

ORIGINAL ARTICLE

The “upside down” systematics of hairstreak butterflies (Lycaenidae) that eat pineapple and other Bromeliaceae

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All Lycaenidae larvae that eat Bromeliaceae belong to the *Strymon ziba* and *S. serapio* species groups, but confusion with taxonomy has resulted in widespread misidentification of the butterflies in both the ecological and agricultural literature. Published food plant records are assessed, and new rearing records are presented. The species that have been recorded eating Bromeliaceae are *Strymon ziba* (Hewitson), *S. megarus* (Godart), *S. lucena* (Hewitson), *S. oreala* (Hewitson), *S. serapio* (Godman & Salvin), *S. azuba* (Hewitson), and *S. gabatha* (Hewitson). The first four are recorded from pineapple, with the sympatric *S. megarus* and *S. ziba* sometimes being especially destructive in commercial fields. Most published records lump these two species and misidentify them under the names *Thecla basilides*, *Thecla basalides*, or *Tmolus echion*. *Strymon ziba* has also been reared from other monocotyledon plant families, such as Heliconiaceae and Haemodoraceae. In most cases, caterpillars eat flowers and fruits, but larvae of *S. megarus* and/or *S. ziba* may also bore into leaves when flowers and fruits are unavailable. The known bromeliad feeders are illustrated, and distinguishing characters are noted. The female butterflies appear to use reddish color as a visual cue, which could be the basis for a non-insecticidal means of controlling outbreaks in commercial pineapple crops.

Todas as larvas de Lycaenidae que se alimentam de Bromeliaceae pertencem aos grupos de espécies de *Strymon ziba* e *S. serapio*, porém confusão com sua taxonomia resultou em erros generalizados de identificação destas borboletas tanto na literatura ecológica como agrícola. Registros publicados de plantas alimentares são aqui avaliados, e novos registros com base em criação são apresentados. As espécies que foram registradas se alimentando de Bromeliaceae são *Strymon ziba* (Hewitson), *S. megarus* (Godart), *S. lucena* (Hewitson), *S. oreala* (Hewitson), *S. serapio* (Godman & Salvin), *S. azuba* (Hewitson), e *S. gabatha* (Hewitson). As quatro primeiras são encontradas em abacaxi, com as espécies simpátricas *S. megarus* e *S. ziba* algumas vezes sendo especialmente destrutivas em áreas comerciais. A maioria dos registros publicados considera estas duas espécies como somente uma, identificando-as erroneamente como *Thecla basilides*, *Thecla basalides*, ou *Tmolus echion*. *Strymon ziba* também foi criada em outras famílias de plantas monocotiledôneas, como Heliconiaceae e Haemodoraceae. Na maioria dos casos, as lagartas comem flores e frutos, mas larvas de *S. megarus* e / ou *S. ziba* também podem perfurar as folhas quando as flores e os frutos não estão disponíveis. As espécies conhecidas que se alimentam de bromélias são aqui ilustradas, e seus caracteres distintivos ressaltados. As borboletas fêmeas parecem usar a cor vermelha como um sinal visual, o que poderia ser a base para um meio não-inseticida de controle de focos em lavouras comerciais de abacaxi.

Keywords: *basilides*; *megarus*; Neotropical Eumaeini; *Strymon*; *Thecla*; *ziba*

