

A NEW SPECIES OF *EUPTYCHIA* HÜBNER, 1818 (NYMPHALIDAE: SATYRINAE: SATYRINI) FROM THE AMAZON BASIN AND THE GUIANAS

Andrew F. E. Neild¹, Shinichi Nakahara², Steven A. Fratello³ and Donald J. Harvey⁴

1. Scientific Associate, The Natural History Museum, London SW7 5BD, UK; andrew.neild@blueyonder.co.uk

2. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; snakahara@ufl.edu

3. 11 First St, W. Islip, NY 11795, USA; sfratell@suffolk.lib.ny.us

4. Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0127, USA; harveyd@si.edu

Abstract - A new species of *Euptychia* Hübner, 1818, from the Amazon basin and the extreme southern edge of the Guianas, *E. alacristata* **sp. nov.**, is described and compared to its congeners, from which it differs in genitalia, wing shape, and the presence of an androconial hair pencil on the dorsal hindwing.

Key words: Amazon, Guianas, Neotropical, Euptychiina, androconia, hair pencil, genitalia

INTRODUCTION

The nymphalid genus *Euptychia* is one of many species-rich genera within the large subtribe Euptychiina, and currently contains about 16 described species (Lamas 2004, Brévignon 2005, Freitas *et al.* 2013). However, several undescribed species are awaiting description by ourselves and a number of colleagues (Lamas 2004), so the genus as currently recognised is estimated to contain some 30 species. The relationship between *Euptychia* and the other genera in its subtribe remains unclear, but its monophyly is supported by recent phylogenetic studies using morphological and molecular data (Murray & Prowell 2005, Peña *et al.* 2006, 2010, Peña *et al.* 2011, Freitas *et al.* 2012). Although the appearance of the various species in this genus allows for easy recognition, diagnostic characters for *Euptychia* have not been formally described (Forster 1964; Miller 1968). In addition to external morphology of the adults, such as their small size, dorsal translucence of the great majority of species, strongly defined contrasting ventral transverse bands, and numerous and often large ventral hindwing ocelli, only a few synapomorphies currently support this genus: they are found in the larvae and their singular hosts (fern allies and mosses in the Selaginellaceae and Neckeraceae: Singer *et al.* 1971; Singer *et al.* 1983; DeVries 1986, 1987; Murray 2001), and in the conspicuous projection of the tegumen over the uncus in male genitalia (Pulido *et al.* 2011; Freitas *et al.* 2012, 2013). Representatives of these butterflies are found throughout the Neotropical region, and a large proportion of *Euptychia* species are widely distributed. Nonetheless, many *Euptychia* are poorly represented in collections - their small size, mostly dull coloration, retiring behaviour in the forest gloom, and, in some cases, genuine scarcity, have all contributed to under-sampling by field workers (pers. obs.). These traits, coupled with their confusingly similar appearance and complicated taxonomy, have inspired predictably little interest in researchers until very recently, and our understanding of the natural history and taxonomy of most species is consequently poor.

The geographical, spatial and temporal distributions of many species are also little known. Although most euptychiine species are inhabitants of lowland forests, where some *Euptychia* species certainly occur (pers. obs.; DeVries 1987; Marin *et al.* 2011), *Euptychia* are also unusually diverse in association with

mountain foothills and montane forest (e.g. Pulido *et al.* 2011; pers. obs.).

The senior author first collected specimens of the species that is the subject of this paper in 1989 in south-western Venezuela, while conducting field work for the *Butterflies of Venezuela* book series (Neild, 1996, 2008). A decade later, one of us (SF) collected three further specimens during an expedition into the interior of Guyana (Fratello 2005). Later still, during research for this paper, we found figures of an additional specimen in Pinzón (2009), this time from the Colombian Amazon, and the junior authors (SF and SN) subsequently located additional specimens in the MGCL from Brazil and Colombia. In this paper we describe and name this new species and summarise the little information that is known about its distribution and natural history.

METHODS

For comparison with our new species, we examined the morphology of *Euptychia* specimens in the collections listed below.

