satyrinae, whose results, as interpreted, do not support my subtribal arrangement, therefore they reject both my taxonomic and biogeographical hypotheses (the latter discussed in Viloria, 2003). What is clear from this and another molecular study devoted to Neotropical satyrines (Murray and Prowell, 2005) is that the current higher classification of the entire subfamily (basically Miller's) is rather artificial. My critique *a priori* to those molecular studies is that they are not universal. The addition of many more taxa that are still missing in the analysis (at least to match the number of South American genera I took on to study) will possibly change the topology of the cladograms obtained. Some genes (as mitochondrial COI, so popular among lepidopterists) might not be very informative in establishing close or distant relationships at the same resolution.

It is puzzling to see how incongruent the results presented by Peña *et al.* (2006) are with respect to morphological evidence, specifically in the case of the genera of Neotropical Erebiina and Hypocystina, which they simply return to the Pronophilina. The name Coenonymphina is applied to the group of Indo-Australasian genera I refer to as Hypocystina (it is not discussed whether the latter is a junior synonym). The authors place *Oressinoma* Westwood within this clade. This is obviously a convenient solution, as the species of this genus are structurally very different either from any euptychiine or the coenonymphine genera included in their analysis. However, I agree with the hypothesis that *Oressinoma* is not an euptychiine, but strongly keep my position that *Amphidecta* is not either.

It is my proposition herein that the name Euptychiina should no longer be applied in the sense it has been to the largely heterogeneous group of satyrines of the lowlands of the Neotropical region. Its type genus, *Euptychia* Westwood, is characterized by a distinctive group of species, whose adults are easily separated from other Neotropical satyrines: they posses a unique larval morphology for the family and very unusual hostplant associations (Viloria, 2003). If we add to this evidence the phylogenetic position occupied by its members in the available cladograms obtained from molecular sequences (Murray and Prowell, 2005; Peña *et al.*, 2006), then there are sufficient elements as to restrict the name of the subtribe to the members of this genus.

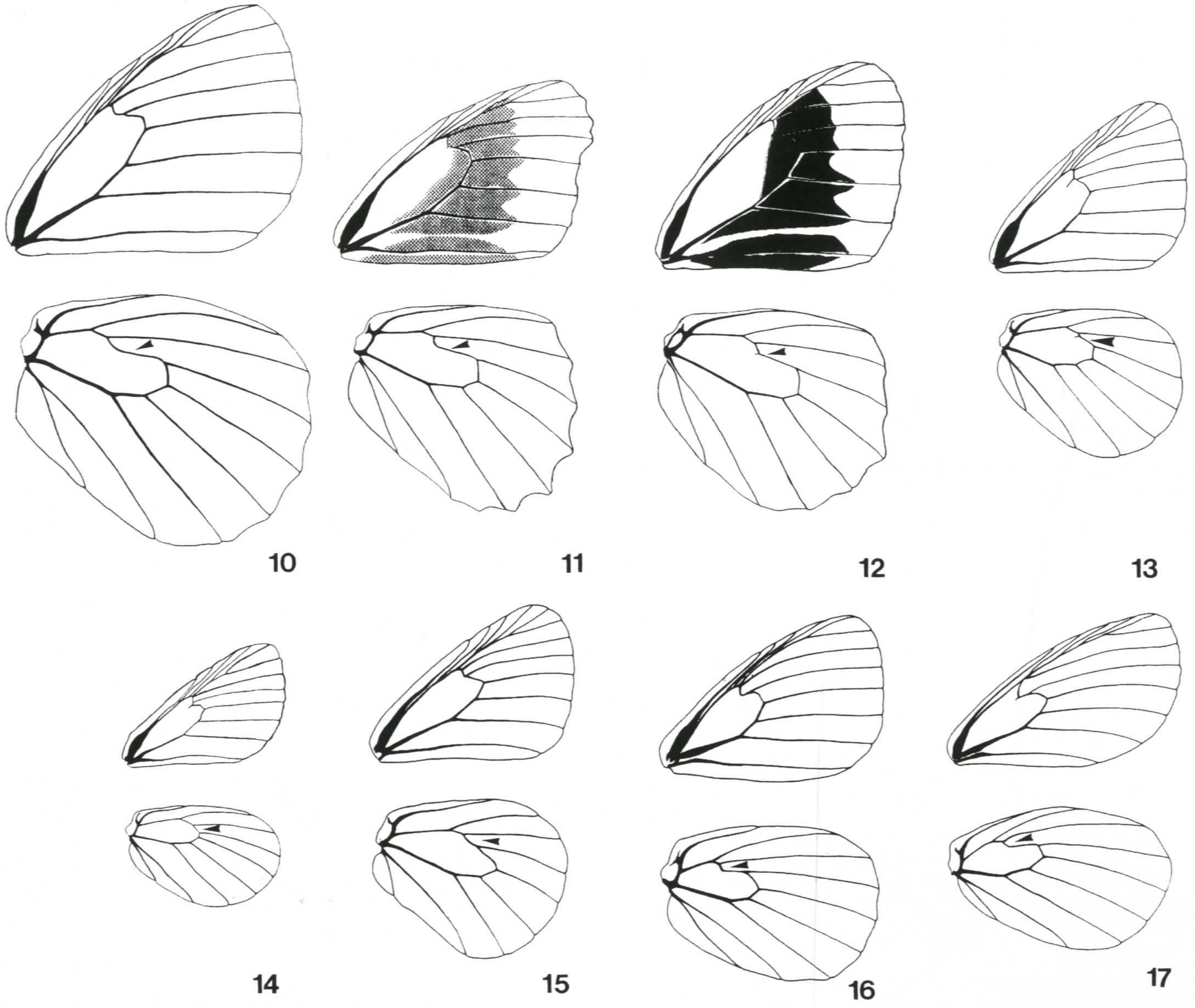


Fig. 10-17. Wing venation of selected satyrine taxa belonging to three different subtribes, showing diagnostic differences in the curvature of the hindwing crossvein m1-m2 (indicated by arrows) and the relative length of the discal cell (dark areas of the wing represent androconial patch when present): **10.** *Protopedaliodes kukenani* Viloria & Pyrcz (male, Neotropical Pronophilina [Pantepui]); **11.** *Praepedaliodes phanias* (Hewitson) (male, Neotropical Pronophilina [Southeasten Brazil]); **12.** *Praepronophila perperna* (Hewitson) (male, Neotropical Pronophilina [Andean-Mesoamerican]); **13.** *Tamania jacquelinae* Pyrcz (male, Neotropical Erebiina [North Andean]); **14.** *Idioneurula erebioides* (C. & R. Felder) (male, Neotropical Erebiina [North Andean]); **15.** *Erebia discoidalis* (Kirby) (male, Holarctic Erebiina [North American]); **16.** *Argyrophorus argenteus* Blanchard (male, Fuego-Patagonian Hypocystina [Chilean]); **17.** *Argyrophenga antipodum* Doubleday (male, Indo-Austral-Asian Hypocystina [New Zealand]).