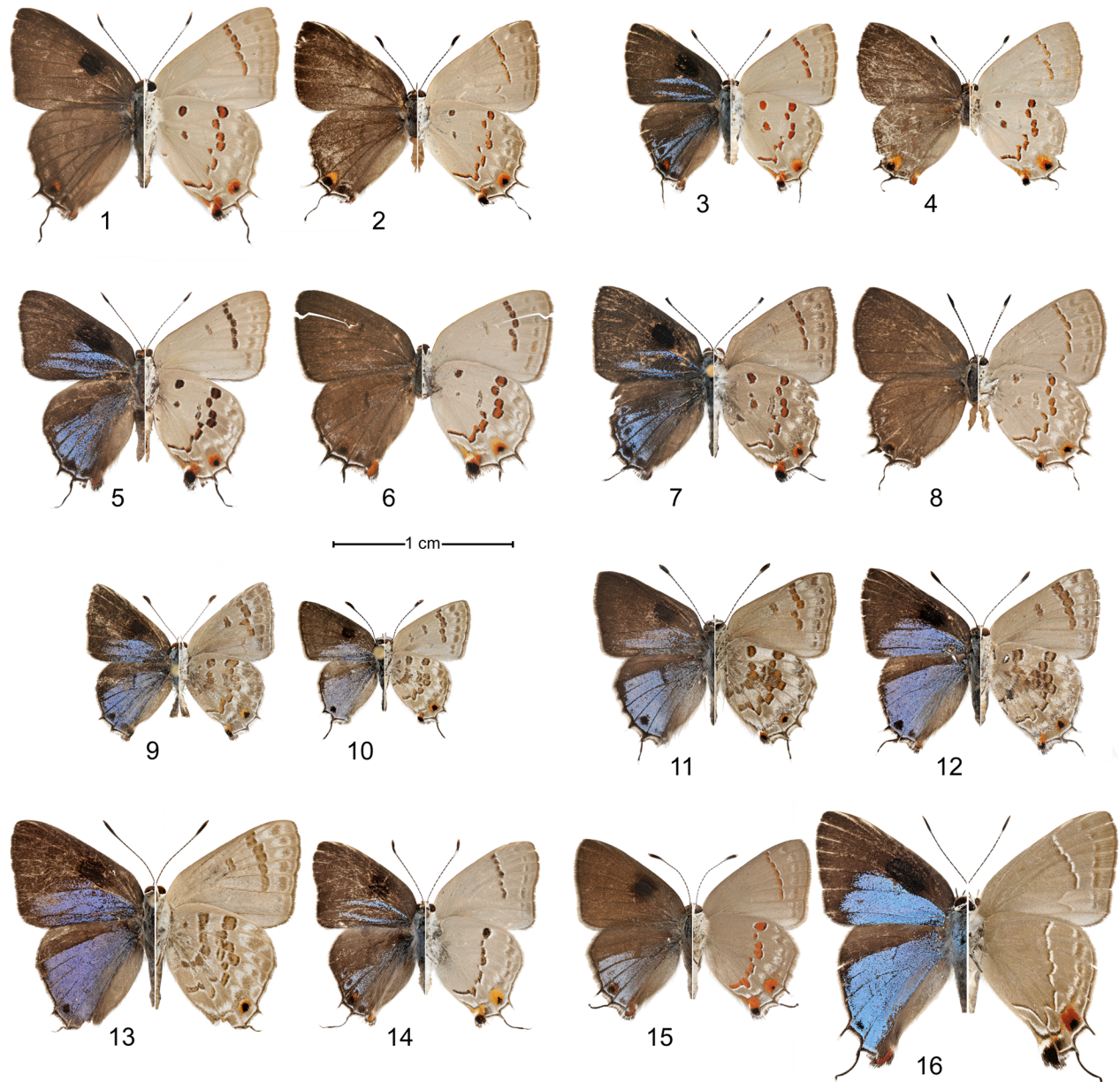
Introduction

Insect interactions with Bromeliaceae, a primarily Neotropical plant family with about 2700 species, are varied (Benzing 2000; Frank & Lounibos 2009). Some insects live in water impounded in leaf axils, some pollinate bromeliad flowers or disperse seeds, and many eat plant leaves, flowers, or fruits. In turn, some bromeliads are insectivores (Ward & Fish 1979; González et al. 1991). Additionally, there is an extensive agricultural literature on the insect “pests” of commercial pineapple (e.g., Collins 1960; Sanches 1981; Marie 1995; Petty et al. 2002; Reinhardt 2009).