AN Andrew Neild collection, London, UK

BMNH The Natural History Museum, London, UK

JFLC Jean François Le Crom collection, Bogota, Colombia

MGCL McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Florida, USA

MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

The abdomens of two Venezuelan males and one Guyanan male were dissected to observe genital structures. We also checked type specimens in the BMNH, plus photographs of additional taxa on the website "Butterflies of America" (available online in Warren *et al.* 2013). Abdomens were dissected using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glycerine. External morphology and dissections were studied using a stereomicroscope and

photographed using digital cameras. The terminology for genital and abdominal structures largely conforms to Klots (1970), nomenclature for wing venation follows the Comstock-Needham system described in the informative paper by Miller (1970), and areas and elements of the wing pattern follow Peña & Lamas (2005) and Neild (2008).

***Euptychia alacristata* Neild, Nakahara & Fratello, sp. nov.**
(Figs. 1-3)

“1320 [n. sp.] Neild, MS Venezuela” in Lamas, 2004: 219
“Undescribed euptychiine” in Fratello, 2005: pp. 31 & 34,
figs. 5-7 (p. 36)
“*Euptychiina* sp.” in Pinzón, 2009: pl. 4

Holotype ♂ (FW length: 16.0 mm) Guyana: Acarai Mts., Sipu R. 900'-2500', 29.X-12.XI.2000, 1°23.2'N 58°56.8'W, Leg. S. Fratello (USNM)

Allotype ♀ (FW length: 18.0 mm) 1♀ Brasil: Amazonas. Maraã, Rio Japura. IX.1995. ex M. Simon / Allyn Museum Acc. 2004-9 (MGCL)

Paratypes: 2♂: Brasil: Amazonas, Manicoré. 18.VIII.1976. C. Callaghan / A. C. Allyn Acc. 1976-15 (MGCL); 1♂ Colombia, Vaupés, N. Mitú. 7.viii.1983. ex M. Simon / Allyn Museum Acc. 1983-25 (MGCL); 1♂ Aug. 26, 1986. Fazenda Este 10 R-1210, Dist. Agr. Da Suframa, Mpio. Manaus, Amazonas, Brazil. R. W. Hutchings (MGCL); 2♂: Maroa-Yavita Rd, km.11 “puente Juda”, Amazonas, Venezuela. Coll. Andrew Neild / 12-15. XI. 1989 ♂ 100m.

/ Genital Vials #261 & #270 (AN; 1 specimen to be deposited in the BMNH); 2♂ Brasil: Amazonas, Manaus, BR-174, km. 64, Faz. Porto Alegre. 2°22'S 59°56'W. Dec. 10, 1993. Roger W. Hutchings & J. Bolling Sullivan R-3304 & Camp (MGCL); 1♂ Brasil – Am. Rio Japura, Maraã. X-95 / Allyn Museum Acc. 2003-9 (MGCL); 1♂ Same data as holotype (genitalic dissection prepared: #2013-05) (USNM); 1♀ Guyana: Acarai Mts, Sipu R. 900', 24.X-12.XI.2000, 1°25.1'N 58°57.2'W, Leg S. Fratello et al. (USNM); 1♂ Colombia, Vaupés, Río Apaporis, Lago Taraira, Estación Biológica Mosiro-Itajura (Caparú). 1° 5' 26.34''S; 69° 29' 52.56''W. J. Pinzón leg. 4.IV.2003 (JFLC); 1♀ *idem*: 22.IV.2003 (JFLC).

MALE (Fig. 1)

Forewing length: 16.0 – 19.0 mm (n = 12). **Antenna:** Orange-brown, about 7.0 mm long (about 3/8ths length of costa from base to apex), dorsally most antennomeres with some fine grey-brown scales which glisten under bright microscope lights (but not to naked eye). **Eyes:** entirely brown, sparsely hairy; a fringe of creamy scales along posterior lateral edge of eye changing posteriorly to brown. **Palpus:** Covered by long creamy hairs (brown beneath where scales are rubbed off), approximately 2.5 mm long. **Foreleg:** Covered by long creamy hairs and scales with two tarsomeres partially fused, first about 9/10ths length of tibia, and second about half length of first. **Wing venation:** Recurrent vein present. Most of FW subcostal vein swollen; base of cubitus barely so. **Wing shape:** Forewing less subtriangular than in most other *Euptychia*, significantly more rounded, including apex; costal and especially outer margin convex, inner margin straight, but rounded towards anterior thorax near base; hindwing less elongate than average, notably rounded; basal half of costal margin strongly lobed (extending anteriorly 2.5 mm from base of Rs to costal margin), outer margin very slightly undulating, slightly angular (concave) inner margin near tornal angle as in other *Euptychia*, anal lobe slightly rounder than average (more convex). **Dorsal surface:** Ground colour dark brown with subtle greyish overtones, slightly translucent, thus subtly revealing ventral dark bands and



Fig. 1 Type specimens of *Euptychia alacristata* sp. nov. Scale bar = 10 mm. Top row (dorsal/ventral): male holotype from the River Sipu, Acarai Mountains, Guyana; bottom row (dorsal/ventral): female allotype from the Rio Japura, Amazonas, Brazil.



