

BULLETIN OF THE ALLYN MUSEUM

Published By
The McGuire Center for Lepidoptera and Biodiversity
Florida Museum of Natural History
University of Florida
P. O. Box 112710
Gainesville, FL 32611-2710

Number 149

16 November 2007

ISSN-0097-3211

TAXONOMIC COMMENTS ON *PSEUDOLYCAENA* WALLENGREN (LEPIDOPTERA: LYCAENIDAE: THECLINAE: EUMAEINI)

George T. Austin, Lee D. Miller, and Jacqueline Y. Miller

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History,
University of Florida, P. O. Box 112710, Gainesville, Florida 32611-2710

ABSTRACT: Five species of *Pseudolycaena* are recognized: *Pseudolycaena marsyas* (Linnaeus, 1758) (widespread in South America), *Pseudolycaena nellyae* Lamas, 1975, **new status** (western Peru and Ecuador), and *Pseudolycaena cybele* (Godman & Salvin, 1896), **reinstated status** (St. Vincent), all of the “marsyas” group with males having vincular brush organs and *Pseudolycaena damo* (H. Druce, 1875), **confirmed status** (Mexico to Colombia) and *Pseudolycaena dorcas* (H. H. Druce, 1907), **reinstated status** (northwestern Peru), both of the “damo” group with males lacking vincular brush organs..

KEY WORDS: brush organ, distribution, genitalia, hairstreak, hostplants, neotropic

INTRODUCTION

The genus *Pseudolycaena* Wallengren, 1858 (type species: *Papilio marsyas* Linnaeus, 1758 by original designation, Hemming 1967), includes very large hairstreaks (Lycaenidae: Theclinae: Eumaeini) distributed through much of tropical America from northern Mexico to Argentina. Besides their large size, members of *Pseudolycaena* are unmistakable with their produced forewing apices (especially prominent on males), bright blue dorsum, very long tail at the end of the vein CuA₂ on the hindwing and a somewhat shorter tail from CuA₁, and purple-gray venter with relatively large black macules. Male *Pseudolycaena* do not have a prominent alar patch of androconial scales as is present on many taxa of Eumaeini. The dorsal color, described as ‘pedaço animado do céu’ (an animated piece of the sky, Brown 1992), is produced by “morpho-type scales” (e.g., Vértessy *et al.* 2006). Clench (1963) thought the genus was allied to *Arcas* Swainson, 1832, and especially *Atlides* Hübner, [1819], based on genital morphology and the tornal cleft on the hindwing (see also Godman and Salvin 1879-1901). Nicolay

(1971), however, while noting overall similarities in the genitalia of the three taxa, pointed out consistent differences. Robbins (2004) similarly placed *Pseudolycaena* in his *Atlides* section of Eumaeini with *Atlides*, *Arcas*, and *Theritas* Hübner, 1818.

Traditionally, two species of *Pseudolycaena* have been recognized (e.g., Robbins 2004): *Papilio marsyas* Linnaeus, 1758, with two additional subspecies (*Thecla cybele* Godman & Salvin, 1896, *Pseudolycaena marsyas nellyae* Lamas, 1981) and the monotypic *Thecla damo* H. Druce, 1875 (including its putative synonym *Thecla dorcas* H. H. Druce, 1907). Several authors (e.g., Clench 1963; Scott 1971; Lamas 1981; Bridges 1988, 1994; D'Abbrera 1995), however, considered all as subspecific taxa and/or synonyms of *P. marsyas*. Smith *et al.* (1994) included *Thecla cybele* as a subspecies of *P. marsyas*, but thought it possibly conspecific with *P. damo* or a species in itself. Despite this, characters of the male genitalia, especially, indicate two distinct species groups within *Pseudolycaena*, each containing more than one species. Our studies of *Pseudolycaena* from several neotropical venues prompted a reexamination of the genus, the results of which are presented below. The material resulting from those investigations consists of 650 individuals deposited at the McGuire Center for Lepidoptera and Biodiversity in Gainesville, Florida, supplemented by 25 specimens at the American Museum of Natural History in New York.

"marsyas" group

Males of the "marsyas" group have large and distinct brush organs on the dorsum of the vinculum of the genitalia (Fig. 36) and the dorsal forewing has a broad to very broad black margin. Three species are recognized.

Pseudolycaena marsyas (Linnaeus)

(Figs. 1-12, 29, 30, 37-42)

Papilio marsyas Linnaeus, 1758

Pseudolycaena marsyas: Wallengren, 1863; Kaye, 1904; Brown and Mielke, 1967, 1968; Barcant, 1970; Scott, 1971; Smart, 1975; Johnson *et al.*, 1986; Emmel and Austin, 1990; Brown, 1992; Lamas *et al.*, 1996; Murray, 1996; Ruzsczyk and Silva, 1997; Debrot *et al.*, 1999; Brown and Freitas, 2000; Motta, 2002; Iserhard and Romanowski, 2004; Robbins, 2004; Emery *et al.*, 2006; Nuñez, 2006; Pinheiro and Emery, 2006; Zárte and Broncales, 2006

Thecla marsyas: Kirby, 1871; Capronnier, 1874; Mathew, 1887; Druce, 1876; Möschler, 1877; Godman and Salvin, 1879-1901; Snellen, 1887; Draudt, 1921-24; Köhler, 1928; Jörgensen, 1935; Lima, 1950; Biezanko *et al.*, 1957; Silva *et al.*, 1968; Ebert, 1969; Hayward, 1973; Lewis, 1973; Watson and Whalley, 1975; D'Abbrera, 1984

Thecla marsyas: Köhler, 1923

(no genus) *marsyas*: Comstock and Huntington, 1961

Pseudolycaena marsyas marsyas: Clench, 1963; Riley, 1975; Lamas, 1975, 1981, 2003; Bridges, 1988, 1994; Mielke and Casagrande, 1991, 1997; Mielke, 1994; D'Abbrera, 1995

Type: Lectotype male (designated by Honey and Scoble 2001) in collection of Museum Ludovica Ulrica housed at the Zoological Museum, University of Uppsala,

labeled as described by Honey and Scoble (2001). Type locality: “*Calidis regionibus*” restricted to Rio de Janeiro, Brazil (Smith *et al.* 1994).

The dorsum of *P. marsyas* is similar to that of its more northerly distributed congener, *P. damo*, but averages a deeper blue in color with less of the green reflections seen on *P. damo*. On males, the distal 2/3 to 7/8 of the forewing costal margin is intensely black, this becoming broad at the apex and narrows along the outer margin to a terminal line at the tornus. The margins of the forewings are usually more broadly black on females, remaining 2-4 mm in width posteriorly at the tornus. The dorsal hindwing of the male has a dark gray costa, a black terminal line, and a variable in size oval to triangular “thecla” spot. Females have a similar costal area, blackish along the outer margin, broadest at the apex and extending to vein CuA_2 , a larger “thecla” spot than males, and usually an adjacent black triangular macule in cell CuA_2-2A . The ventral surface of both sexes is largely purple-gray with a pattern of black (outlined with white) macules centrally on both wings and more lineal and curvilinear elements distad on the hindwing. The forewing is largely pale brown posterior to vein CuA_2 ; males usually have a narrow line of blue along the lower discal cell vein often extending distad along vein CuA_2 . The tornal area of the hindwing is shaded with greenish-gray; the tornal macule and “thecla” spot are prominent black oval macules. Otherwise, the ventral marginal and submarginal patterns are absent or very faint on the forewing and poorly developed on the hindwing, usually as dark lines in each cell vaguely highlighted on both sides by whitish. The end of the discal cell is a thin black line on the forewing and unmarked or with a thin black line (sometimes incomplete) on the hindwing.

Pseudolycaena marsyas exhibits both local individual and clinal variation. Such superficial variation includes size, shape of the wing, intensity and hue of the dorsal blue, width of the black margins especially at the apex of the forewing, darkness of the ventral ground color, and size of ventral macules. Variation in size among individuals can be considerable. The forewing, particularly of males, typically has an elongated apex, but on some individuals, the apex may be very weakly produced giving a squared aspect. Those intrapopulation variations do not appear as seasonal phenomena within available samples. Males, especially, show variation in color on the dorsum. This may vary locally; males from Rondônia, Brazil, for example, range from blue to lavender. Individuals seen from French Guiana and Guyana are blue, approaching the color of *P. nellyae*. That phenotype (Fig. 5) is also frequent, but not nearly as universal, among males westward into Venezuela (including Tobago and Trinidad) and eastward into the lower Amazonian drainage of Brazil (especially Pará). Populations of *P. marsyas* in northern South America also tend to have a darker, more purplish, venter compared with more southern populations that have a grayer aspect. Most females in northern South America (Venezuela to French Guiana) have especially broad black margins on the dorsal forewings, often covering more than half of the wing (Fig. 11). Southward, the margins are much narrower and exhibit individual and apparent clinal variation with some approaching the yet narrower margins of *P. damo* (e.g., 11 of 52 females from Pará, Amazonas, and Rondônia within the Amazonian basin have narrow margins compared with 12 of 26 from Espírito Santo and 9 of 11 females from Argentina). Since these several characters appear to vary clinally and are not accompanied by observable differences in genital morphology, taxonomic recognition is not justifiable for northern South American populations given the present state of knowledge.

Pseudolycaena marsyas and *P. damo* are readily separated by their genitalia. Males of *P. marsyas* have distinct, large, dark brown to black brush organs on the dorsum of the

vinculum (absent on *P. damo*) and females have a broad lamella with its lateral margins developed into prominent caudally directed and sharply pointed projections (no projections on *P. damo*). The brush organs were not noted by Clench (1963), but his figure of male genitalia seems otherwise to be that of typical *P. marsyas*. The genitalia of both sexes of *P. marsyas* exhibit variation both locally and geographically. This appears to be intraspecific, continuous, and with no consilient superficial variation. On males, this variation includes the breadth of the valvae, width and orientation of the central lobes at the juncture of the bilobes and caudal extensions, shape of the vincular spur, and shape of the cephalic end of the aedeagus (Figs. 29, 30). On females, variation involves the breadth and shape of the lamella including the length of the lateral lamellar teeth and configuration of the opening of the ostium bursae (Figs. 37-42).