Among Lycaenidae (Lepidoptera), caterpillars of the *Strymon serapio* (Godman & Salvin) species

group (~15 species) and *S. ziba* species (Hewitson) group (one species) (Theclinae: Eumaeini) eat Bromeliaceae, including pineapple (Robbins & Nicolay 2002) (representative adults in Figure 1–16). These species groups are the only *Strymon* species in which there are two cornuti in the penis (Figures 17, 18). They are also the only ones in which males typically perch on vertical surfaces, such as tree trunks, when occupying a mating territory. However, *S. ziba* was tentatively placed in its own species group because its genitalic morphology is divergent from all other *Strymon* and because its larvae eat both Bromeliaceae and plants in related families, unlike members of the *S. serapio* species group (Robbins & Nicolay 2002). It is

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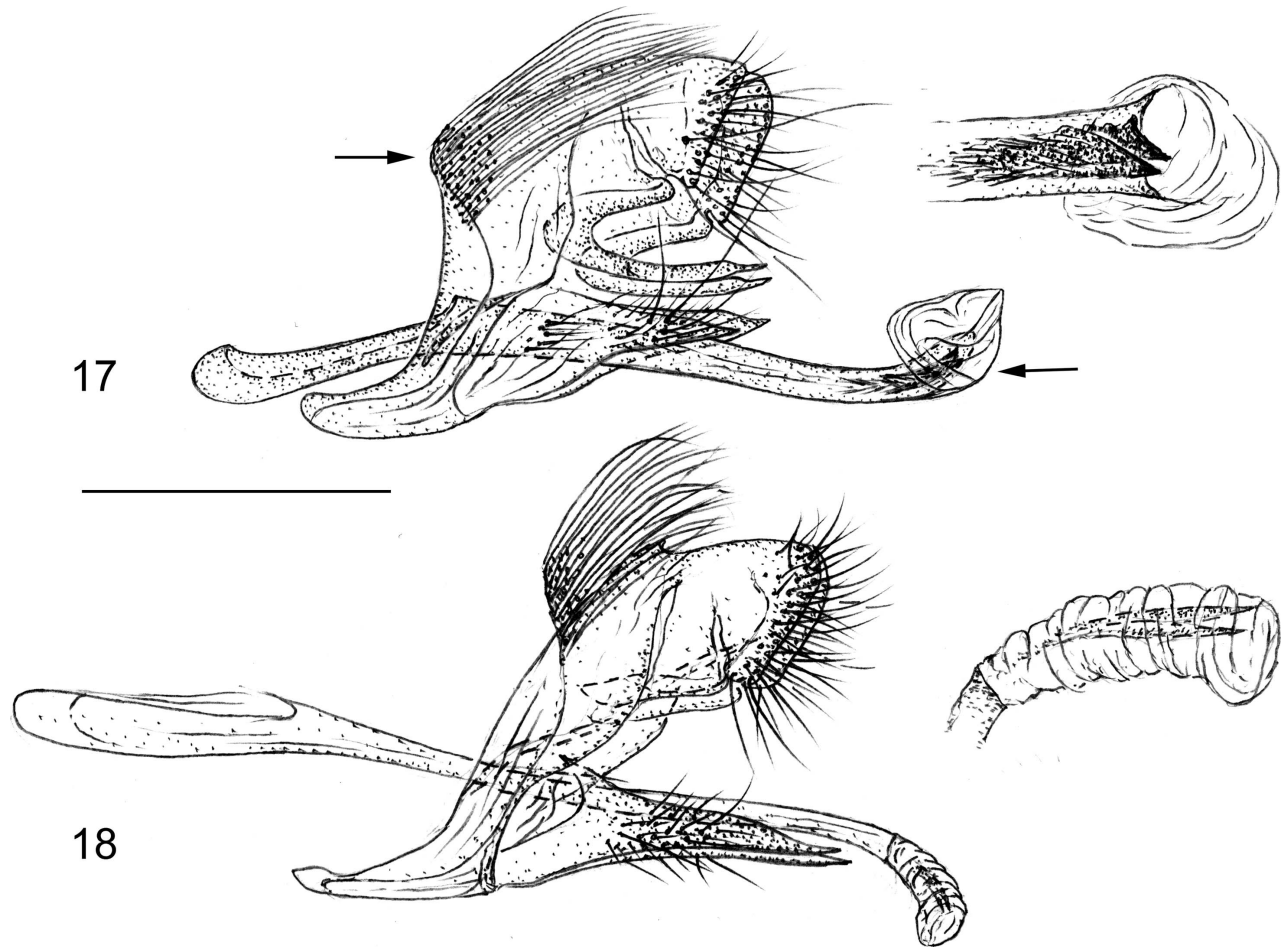