Fig. 2 Hair pencils on the DHW (left) and corresponding contact area on the VFW (right) (male paratype of *E. alacristata* sp. nov. from Maroa, Venezuela).

ocelli; forewing with a short and barely visible recurrent vein extending basad from angle on middle discocellular; hindwing humeral vein present, shorter than 0.5 mm; a blackish androconial brush (“hair pencil”) (see Fig. 2) lying at approximately a 45 degree angle to cubital vein, about 0.5 mm wide at its base by 3.0 mm long, extending from basal area of discal cell and distally gradually fanning out somewhat, reaching into space M1 approximately 2.0 mm distal to union of Rs and M1; modified greyish scales, much thinner and longer than others, are present immediately anterior to this hair pencil, from around union of Rs and M1 and extending approximately 2.0 mm distad along Rs, and about 1.0 mm anterior to vein. **Ventral surface:** ground colour pale greyish-brown, paler towards outer margins, especially on forewing; both wings with several dark brown transverse bands, with subtle chestnut overtones in places, a little darker on hindwing. **Ventral forewing:** older specimens with a bare area, opposite dorsal HW hair pencil, presumably resulting from removal of naturally loose modified grey scent scales (some still present) by this brush-like structure (see Fig. 2); submedian dark band extending at an angle from subcostal vein near cell apex to just beyond cubital vein, a little basad to stem of Cu2; median band almost straight, thicker than submedian band, broadening slightly from subcosta to cell Cu1, then narrowing slightly, extends from subcostal vein, traversing base of spaces R5 – Cu1, reaching vein 2A approximately 7.0 mm distance from wing base to apex; irregular submarginal band, slightly undulating, extends from apical to tornal regions, approximately parallel to margin in apical and subapical regions then moving inwards below vein M3, gradually broadening towards vein Cu2, then slightly narrower after this vein and slightly angled back towards outer margin; a darker brown, narrow marginal band extends from near apex towards tornus, aligned parallel to outer margin in some specimens, in others zigzagging in anterior section (and pointing basad in centre of each interspace) from apex to vein M3, and then straight in all specimens but wider in spaces M3 and Cu1, then narrowing towards inner margin at tornus; brownish band along outer margin, fading gradually inwards into pale ground colour before dark marginal band; fringe brown; a large black ocellus in cell M1, touching vein M1 and exceeding width of interspace across vein M2, ringed narrowly in pale yellow inside a narrow brown ring nearly 2.0 mm in diameter, with one centred white pupil in black area; a further back ocellus in cell M3, touching vein M3 but not quite reaching Cu1, narrowly ringed in pale grey (or very pale yellow) inside a narrow brown ring over 2.0 mm in diameter, with one centred white pupil in black area; in two specimens nearest adjacent parts of yellow rings of these two ocelli are drawn out towards each other and enclose a small dark satellite spot; an indistinct suffusion of brown scales surrounds these ocelli, barely darker than ground colour, hinting at an indistinct band. **Ventral hindwing:** basal area with a dark band of regular width extending from costal margin to inner margin; postbasal band slightly irregular, extending from costal margin to inner margin, slightly narrower in anal fold area, slightly curved distally in discal cell; median band slightly thicker than postbasal band, extending from costal margin to inner margin, slightly narrowing posteriorly; very irregular zigzagging submarginal band, very narrow in apical region, broadens notably and M-shaped between vein M2 and Cu1, and then narrowing towards tornus; a darker brown marginal band, thin and undulating between vein M1 and M3, traverses margin from apical area to tornal; brownish band along outer margin, enclosing a narrow pale band between it and dark marginal band; fringe brown; a postmedian series of black ocelli, each with one centred white pupil, narrowly yellow-ringed (yellowish than on FW), and encircled in a narrow brown ring; smallest of all, filling width of cell Rs; second largest exceeding width of cell

