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SOME GONDWANAN AND LAURASIAN ELEMENTS IN THE SATYRINE FAUNA OF SOUTH AMERICA (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.– A summary of the current knowledge on the satyrine butterflies in South America is given, and 27 American satyrine genera, most of them Fuego-Patagonian or high Andean, are transferred to other subtribes: 19 to the Hypocystina, and 8 to the Erebiina. Two genera formerly believed to belong to the Pronophilina remain in uncertain positions.

RESUMEN.– Se transfieren a otras tribus veintisiete géneros de satirinos americanos, la mayoría de ellos fuego-patagónicos o altiandinos: diecinueve pasan a Hypocystina, y ocho a Erebiina. Dos géneros, anteriormente considerados como pertenecientes a Pronophilina permanecen por el momento en posición incierta.

KEY WORDS.– *Amphidecta*, *Argyrophorus*, *Auca*, biogeography, *Chillanella*, *Cosmosatyrus*, *Diaphanos*, *Elina*, *Erebia*, *Erebiola*, Erebiina, *Etcheverrius*, *Faunula*, *Gyrocheilus*, *Haywardella*, *Homoeonympha*, Hypocystina, *Idioneurula*, *Lymanopoda*, *Manerebia*, *Nelia*, *Neomaenas*, *Neomaniola*, *Neosatyrus*, Neotropical, New Caledonia, New Zealand, *Oreixenica*, *Palmaris*, *Pampasatyrus*, *Pamperis*, *Paratisiphone*, *Percnodaimon*, Pronophilina, *Punargentus*, *Quilaphoetosus*, *Sabatoga*, South America, *Spinantenna*, *Stuardosatyrus*, *Tamania*, Tasmania, taxonomy, *Tetraphlebia*, *Tisiphone*, *Xenica*.

In a previous paper (Viloria, 2007, this issue) I have proposed a reviewed morphological typification for the pronophiline butterflies. A number of South American genera, hitherto considered members of the Pronophilina Reuter (equivalent to Pronophilini *sensu* Miller, 1968) do not show the character combination recently detected as diagnostic for this subtribe. Extensive labors of comparison conducted in the butterfly collections of the Natural History Museum (London) have led to the discovery of simple structural features that allowed the tribal reallocation of 27 of those 'alien' genera. As presently understood, only two genera from the region remain systematically conflictive.

A number of genera of the Neotropical Satyrinae show clear affinities with other continent's taxa belonging to subtribes or tribes formerly overlooked by entomologists in the American continent. Taxonomic heterogeneity revealed by this study is remarkable because of the unusual assemblage of diverse elements within a continental fauna. Preliminary phylogenetic analyses performed by the author (Viloria, 1998) seem to support the new systematic arrangement and might help unraveling the historical biogeography of these butterflies (Viloria, 2003). However, see discussion in Viloria (2007, this issue) concerning new molecular evidence and hypotheses emerged from them.

SUBTRIBE HYPOCYSTINA Miller, 1968[2]

In contrast to the members of the Pronophilina *sensu novum*, that are strict denizens of the temperate zones of the American intertropical belt (with the exception of the Antillean *Calisto*; see Viloria, 2007), many of the species and genera of Satyrinae found in the southern temperate extremity of South America seem to belong to a different group, the hitherto Indo-Australian subtribe Hypocystina. Most of them were first placed by Miller (1968) in the *Elina*-, and *Lymanopoda*-series of the Pronophilini. They have the hindwing cross-vein m1-m2 curved into the discal cell (Fig. 16-17, Viloria, 2007), and tibial spurs. These characters are not exclusive to the true pronophilines, but have traditionally been considered their major morphological features by all authors following Miller (1968). However, the majority of the austral South American genera (some of them ranging as north as southern Peru) possesses a combination of structural characters not represented within what I consider the true Pronophilina: their hindwing discal cell is either exactly equal to (in very few cases) or notably shorter than half the total length of the hindwing (see Fig. 16-17, Viloria, 2007); their eyes are naked; the antennae are always very well developed; the male genitalia (not considered by Miller) are generally simple but uniformly distinctive: characterized by the moderate dome-like tegumen, which is produced posteriorly; the absence of a well defined uncal suture; the long, well-developed uncus; the subunci prominent, but considerably shorter than uncus; the saccus sub-globular, the valvae without ornamentation or processes, and the aedeagus slightly curved to straight, often laterally ornamented with spines (see Herrera, 1965, 1966, and Herrera and Howarth, 1966; and Fig. 24-25 of Viloria, 2001).The unique combination of these characters is also invariably found in genera of the "*Tisiphone*-series" (= *Xenica*-series, see Craw 1978) of the subtribe Hypocystina[3], including *Argyrophenga* Butler, *Erebiola* Fereday, and *Percnodaimon* Butler from New Zealand (see Craw, 1978 and Gibbs, 1980), *Oreixenica* Waterhouse & Lyell from Tasmania (pers. observations), and *Paratisiphone* Watkins from New Caledonia (see Holloway, 1974). Wing patterns, general aspects, and habits observed in members of both the South American and the "Indo-Australian