Figures 1–16. Adults of bromeliad feeding *Strymon* in dorsal (left) and ventral aspect. (1) ♂ *Strymon ziba* (Panama). (2) ♀ *S. ziba* (Panama). (3) ♂ *S. megarus* (Panama). (4) ♀ *S. megarus* (Panama). (5) ♂ *S. megarus* (Amazonian Peru). (6) ♀ *S. megarus* (Amazonian Peru). (7) ♂ *S. megarus* (Brazil, Rio de Janeiro state). (8) ♀ *S. megarus* (Brazil, Rio de Janeiro state). (9) ♂ *S. lucena* (Argentina, Buenos Aires). (10) ♂ *S. lucena* (Brazil, Rio de Janeiro state). (11) ♂ *S. lucena* (Brazil, Minas Gerais). (12) ♂ *S. dindus* (Brazil, Rio de Janeiro state). (13) ♂ *S. oreala* (Brazil, Rio de Janeiro state). (14) ♂ *S. serapio* (Panama). (15) ♂ *S. azuba* (Brazil, Distrito Federal). (16) ♂ *S. gabatha* (Panama).

likely that the *S. serapio* species group is paraphyletic in terms of *S. ziba*, but the morphological evidence is not definitive.

The historical literature on the *Strymon* that eat Bromeliaceae is almost universally incorrect because the identification of *Strymon* species has been confused since the time of Linnaeus. Although a bit oversimplified, there are three taxonomic problems. First, the very similar ventral wing patterns of *Strymon ziba*, *S.*

megarus (Godart) (= *Thecla basilides* [Geyer]), and the dicotyledon-feeding *Tmolus echion* (Linnaeus) (= *Thecla echion*) have generated misidentifications. It is the reason why Ehrlich & Raven (1965) mistakenly noted that *T. echion* uses a variety of dicotyledons and bromeliads as larval food plants. It is the reason why entomologists in the agricultural literature (e.g., Harris 1927) were baffled by the purposeful introduction of *T. echion* – supposedly a pineapple pest – from



Figures 17, 18. Male genitalia in lateral aspect, anterior to left, enlarged penis tip on right. (17) *Strymon ziba* (Brazil, Rio de Janeiro state), arrow at left shows the prominent angle of the anterior margin of the vinculum (absent in *S. megarus*) and arrow at right shows the upturned penis tip (downturned in *S. megarus*), with two heavily sclerotized cornuti (lightly sclerotized in *S. megarus*). (18) *S. megarus* (Brazil, Rio de Janeiro state). Scale bar: 1 mm.

Mexico to Hawaii as a biological control for *Lantana* (Verbenaceae). It is the reason why virtually all papers in the agricultural literature discussed herein treated *S. ziba* and *S. megarus* as one species.

Second, the generic nomenclature of Neotropical Eumaeini has been markedly unstable (Robbins 2004a), but all literature records of bromeliad-feeding species belonging to *Thecla*, *Tmolus*, and *Ziegleria* are based on incorrect taxonomy (Robbins & Nicolay 2002, see Results below).

Third, species-level identification has been difficult because there is little morphological variation among the *S. serapio* group of species. It is the reason why some papers used the identification *Thecla* sp. (e.g., Carter 1949; Velasco 1972). It is the reason why recent references to *Strymon megarus* as a pineapple pest (e.g., Inclán et al. 2007, 2008; Faria et al. 2009; Frank & Lounibos 2009; Matos & Reinhardt 2009) may actually

refer to *S. ziba*. It is one reason why many of the *Strymon* rearing records from bromeliads in museums and agricultural institutions are unpublished.

The purpose of this paper is to review and correct the published information on bromeliad-feeding *Strymon* – at least as well as can be done with current taxonomic knowledge and without vouchers in many cases – and to present the previously unpublished information in museums and agricultural institutions. Using these records as a foundation, I then discuss (1) a scenario by which specialization on Bromeliaceae could have evolved within *Strymon*; (2) how the widespread eumaeine trait of boring into plant parts affects the phenology of bromeliad–lycaenid interactions; and (3) the evidence that adults of bromeliad-feeding *Strymon* use reddish color as a visual cue and how this information might be useful for non-pesticide biological control of these pineapple pests.