DISTRIBUTION OF THE PRONOPHILINA

The genera included in the subtribe Pronophilina are restricted to the Neotropical region. *Calisto* Hübner is endemic in the West Indies, and is the only genus of satyrine butterflies to be found in those islands (Smith *et al.*, 1994). It also represents the only pronophiline to exist at very low elevations in the tropical zone. Some speciose genera, like *Pedaliodes* and *Lymanopoda*, are widely distributed from northern Argentina to southern Mexico. A number of Andean or Mesoamerican genera only adapted to middle elevations have a restricted range of distribution, a phenomenon already studied by Adams (1977, 1983, 1985, 1986), Adams and Bernard (1977, 1979, 1981), Pyrcz and Wojtusiak (1999, 2002), and Pyrcz (2004b). Some additional ideas to explain this generalized trend are put forth by Viloria (1998, Chapter 5). Several high Andean genera are strongly insular, sometimes being monobasic, and always endemic to the top of specific mountain ranges.

CONSERVATION AND PRONOPHILINE BUTTERFLIES

Because of the notable levels of endemism and the specificity in habitat preferences within the subtribe Pronophilina, Adams (1983, 1985) remarked that they might have potential value as ecological indicators of habitat condition in cloud forests and páramo. Neat altitudinal distribution of the species seems to be highly dependent on pristine conditions of the forests, and it has been observed that patterns of vertical distribution are strongly altered by disturbance of the original vegetation (Adams, 1985).

Having, in general, very small areas of distribution, most species of pronophiline butterflies should be considered vulnerable to habitat destruction. There are persistent threats to cloud forests

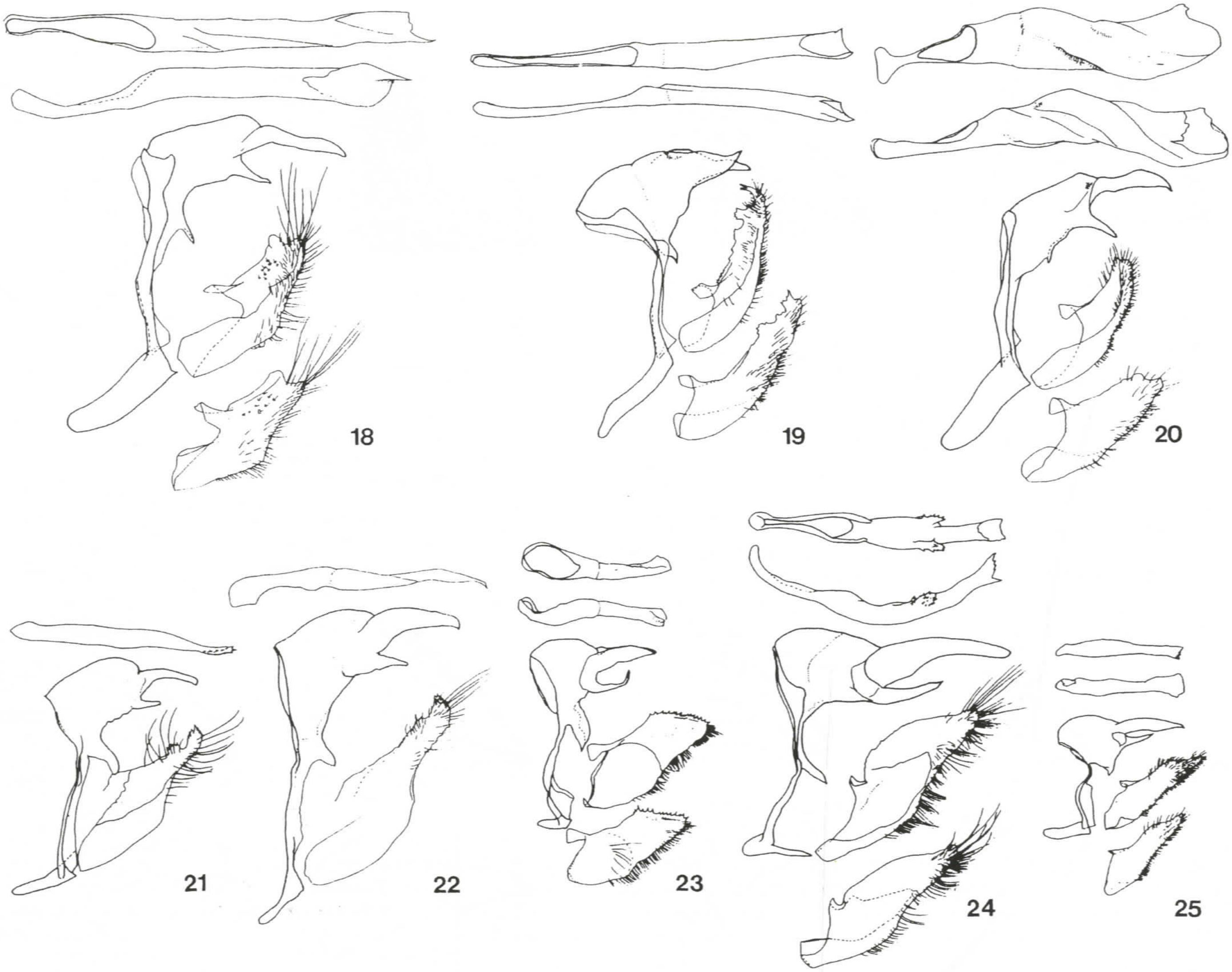


Fig. 18-25. Male genitalia of selected satyrine taxa belonging to three different subtribes (upper structures detached from main armature represent the dorsal and lateral views of the aedeagus; left valva also detached); **18.** *Protopedaliodes kukenani* Viloria & Pyrcz (Neotropical Pronophilina [Pantepui]); **19.** *Praepedaliodes phanias* (Hewitson) (Neotropical Pronophilina [Southeasten Brazil]); **20.** *Praepronophila perperna* (Hewitson) (Neotropical Pronophilina [Andean-Mesoamerican]); **21.** *Tamania jacquelinae* Pyrcz (Neotropical Erebiina [North Andean]); **22.** *Idioneurula erebioides* (C. & R. Felder) (Neotropical Erebiina [North Andean]); **23.** *Erebia discoidalis* (Kirby) (Holarctic Erebiina [North American]); **24.** *Argyrophorus argenteus* Blanchard (Fuego-Patagonian Hypocystina [Chilean]); **25.** *Argyrophenga antipodum* Doubleday (Indo-Austral-Asian Hypocystina [New Zealand]).

and páramos in the Neotropics, in particular the poorly controlled process of colonization for agricultural purposes, which involves deforestation by any possible means (often extensive burning). In Latin America not even the areas under special legislation (National Parks, Forestal Reserves, Biosphere Reserves, etc.) can guarantee the preservation of natural montane habitats, because most governments lack the means to control invasive colonization and/or cultivation of drug plants, or different environmentally destructive kinds of mining. These activities, illegal as they are, are supported by international networks that are sometimes far more powerful than local governments.