Pseudolycaena marsyas is widespread and often common in much of South America, extending northward to Tobago, Trinidad and southernmost Central America. Records of *P. marsyas* exist for Argentina, Bolivia, Brazil (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Pará, Paraíba, Paraná, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo), Colombia, Curaçao (where apparently extirpated, Debrot *et al.* 1999), Ecuador, French Guiana, Guyana, Panama, Paraguay, Peru, Suriname, Tobago, Uruguay, and Venezuela (Möschler 1877; Godman and Salvin 1879-1901; Snellen 1887; Kaye 1904; Biezanko *et al.* 1957; Brown and Mielke 1967, 1968; Silva *et al.* 1968; Ebert 1969; Barcant 1970; Hayward 1973; Lewis 1973; Lamas 1975, 1981, 2003; Smart 1975; D'Abrera 1984, 1995; Emmel and Austin 1990; Mielke and Casagrande 1991, 1997; Brown 1992; Mielke 1994; Smith *et al.* 1994; Lamas *et al.* 1996; Murray 1996; Ruszczyk and Silva 1997; Brown and Freitas 2000; Motta 2002; Iserhard and Romanowski 2004; Emery *et al.* 2006; Nuñez 2006; Pinheiro and Emery 2006; K. Brown *in litt.*; this study), but east of the Andes (Lamas 1981). The male identified as *P. marsyas* illustrated by D'Abrera (1984) from the "Leeward Islands" is *P. cybele* (note data with holotype of that species below) or mislabeled. A short series at the McGuire Center for Lepidoptera and Biodiversity labeled as from Chiapas, Mexico, are typical *P. marsyas*; these are considered mislabeled.

Barcant (1970) found *P. marsyas* in numbers at the nectar of *Eupatorium* (Asteraceae) in swampy areas on Tobago. In Rondônia, Brazil, the species was encountered in disturbed areas especially within open second growth and along forest edges (Austin, pers. obs.); Brown (1992) found it to be migratory and common in cities and open country, although Kaye (1904) observed that it only flew for short periods and often landed on the ground. The species is polyphagous (Brown 1992), with reported larval hostplants within several families: Anacardiaceae, Celastraceae, Combretaceae, Myrtaceae, Rosaceae, Ulmaceae, and Urticaceae (Jørgensen 1935, Silva *et al.* 1968, Hayward 1973). Larvae apparently feed on flowers and leaves (Silva *et al.* 1968). The flight period may vary with location; records are from July through April in Colombia, February through September in Espírito Santo, Brazil, during every month except February in Rondônia, Brazil, and from February to August in Salta, Argentina.

***Pseudolycaena nellyae* Lamas, new status**

(Figs. 13-16, 31, 43)

Pseudolycaena marsyas dorcas: Lamas, 1975, 1976

Pseudolycaena marsyas nellyae Lamas, 1981; Bridges, 1988, 1994

Pseudolycaena marsyas marsyas: D'Abbrera, 1995

Pseudolycaena marsyas: Robbins, 2004; Zárata and Broncales, 2006

Type: Holotype male at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru, with the following data: "Lima, Cieneguilla, 360 m, 24.iii.74 (G. Lamas & N. Medina)" (Lamas 1981).

Lamas (1981) described and illustrated this taxon from populations of *Pseudolycaena* occurring west of the Andes Mountains in Peru (a male from Lima, Peru, was also illustrated by D'Abbrera 1995 as *P. marsyas marsyas*). It was treated as a synonym of *P. marsyas* by Robbins (2004). *Pseudolycaena nellyae* is characterized by its intense and dark blue dorsal color and usually smaller (than on *P. marsyas*) ventral macules. The macules are placed as on *P. marsyas*. The markings at the ends of the discal cells are like those of *P. marsyas*. Males have broad black margins on the forewings like *P. marsyas*; females have narrow margins as on females of *P. damo* and some *P. marsyas*.

Male genitalia of *P. nellyae* are similar to those of *P. marsyas* in having vincular brush organs, but are broader overall and have a proportionally shorter aedeagus (Fig. 31). Female genitalia (Fig. 43), however, are different and resemble those of *P. damo* and *P. dorcas*. The lamella is broad and lacks the lateral caudal pointed processes seen on *P. marsyas* and the ductus bursae has a very shallow caudal excavation. Too few specimens were examined to assess individual variation.

Because of constant differences from other *Pseudolycaena* in color and genital characters, *P. m. nellyae* is herein raised to a species-level taxon.

Lamas (1981) recorded *P. nellyae* from the departments of Ancash, Lima, and Tumbes in western Peru, and suggested its occurrence both southward in Peru and northward into western Ecuador; other Peruvian records are for La Libertad (Zárata and Broncales 2006). Additional material examined as part of the present study was seen from Loja (Vilcabamba, 1600 m, May), and Guayas (82 km west of Guayaquil on road to Salinas, March) provinces in western Ecuador; the western Ecuadorian record of *P. damo* of Godman and Salvin (1879-1901) may well be of this species (see also Draudt 1921-1924). A female in the American Museum of Natural History labeled (possibly erroneously) as from Latas, Ecuador (Napo Province) appears to be this species. *Pseudolycaena nellyae* is apparently confined (or largely confined) to regions of arid or seasonally dry climate along the west coast of South America in Ecuador and Peru.

The life history of *P. nellyae* was reported by Cisneros and Gazani (1973, cited by Lamas 1981); reported hostplants include plants of the families Anonaceae, Fabaceae, Malpighiaceae, Meliaceae, and Sapotaceae (Lamas 1975, 1976). The species may be a pest on *Pouteria lucuma* (Sapotaceae) and other cultivated plants (Lamas 1975, Zárata and Broncales 2006). Lamas (1981) found *P. nellyae* commonly within the city of Lima, often visiting flowers of *Lantana* (Verbenaceae). The flight period in Peru was reported from December through July with the species being most common until March (Lamas 1981); the few records from Ecuador are in March and May.

***Pseudolycaena cybele* (Godman & Salvin), reinstated status**
(Figs. 17-20, 32, 36, 49)

Thecla cybele Godman & Salvin, 1896: Draudt, 1921-24

Pseudolycaena marsyas cybele: Comstock and Huntington, 1943; Clench, 1963; Riley, 1975; Brown, 1978; Lamas, 1981; Bridges, 1988, 1994; Smith *et al.*, 1994; D'Abrera, 1995

(no genus) *marsyas cybele*: Comstock and Huntington, 1959

Pseudolycaena marsyas: Scott, 1971; Miller and Miller, 2001; Robbins, 2004

Type: Holotype male at The Natural History Museum, London, with the following labels: "Godman-Salvin / Coll. / Thecla / cybele G&S.", "Leeward side / St. Vincent, W.I. / H. H. Smith", "Type", "B. M. TYPE / No. Rh. 518"

Pseudolycaena cybele is the darkest-colored species of the genus. It is deeper blue on the dorsum, purple-blue rather than cobalt blue or paler, than are *P. nellyae* and *P. dorcas* and does not have the greenish aspect, except at the very bases of the wings, of *P. marsyas*, or especially *P. damo*. The wings are, on average, much less produced than on any congener; forewings of the female are particularly short and quadrate (note that some individuals of other species of *Pseudolycaena* have foreshortened apices to the forewings). The black margins of the dorsal forewings are very broad on both sexes, these similar to, but even broader than on most *P. marsyas* and *P. nellyae*. The venter is a very dark purplish brown, more so than other species of *Pseudolycaena*, with large and bold black macules outlined distinctly by pale greenish, has a distinctly blue-green cast posteriorly on forewing, and has the tornal area of the hindwing intensely blue-green. The male has a blue streak along the base of the discal cell vein as on *P. marsyas*. The ventral submarginal pattern, especially on the hindwing, is much more distinctly developed on *P. cybele* than on its congeners. Both wings have black at the distal end of the discal cell (this as a macule on the forewing), with the macules on the forewing in R₂-R₃ and M₂-M₃ occurring near the bases of their respective cells (as on *P. marsyas*, see below under *P. damo*) and forming nearly a straight line with the macule in the discal cell. The "thecla" spot is bar-shaped on the venter of *P. cybele* rather than an oval macule as on other species of *Pseudolycaena*.

Male genitalia of *P. cybele* resemble those of *P. marsyas* and *P. nellyae* in the presence of prominent, thick brush organs on the dorsum of the vinculum (Fig. 36). The genital capsule of *P. cybele* is broader and stouter than that of *P. marsyas*, the valvae are somewhat broader, the lateral and caudal lobes at the juncture of the bilobes and caudal extensions are thinner, and the saccus is relatively shorter and broader (Fig. 32). Female genitalia have a wide lamella and one or two pairs of caudally directed teeth. The ductus bursae is more robust than on any other *Pseudolycaena* and the signa are broader (Fig. 49). No individual variation was noted within the small sample examined.

Thecla cybele had been considered a subspecies of *P. marsyas*. Riley (1975) noted that it was sometimes considered a distinct species, but included it as a subspecies of *P. marsyas*. The latest work dealing with the West Indian fauna (Smith *et al.* 1994) retained it as such, but suggested it as possibly conspecific with *P. damo* or a separate species. Robbins (2004) considered *T. cybele* synonymous with *P. marsyas*. Because of differences in superficial and genital morphology resulting in a unique combination of characters, and the apparently long period of isolation from other *Pseudolycaena* (Maury *et al.* 1990), *Thecla cybele* is here returned to a species-level taxon. It is similar to *P. marsyas* in its ventral maculation, the presence of brush organs on males, and the overall form of the lamella of females. This appears to substantiate the suggestions by Clench (1963) and Brown (1978) of a South American origin for *P. cybele*.