M1, touching vein M1 and spilling over vein M2, with a tiny closely-satellited ocellus (mostly yellow) in cell M2 in one specimen, barely 0.5 mm in diameter, and same in another specimen, albeit double size, black-pupilled, and yellow-ringed; another ocellus, slightly smaller than former, occupying width of cell M3; largest ocellus filling width of cell Cu1, its yellow ring joining partially with that of ocellus in M3; a further tiny satellited ocellus in cell Cu2 in one specimen, mostly yellow with a tiny black pupil, barely 0.5 mm in diameter (present on only one wing in one of these specimens); an irregular suffusion of brown scales surrounds these ocelli, forming an indistinct band, far more prominent than that around forewing ocelli; this ocellar band is linked by brown veins to both submarginal and median brown bands, and to submarginal band by a thin brown line along centre of interspace M2 and less obviously also in M3.

Genitalia (Fig. 3): (3 male specimens prepared: vials #261 & #270 (AN); vial #2013-05 (USNM)). Tegumen dorsally flattened, ventral edges concave, trapezium in dorsal view, a conspicuous posterior projection of tegumen above uncus, one third length of uncus; uncus, sparsely hairy, rather thick and short, posterior tapered and slightly hooked in lateral view, somewhat triangular in dorsal view; gnathos huge, wide, dorsal two-thirds subtriangular in lateral view, extending ventrally to meet and fuse with opposite gnathos to form a dark (near black) truncated “boot”-shaped “keel”; vinculum fused to anterior ventral margin of tegumen and medially divided; appendices angulares absent; saccus short and slightly rounded, almost same length of uncus plus tegumen, anteroventrally a continuation of vinculum; dark oval androconia patch between cuticle and base of valvae; valvae sparsely hairy, positioned at approximately a 45 degree angle to horizontal; valva vaguely trapezoidal, with anterior margin concave and highly translucent, posterior margin gently convex, slightly concave dorsal surface projecting further posterior than ventral and forming a posterior apex, rounded and curved upwards to a broad rounded tip, from which a prominent single spike projects towards valve apex opposite; aedeagus elongate and tubular, in dorsal view straight and with broadening anterior portion which opens anterodorsally, in lateral view posterior one third of aedeagus narrower, medial section curved upwards, broadening anteriorly, approximately length of saccus plus valva. Cornuti absent.

FEMALE (Fig. 1)

Forewing length: 17.0 – 19.0 mm (n = 3). Similar to male, except as follows: both wings a little wider and rounder. Dorsally lighter brown, more translucent, with ventral bands and ocelli clearly visible, and lacking hair pencils. Ventrally with more contrast between dark bands and paler ground colour, latter being a lighter greyish-brown; reddish-brown transverse bands are narrower than those of male; thin dark brown marginal line is same as male or a little more scalloped between M1 and Cu1, especially so in Guyanese female; ocelli are similar in size to male holotype, and in same positions, but possibly subject to same variation as seen in males (e.g. on allotype, yellow ring of anterior ocellus of left VFW is slightly extended towards centre of cell M2 and encloses a minute black spot, while a tiny satellited ocellus lies in cell Cu2 of right VHW, mostly yellow with a tiny black pupil, barely 0.5 mm in diameter).

Etymology

Derived from the feminine Latin noun *ala* (wing) and adjective *cristatus* (possessing a tuft or crest, referring to the hair pencil on the dorsal hindwing).

Diagnosis and discussion

As previously hypothesised by one of the authors (Fratello 2001), *E. alacristata* **sp. nov.** appears to be a member of the genus *Euptychia*, at least to judge from wing pattern elements and the prominent projection of the tegumen over the uncus in the male genitalia. This projection is thought to be a diagnostic character for *Euptychia* (Forster 1968; Freitas *et al.* 2012, 2013), and its presence has influenced our decision to place this species here. However, *E. alacristata* differs in significant ways from its supposed congeners. Externally the wing shape is remarkably different from most *Euptychia*, with both wings dramatically broadened and rounded, and with the basal half of the hindwing costal margin strongly lobed. More notable, however, is the presence on male specimens of a single androconial hair pencil near the base of the dorsal hindwing cell. This character, and other brush organs and androconia patches, are found in the mycalesine satyrs, notably the African genus *Bicyclus* Kirby, 1871 (Larsen 2005) and Asian *Mycalesis* Hübner, 1818 (Parsons 1999), but it occurs only rarely among Neotropical euptychiine species (*pers. obs.*; notable exceptions include various members of *Caeruleuptychia* Forster, 1964 – these are currently the subject of a revision by one of us (SN)). In fact, one of several reasons that *E. ernestina* Weymer, 1911, was removed from *Euptychia* is precisely because of the presence of dorsal hindwing hair pencils (Freitas *et al.* 2013). However, detailed studies of these secondary sexual organs have shown that they may be present