Nowadays, a vast variety of montane habitats is however represented in the National Parks systems throughout Latin America, intended to offer protection to the entire biota, without particular interest in endemic butterflies. Adams (1983) has especially recommended for pronophiline butterflies to concentrate efforts in the preservation of tropical montane habitats at elevations above 2500m, although some emphasis should also be put in trying to protect the integrity of original habitats along complete altitudinal gradients. A similar proposal for Venezuela (this time intended to protect the vanishing populations of spectacled bears) considered the establishment of montane ecological corridors in the Andes (Yerena, 1994), which at least has begun to be considered seriously by the national environmental authorities.

Based on Adams' sensible criteria (1983), I emphasized the vulnerability of the high Andean genera of Pronophilina in Venezuela, in a special meeting about threatened Venezuelan invertebrates organized by Fundación Provita during the Latin American Congress of Entomology held on Margarita Island, Venezuela, in 1993. I have been one of the few who actually sent a formal written proposal to the organizers after the event, and I have to regret having done so, because it made me, and other researchers on this group the victims of a terrible irony. For a certain time, the Venezuelan authorities totally banned the collecting of a number of taxa that were listed in the *Red Data Book of the Venezuelan Fauna* (Rodríguez and Rojas-Suárez, 1995), where my contribution has obviously been acknowledged. Permits for scientific collecting of these taxa were rejected for the same reason, no matter whether it was for the only goal of discovering their biological attributes which are currently unknown, or whether the scientists applying were actually the only ones who care about the fate of this fauna, otherwise certainly only known to the authorities because of the Latin names included in the publication referred to above.

CONCLUSIONS

Recent faunistic surveys in selected localities of the Andes and the Tepuyes of the Guayana Shield have shown that even the basic alpha-taxonomic knowledge of the subtribe Pronophilina is still far from complete. Previously unknown species, and even genera, are regularly being discovered, both in old museum material and in nature.

In spite of the systematic, biogeographical, ecological, and evolutionary interest of the Pronophilina (Adams, 1983), many lepidopterists are still unaware of their potential, and so they continue to be neglected. Useful distributional and biogeographical information of the subtribe has been generated from the work of only a handful researchers during the last 40 years. As summarized above, we know practically nothing about the ecological relationships of these butterflies and their environments. Almost complete ignorance prevails on their larval host plants and life cycles, as on every biological aspect of this, probably the most diverse satyrine tribe on Earth. Considering how better known other groups of butterflies are in the Neotropics and elsewhere, this is almost a scandal.

This annotated compilation is intended to bring together all potentially useful information to foster and promote future research on this butterfly group. A taxonomic framework is presented, and I have also presented what is known about host plants, important for understanding spatial distribution (discussed elsewhere). Next papers will deal with the alpha-taxonomy and phylogeny of the *Pedaliodes* generic complex, and their implications for biogeography in two different contexts. These contributions are only inevitably first steps that will be superseded as more biological information becomes available.

In the meantime, continuing exploration of remote montane regions of the Neotropics, together with the study of early stages and life cycles, are first priorities to accelerate progress in our understanding of the pronophiline butterflies. Only in this way can biologists make the most of what these wonderful insects have to say about the intriguing phenomenon of life.

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REFERENCES

Acosta, D.
1999. Mariposas altoandinas: sobre una población de *Lymanopoda samius* Westwood 1851 (Lep: Nymphalidae: Satyrinae) en la región oriental. *Bol. Cient. Mus. Hist. Nat. Univ. Caldas* (Manizales), 3:33-35.

Adams, M. J.
1983. Andean brown butterflies. *In* S. M. Wells, R. M. Pyle, and N. M. Collins (eds.), *The IUCN Invertebrate Red Data Book*, 473-476. Gland: IUCN.
1984. Northern Andean butterflies – search and research. *Alpine J.* (London), 1984:90-96.
1985. Speciation in the pronophiline butterflies (Satyridae) of the Northern Andes. *J. Res. Lepid.* (Beverly Hills), 1985 (suppl.): 33-49.
1986. Pronophiline butterflies (Satyridae) of the three Andean Cordilleras of Colombia. *Zool. J. Linn. Soc.* (London), 87:235-320.
1987. Butterfly search and research in the northern Andes. *Proc. Trans. Br. Ent. Nat. Hist. Soc.* (London), 20:35-40.

Adams, M. J., and G. I. Bernard
1977. Pronophiline butterflies (Satyridae) of the Sierra Nevada de Santa Marta, Colombia. *Syst. Ent.* (London), 2:263-281.
1979. Pronophiline butterflies (Satyridae) of the Serranía de Valledupar, Colombia-Venezuela border. *Syst. Ent.* (London), 4:95-118.
1981. Pronophiline butterflies (Satyridae) of the Cordillera de Mérida, Venezuela. *Zool. J. Linn. Soc.* (London), 71:343-372.

Alayo-D., P., and L. R. Hernández
1987. *Atlas de las Mariposas Diurnas de Cuba (Lepidoptera: Rhopalocera)*. Havana: Edit. Cientif.-Técn. 148pp, 49 pl.

Apolinar, Hno.
1914. Apuntes entomológicos. *Pedaliodes nebris* Th. *Bol. Soc. Cienc. Nat. Inst. La Salle* (Bogota), 2:74-80.

Beccaloni, G. W., A. L. Viloria, S. K. Hall, and G. S. Robinson
(in press). *Host Plants of the Neotropical Butterflies: a catalogue. Catalogo de las Plantas Huésped de las Mariposas Neotropicales*. Zaragoza: Soc. Ent. Aragonesa. RIBES-CYTED.