Pseudolycaena cybele is known only from the island of St. Vincent in the West Indies (Comstock and Huntington 1943, Riley 1975, Smith *et al.* 1994). Although it has been recorded elsewhere on St. Vincent (Clark 1904, Smith *et al.* 1994; K. Brown, pers. comm.), the Millers first saw this species at the type locality in mixed tropical forest of Wallilabou Valley of western St. Vincent in the shadow of the active Soufrière volcano. Here the mornings dawn bright and sunny, but usually by noon it is overcast with brief showers, mist, and fog. *Pseudolycaena cybele* was usually seen active from about 1100 hours and later, with very brief periods of activity despite cloudy weather. Populations of this species appear to be localized and small where it occurs on the island. We have records for September and October.

The favorite nectar source of *P. cybele* on St. Vincent is *Eupatorium* (Asteraceae), and the butterfly is particularly fond of the sticky nectar available at the base of the flowers and also at extrafloral nectaries (Smith *et al.* 1994). The behavior of *P. cybele* while taking nectar, noted on several occasions, is distinct. Individuals of *P. cybele* literally "walk" (actually wobble) from the end to the base of the inflorescence while taking nectar. The wings are folded above the body. This is in contrast with observations of *P. damo* made by the Millers in February 1969 outside of Nautla, Veracruz, Mexico. Here, *P. damo* fed from the flowers of *Senecio* (Asteraceae) with the wings outstretched. This behavior occurred on several occasions over three days. A. Warren (pers. comm.), however, indicated that the wings of *P. damo* are typically upright above the body while taking nectar.

"damo" group

Males of the "damo" group have no brush organs on the dorsum of the vinculum of the genitalia and the black margin on the dorsal forewing is narrow to absent. Two species are recognized.

Pseudolycaena damo (H. Druce), confirmed status

(Figs. 21-26, 33, 34, 44-47)

Thecla marsyas: Boisduval, 1870; Davis, 1928; Meerman and Boomsma, 1993

Thecla damo H. Druce, 1875; Godman and Salvin, 1879-1901; Dyar, 1914; Draudt, 1921-24; Hoffmann, 1941; Lewis, 1973; Beutelspacher, 1982; Routledge, 1977; D'Abrera, 1984

(no genus) *damo*: Comstock and Huntington, 1959

Pseudolycaena marsyas damo: Clench, 1963; Kendall, 1975; Riley, 1975; Lamas, 1981; Llorente *et al.*, 1986; Bridges, 1988, 1994; de la Maza *et al.*, 1989; de la Maza and White, 1990; de la Maza and Gutiérrez, 1992; de la Maza and de la Maza, 1993; D'Abrera, 1995; Maes, 2004

Thecla marsyas damo: Ross, 1964, 1976; Monroe *et al.*, 1967; de la Maza and White, 1990

Pseudolycaena marsyas: Scott, 1971; Pyle, 1981; Opler, 1992; Durden, 2006

"Strymon" *damo*: Kitching and Kitching, 1973

Pseudolycaena damo: Smart, 1975; Robbins and Small, 1981; Robbins and Aiello, 1982; DeVries, 1983; Downey and Allyn, 1984; de la Maza and de la Maza, 1985; de la Maza, 1987; Luis *et al.*, 1991, 1995, 2004; Raguso and Llorente, 1991, 1997; Vargas *et al.*, 1991, 1992, 1996; Johnson and Llorente, 1992; Balcázar, 1993; Austin *et al.*,

1996; Warren *et al.*, 1998; Meerman, 1999; Warren and Llorente, 1999; Monteagudo *et al.*, 2001; Pozo *et al.*, 2003; Llorente *et al.*, 2004; Robbins, 2004; Salinas *et al.*, 2004; Janzen and Hallwachs, 2005

Type: Holotype male at The Natural History Museum, London, with the following labels - "Godman-Salvin / Coll. 1911--93. / B.C.A. Lep. Rhop. / Thecla / damo / Druce", "Calobre / Panama / Arcé.", "T. Damo / Type / H Druce.", "Sp. figured" , "Type", "B. M. TYPE / No. Rh. 516".

As noted above, the wings of *P. damo* are generally similar to those of *P. marsyas*. The dorsum of *P. damo* is a paler and more greenish blue than that of *P. marsyas*. The black of the margins of the male's forewing is less intense and does not broaden along the costa (on some specimens it becomes narrower) towards the apex or extend posterior to vein M_1 proximad to the apex. The outer margin has little black, this usually no more than a terminal line. Females also have narrow black margins (although broader than on males) that are nearly as broad at the tornus (2 mm) as at the apex. The "thecla" spot is usually larger than that of *P. marsyas* and there is nearly invariably a triangular spot adjacent to it in cell CuA_2-2A . The venter of *P. damo* is grayer than on *P. marsyas* and is not as intensely purple; this grayness is also seen in the brown posterior portion of the forewing. Males lack or have much more restricted blue along the lower vein of the discal cell than seen on *P. marsyas*. The discal cell on the forewing of *P. damo* has a distinct black bar at its distal end; this is at most a thin and inconspicuous black line on *P. marsyas*. The black macules distad of the discal cell in cells R_2-R_3 , R_3-M_1 and M_2-M_3 are offset more towards the termen than on *P. marsyas* where the macules in R_2-R_3 and M_2-M_3 approximate the end of the discal cell, occurring near the bases of their respective cells. Similarly, the macule in cell CuA_1-CuA_2 on the forewing tends to be more distad on *P. damo* (and *P. dorcas*) than on *P. marsyas*, resulting in a lineal series of the macules in that cell, CuA_2-2A , and M_3-CuA_1 with that in M_1-M_2 . Those macules on *P. marsyas*, *P. cybele*, and *P. nellyae*, more often than not, are aligned with the end of the discal cell. A similar pattern occurs on the hindwing. *Pseudolycaena damo* has a more prominent black bar at the distal end of the discal cell than does *P. marsyas* (where it may be altogether absent) and the macules in $Rs-M_1$ and M_2-M_3 are more distad than on *P. marsyas*. The tornal area of the ventral hindwing is more grayish (often grayish blue) and less intense than the greenish on *P. marsyas*.

Male genitalia of *P. damo* generally resemble those of *P. marsyas*, but lack the vincular brush organs and the genital capsule is broader (Figs. 33, 34). In addition, they exhibit considerable variation as was also seen in *P. marsyas*. This variation includes the breadth of the genital capsule, robustness of the valvae, and relative length of the saccus. Female genitalia differ from *P. marsyas* in the absence of prominent caudally directed teeth laterad on the lamella; in this respect they resemble those of *P. nellyae* and *P. dorcas*. The lamella of *P. damo* is broadly triangular and exhibits continuous local and apparent geographical variation in its width and overall shape and in the configuration at the opening of the ostium bursae (Figs. 44-47). The lamella of *P. nellyae* tends to be narrower and more angular without the more rounded corners typical of *P. damo*, especially northward.

This widely distributed species occurs in the northern neotropics south through Central America to at least Colombia (Cauca and Magdalena valleys, Casabe) in northern South America. Records of *P. damo* were found for Belize, Colombia, Costa Rica, El

Salvador, Guatemala, Honduras, Mexico (Campeche, Chiapas, Colima, Guerrero, Hidalgo, Jalisco, Michoacan, Nayarit, Oaxaca, Puebla, Quintana Roo, San Luis Potosi, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatan), Nicaragua, and Panama (Boisduval 1870; Godman and Salvin 1879-1901; Dyar 1914; Davis 1928; Hoffmann 1941; Ross 1964, 1976; Monroe *et al.* 1967; Kitching and Kitching 1973; Kendall 1975; Routledge 1977; Robbins and Small 1981; Beutelspacher 1982; Robbins and Aiello 1982; de la Maza and de la Maza 1983, 1985; DeVries 1983; D'Abbrera 1984, 1995; Llorente *et al.* 1986, 2004; de la Maza 1987; de la Maza and White 1990; Luis *et al.* 1991, 1995, 2004; Raguso and Llorente 1991; de la Maza and Guitiérrez 1992; Vargas *et al.* 1992, 1996; Balcázar 1993; Meerman and Boomsma 1993; Austin *et al.* 1996; Warren *et al.* 1998; Meerman 1999; Warren and Llorente 1999; Pozo *et al.* 2003; Maes 2004; Salinas *et al.* 2005; A. Luis, pers. comm.; this study). The species has also been reported as a stray in southern Texas (Pyle 1981, Opler 1992, Durden 2006), but this has not been confirmed. Godman and Salvin's (1879-1901) report for western Ecuador may refer to *Pseudolycaena nellyae* as may Draudt's (1921-1924).

In Mexico, Kendall (1975) reared *P. damo* on *Croton niveus* (Euphorbiaceae) and Robbins and Aiello (1982) recorded oviposition of *Pterocarpus* (Fabaceae) in Panama. Maes (2004) indicated hostplants in the families Bromeliaceae, Fabaceae, Malpighiaceae, Meliaceae and Sapotaceae in Nicaragua. In Costa Rica, larvae have been found on Asteraceae, Chrysobalanaceae, Connaraceae, Fabaceae, Malpighiaceae, and Sapindaceae (Janzen and Hallwachs 2005). Larvae were not found to produce calls (DeVries 1991). The species is a broadly distributed habitat generalist found commonly along edges of a variety of forests in Mexico (Ross 1976, Pozo *et al.* 2003, Llorente *et al.* 2004). In Guatemala (Austin *et al.* 1996) and Costa Rica (this study), it has been found in second growth habitats, on forest edges, and often in towns. Ross (1964) found this species common in shrubby fields in Belize and (1976) along edges of forests and hedgerows in Veracruz, Mexico. Godman and Salvin (1879-1901) noted that the species "flies high" and settles on "foliage at the borders of the forest." In Panama, the species may exhibit dispersal by seasonal winds (Robbins and Small 1981). At Tikal, Guatemala, *P. damo* was encountered in every month (Austin *et al.* 1996) as it has been in Panama (this study); records for Mexico were reported from May to December (de la Maza 1987), but the species apparently flies at some locations throughout the year (*e.g.*, Vargas *et al.* 1991, 1992, 1996; Balcazar 1993; Warren *et al.* 1998; Llorente *et al.* 2004; A. Luis, pers. comm.).