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[3] Holloway (1974) explored the morphology of all Miller's (1968) hypocystine genera. Regarding male and female genitalia, he found no consistency in the series division proposed for the tribe by Miller (1968). On the other hand, Craw (1978) compared his results of length ratio of palpal segments to those obtained by Miller (1968) for several of the same genera, finding no support for the definition of series. Additionally, Craw noticed ambiguities in Miller's (1968) morphological criteria. The general conclusion to be drawn from these contributions is that generic affinities within the tribe Hypocystini are far from well known. A general recommendation is to avoid using the series arrangement of Miller (1968), until further morphological reassessments or molecular analyses can be made that reliably help suprageneric definitions in the tribe.

region" faunas are uniform and remarkably similar; therefore, suggesting a true phylogenetic relationship, instead of a rather unlikely multistructural convergence. Based on these considerations a number of South American genera are here removed from the subtribe Pronophilina, and transferred to the Hypocystina. Thus, this paper and the previous one (Viloria, 2007) represent the formal justification for the subtribal changes in Lamas (2004). Biogeographic implications of this important discovery appeared in a controversial chapter written in 1998 (Viloria, 2003).

Neotropical genera formally transferred to the subtribe Hypocystina (type species in bold italics):

1. ***Argyrophorus*** Blanchard, 1852; species: ***A. argenteus*** Blanchard.
2. ***Auca*** Hayward, 1953; species: *A. barrosi* (Silva), *A. coctei* (Guérin-Ménéville), *A. nycteropus* (Reed), ***A. pales*** (Philippi).
3. ***Chillanella*** Herrera, 1966; species: ***C. stelligera*** (Butler).
4. ***Cosmosatyrus*** C. & R. Felder, 1867; ***C. leptoneuroides*** C. & R. Felder.
5. ***Elina*** Blanchard, 1852; species: *E. montrolii* (Feisthamel), ***E. vanessoides*** Blanchard.
6. ***Etcheverrius*** Herrera, 1965; species: ***E. chiliensis*** (Guérin-Méneville), *E. tandilensis* (Köhler).
7.. ***Faunula*** C. & R. Felder, 1867; species: ***F. leucoglene*** C. & R. Felder, *F. patagonica* (Mabille).
8. ***Haywardella*** Herrera, 1966; species: ***H. edmondsii*** (Butler).
9. ***Homoeonympha*** C. & R. Felder, 1867; species: ***H. boisduvalii*** (Blanchard), *H. humilis* C. & R. Felder, *H. schajovskoii* Hayward, *H. vesagus* (Doubleday).
10. ***Nelia*** Hayward, 1953; species: *N. calvertii* (Elwes), ***N. nemyroides*** (Blanchard).
11. ***Neomaenas*** Wallengren, 1858; species: *N. coenonymphina* Butler, *N. edmondsii* (Butler), *N. fractifascia* Butler, *N. inornata* Elwes, *N. poliozona* (C. & R. Felder), ***N. servilia*** Wallengren, *N. simplex* (Butler), *N. wallengrenii* Butler.
12. ***Neosatyrus*** Wallengren, 1858; species: ***N. ambiorix*** Wallengren.
13. ***Palmaris*** Herrera, 1965; species: *P. antarcticus* (Mabille), ***P. monticolens*** (Butler), *P. gustavi* (Staudinger), *P. penai* (Hayward).
14. ***Pampasatyrus*** Hayward, 1953; species: *P. glaucope* (C. & R. Felder), ***P. gyrtone*** (Berg), *P. imbrialis* (Weeks), *P. nilesi* (Weeks), *P. ocelloides* (Schaus), *P. periphas* (Godart), *P. quies* (Berg), *P. reticulata* (Weymer), *P. yacantoensis* (Köhler).
15. ***Pamperis*** Heimlich, 1959; species: ***P. poaoeneis*** Heimlich.
16. ***Punargentus*** Heimlich, 1963 ; species: *P. angusta* (Weymer), ***P. lamna*** (Thieme), *P. penai* Hayward.
17. ***Quilaphoetosus*** Herrera, 1966; species: *Q. janirioides* (Blanchard), ***Q. monachus*** (Blanchard).
18. ***Spinantenna*** Hayward, 1953; species: ***S. tristis*** (Guérin-Méneville).
19. ***Tetraphlebia*** C. & R. Felder, 1867; species: ***T. germainii*** C. & R. Felder.