in numbers or entirely absent within the same genus – see for example Condamin (1973) in conjunction with the phylogeny of Monteiro & Pierce (2001), Larsen (2005), Parsons (1999), and (with a host of useful references) Robbins *et al.* (2012). Along with this distinctive character, the male genitalia of *E. alacristata* are unusual among *Euptychia* in having a long aedeagus, a rather distinctive valva, and a massive gnathos, this last being absent or very small in most *Euptychia*. However, the gnathos (and valva) does somewhat resemble that of the otherwise dissimilar Central American species *E. rubrofasciata* Miller & Miller (1988: fig. 5), in which this structure is also fused (Jacqueline Miller, *pers. comm.*). In addition to these two species, we are aware of only a few described species of *Euptychia* with gnathi, and these are relatively small: *E. hannemanni* Forster, 1964, & *E. mollina* (Hübner, [1813]) (both figured in Forster 1964: p. 81), *E. neildi* (Brévignon, 2008: fig. 52), and several undescribed Guianan species under study with Christian Brévignon. The absence of a gnathos is considered to be a non-exclusive character of *Euptychia* in Freitas *et al.* (2012, 2013). Despite the various differences catalogued above, it seems prudent to classify this new species as a *Euptychia* and to await a full revision of the genus before deciding upon its correct systematic placement.

Behaviour and habitat

All the known specimens were encountered in lowland tropical rain forest below a maximum of 800 m, predominantly at very



Fig. 3 Male genitalia of paratype of *E. alacristata* **sp. nov.** from the River Sipu, Acarai Mountains, Guyana. Scale bar = 1 mm (photo courtesy Karie Darrow, USNM).



Fig. 4: Local Amerindians repairing “Puente Juda” on the track from Maroa to Yavita, Amazonas, Venezuela. Paratypes were collected in the immediate vicinity inside this forest.

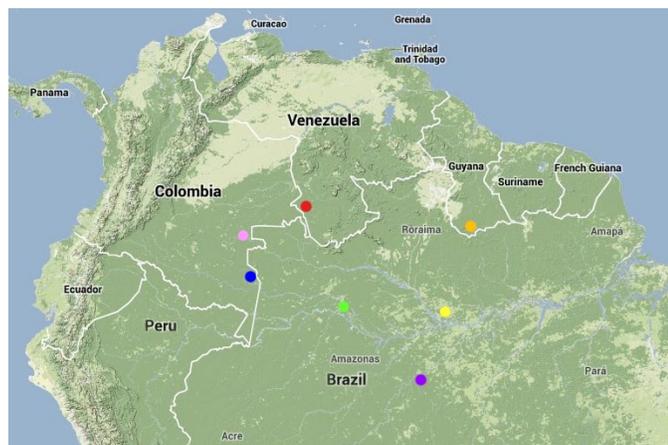


Fig. 5: Map showing collecting localities for *Euptychia alacristata* sp. nov. (clockwise from top): red dot = Maroa, Venezuela; orange dot = Acarai Mountains, Guyana; yellow dot: Manaus, Brazil; purple dot = Manicoré, Brazil; green dot = Maraã, Brazil; blue dot = Lago Taraira, Colombia; pink dot = Mitú, Colombia. (Map data: © 2013 Google, MapLink).

low elevations above sea level. The Brazilian specimens from Manicoré and those from Maroa in Venezuela were taken in pristine terra firme forest at about 50 m and 100 m a.s.l. respectively. The latter specimens were found near a river in close proximity to alluvial forest (with lower canopy and many emergent palms) which might be seasonally inundated (see Fig. 4). Those from Guyana were taken at the highest elevations. The female was found in alluvial forest at 275 m a.s.l., probably seasonally inundated, but very dry at the time of capture. Data for the Guyanese males is vague, with all captures recorded en masse as sampled between about 300 and 800 metres, thus either on the slopes of the Acarai mountain range, and/or in alluvial forest at the very base of the range. Jaime Pinzón, who collected the two Colombian individuals along the edge of Lago Taraira (Vaupés), made detailed notes regarding his captures. These were found at about 80 m a.s.l. in an area of forested old natural terraces that were at one time seasonally flooded by the Apaporis River (a black water river system). However, Pinzón notes (pers. comm.) that occasional flooding may occur during the rainy season by water overflowing from the main stream that drains into the horseshoe lake. He also observes that the forest

is pristine, with a continuous canopy of 25-30m in height with some occasional natural gaps created by fallen trees, that the mean annual temperature inside the forest is about 25°C (with a minimum of 23°C, and a maximum of 27°C), and the mean annual precipitation is approximately 4000 mm. Regrettably, none of the collectors of the type series remembers anything about the behaviour of the specimens.