***Pseudolycaena dorcas* (H. H. Druce), reinstated status**

(Figs. 27, 28, 35, 48)

Thecla dorcas H. H. Druce, 1907: Draudt, 1921-24; D'Abbrera, 1984

(no genus) *damo dorcas*: Comstock and Huntington, 1959

Pseudolycaena marsyas dorcas: Lamas, 1981; D'Abbrera, 1995

Pseudolycaena marsyas damo: Bridges, 1988, 1994

Pseudolycaena marsyas: Robbins, 2004

Type: Holotype male at The Natural History Museum, London, with the following labels - "Godman-Salvin / Coll. 1911.--93. / Vina. / N.W. Peru. / 5500 ft. / O.T. Baron.", "T. dorcas ♂ / type H. H. Druce.", "Type", "♂", "B.M. TYPE / No. Rh. 517".

The wings of *P. dorcas* are shining pale blue similar to *P. damo*, but the strong green reflections of that species are absent. Males are unlike all other *Pseudolycaena* in lacking black margins on the dorsum; on females, the black margins are narrow (e.g., see D'Abbrera 1995, p. 1113), reminiscent of *P. damo* and *P. nellyae*. The ventral maculation, however, is like that of *P. marsyas*, *P. nellyae*, and *P. cybele*.

Male genitalia of *P. dorcas*, without brush organs, presumably indicate affinity with *P. damo*. The genital capsule is robust, more so than that of other congeners, except *P. cybele* (Fig. 35). The falces are longer and thinner than on *P. damo* and the valvae, especially the bilobes, are less broad than on other *Pseudolycaena*. The lamella of the female genitalia is broad as on *P. marsyas*, but lacks the caudally directed processes (Fig. 48), similar in this respect to *P. damo* and *P. nellyae*. Insufficient material was available to assess any variation that may occur.

Thecla dorcas has a varied history having been regarded as a synonym of *P. damo* or *P. marsyas*, a subspecies, or a full species (see synonymy above). Lamas (1981) considered *P. nellyae* and *P. dorcas* to be well differentiated subspecies of *P. marsyas*. The absence of brush organs on the male genitalia of *P. dorcas* suggests possible affinity with *P. damo*. Because of distinct differences from other species of *Pseudolycaena* in wing markings and genital morphology, *P. dorcas* is herein considered a species-level taxon. *Pseudolycaena dorcas* and *P. nellyae* differentially have characteristics similar to *P. damo* and *P. marsyas* (Table 1). Both are like *P. marsyas* in the placement of macules on the ventral surface. Male *P. nellyae* have the broad black dorsal margins of *P. marsyas* while *P. dorcas* lack black margins, a character state approached by some *P. damo*. Females of both *P. nellyae* and *P. dorcas* have narrow margins most typical of *P. damo*. Male genitalia of *P. nellyae* have vincular brush organs as does *P. marsyas*, but these are absent on *P. dorcas* and *P. damo*. The lamellae of female genitalia of both *P. nellyae* and *P. dorcas* lack the prominent caudal projections seen on *P. marsyas*. The lamella of *P. dorcas* is, however, broad and angular similar to *P. marsyas*; that of *P. nellyae* is angular (not rounded as on *P. damo*), but narrower than that of *P. dorcas*.

This species is known at present only from northwestern Peru along the upper Rio Marañon and some of its tributaries (Lamas 1981), including Vina and Rio Huayabamba (Druce 1907, D'Abbrera 1995); a male of this subspecies from Pacava, Peru (American Museum of Natural History) is also of this taxon. Apparently nothing has been reported on its behavior or life history.

DISCUSSION

The neotropical thecline genus *Pseudolycaena*, previously considered monotypic or at most including two species, appears to embrace several species differing in characters of the wings and genitalia of both sexes (Table 1). Eliot (1973) placed *Pseudolycaena* with a group of genera possessing brush organs on the male genitalia. Examination of series from across the distribution of the genus, however, indicated the existence of five species in two species groups differentiated, in part, by the presence or absence of brush organs. Although another species of Eumaeini, *Strymon istapa* (Reakirt, [1867]), exhibits intrapopulational variation in the presence of brush organs (Robbins and Nicolay 1998), this character appears constant within populations of *Pseudolycaena* and consilient with variations of wing patterns and has geographic integrity.

There is a potential sympatry of *P. marsyas* with *P. damo* in Panama, southwestern Colombia, and possibly northwestern Ecuador (recorded from Cauca Valley, Colombia;

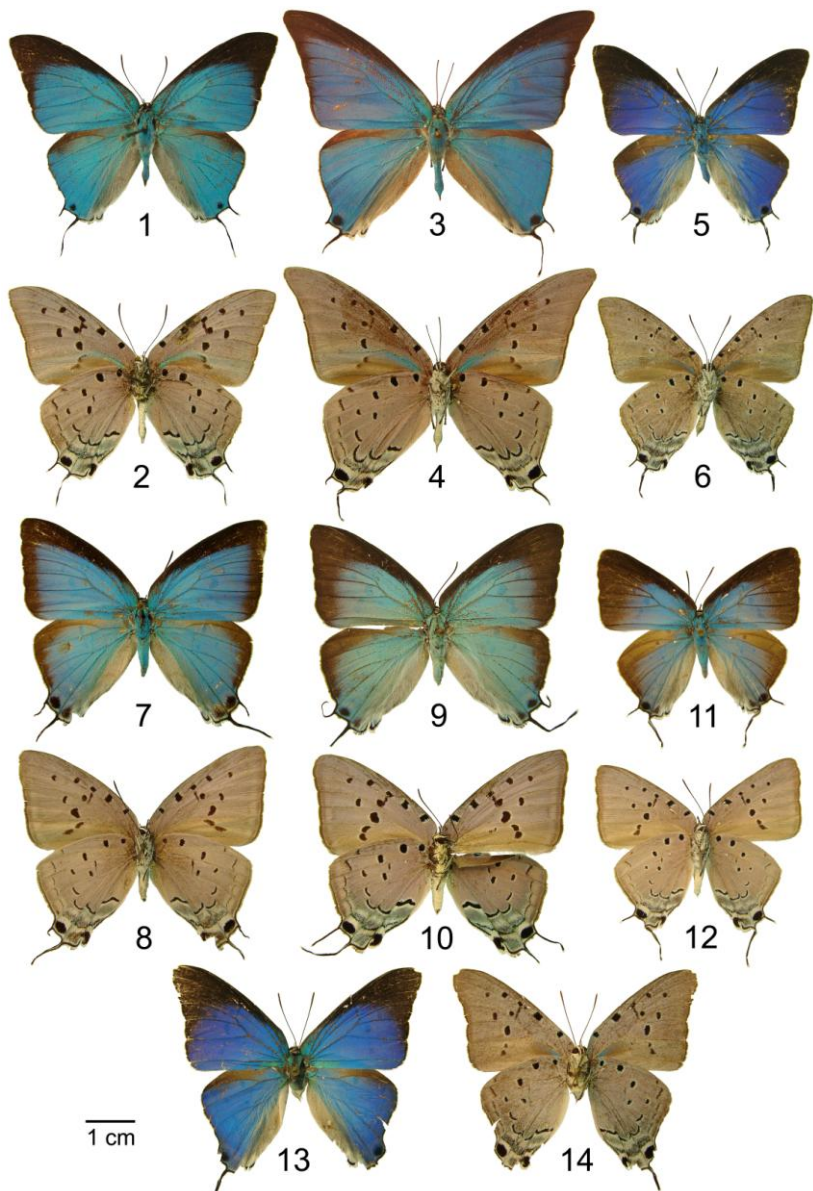
they are apparently sympatric there and elsewhere in Colombia, *vide* J. Salizar), with *P. nellyae* (near Guayaquil, Ecuador) and perhaps elsewhere, and with *P. dorcas* in northern Peru. Field investigations in these areas should prove fruitful and all southern Central American and northern South American populations require further study and elaboration.