Beebe, W.
1951. Migration of Nymphalidae (Nymphalinae), Brassolidae, Morphidae, Libytheidae, Satyridae, Riodinidae, Lycaenidae and Hesperiidae (butterflies) through Portachuelo Pass, Rancho Grande, north-central Venezuela. *Zool.* (New York), 36:1-16, pls. 1-2.

Biezanko, C. M.
1960. Satyridae, Morphidae et Brassolidae da Zona Sueste do Rio Grande do Sul (Contribução ao conhecimento da fisiografia do Rio Grande do Sul). *Arq. Ent.* (Pelotas), (A) 4:1-12, 1 pl.

Biezanko, C. M.; Ruffinelli, A. & D. Link
1974. Plantas y otras sustancias alimenticias de las orugas de los lepidópteros uruguayos. *Revta. Centro Ciênc. Rurais* (Santa Maria), 4:107-147.

Brown, F. M.
1941. Notes on Ecuadorian butterflies – I. *Steroma*, *Pseudosteroma* and *Steremnia* (Satridae [*sic*], Rhop.). *Ann. Ent. Soc. Amer.* (Lanham), 34:432-436.

Brown, F. M., and B. Heineman
1972. *Jamaica and its Butterflies*. London: E. W. Classey. 478pp, 10 pls.

Brown, K. S., Jr.
1992. Borboletas da Serra do Japi: Diversidade, hábitats, recursos alimentares e variação temporal. *In* L. P. C. Morellato (ed.), *História natural da Serra do Japi: Ecologia e preservação de uma área florestal do Sudeste do Brasil*, 142-187. Campinas: Edit. Unicamp/Fapesp.

Butler, A. G.
1867. Revision of the group of lepidopterous insects hitherto included in the genus *Pronophila* of Westwood. *Ann. Mag. Nat. Hist.* (London), (3) 20:266-268

1872. Descriptions of new butterflies from Costa Rica. *Cist. Ent.* (New York), 1:72-90.

Calderón, C. E., and T. R. Soderstrom

1980. The genera of Bambusoideae (Poaceae) of the American continent: keys and comments. *Smithson. Contr. Botany* (Washington), 44:1-27.

Clark, A. H.

1947. The interrelationships of the several groups within the butterfly superfamily Nymphaloidea. *Proc. Ent. Soc. Washington*, 49:148-149.

1948. Classification of the butterflies, with the allocation of the genera occurring in North America north of Mexico. *Proc. Biol. Soc. Washington*, 61:77-81.

Clark, L. G.

1989. Systematics of *Chusquea* sect. *Swallenochloa*, sect. *Verticillatae*, sect. *Serpentes*, and sect. *Longifoliae* (Poaceae: Bambusoideae). *Syst. Bot. Monog.* (Ann Arbor), 27:1-127.

1990. Diversity and biogeography of Neotropical bamboos (Poaceae: Bambusoideae). *Acta Botanica Brasil.* (São Paulo), 4:125-132.

1995. Diversity and distribution of the Andean woody bamboos (Poaceae: Bambuseae). *In* S. P. Churchill *et al.* (eds.), *Biodiversity and conservation of Tropical montane forests*, 501-512. New York: New York Botanical Garden.

Craw, R. C.

1978. Revision of the genus *Argyrophenga* (Lepidoptera: Satyridae). *New Zealand J. Zool.* (Wellington), 5:751-768.

Cubero, R.

1985. Notes on the life cycle and natural history of *Opsiphanes quiteria quirinus* Godman and *Eryphanis aesacus buboculus* Butler (Brassolidae). *J. Lepid. Soc.* (Los Angeles), 39:33-42.

De Marmels, J., J. A. Clavijo, and M. E. Chacín

1996. A new subspecies of *Xylophanes tersa* (Sphingidae) from Venezuela. *J. Lepid. Soc.* (Los Angeles), 50:303-308.

Dethier, V. G.

1940. Life histories of Cuban Lepidoptera. *Psyche* (Cambridge, Ma), 47: 14-26, pl. 3.

DeVries, P. J.

1980. Description, natural history, and distribution of a new species of *Eretris* (Satyridae) from Costa Rica. *J. Lepid. Soc.* (Los Angeles), 34:146-151.

1986. Hostplant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae & Nymphalidae). *J. Res. Lepid.* (Beverly Hills), 24:290-333.

1987. *The Butterflies of Costa Rica and their Natural History: Papilionidae, Pieridae, Nymphalidae*. Princeton: Princeton Univ. Pr. 327 pp, 50 pls.

Díaz, A., J. E. Péfaur, and P. Durant

1997. Ecology of South American páramos with emphasis on the fauna of the Venezuelan páramos. *In* F. E. Wielgolaski (ed.), *Ecosystems of the World 3. Polar and Alpine Tundra*, 263-310. Amsterdam: Elsevier.

Doubleday, E.

1848. *List of the Specimens of Lepidopterous insects in the Collection of the British Museum. Appendix*. London: Spottiswoode and Shaw. 37pp.

[1849]. *The Genera of Diurnal Lepidoptera, 1*. London: Longman, pls. 60-62.

Drummond, B. A., III

1988. Zone 13. South America. *In* 1987 Season Summary. *News Lepid. Soc.* (Los Angeles), 1988(2):39-42.

Felder, C., and R. Felder

1859. Lepidopterologische Fragmente. *Wien. Ent. Monatsch.* (Vienna), 3: 321-328, pl. 6.

Ferrer-Paris, J. R., and A. L. Viloria

[2004]. Mariposas altiandinas (Lepidoptera: Nymphalidae, Satyrinae) y la conservación de los páramos en Venezuela. *In*, C. A. Jaramillo, C. Castaño Uribe, F. Arjona Hincapié, J. V. Rodríguez, and C. L. Durąn (eds.), *Congreso Mundial de Páramos. Memorias*, 1:626-633. Bogotá: Conserv. Internac. Colombia.

Forno, E.

1991. Mariposas. *In* E. Forno and M. Baudoin (eds.), *Historia Natural de un Valle en los Andes: La Paz*, 481-497. La Paz: Univ. Mayor de San Andrés, Inst. Ecol.

Forster, W.

1964. Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. *Veröff. Zool. Staatssamml. München*, 8: 51-188, pls. 27-35.

Guala, G. F., II

1993. Cyanogenesis in the bamboos: a phylogenetic perspective. *J. Amer. Bamboo Soc.* (Solano Beach), 10:1-8.

Harvey, D.

1991. Appendix B. Higher classification of the Nymphalidae. *In* H. F. Nijhout, *The Development and Evolution of Butterfly Wing Patterns*, 255-273. Washington: Smithson. Inst. Pr.