Distribution

Euptychia alacristata is currently known from seven widely scattered localities (see map, Fig. 5). Six sites lie within the Amazon basin: three from the centre (Manaus, Manicoré, & Maraã, Amazonas, Brazil), and three from the upper (Lago Taraira & Mitú, Vaupés, Colombia; Maroa, Amazonas, Venezuela). One additional site (Acarai Mountains, Guyana) lies on the southern margin of the Guianan basin watershed, just shy of the extreme northern edge of the Amazon basin. The area that these seven sites demarcate already includes nearly a million square kilometres of tropical lowland forest. Nonetheless, the distribution of this scarce species undoubtedly extends far further than this data indicates; we anticipate that it will be found elsewhere in the upper and central Amazon basin at least (most likely in the Peruvian Amazon), and elsewhere in the southern Guianas.

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REFERENCES CITED

- Brévignon, C.**
2005. Description de nouveau Satyrinae provenant de Guyane française (Lepidoptera, Nymphalidae). *Lambillionea* 105(3)(1): 393-404, 60 figs.
- Condamín M.**
1973. Monographie du genre *Bicyclus* (Lepidoptera: Satyridae). *Mémoires de l'Institut fondamental d'Afrique Noire* 88: 1-324.
- DeVries, P. J.**
1986. Hostplant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae & Nymphalidae). *Journal of Research on the Lepidoptera* 24(4): 290-333, 3 tabs.
1987. *The Butterflies of Costa Rica and their Natural History*. Papilionidae, Pieridae, Nymphalidae. Princeton, Princeton University Press. xxii + 327 pp., 50 pls., 35 figs., 3 tabs., 2 maps
- Forster, R.**
1964. Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. *Veröffentlichungen der zoologischen Staatssammlung München* 8: 51-188, pls. 27-35, 264 figs.
- Fratello, S. A.**
2005. An expedition to Guyana's Acarai Mts. Including two new and one undescribed butterfly species. *News of the Lepidopterists' Society* 47(1): 29-31, 34-37, 12 figs.
- Freitas, A. V. L., N. Wahlberg, P. F. Matos-Maravi, M. A. Marín and O. H. M. Mielke**
2012. *Euptychia bouletti* (Le Cerf) n. comb. (Lepidoptera: Nymphalidae: Satyrinae), a rare and endangered butterfly from Southeastern Brazil. *Neotropical entomology* 41(6): 461-467, 4 figs., 1 tab.
- Freitas, A. V. L., E. P. Barbosa, J. P. Santos and O. H. H. Mielke**
2013. A new genus, *Atlanteuptychia* gen. nov., for *Euptychia ernestina* (Lepidoptera: Nymphalidae: Satyrinae). *Zoologia* 30(6): 661-668, 19 figs., 1 tab.
- Klots, A. B.**
1970. *Lepidoptera*, pp. 115-130. In: Tuxen S. L. (Ed.), *Taxonomists's Glossary of Genitalia in Insects*. Copenhagen, Munksgaard.
- Lamas, G.**
2004. *Nymphalidae. Satyrinae. Tribe Satyrini. Subtribe Euptychiina*, pp. 217-223. In: Lamas, G. (Ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea*. In: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera. Volume 5A*. Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Larsen, T. B.**
2005. *Butterflies of West Africa*. Apollo Books, Stenstrup, Denmark. 2 vols., 596 pp., 125 pls.
- Marín, M. A., C. Peña, A. V. L. Freitas, N. Wahlberg and S. I. Uribe**
2011. From the phylogeny of the Satyrinae butterflies to the systematics of Euptychiina (Lepidoptera: Nymphalidae): History, progress and prospects. *Neotropical Entomology* 40(1): 1-13, 3 figs., 2 tabs.
- Miller, L. D.**
1968. The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). *Memoirs of the american entomological Society* 24: [6] + iii + 174 pp., 327 figs., 7 tabs.
- Miller, L. D.**