Key to the species of *Pseudolycaena*

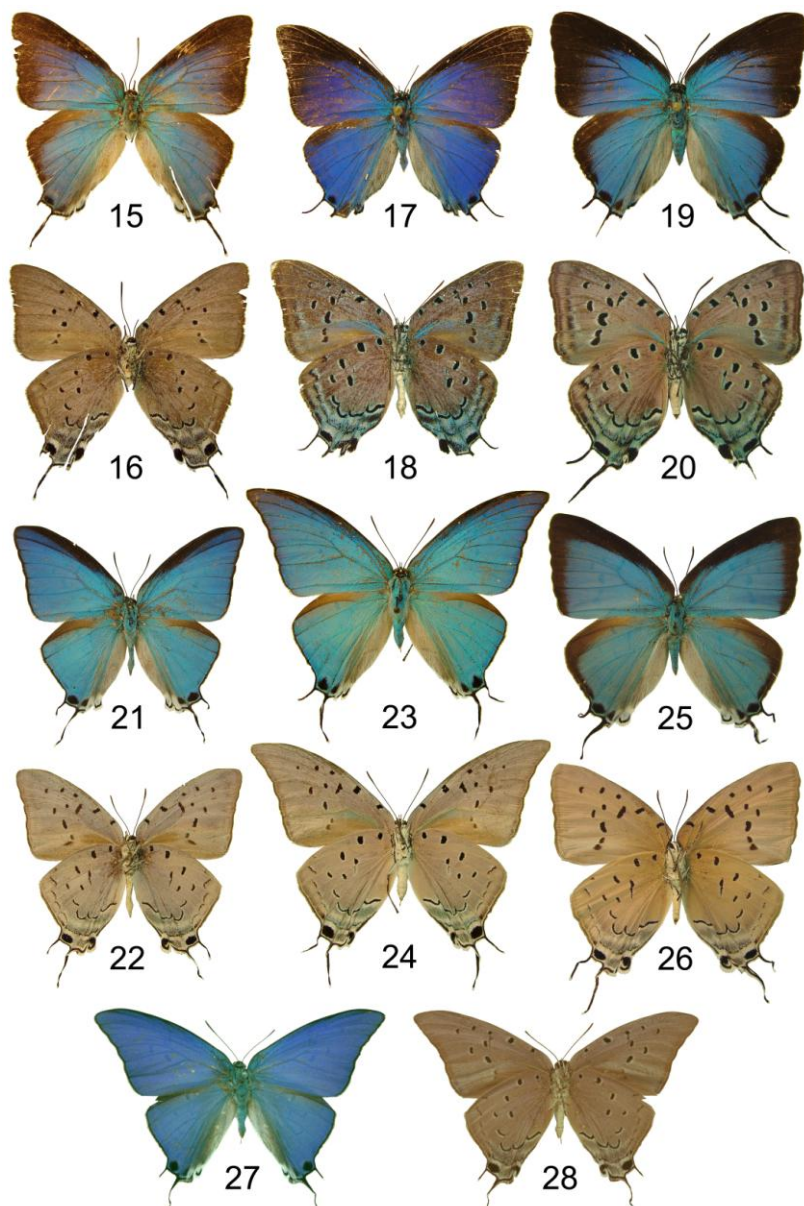
1. Male genitalia with brush organ and dorsal forewing with broad black margin "marsyas" group 2
Male genitalia without brush organ and dorsal forewing with no or narrow black margin "damo" group 4
2. Dorsum purple-blue, venter with extensive green scaling, St. Vincent only *P. cybele*
Dorsum more blue or blue-green, venter without extensive greenish scaling, not St. Vincent 3
3. Dorsum pale blue, female lamella pointed, east of Andes *P. marsyas*
Dorsum cobalt blue, female lamella not pointed, west of Andes *P. nellyae*
4. Dorsum of males without black margins, northern Peru *P. dorcas*
Dorsum of males with black margin (at least along costa), Mexico to Colombia *P. damo*

ACKNOWLEDGEMENTS

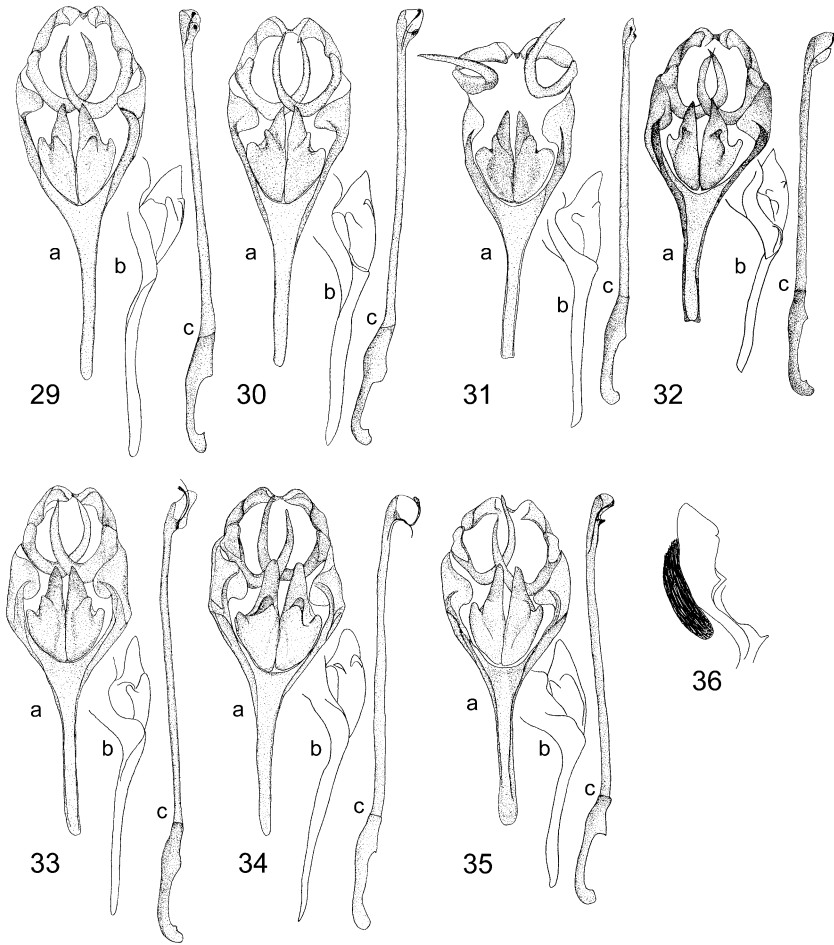
We thank P. Ackery at The Natural History Museum (London) for the loan of abdomens of types in his care and for permission to dissect these. K. Johnson graciously loaned specimens from the American Museum of Natural History. G. Lamas kindly sent a copy of his paper describing *P. nellyae*. J. Salizar shared his observations on the genus in Colombia. J. Llorente B, A. Luis M, and K. Brown, Jr. sent data and/or shared observations. Numerous people assisted with field studies, but especially N. M. Haddad, C. Mendez, and V. and G. Orellana in Guatemala and J. P. Brock, O. Gomes, and J. D. Turner in Brazil. We especially thank J. Calhoun and A. D. Warren for their careful review of the manuscript and offering helpful suggestions for its improvement. We also thank L. Buss, Dept. of Entomology and Nematology, University of Florida, for his invaluable assistance in scanning negatives. We are indebted to D. Matthews Lott for critically commenting on the manuscript, photographing specimens, and expertly organizing text and figures into this final product and to D.-M. Mintz for assistance in the production of this publication. Investigations in Guatemala were supported by several institutions including Centro de Estudios Conservacionistas (CECON) of the Universidad de San Carlos, the Parque Nacional de Tikal, The Peregrine Fund, and Consejo Nacional de Areas Protegidas (CONAP). The Conselho Nacional de Desenvolvimento Científico e Tecnológico kindly issued the authorization permits from the Ministério da Ciência e Tecnologia for studies in Rondônia, Brazil, in collaboration with EMBRAPA/CPAC and the Universidade Federal do Paraná. Partial financial support for Austin's field studies was provided by the John D. and Catherine T. MacArthur Foundation through Stanford University.



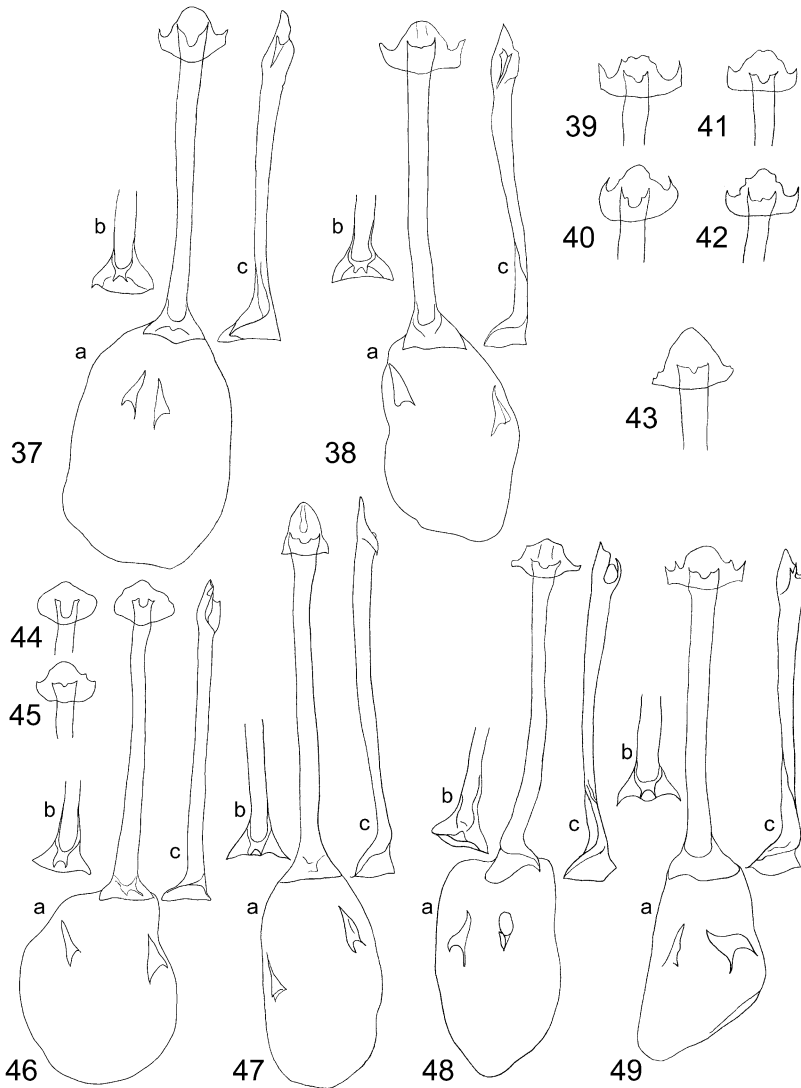
Figures 1-14. *Pseudolycaena* (D = dorsum, V = venter). **1-2)** *P. marsyas* ♂, D,V, PERU: Andes Orient, no date; **3-4)** *P. marsyas* ♂, D,V, COLOMBIA: Boyaca, Muzo, no date; **5-6)** *P. marsyas* ♂, D,V, VENEZUELA: La Sierra, Margarita, 19.ii.1981; **7-8)** *P. marsyas* ♀, D,V, COLOMBIA: Boyaca, Muzo, no date; **9-10)** *P. marsyas* ♀, D,V, PERU: Andes Orient, no date; **11-12)** *P. marsyas* ♀, D,V, VENEZUELA: La Sierra, Margarita, 19.ii.1981; **13-14)** *P. nellyae* ♂, D,V, ECUADOR: Guayas Prov.; 82km W Guayaquil on rd. to Salinas, 8.iii.1977.