Hayward, K. J.

1969. Datos para el estudio de la ontogenia de lepidópteros argentinos. *Misc. Inst. Lillo, Univ. Nac. Tucumán*, 31:1-142.

Hemming, F.

1964. XXXVI. Introduction, as replacements for names invalid under the Law of Homonymy, of names for three genera in the family Satyridae. In *Annotationes Lepidopterologicae. Part 4*, 137-138. London: Hepburn & Sons.

Heredia, M. D., and A. L. Viloria

2004. Description and life history of *Pedaliodes zingara*, a new satyrine species from Colombia (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 58:80-87.

Hewitson, W. C.

[1849]. Description of a new genus and species of Satyridae. *Proc. Zool. Soc. London*, 1848:115-117.

[1858]. Satyridae. *Daedalma*. In *Illustrations of new species of exotic butterflies, selected chiefly from the collections of W. Wilson Saunders and William C. Hewitson. Vol. II*, 85-86, pl. [43]. London: John van Voorst.

Hoffman, F.

1937. Beiträge zur Naturgeschichte brasilianischer Schmetterlinge. II. *Int. Ent. Zeit.* (), 50(37/38):430, (42):487-488, (43):498-501, (44):511--512, (45):525-528, (46):538-539; 51(5):49-52, (6):56-59, (7):73-76, (17):175-176, (18):181-184, (20):203-204, (21):212-213, (23): 231-232, (24):237-240, (26):253-256, (29):275-277.

Holloway, J. D.

1974. The endemic Satyridae (Lepidoptera: Rhopalocera) of New Caledonia. *J. Ent.* (London), (B) 43:89-101.

Hübner, J.

[1823]. *Zuträge zur Sammlung exotischer Schmettlinge* [*sic*], *bestehend in Bekundigung eizelner Fliegmuster neuer oder rarer nichteuropäischer Gattungen, 2*, 1-40. Augsburg.

Janzen, D. H.

1976. Why bamboos wait so long to flower?. *Ann. Rev. Ecol. Syst.* (Palo Alto), 7:347-391.

Lamas, G.

1999. A remarkable new species of *Pedaliodes* (Lepidoptera: Nymphalidae, Satyrinae) from the Cordillera de Vilcabamba, Cuzco, Peru. *Revta. Peruana Ent.* (Lima), 41:28-30.

Lamas, G. (ed.)

2004. *Checklist: Part 4A. Hesperioidea - Papilionoidea. In* J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A. Gainesville: Assoc. Trop. Lepid. 439 pp.

Lamas, G., A. L. Viloria, and T. W. Pyrcz

2004. Tribe Satyrini, Subtribe Pronophilina. *In*, G. Lamas (ed.), Checklist: Part 4A. Hesperioidea - Papilionoidea. *In*, J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A:206-215. Gainesville: Assoc. Trop. Lepid.

Lichy, R.

1946. Documents pour servir a l'etude des Lépidoptérès du Vénézuéla (3e. Note). Un cas de parasitisme sur les ailes des Lépidoptérès. *Bol. Ent. Venez.* (Caracas), 5:1-4, 1 pl.

Londoño, X.

1990. Aspectos sobre la distribución y la ecología de los bambúes de Colombia (Poaceae: Bambusoideae). *Caldasia* (Bogota), 16: 139-153.

McClure, F. A.

1966. *The Bamboos: a Fresh Perspective*. Cambridge: Harvard Univ. Pr. 347pp.

1973. Genera of bamboos native to the New World (Gramineae: Bambusoideae). *Smithson. Contr. Botany* (Washington), 9:1-148.

Maes, J. M.

1997. *Oxeoschistus hilarus* Bates (Lepidoptera: Nymphalidae: Satyrinae) nuevo reporte para la fauna de Nicaragua. *Revta. Nicarag. Ent.* (Leon), 40:5-6.

Miller, L. D.

1968. The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). *Mem. Amer. Ent. Soc.* (Philadelphia), 24:1-174.

1970. Nomenclature of wing veins and cells. *J. Res. Lepid.* (Beverly

Hills), 8:37-48.
1986. The relationship between *Pedaliodes perperna* and *petronius* (Satyridae), with the description of a new subspecies. *J. Lepid. Soc.* (Los Angeles), 39:187-195.

Müller, W.
1886. Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. *Zool. Jahrb. (Syst.)* (Jena), 1:417-678, pls. 12-15.

Murray, D., and D. P. Prowell
2005. Molecular phylogenetics and evolutionary history of the Neotropical satyrine subtribe Euptychiina (Nymphalidae: Satyrinae). *Mol. Phyl. Evol.* (Amsterdam), 34:67-80.

Pelz, V.
1996. Life history of *Pedaliodes parepa* from Ecuador (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 8:41-45.

Peña, C., N. Wahlberg, E. Weingartner, V. Kodandaramaiah, S. Nylin, A. V. L. Freitas, and A. V. Z. Brower
2006. Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molec. Physiol. Evol.* (Amsterdam), 40:29-49.

Pyrcz, T. W.
1995. A new genus, *Tamania*, and a new species, *Tamania jacquelinae*, from the Tama Range, Venezuela Colombia border, and some thoughts on the diagnosis of the tribe Pronophilini (Nymphalidae: Satyrinae). *Lambill.* (Tervuren), 95:519-525.
2004a. Nymphalidae: Satyrinae. *Apexacuta* Pyrcz, new genus. *In* Appendix. Descriptions of new butterfly genera (Lepidoptera: Nymphalidae, Lycaenidae). *In*, G. Lamas (ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea*. 283. *In* J. B. Heppner (ed.): *Atlas of Neotropical Lepidoptera*. Vol. 5A:283. Gainesville, Fl.: Assoc. Trop. Lepid.
2004b. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus* (Wroclaw), 15: 455-622.

Pyrcz, T. W., and A. L. Viloria
2007. Pronophiline and erebiine butterflies of the Serranía del Tamá, Venezuela-Colombia border (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 15:16-50. (2004)

Pyrcz, T. W., K. R. Willmott, and J. P. W. Hall
1999. Contribution to the knowledge of Ecuadorian Pronophilini. Part III. Three new species and five new subspecies of *Lymanopoda* (Lepidoptera: Nymphalidae: Satyrinae). *Genus* (Wroclaw), 10: 497-522

Pyrcz, T. W., and J. Wojtusiak
1999. Mariposas de la tribu Pronophilini de la Reserva Forestal Tambito, Cordillera Occidental, Colombia. Segunda parte. Patrones de distribución altitudinal (Lepidoptera: Nymphalidae, Satyrinae). *SHILAP Revta. Lepid.* (Madrid), 27:203-213.
2002. The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational trnasect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecol. Biogeog.* (Oxford), 11: 211-221.