Materials and methods

Food plant records were accumulated from the butterfly literature by tracing citations and from the agricultural literature by searching the AGRICOLA database (agricola.nal.usda.gov/, accessed 6 November 2009). The most useful and complete bibliographic reference, however, was Lamas (2008). To avoid repeating potentially dubious records, secondary citations of rearings, such as the compilations in D'Araujo e Silva et al. (1967–1968) and in Beccaloni et al. (2008), were generally omitted, especially if vouchers were lacking. Identifications were done from vouchers or from illustrations in the articles, as noted. Reared specimens in the museums and agricultural institutions listed below were identified by personal examination unless noted otherwise. To minimize errors in standardizing the format of latitude and longitude, coordinates are given as they were written on data labels, in publications, and on websites.

The butterfly generic, species-group, and species-level taxonomy follows Robbins & Nicolay (2002) and Robbins (2004b). However, the taxonomy that is used for the unresolved "*Thecla basilides*" and "*Thecla legota*" complexes is detailed in the text. Characters for identifying each of the other butterfly species are given along with the distribution of the species from both literature sources and museum collections. Data on habitat and the time (all are standard times) at which males set up "mating territories" are from the author's field work, unless otherwise noted. Brazilian states are noted by their standard two letter abbreviations.

For each plant species name, the author, genus, and family follow the Tropicos database of the Missouri Botanical Garden (www.Tropicos.org, accessed 27 October 2009). If there is an accepted senior synonym in the database, then the name given in the rearing record is placed after an equals (=) sign. When a common name for a food plant was given (other than pineapple), it is listed in parentheses. For example, "*Bromelia fastuosa* Lindl. = *Bromelia antio-cantha* Bertol. (gravatá)" means that *Bromelia antio-cantha* was listed in the rearing record with the common name gravatá, but *Bromelia fastuosa* is the accepted name for this species in the Tropicos database.

Museums and other institutions where vouchers are deposited are: CIBC: Trinidad and Tobago, Curepe, International (formerly Commonwealth) Institute of Biological Control; CPAC: Brazil, Distrito Federal, Planaltina, EMBRAPA, Centro de Pesquisas, Agropecuárias do Cerrado; DZUP: Brazil, Paraná, Curitiba, Universidade Federal do Paraná, Museu de Entomologia Pe. Jesus Santiago Moure; FIOC: Brazil, Rio de Janeiro, Rio de Janeiro, Fundação Instituto Oswaldo Cruz, Zikán Collection;

IBUNAM: Mexico, Mexico D.F., Universidad Nacional Autónoma de México, Instituto de Biología; LANUFSC: Entomological Collection of J. Steiner at the Native Bee Laboratory, BEG, Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil; MCZ: USA, Massachusetts, Cambridge, Harvard University, Museum of Comparative Zoology; MIZA: Venezuela, Maracay, Museo del Instituto de Zoología Agrícola, including the Fusagri Collection; MJWC: Collection of M.J.W. Cock of CIBC, currently stationed in the UK; MUSM: Peru, Lima, Universidad Nacional Mayor de San Marcos, Museo de Historia Natural; RSME: UK, Edinburgh, National Museum of Scotland; TAMU: USA, Texas, College Station, Texas A & M University, Roy and Connie Kendall Collection; and USNM: USA, Washington, DC, National Museum of Natural History.