Figures 15-28. *Pseudolycaena* (D = dorsum, V = venter). **15-16** *P. nellyae* ♀, D,V, ECUADOR: Loja, Vilcabamba, 1600m, v.1974; **17-18** *P. cybele* ♂, D,V, ST VINCENT: St. Patrick Par., 2km N Layou, 20m, 29.ix.1989, **19-20** *P. cybele* ♀, D,V, ST VINCENT: Charlotte Par.; Rabacca Dry River, 0.5-1.0km N Georgetown, 3.x.1989; **21-22** *P. damo* ♂, D,V, MEXICO: Veracruz; Catemaco, x.1960; **23-24** *P. damo* ♂, D,V, PANAMA: Colon; Piña, 100m, 22.ii.1971; **25-26** *P. damo* ♀, D,V, MEXICO: Veracruz; Catemaco, x.1960; **27-28** *P. dorcas* holotype ♂, D,V.



Figures 29-36. Male genitalia of *Pseudolycaena* (a. ventral view of genital capsule, b. lateral view of saccus and valva, c. lateral view of aedeagus). **29)** *P. marsyas* – BRAZIL: Rondônia, GTA #4749; **30)** *P. marsyas* – same location, GTA #4733; **31)** *P. nellyae* – ECUADOR: Guayas Province, GTA #4741; **32)** *P. cybele* – WEST INDIES: St. Vincent, GTA #5045; **33)** *P. damo* – MEXICO: Veracruz, GTA #4739; **34)** *P. damo* – PANAMA: Calobre (holotype), GTA #5961 (BM #3783); **35)** *P. dorcas* – PERU: Vina (holotype), GTA #5962 (BM #3784); **36)** *P. cybele* – same specimen as in Fig. 32, lateral view of tegumen and brush organ.



Figures 37-49. Female genitalia of *Pseudolycaena*; structures for Figs. 37, 38, 46-49 are (a) ventral view of lamellae, ductus bursae, and corpus bursae, (b) dorsal view of juncture of ductus bursae and corpus bursae, (c) lateral view of lamella and ductus bursae; structures for Figs. 39-45 are ventral view of lamella and anterior ductus bursae. **37)** *P. marsyas* – same location, GTA #4750; **38)** *P. marsyas* – BRAZIL: Rondônia, GTA #4753; **39)** *P. marsyas* – BRITISH GUIANA, GTA #5048; **40)** *P. marsyas* – FRENCH GUIANA, GTA #5047; **41)** *P. marsyas* – ECUADOR: Manigal, GTA #5053; **42)** *P. marsyas* – ECUADOR: Mishahualli, GTA #5050; **43)** *P. nellyae* – ECUADOR: Latas, GTA #5051; **44)** *P. damo* – GUATEMALA: Petén, GTA #4737; **45)** *P. damo* – same location, GTA #4743; **46)** *P. damo* – same location, GTA #4742; **47)** *P. damo* – COLOMBIA: Cali, GTA #5049; **48)** *P. dorcas* – associated with holotype, GTA #5963 (BM #3785); **49)** *P. cybele* – WEST INDIES: St. Vincent, GTA #5046.

Table 1. Wing and genital characters of *Pseudolycaena*.

character	<i>marsyas</i>	<i>nellyae</i>	<i>cybele</i>	<i>damo</i>	<i>dorcas</i>
dorsal color	pale blue	cobalt	blue-purple	pale blue-green	cobalt
♂ forewing margin	broad	very broad	very broad	narrow	narrow
♀ forewing margin	usually broad	narrow	very broad	narrow	narrow
ventral color	purple-gray	purple-gray	deep purplish	purple-gray	purple-gray
ventral maculation	<i>marsyas</i> type	<i>marsyas</i> type	<i>marsyas</i> type	<i>damo</i> type	<i>marsyas</i> type
VHW thecla spot	oval	oval	bar	oval	oval
VFW blue streak	present	present	present	absent	absent
genital capsule	narrow	medium	broad	medium	broad
brush organ	present	present	present	absent	absent
saccus	long	short	short	long	short
valvae	medium	broad	narrow	medium	narrow
aedeagus	long	short	long	long	long
lamella	medium, pointed	narrow, not pointed	broad, pointed	narrow, not pointed	medium, not pointed

LITERATURE CITED

- Austin, G. T., N. M. Haddad, C. Mendez, T. D. Sisk, D. D. Murphy, A. E. Launer, and P. R. Ehrlich. 1996. Preliminary annotated checklist of the butterflies of Tikal National Park and vicinity, Guatemala (Lepidoptera). *Trop. Lepid.* 7:21-37.
- Balcázar L., M. A. 1993. Butterflies of Pedernales, Michoacán, Mexico, with notes on seasonality and faunistic affinities (Lepidoptera: Papilionoidea and Hesperioidea). *Trop. Lepid.* 4:93-105.
- Barcant, M. 1970. *Butterflies of Trinidad and Tobago*. London: Collins. 314pp.
- Beutelspacher B, C. R. 1982. Mariposas diurnas de "El Chorreadero", Chiapas (Insecta: Lepidoptera). *Ann Inst. Biol. UNAM* 53:341-366.
- Biezanko, C. M., A. Ruffinelli, and C. S. Carbonell. 1957. Lepidoptera del Uruguay. Lista anotada de especies. *Revta Fac. Agron., Univ. Rep.* 46:1-152.
- Boisduval, J. B. A. D. de 1870. *Considérations sur des Lépidoptères Envoyés du Guatemala a M. de l'Orza*. Rennes: Oberthür et fils. 100pp.
- Bridges, C. A. 1988. *Catalogue of Lycaenidae & Riodinidae (Lepidoptera: Rhopalocera)*. Urbana, IL: published by author. 795pp.
- Bridges, C. A. 1994. *Catalogue of the family-group, genus-group and species-group names of the Riodinidae & Lycaenidae (Lepidoptera) of the world*. Urbana, IL: published by author. 1115pp.

- Brown, F. M. 1978. The origins of the West Indian butterfly fauna. Pp. 5-30 in *Zoogeography in the Caribbean*. Special Publication 13: Acad. Nat. Sci. Philadelphia.
- Brown, K. S., Jr. 1992. Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal. Pp. 142-187 in L. P. Morellato (Org.), *História Natural da Serra do Japi, Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil*. Campinas: Editora UNICAMP/FAPESP. 321pp.
- Brown, K. S., Jr., and A. V. L. Freitas. 2000. Diversidade de Lepidoptera em Santa Teresa, Espírito Santo. *Bol. Mus. Biol. Mello Leitão* 11/12:71-118.
- Brown, K. S., Jr., and O. H. H. Mielke. 1967. Lepidoptera of the central Brazil Plateau. I. Preliminary list of Rhopalocera (continued): Lycaenidae, Pieridae, Papilionidae, HesperIIDae. *J. Lepid. Soc.* 21:145-168.
- Brown, K. S., Jr., and O. H. H. Mielke. 1968. Lepidoptera of the central Brazil Plateau. III. Partial list for the Belo Horizonte area, showing the character of the southeastern "blend zone". *J. Lepid. Soc.* 22:147-157.
- Capronnier, J. B. 1874. Notice les époques d'apparition des lépidoptères du Brésil recueillis par M. C. Van Volxem dans son voyage en 1872. *Ann. Soc. Ent. Belgique* 17:5-39.
- Cisneros, F., and R. Gazani. 1973. *Pseudolycaena marsyas* (L.) (Lep.-Lycaenidae), el gusano verde del brote del lúcumo, *Lucuma obovata* HBK. *Resúm XVI Con. Soc. entomol. Perú (Tumbes y Guayaquil, 19-24 agosto 1973)*: 48 (mimeog.) [cited after Lamas 1981].
- Clark, A. H. 1904. Notes on the insects of Barbados, St. Vincent, the Grenadines, and Granada. *Psyche* 11:114-117.
- Clench, H. K. 1963. A synopsis of the West Indian Lycaenidae with remarks on their zoogeography. *J. Res. Lepid.* 2:247-270.
- Comstock, W. P., and E. I. Huntington. 1943. Lycaenidae of the Antilles (Lepidoptera: Rhopalocera). *Ann. New York Acad. Sci.* 45:49-130.
- Comstock, W. P., and E. I. Huntington. 1959. An annotated list of the Lycaenidae (Lepidoptera, Rhopalocera) of the Western Hemisphere. *J. New York. Ent. Soc.* 67:163-212.
- Comstock, W. P., and E. I. Huntington. 1961. An annotated list of the Lycaenidae (Lepidoptera, Rhopalocera) of the Western Hemisphere. *J. New York. Ent. Soc.* 69:157-176.
- D'Abrera, B. 1984. *Butterflies of South America*. Victoria, Australia: Hill House. 256pp.
- D'Abrera, B. 1995. *Butterflies of the Neotropical Region. Part VII. Lycaenidae*. Victoria, Australia: Hill House. Pp. 1098-1270.
- Davis, F. L. 1928. *Notes on the Butterflies of British Honduras*. London: Old Royalty Book Publishers. 101pp.
- de la Maza, J., and R. G. de la Maza. 1985. La fauna de mariposas de Boca del Chajul, Chiapas, Mexico (Rhopalocera). Parte I. *Revta Soc. mex. Lepid.* 9:23-44.
- de la Maza, R. G. 1987. *Mariposas Mexicanas, Guía para su Colecta y Determinación*. Mexico City: Fondo de Cultura Económica. 302pp.
- de la Maza, R. G., and J. de la Maza E. 1993. *Mariposas de Chiapas*. México: Gobierno del Estado de Chiapas. 224pp.