Reuter, E.
1896. Über die Palpen der Rhopaloceren. Ein Beitrag zur Erkenntnis der Verwandtschftlichen Beziehungen unter den Tagfaltern. *Acta Soc. Sci. Fenn.* (Helsinki), 22:1-577.

Riley, N. D.
1975. *A Field Guide to the Butterflies of the West Indies*. London: Collins. 224pp., 24 pls.

Rodríguez, J. P. & F. Rojas-Suárez
1995. *Libro Rojo de la Fauna Venezolana*. Caracas: Provit Fund. Polar, 444pp.

Röber, J.
1889. X. Satyriden. *In* O. Staudinger and E. Schatz (eds.), *Exotische Schmetterlinge. II. Theil. Die Familien und Gattungen der Tagfalter systematisch und analytisch baarbeitet*. 2:181-225, pl. 35-42. Fürth: G. Löwensohn.

Santin, A.
1998. *Repertoire des Plantes-hôtes et de Substitution des Chenilles de lepidoptères du Monde*. Guyancourt: Office l'Inform. Eco-ent. 1: 1-616, 2:617-1238.

Schultze, A.
1930. Die ersten Stände von drei kolumbianischen hochandinen Satyriden. *Dtsch. Ent. Zeit. Iris* (Dresden), 43:157-165, pl. 3.

Schwartz, A.
1989. *The Butterflies of Hispaniola*. Gainesville: Univ. Florida Pr. 580pp., 8 pls.

Silva, A. G. D'A., C. R. Gonçalves, D. M. Galvão, J. L. Gonçalves, J. Gomes, M. N. Silva, and L. de Simoni
1968. *Quarto catálogo dos insetos que vivem nas plantas do Brasil, seus parasitos e predadores. Edição ampliada do "3° catálogo dos insetos que vivem nas plantas do Brasil" de autoria do Prof. A. M. da Costa Lima. Parte II. Insetos, hospedeiros, e inimigos naturais. Índice de insetos e índice de plantas*. Rio de Janeiro: Minist. Agric. 1:1-622; 2:1-265.

Smith, D. S., L. D. Miller, and J. Y. Miller
1994. Family Satyridae. In *The Butterflies of the West Indies and South Florida*, 46-60, pl. 3. Oxford: Univ. Pr.

Soderstrom, T. R., E. J. Judziewicz, and L. G. Clark
1988. Distribution patterns of Neotropical bamboos. *In* W. R. Heyer and P. E. Vanzolini (eds.), *Proceedings of a Workshop on Neotropical Distribution Patterns*, 121-157. Rio de Janeiro: Acad. Brasil. Ciênc.

Sourakov, A.
1996. Notes on the genus *Calisto*, with descriptions of the immature stages (Part 1) (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 7:91-112.
1997. *Morphology of Immature Stages in Satyrinae (Lepidoptera: Nymphalidae) and its Application to Systematics*. Ph.D. Diss., Univ. Fla., Gainesivlle.
2001. Notes on the genus *Calisto*, with descriptoins of immature stages (Part 2) (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 10:73-79. (1999)

Sourakov, A., and T. C. Emmel
1995. Early stages of *Calisto grannus* Bates on Hispaniola (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 6:27-30.

Thieme, O.
1905. Monographie der Gattung *Pedaliodes* Butl. (Lepidoptera Rhopalocera. Satyridae). *Berl. Ent. Zeit.* (Berlin), 50:43-141, pls. 1-3.
1907. Monographische Bearbeitung der Gattungen *Lasiophila* Felder, *Daedalma* Hew., *Catargynnis* Röber, *Oxeoschistus* Butl., *Pronophila* Westw., *Corades* Doubl. Hew. (Lepidoptera Rhopalocera. Satyridae.). Mit Begründung neuer Gattungen und einer Anzahl Neubeschreibungen. *Berl. Ent. Zeit.* (Berlin), 51:101-234, 3 pls.

Tjon Sie Fat, L.
1979. Contributions to the knowledge of cyanogenesis in angiosperms 11. Communication. Cyanogenesis in some grasses IV. The genus *Cortaderia*. *Proc. Koninkl. Nederl. Akad. Wetens. Series C* (Amsterdam), 82(2):165-170.

Torres-Núñez, R., J. P. W. Hall, K. R. Willmott, and K. Johnson
1996. A new genus of "elfin" butterflies from the northern high Andes (Lepidoptera: Lycaenidae). *Trop. Lepid.* (Gainesville), 7:81-86.

Vane-Wright, R. I.
1976. A unified classification of mimetic resemblances. *Biol. J. Linn. Soc.* (London), 8:25-56.
1991. A case of self-deception. *Nature* (London), 350:460-461.

Vane-Wright, R. I, and M. Boppré
2005. Adult morphology and the higher classification of *Bia* Hübner (Lepidoptera: Nymphalidae). *Bonn. Zool. Beitr.* (Bonn), 53: 235-254.

Van Someren, V. G. L., and T. H. E. Jackson
1959. Some comments on protective resemblance amongst African Lepidoptera (Rhopalocera). *J. Lepid. Soc.* (Los Angeles), 13: 121-150.

Vélez, J. H., and J. A. Salazar
1991. *Mariposas de Colombia*. Bogotá: Villegas Edit. 168pp.

Viloria, A. L.
[1991]. Los páramos de Perijá. *Natura* (Caracas), 93:25-29.
1994. High Andean Pronophilini from Venezuela:Two new species of *Diaphanos* (Nymphalidae:Satyrinae). *J. Lepid. Soc.* (Los Angeles), 48:180-189.
1998. Studies on the Systematics and Biogeography of some Montane Satyrid Butterflies (Lepidoptera). Ph.D. diss., King's College and The Natural History Museum, London. 493pp.
2003. Historical biogeography and the origins of the satyrine butterflies of the Tropical Andes (Insecta: Lepidoptera, Rhopalocera). *In*, J. J. Morrone and J. Llorente-B. (eds.), *Una Perspectiva Latinoamericana de la Biogeografía*, 247-261. Mexico City: Prensas Ciencias, Fac. Ciencias, UNAM.
2007a. Some Gondwanan and Laurasian elements in the satyrine fauna of South America (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 15:53-55. (2004)
2007b. The Brazilian genus, *Foetterleia* and its systematics (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid.* (Gainesville), 15:56-58.