SUBTRIBE EREBIINA Tutt, 1896

Although it is not clear from Miller's diagnosis (1968: 101-105) whether the hitherto Holarctic subtribe Erebiina is truly monophyletic, he gave a number of morphological characters that can be found combined in one Patagonian and seven Neotropical montane genera previously considered atypical pronophilines (see Herrera and Etcheverry, 1965; Adams and Bernard, 1977, 1981; Adams, 1985; Viloria, 1994; Pyrcz, 1995; Pyrcz and Viloria, 2001). These are, the hindwing cross-vein m1-m2 entirely straight or only very slightly curved (almost imperceptible) (Fig. 13-15, Viloria, 2007), absence of hairs covering the eyes (eyes glabrous), and hindwing discal cell short, equal to half the total length of the hindwing or less (Fig. 13-15, Viloria, 2007). Again, close examination of the male genitalia of the species belonging to these South American genera reveals strong similarities to the Holarctic genus *Erebia* Dalman, which is extremely well known in structural aspects due to the unsurpassed monograph of Warren (1936). Male genitalia of *Erebia* and of the Erebiina in general are distinguished from other South American Satyrinae by the high-domed (almost globular) tegumen; a very well-defined suture between the tegumen and the uncus (generally a constriction); the long, curved, and usually stylized uncus; the well developed subunci, always much shorter than the uncus (rarely rudimentary), with little basal expansion; the saccus semi-globular; the valvae generally dorsally ornamented (with teeth or toothed processes); and the aedeagus straight or slightly curved (sometimes with lateral, dorsal or apical tooth-like processes) (Fig. 21-23, Viloria, 2007). In the case of the genus *Tamania* Pyrcz (1995), the diagnostic characters are almost indistinguishable from those of *Erebia*, but the case for synonymy is possibly not well supported by biogeography (Viloria, 2003). Wing scales in the genus *Diaphanos* (see illustrations in Viloria, 1994) are unlike those of any other true member of the Pronophilina, but closely similar to those of several species of *Erebia* (see illustrations in Warren, 1936).

Most of the Holarctic erebiines are either Alpine or high Arctic, an ecological condition recurrent in the majority of the Andean examples (*i. e.*, *Diaphanos* Adams & Bernard, *Idioneurula* Strand, *Manerebia* Stgr., and *Sabatoga* Stgr.), and in the Magellanic *Stuardosatyrus* Herrera & Etcheverry. It is also interesting to note that several cases of marked seasonality are known within the high elevation species of *Diaphanos* and *Manerebia*, a condition that could have been developed in the group in extra-tropical latitudes, prior to its arrival in the tropics (Viloria, 2007, this issue).

Neotropical genera formally transferred to the subtribe Erebiina (type species in bold italics):

1. ***Diaphanos*** Adams & Bernard, 1981; species: *D. curvignathos* Viloria, *D. fuscus* Viloria, ***D. huberi*** Adams & Bernard.
2. ***Ianussiusa*** Pyrcz & Viloria (2004); species: ***Ianussiusa maso*** (Godman).
3. ***Idioneurula*** Strand, 1932; species: ***I. erebioides*** (C. & R. Felder), *Idioneurula eremita* Viloria & Pyrcz (in Pyrcz and Viloria, 2007).
4. ***Manerebia*** Staudinger, 1897 (includes *Penrosada* Brown and *Posteuptychia* Forster; synonymy given by Lamas & Viloria, 2004. Taxonomy partly revised by Pyrcz et al., 2006); species: *M. apiculata* (C. & R. Felder), *M. cyclopella* Staudinger, *M. cyclopina* Staudinger, *M. cyclops* Staudinger, *M. franciscae* (Adams & Bernard), *M. germaniae* Pyrcz & Hall, *M. golondrina* Pyrcz & Willmott, *M. ignilineata* (Dognin), *M. inderena* (Adams), *M. insulsa* (Hewitson), *M. interrupta* (F. M. Brown), *M. leaena* (Hewitson), *M. levana* (Godman), *M. lisa* (Weymer), *M. magnifica* Pyrcz & Willmott, *M. mammuthus* Pyrcz & Willmott, *M. mycalesoides* (C. & R. Felder), *M. navarrae* (Adams & Bernard), *M. nevadensis* (E. Krüger), *M. pervaga* Pyrcz & Viloria, *M. pluviosa* Pyrcz & Viloria, *M. prattorum* Pyrcz & Willmott, *M. quinterae* (Adams & Bernard), *M. reducta* (F. M. Brown), *M. rubescens* (Butler), *M. rufanalis* Pyrcz & Hall, *M. satura* (Weymer), *M. seducta* Pyrcz & Willmott, *M. staudingeri* Forster, *M. trimaculata* (Hewitson), *M. typhlops* Staudinger, *M. undulata* Pyrcz & Hall, *M. zoippus* (H. Druce)
5. ***Neomaniola*** Hayward, 1949; species: ***N. euripides*** Weymer.
6. ***Sabatoga*** Staudinger, 1897; species: ***S. mirabilis*** Staudinger.
7. ***Stuardosatyrus*** Herrera & Etcheverry, 1965; species: ***S. williamsianus*** (Butler).
8. ***Tamania*** Pyrcz, 1995; species: ***T. jacquelinae*** Pyrcz.

Neotropical genera formerly placed in the Pronophilina, but of uncertain position. Further studies are required to determine their affinities:

1. ***Amphidecta*** Butler, 1867b, species: ***A. calliomma*** (C. & R. Felder), *A. picnerator* Butler, *A. reynoldsi* Sharpe.
2. ***Gyrocheilus*** Butler, 1867a: ***G. patrobas*** (Hewitson)

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