- de la Maza E., R., J. de la Maza E., and A. White Lopez. 1989. La fauna de mariposas de Mexico. Parte I. Papilionoidea (Lepidoptera: Rhopalocera). *Revta Soc. mex. Lepid.* 12:39-98.
- de la Maza, R. G., and D. Gutiérrez C. 1992. Rhopalóceros de Quintana Roo, su distribución, origen y evolución. *Revta Soc. mex. Lepid.* 15:1-44.
- de la Maza E., R. G., and A. White L. 1990. Rhopalocera de la Huasteca Potosina, su distribución, composición, origen y evolución. *Revta Soc. mex. Lepid.* 13:31-88.
- Debrot, A. O., J. Y. Miller, L. D. Miller, and B. T. Leysner. 1999. The butterfly fauna of Curaçao, West Indies: 1996 status and long-term species turnover. *Carib. J. Sci.* 35:184-194.
- DeVries, P. J. 1983. Checklist of the butterflies. Pp. 654-678 in D. H. Janzen (ed.), *Costa Rican Natural History*. Chicago: Univ. of Chicago Press. 816pp.
- DeVries, P. J. 1991. Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. *Amer. Mus. Novit.* 3025:1-23.
- Downey, J. C., and A. C. Allyn. 1984. Chorionic sculpturing in eggs of Lycaenidae. Part II. *Bull. Allyn Mus.* 84:1-44.
- Draudt, M. 1921-1924. Die amerikanischen Tagfalter. Lycaenidae and Grypocera. Pp. 836-1011 in A. Seitz, *Gross-Schmetterlinge der Erde*. Stuttgart: Alfred Kernen, vol. 5. 1141pp.
- Druce, H. 1875. Descriptions of new species of diurnal Lepidoptera. *Cistula Entom.* 1:357-363.
- Druce, H. 1876. List of the butterflies of Peru, with descriptions of new species. With some notes by Edward Bartlett. *Proc. Zool. Soc. London* 1876:205-250.
- Druce, H. H. 1907. On neotropical Lycaenidae with descriptions of new species. *Proc. Zool. Soc. London* 1907:566-632.
- Durden, C. 2006. Checklist of Texas Butterflies. (accessed November 2006). <http://www.utexas.edu/tmm/tnhc/entomology/butterfly/butterfly.list.html>
- Dyar, H. G. 1914. Report on the Lepidoptera of the Smithsonian biological survey of the Panama Canal Zone. *Proc. U.S. Natl. Mus.* 47:139-350.
- Ebert, H. 1969. On the frequency of butterflies in eastern Brazil with a list of the butterfly fauna of Pocos de Caldas, Minas Gerais. *J. Lepid. Soc.* 23(suppl. 3):1-48.
- Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bull. British Mus. (NH) Ent.* 28:373-505.
- Emery, E. O., K. S. Brown, Jr., and C. F. G. Pinheiro. 2006. As borboletas (Lepidoptera, Papilionoidea) do Distrito Federal, Brasil. *Rev. bras. Ent.* 50:85-92.
- Emmel, T. C., and G. T. Austin. 1990. The tropical rain forest butterfly fauna of Rondonia, Brazil: species diversity and conservation. *Trop. Lepid.* 1:1-12.
- Godman, F. D., and O. Salvin. 1879-1901. *Biologia Centrali-Americana. Zoologia, Lepidoptera-Rhopalocera*. London: Taylor & Francis. 1269pp.
- Godman, F. C., and O. Salvin. 1896. On the butterflies of St. Vincent, Grenada, and the adjoining islands of the West Indies. *Proc. Zool. Soc. London* 1896:513-520.
- Hayward, K. J. 1973. Catálogo de los ropalóceros argentinos. *Opera Lilloana* 23:1-318.
- Hemming, A. F. 1967. The generic names of the butterflies and their type-species (Lepidoptera: Rhopalocera). *Bull. British Mus. NH (Entomology) suppl.* 9:1-509.
- Hoffmann, C. C. 1941. Catalogo sistematico y zoogeografico de los Lepidopteros Mexicanos. Primera Parte. Papilionoidea. *Ann. Inst. Biol. UNAM* 11:639-739.

- Honey, M. R., and M. J. Scoble. 2001. Linnaeus's butterflies (Lepidoptera: Papilionoidea and Hesperioidea). *Zool. J. Linn. Soc.* 132:277-399.
- Iserhard, C. A., and H. P. Romanowski. 2004. Lista de espécies de borboletas (Lepidoptera, Papilionoidea e Hesperioidea) da região do vale rio Maquiné, Rio Grande do Sul, Brasil. *Revta bras. Zool.* 21:649-662.
- Janzen, D. H., and W. Hallwachs. 2005. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica.
<http://janzen.sas.upenn.edu>
- Johnson, K., and J. Llorente-Bousquets. 1992. Taxonomic additions to recent studies of neotropical butterflies. IV. Additions to the Mexican fauna. *Reports Mus. Nat. Hist. Univ. Wisconsin, Stevens Point* 23:9-12.
- Johnson, K., B. MacPherson, and J. I. Ingraham. 1986. A new genus and species of Eumaeini (Theclinae) from western Argentina (Lepidoptera: Lycaenidae). *Bull. Allyn Mus.* 102:1-7.
- Jørgensen, P. 1935. Lepidópteros nuevos o raros de la Argentina y del Paraguay. *An. Mus. arg. de Cienc. nat.* 38:85-129.
- Kaye, W. J. 1904. A catalogue of the Lepidoptera Rhopalocera of Trinidad. *Trans. ent. Soc. London* 1904:159-228.
- Kendall, R. O. 1975. Larval foodplants for seven species of hairstreaks (Lycaenidae) from Mexico. *Bull. Allyn Mus.* 24:1-4.
- Kirby, W. F. 1871. *A Synonymic Catalogue of Diurnal Lepidoptera*. London: John Van Voorst. 690pp.
- Kitching, R. L., and B. M. Kitching. 1973. Notes on a collection of butterflies from western Mexico. *Entomologist* 196:269-276.
- Köhler, P. 1923. Fauna argentina. Lepidoptera e collectione Alberto Breyer. I. Teil. Rhopalocera. Systematischer Katalog und Studien, Berichtigungen u. Neubeschreibungen. *Zeit. wissenschaft. Insektenbiol.* 18(12):1-34.
- Köhler, P. 1928. *Catalogo de Lepidópteros Argentinos*. Buenos Aires: Publ. Breyer. 12pp.
- Lamas, G. 1975. Mariposas diurnas (Lepidoptera, Rhopalocera) que atacan plantas de interes agricola en el Peru. *Revta per. Ent.* 18:1-5.
- Lamas, G. 1976. Notas sobre mariposas peruanas (Lepidoptera). III. Sobre una colección efectuada en el Departamento de Tumbes. *Revta per. Ent.* 19:8-12.
- Lamas, G. 1981 [1980]. Una nueva subespecie de *Pseudolycaena marsyas* (Lepidoptera: Lycaenidae) del oeste del Perú. *Revta per. Ent.* 23:143-144.
- Lamas, G. 2003. *Las Mariposas de Machu Picchu*. Lima: PROFONANPE. 221pp.
- Lamas, G., R. K. Robbins, and D. J. Harvey. 1996. Mariposas del alto Río Napo, Loreto, Perú (Lepidoptera: Papilionoidea y Hesperioidea). *Rev. per. Ent.* 39:63-74.
- Lewis, H. L. 1973. *Butterflies of the World*. Chicago: Follett. 312pp.
- Lima, A. C. 1950. *Insetos do Brasil. 6º Tomo. Lepidópteros 2a parte*. Rio de Janeiro: Escol Nac. Agronomia. 420pp.
- Linnaeus, C. 1758. *Systema naturae por regna tria naturae, secundum Classes, Ordines, Genera, Species, com Characteribus, Differentiis, Synonymis, Locis*. Holmiae, Laurentii Salvii (Edition 10) 1 (Animalia). 824pp.
- Llorente-Bousquets, J. E., A. R. Garcés-Medina, and M. A. Luis-Martínez. 1986. Las mariposas de Jalapa-Teocelo, Veracruz. *Revta Teocelo* 4:14-27.