(2004)

Viloria, A. L., M. J. Adams, T. W. Pyrcz, and F. Romero-M.
2001a. Noticia histórica sobre satíridos venezolanos coleccionados por Karl Moritz (1797-1866) y discusión de la identidad taxonómica y la distribución de *Pedaliodes pisonia* (Hewitson, 1862) (Lepidoptera:Nymphalidae, Satyrinae). *SHILAP Revta. Lepid.* (Madrid), 29:31-42.

Viloria, A. L., and J. Camacho
1999. Three new pronophiline butterflies from the Serranía del Turimiquire, eastern Venezuela, and type designation for *Corades enyo enyo* (Lepidoptera, Nymphalidae). *Frag. Ent.* (Rome), 31:173-188.

Viloria, A. L., L. D. Miller, and J. Y. Miller
2004. Nymphalidae: Satyrinae. *Neopedaliodes* Viloria, L. D. Miller & J. Y. Miller, new genus. *In* Appendix. Descriptions of new butterfly genera (Lepidoptera: Nymphalidae, Lycaenidae). *In*, G. Lamas (ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea. In* J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A:284. Gainesville: Assoc. Trop. Lepid.
(in press). A reassessment of *Parapedaliodes* with description of new taxa (Lepidoptera: Nymphalidae: Satyrinae). *Bull. Allyn Mus.* (Gainesville).

Viloria, A. L., and T. W. Pyrcz
1994. A new genus, *Protopedaliodes* and a new species, *Protopedaliodes kukenani* from the Pantepui, Venezuela. *Lambill.* (Tervuren), 94: 345-352.
2001. Revalidación y revisión de *Steromapedaliodes* Forster, con descripción dos especies nuevas (Lepidoptera: Nymphalidae, Satyrinae). *Anartia* (Maracaibo), 15:1-22.
(MS). The genus *Redonda* of the Venezuelan Andes (Lepidoptera: Nymphalidae: Satyrinae).

Viloria, A. L., T. W. Pyrcz, J. Wojtusiak, J. R. Ferrer-Paris, G. W. Beccaloni, K. Sattler, and D. C. Lees
2003. A brachypterous butterfly? *Proc. Roy. Soc. London. (B. Biol. Lett.)*, 270 (Suppl. 1):21-24.

Westwood, J. O.
[1850]. *In* E. Doubleday, *The genera of diurnal Lepidoptera, 2*, 315-326, pl. 54, 63, 65-66. London: Longman.
[1851]. *In* E. Doubleday, *The genera of diurnal Lepidoptera, 2*, 375-386, pl. 67. London: Longman.

Wetherbee, D. K.
1988. *Larval Host-plants, newly Determined of several Hispaniolan Butterflies (Rhopalocera), and Notes of some Early Stages*. Shelbourne, Ma. 20pp.
1992. *The Butterfly / Larva Flora, with a Theory of* Calisto *(Satyridae) Origin and Endemicity*. Shelbourne, Ma. 173pp.
1996. *La Xaiba prieta and la Xaiba piñita (Epilobocera, Decapoda) in Hispaniola, and 20+ further contributions on Hispaniolan fauna*. Santo Domingo. 465pp.

Weymer, G.
1912. 4 Familie:Satyridae. *In* A. Seitz (ed.), *Die Gross-Schmetterlinge der Erde, 2. Exotische Fauna. 5*, 265-272. Stuttgart: A. Kernen.

Widmer, Y.
1997a. Life history of some *Chusquea* species in old-growth oak forest in Costa Rica. *In* G. P. Chapman (ed.), *The Bamboos: Papers Presented at an International Symposium Organised by the Linnean Society of London, the Royal Botanic Gardens Kew and Wye College, University of London, held at the Linnean Society's Rooms, London, 25th to 29th March, 1996*, 17-31. London: Academic Pr.
1997b. Flowering phenology of *Chusquea* bamboos with special reference to *Chusquea talamancensis* in Costa Rica. *J. Amer. Bamboo Soc.* (Solano Beach), 12:1-20.

Yerena, E.
1994. *Corredores Ecológicos en los Andes de Venezuela. Parques Nacionales y Conservación Ambiental No. 4*. Caracas: S. & T. Amend. 186pp, 1 map.

ADDENDUM TO REFERENCES

Since this article was written in its original version (1998), a number of papers related to the Pronophilina have been published. Here is a list of the most relevant ones:

Johnson, K., J. A. Salazar E., J. I. Vargas Ch., and E. R. Henao
2004. Nuevas especies y subespecies de Rhopalocera para Colombia (Insecta, Lepidoptera: Lycaenidae, Riodinidae, Satyridae). *Bol. Cient. Centro Museos* (Manizales), 8:303-316.

Lamas, G., J. Grados, and G. Valencia
1999. Las mariposas de Machu Picchu, Cuzco, Perú: un inventario preliminar (Lepidoptera: Rhopalocera). *Rev. Peru. Ent.* (Lima), 41: 1-8.

Lamas, G., and A. L. Viloria
2004. Tribe Satyrini, Subtribe Erebiina; Subtribe Hypocystina; Subtribe incertae sedis. *In*, G. Lamas (ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea. In*, J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A:215-217. Gainesville: Assoc. Trop. Lepid.

Pyrcz, T. W.
1999a. The E. Krüger Collection of pronophiline butterflies Part I: introduction, genera *Altopedaliodes* to *Lymanopoda* (Lepidoptera: Nymphalidae: Satyrinae). *Lambill.* (Tervuren), 99:221-240.
1999b. The Krüger Collection of pronophiline butterflies Part II: genera *Manerebia* to *Theimeia* [sic] (Lepidoptera: Nymphalidae: Satyrinae). *Lambill.* (Tervuren), 99:351-376.
1999c. Contributions to the knowledge of Ecuadorian Pronophilini, Part II. The genus *Lasiophila* (Lepidoptera: Nymphalidae: Satyrinae). *Genus* (Wroclaw), 10:479-495.
2003a. Datos sistemáticos y zoogeográficos sobre *Lymanopoda huilana* Weymer con la descripción de una nueva subespecie (Nymphalidae: Satyrinae: Satyrini: Pronophilina). *Bol. Cient. Centro Museos* (Manizales), 7:235-243.
2003b. Una nueva especie de lepidóptero altoandino de Chanchamayo (Peru central) — *Pedaliodes franzi* (Nymphalidae: Satyrinae: Satyrini: Pronophilina). *Bol. Cient. Centro Museos* (Manizales), 7: 245-253.
2004a. La trayectoria del lepidopterólogo alemán Eugen Krüger. *Bol. Cient. Centro Museos* (Manizales), 8:173-187.
2004b. Notas taxonómicas sobre el género *Pronophila* Doubleday con la descripción de cuatro nuevas subespecies de *Pronophila unifasciata* Lathy (Nymphalidae: Satyrinae: Pronophilini). *Bol. Cient. Centro Museos* (Manizales), 8:233-246.
2004c. New oreal pedaliodine butterflies from Ecuador and Colombia (Nymphalidae: Satyrinae: Pronophilini). *Bol. Cient. Centro Museos* (Manizales), 8:287-301.