[1970]. Nomenclature of wing veins and cells. *Journal of Research on the Lepidoptera* 8(2): 37-48, 5 figs.
- Miller, L. D. and J. Y. Miller.**
1988. A New *Euptychia* Species from Northwestern Mexico (Satyridae). *Journal of the Lepidopterists' Society* 42(4): 276-280, 9 figs.
- Monteiro A. and N. E. Pierce**
2001. Phylogeny of *Bicyclus* (Lepidoptera: Nymphalidae) inferred from COI, COII and EF-1 α gene sequences. *Molecular Phylogenetics & Evolution* 18: 264-281, 7 figs., 9 tabs.
- Murray, D.L.**
2001. *Systematics of euptychiine butterflies (Nymphalidae: Satyrinae: Euptychiina) based on larval morphology and DNA sequence data and the evolution of life history traits*. Ph.D. dissertation, Louisiana State University, Baton Rouge, LA.
- Murray, D. L. and D. P. Prowell**
2005. Molecular phylogenetics and evolutionary history of the Neotropical satyrine subtribe Euptychiina (Nymphalidae: Satyrinae). *Molecular Phylogenetics and Evolution* 34(1): 67-80, 4 figs., 4 tabs.
- Neild, A. F. E.**
1996. *The Butterflies of Venezuela. Part 1: Nymphalidae I (Limentitidinae, Apaturinae, Charaxinae)*. A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae. Meridian Publications, Greenwich. 144 pp., 32 pls., 18 figs., 4 maps.
2008. *The Butterflies of Venezuela. Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae)*. A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae. Meridian Publications, London. 276 pp., 84 pls., 31 figs., 2 tabs, 4 maps.
- Parsons, M.**
1999. *The Butterflies of Papua New Guinea*. Academic Press, London & San Diego. 736 pp., 136 pls., 57 figs., 8 tabs.
- Peña, C. and G. Lamas**
2005. Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista peruana de Biología* 12(1): 5-48, 14 figs.
- Peña, C., S. Nylin, A. V. L. Freitas and N. Wahlberg**
2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae). *Zoologica Scripta* 39(3): 243-258, 4 figs., 3 tabs.
- Peña, C., S. Nylin and N. Wahlberg**
2011. The radiation of Satyrini butterflies (Nymphalidae: Satyrinae): a challenge for phylogenetic methods. *Zoological Journal of the Linnean Society* 161(1): 64-87, 8 figs., 2 tabs.
- Peña, C., N. Wahlberg, E. Weingartner, U. Kodandaramaiah, S. Nylin, A. V. L. Freitas and A. V. Z. Brower**
2006. Higher level phylogeny of satyrine butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phylogenetics and Evolution* 40(1): 29-49, 7 figs., 3 tabs.
- Pinzón, J.**
2009. Mariposas del bajo Río Caquetá y Apaporis (Amazonía colombiana). Nymphalidae: Satyrinae. Online "Rapid Color Guide" available from the Field Museum (Chicago, USA): http://fm2.fieldmuseum.org/plantguides/rcg_intro.asp
- Pulido, H. W., M. G. Andrade, C. Peña and G. Lamas**
2011. Two new taxa of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae) from the Andes of Colombia and Peru. *Zootaxa* 2906: 43-51, 6 figs.
- Robbins, R. K., A. R. P. Martins, R. C. Busby and M. Duarte**
2012. Loss of male secondary sexual structures in allopatry in the Neotropical butterfly genus *Arcas* (Lycaenidae: Theclinae: Eumaeini). *Insect Systematics & Evolution* 43: 35-65, 36 figs.
- Singer, M. C., P. J. DeVries and P. R. Ehrlich**
1983. The *Cissia confusa* species-group in Costa Rica and Trinidad (Lepidoptera: Satyrinae). *Zoological Journal of the Linnean Society* 79(2): 101-119, 4 figs.
- Singer, M. C., P. R. Ehrlich and L. E. Gilbert**
1971. Butterfly feeding on lycopsid. *Science* 172(3990): 1341-1342
- Warren, A. D., K. J. Davis, E. M. Stangeland, J. P. Pelham and N. V. Grishin**
2013. *Illustrated Lists of American Butterflies*. <http://www.butterfliesofamerica.com>