- Llorente-Bousquets, J., A. Luis-Martínez, I. Vargas-Fernández, and A. D. Warren. 2004. Butterflies of the state of Nayarit, Mexico. *J. Lepid. Soc.* 58:203-222.
- Luis-Martínez, A., J. Llorente-Bousquets, A. D. Warren, and I. Vargas-Fernández. 2004. Lepidópteros: Papilionoideos y Hesperioideos. Pp. 335-355 in A. J. Garcia-Mendoza, M. J. Ordoñez, and M. Briones-Salas (eds.), *Biodiversidad de Oaxaca*. Inst. Biol. UNAM - Fondo Oaxaqueño para la Conservación de la Naturaleza - World Wildlife Fund, México.
- Luis-Martínez, A., I. Vargas-Fernández, and J. Llorente-Bousquets. 1991. Lepidoptero fauna de Oaxaca I: Distribución y fenología de los Papilionoidea de la Sierra de Juárez. *Publ. esp. Mus. Zool. UNAM, D.F., Mexico* 3:1-199.
- Luis-Martínez, A., I. Vargas-Fernández, and J. Llorente-Bousquets. 1995. Síntesis de los Papilionoidea (Lepidoptera: Rhopalocera) del estado de Veracruz. *Folia ent. Mex.* 93:91-133.
- Maes, J.-M. 2004. Insectos asociados a algunos cultivos tropicales en el Atlántico de Nicaragua. Parte XXV. Maderas preciosas. Cedro real (*Cedrela odorata*, Melicaceae). Caoba (*Swietenia macrophylla*, Melicaceae). Cedro macho (*Carapa guianensis*, Melicaceae). *Rev. Nica. Ent.* 64(suppl. 1), parte xxv:1-71.
- Mathew, G. F. 1874. List of Lepidoptera forwarded to Edward Newman. *Entomologist* 7:62-66.
- Maury, R. C., G. K. Westerbrook, P. E. Baker, P. Bouysse, and D. Westercamp. 1990. Geology of the Lesser Antilles. Pp. 141-146 in G. Dengo, and J. E. Case (eds.), *The Caribbean Region. The Geology of North America, Vol. H.*, Geological Society of America.
- Meerman, J. C. 1999. Lepidoptera of Belize. 1. Catalog of butterflies (Lepidoptera: Papilionoidea). *Trop. Lepid.* 10(suppl. 1):7-32.
- Meerman, J. C., and T. Boomsma. 1993. Checklist of the butterflies of the Shipstern Nature Reserve. *Occ. Pap. Belize Nat. Hist. Soc.* 2:37-46.
- Mielke, C. G. C. 1994. Papilionoidea e Hesperioidea (Lepidoptera) do Curitiba e seus arredores, Paraná, Brasil, com notas taxonômicas sobre Hesperíidae. *Revta bras. Zool.* 11:759-776.
- Mielke, O. H. H., and M. N. Casagrande. 1991. Lepidoptera: Papilionoidea e Hesperioidea coletados na Ilha de Maracá, Alto Alegre, Roraima, parte do Projeto Maracá, com uma lista complementar de Hesperíidae de Roraima. *Acta amazonica* 21:175-210.
- Mielke, O. H. H., and M. N. Casagrande. 1997. Papilionoidea e Hesperioidea (Lepidoptera) do parque estadual do Morro do Diabo, Teodora Sampaio, São Paulo, Brazil. *Revta bras. Zool.* 14:967-1001.
- Miller, J. Y., and L. D. Miller. 2001. The biogeography of the West Indian butterflies (Lepidoptera): an application of a vicariance/dispersalist model. Pp. 127-154 in C. A. Woods and F. E. Sergile (eds.), *Biogeography of the West Indies, Patterns and Perspectives*. 2nd ed. Boca Raton, FL: CRC Press.
- Monroe, R. S., G. N. Ross, and R. N. Williams. 1967. A report of two recent collections of butterflies from Honduras. *J. Lepid. Soc.* 21:185-197.
- Monteagudo-Sabaté, D., A. Luis-Martínez, I. Vargas-Fernández, and J. Llorente-Bousquets. 2001. Patrones altitudinales de diversidad de mariposas en la Sierra Madre del Sur (México) (Lepidoptera: Papilionoidea). *SHILAP Revta lepid.* 29:207-237.

- Möschler, H. B. 1877. Beiträge zur Schmetterlings-Fauna von Surinam. *Verh. kais.-könig. zool.-botan. Ges. Wien* 26:293-352.
- Motta, P. C. 2002. Butterflies from the Uberlândia region, central Brazil: species list and biological comments. *Braz. J. Biol.* 62:151-163.
- Murray, D. L. 1996. A survey of the butterfly fauna of Jatun Sacha, Ecuador (Lepidoptera: Hesperioidea and Papilionoidea). *J. Res. Lepid.* 35:42-60.
- Nicolay, S. S. 1971. A review of the genus *Arcas* with descriptions of new species (Lycaenidae, Strymonini). *J. Lepid. Soc.* 25:87-108.
- Núñez Bustos, E. O. 2006. Inventory of Rhopaloceran Lepidopterans (diurnal butterflies) of Yacutinga Wildlife Refuge (General Belgrano Department, Misiones Province, Argentina).
http://www.yacutinga.com/html/vz/i_ing/estacion_biologica
- Opler, P. A. 1992. *A Field Guide to Eastern Butterflies*. Boston: Houghton Mifflin. 396pp.
- Pineiro, C. E. G., and E. O. Emery. 2006. As borboletas (Lepidoptera: Papilionoidea e Hesperioidea) da Área de Proteção Ambiental do Gama e Cabeça de Veado (Distrito Federal, Brasil). *Biota Neotrop.* 6(no. 3)
<http://www.biotaneotropica.org.br/v6n3/pt/abstract?inventory+bn1506032006>
- Pozo, C., A. Luis-Martínez, S. U. Tescum, N. S. Saúrez, and A. M. Martínez. 2003. Butterflies (Papilionoidea and Hesperioidea) of Calakmul, Campeche, México. *Southwest. Nat.* 48:505-525.
- Pyle, R. M. 1981. *The Audubon Society Field Guide to North American Butterflies*. New York: Knopf. 916pp.
- Raguso, R. A., and J. Llorente-Bousquets. 1991 (1990). The butterflies (Lepidoptera) of the Tuxtla Mts., Veracruz, Mexico, revisited: species-richness and habitat disturbance. *J. Res. Lepid.* 29:105-133.
- Raguso, R. A., and J. Llorente-Bousquets. 1997. Papilionoidea. Pp. 257-291 in E. González Soriano, R. Dirzo, and R. C. Vogt (eds.), *Historia Natural de Los Tuxtlas*. Instituto de Biología, UNAM: México, D.F.
- Riley, N. D. 1975. *A Field Guide to the Butterflies of the West Indies*. London: Collins. 223pp.
- Robbins, R. K. 2004. Tribe Eumaeini. Pp. 118-137 in G. Lamas (ed.), *Atlas of Neotropical Lepidoptera. Checklist: Part 4A. Hesperioidea-Papilionoidea*. Gainesville, FL: Scientific Publ.
- Robbins, R. K., and A. Aiello. 1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *J. Lepid. Soc.* 36:65-75.
- Robbins, R. K., and S. S. Nicolay. 1998. Taxonomy and nomenclature of *Strymon istapa* and *S. columella* (Lycaenidae: Theclinae: Eumaeini). *J. Lepid. Soc.* 52:318-327.
- Robbins, R. K., and G. B. Small, Jr. 1981. Wind dispersal of Panamanian hairstreak butterflies (Lepidoptera: Lycaenidae) and its evolutionary significance. *Biotropica* 13:308-315.
- Ross, G. N. 1964. An annotated list of butterflies collected in British Honduras in 1961. *J. Lepid. Soc.* 18:11-26.
- Ross, G. N. 1976. An ecological study of the butterflies of the Sierra de Tuxtla in Veracruz, Mexico. *J. Res. Lepid.* 15:185-200.
- Routledge, C. E. 1977. El suborden Rhopalocera (Lepidoptera) del estado de Tabasco. Su lista, frecuencia, diversidad y distribución. *Revta Soc. mex. Lepid.* 3:57-73.

- Ruszczuk, A., and C. F. Silva. 1997. Butterflies select microhabitats on building walls. *Landsc. Urban Planning* 38:119-127.
- Salinas-Gutiérrez, J. L., A. Luis-Martínez, and J. Llorente-Bousquets. 2004. Papilionoidea of the evergreen tropical forests of Mexico. *J. Lepid. Soc.* 58:125-142.
- Scott, J. A. 1971. A list of Antillean butterflies. *J. Res. Lepid.* 9:249-256.
- Silva, A. G. A., C. R. Gonçalves, D. M. Galvão, A. J. L. Gonçalves, J. Gomes, M. N. Silva, and L. Simoni. 1968. *Quarto catálogo dos insetos que vivem nas plantas do Brasil seus parasitos e predadores. Edição ampliada do "3o 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: Ministério da Agricultura. 622pp.
- Smart, P. E. 1975. *The Illustrated Encyclopedia of the Butterfly World in Colour.* London: Hamlyn. 275pp.
- Smith, D. S., L. D. Miller, and J. Y. Miller. 1994. *The Butterflies of the West Indies and South Florida.* Oxford: Oxford Univ. Press. 264pp.
- Snellen, P. C. T. 1887. Bijrage tot de Kennis der Lepidoptera van het Eiland Curaçao met Afbeeldingen door Prof. Dr. J. Van Leeuwen Jr.. *Tijds. Ent.* 30:9-66.
- Vargas-Fernández, I., J. E. Llorente-Bousquets, and M. A. Luis-Martínez. 1991. Lepidopterofauna de Guerrero I: Distribución y fenología de los Papilionoidea de la Sierra de Atoyac. *Publ. esp. Mus. Zool. UNAM, D.F., Mexico* 2:1-127.
- Vargas-Fernández, I., J. Llorente-Bousquets, and A. Luis-Martínez. 1992. Listado lepidopterofaunístico de la Sierra de Atoyac de Alvarez en el estado de Guerrero: notas acerca de su distribución local y estacional (Rhopalocera: Papilionoidea). *Folia ent. Mex.* 86:41-178.
- Vargas-Fernández, I., A. Luis-Martínez, J. Llorente-Bousquets, and A. D. Warren. 1996. Butterflies of the state of Jalisco, Mexico. *J. Lepid. Soc.* 50:97-138.
- Vértesy, Z., Z. Bálint, K. Kertész, J. P. Vigneron, V. Lousse, and L. P. Biró. 2006. Wing scale microstructures and nanostructures in butterflies – natural photonic crystals. *J. Microscopy* 224:108-110.
- Wallengren, H. D. J. 1858. Nya Fjäril-slågten. *Öfversigt kungliga Vetenskaps-Akademiens Förhandlingar* 15:75-84.
- Wallengren, H. D. J. 1863. Die während der Reise der königl. Schwed. Fregatte Eugenie gesammelten schon bekannten Schmetterlinge. *Wein. ent. Monat.* 7:65-76.
- Warren, A. D., and J. E. Llorente-Bousquets. 1999. Butterflies of Mismaloya, Jalisco, and adjacent parts of Banderas Bay and southern Nayarit, Mexico. *Dugesiana* 6:17-32.
- Warren, A. D., I. Vargas-Fernández, A. Luis-Martínez, and J. Llorente-Bousquets. 1998. Butterflies of the state of Colima, Mexico. *J. Lepid. Soc.* 52:40-72.
- Watson, A., and P. E. S. Whalley. 1975. *The Dictionary of Butterflies and Moths in Color.* New York: Exeter Books. 296pp.
- Zárate, L. L., and J. C. Broncales. 2006. Plagas insectiles en el cultivo lúcumo *Pouteria lucuma* (R. et P.) O. Kze., en la provincia de Trujillo, La Libertad. *Pueblo cont.* 17:5-10.