Pyrcz, T. W., and S. Fratello
2005. Cloud forest butterfly fauna of the Pantepui — poor or poorly known? Description of new species and records of new genera of Pronophilina: *Eretris agata* and *Oxeoschistus romeo* (Nymphalidae: Satyrinae). *J. Lepid. Soc.* (Los Angeles), 59:200-211.

Pyrcz, T. W., and G. Rodríguez
2005a. Notas sobre el grupo *Panyapedaliodes muscosa* (Thieme) con la descripción de una nueva especie y dos nuevas subespecies (Lepidoptera, Nymphalidae, Satyrinae, Pronophilini). *Lambill.* (Tervuren), 105:187-194.
2005b. *Pherepedaliodes angela* — una nueva especie para la ciencia y un nuevo género para Colombia (Lepidoptera: Nymphalidae: Satyrinae). *Bol. Cient. Centro Museos* (Manizales), 9:179-191.

Pyrcz, T. W., and A. L. Viloria
1999a. Contribution to the knowledge of Ecuadorian Pronophilini, part 1; new pedaliodines (Lepidoptera: Nymphalidae: Satyrinae). *Genus* (Wroclaw), 10:117-150.
1999b. Mariposas de la tribu Pronophilini (Nymphalidae, Satyrinae) de la Reserva Forestal Tambito, Cordillera Occidental, Colombia. 1ra. Parte. Convergencia de los patrones de coloración en mariposas andinas: siete nuevas especies del género *Pedaliodes* Butler. *SHILAP Revta. Lepid.* (Madrid), 27:173-187.
2004. Nymphalidae: Satyrinae. *Ianussiusa* Pyrcz & Viloria, new genus. *In* Appendix. Descriptions of new butterfly genera (Lepidoptera: Nymphalidae, Lycaenidae). *In*, G. Lamas (ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea. In*, J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A:284-285. Gainesville: Assoc. Trop. Lepid.
2005. Adiciones a la fauna de mariposas de la Reserva Forestal de Tambito (Colombia): descripción de cuatro subespecies nuevas de la subtribu Pronophilina (Nymphalidae: Satyrinae). *Bol. Cient. Centro Museos* (Manizales), 9:258-277.
2006. Systematics, zoogeography and bionomics of high Andean pedaliodines. Part 2: *Pedaliodes praxia* (Hewitson) and related species (Lepidoptera, Nymphalidae, Satyrinae). *Genus* (Wroclaw), 17:427-436.

Pyrcz, T. W., K. R. Willmott, J. P. W. Hall, and A. L. Viloria
2006. A review of the genus *Manerebia* Staudinger (Lepidoptera: Nymphalidae: Satyrinae) in the northern Andes. *J. Res. Lepid.* (Berverly Hills), 39:37-79.

Vargas Ch., J. I., and E. R. Henao-B.

2004. Muestreo preliminar de mariposas (Lepidoptera - Rhopalocera) del Municipio de Samaná – Caldas. *Bol. Cient. Centro Museos* (Manizales), 8:329-351.

Vargas Ch., J. I., and J. Salazar

2004. Mariposas colombianas VII. Breve nota sobre las especies de los géneros *Junea* Hemming 1964, *Daedalma* Hewitson 1858 y *Thiemeia* Weymer 1912 depositadas en algunas colecciones colombianas (Lepidoptera, Satyridae). *Bol. Cient. Centro Museos* (Manizales), 8:247-259.

Viloria, A. L.

1998. Un nuevo *Pedaliodes* Butler, 1867 de la Serranía de Tapirapecó, Venezuela (Lepidoptera: Nymphalidae, Satyrinae, Pronophilini). *SHILAP Revta. Lepid.* (Madrid), 26:13-18.

2000. Estado actual del conocimiento taxonómico de las mariposas (Lepidoptera: Rhopalocera) de Venezuela. *In*, F. Martín-Piera, J. J. Morrone, and A. Melic (eds.), *Hacia un Proyecto Cyted para el inventario y estimación de la diversidad entomológica en Iberoamérica: PrIBES-2000. m3m-Monografías Tercer Milenio*. Vol. 1:261-274. Zaragoza: Soc. Ent. Aragonesa.

2002. Limitaciones que ofrecen distintas interpretaciones taxonómicas y biogeográficas al inventario de lepidópteros hiperdiversos de las montañas neotropicales y a sus posibles aplicaciones. 173-190. *In*, C. Costa, S. A. Vanin, J. M. Lobo, and A. Melic (eds.), *Proyecto de Red Iberoamericana de Biogeografía y Entomología Sistemática PrIBES 2002. m3m-Monografías Tercer Milenio*. Vol. 2:173-190. Zaragoza: Soc. Ent. Aragonesa.

2004. Nymphalidae: Satyrinae. *Foetterleia* Viloria, new genus. *In* Appendix. Descriptions of new butterfly genera (Lepidoptera: Nymphalidae, Lycaenidae). *In*, G. Lamas (ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea. In*, J. B. Heppner (ed.), *Atlas of Neotropical Lepidoptera*. Vol. 5A:283-284. Gainesville: Assoc. Trop. Lepid.

2005. Las mariposas (Lepidoptera: Papilionoidea) y la regionalización biogeográfica de Venezuela. *In*, J. E. Llorente-B., and J. J. Morrone (eds.), *Regionalización Biogeográfica en Iberoamérica y Tópicos Afines. Primeras Jornadas Biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES XII.I-CYTED)*, 441-459. Mexico City: Prensas Cienc., Fac. Cienc., UNAM.

Viloria, A. L., L. D. Miller, and J. Y. Miller

2003. *Pedaliodes pheretias* (Hewitson) form *griseola* Weymer (Nymphalidae: Satyrinae): its identity and availability, with description of a new species. *J. Lepid. Soc.* (Los Angeles), 57:62-67.

Viloria, A. L., and T. W. Pyrcz

2000. New pronophiline butterflies from the Venezuelan tepuyes (Nymphalidae: Satyrinae). *J. Lepid. Soc.* (Los Angeles), 53:90-98.