Results

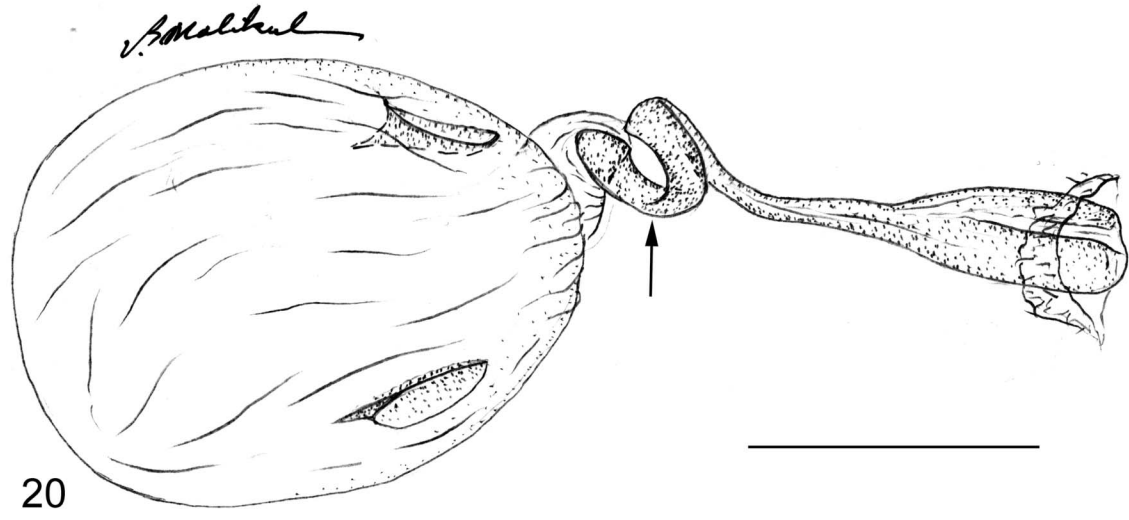
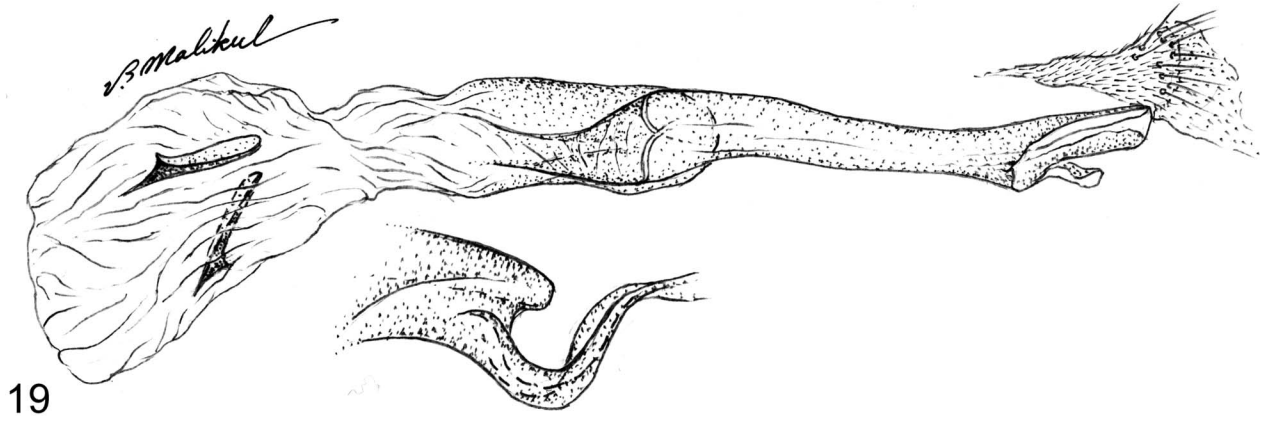
The tangled history of "Thecla basilides"

"*Thecla basilides*" is the name applied most often to the pineapple-feeding Neotropical eumaeine hairstreak "species" that arguably causes more damage to commercial crops than any other. The caterpillars bore into flowers, fruits (frequently destroying the fruit), and leaves when flowers and fruits are unavailable. The efficacy of different insecticides in controlling this species has been investigated (e.g., Zunti & Cardinale 1970; Velasco 1972; Martinez 1976; Azambuja & Mielitz 1981; Chalfoun & Cunha 1984, many more citations are listed below) as have aspects of the biology of this "species" (e.g., Choairy & Fernandes 1983; Sanches et al. 1985; Sanches 1985).

In the agricultural literature the pineapple feeding "species" has been referred to as *Thecla basalides*, *Thecla basilides*, *Thecla echion*, or *Tmolus echion*, but none of these names is nomenclaturally correct. In the beginning, Linnaeus named *Papilio echion* from a written description and a referenced illustration that refer to two unrelated species with similar ventral wing patterns. The nomenclatural identification of *Tmolus echion* that has been accepted almost universally in the taxonomic literature for over a century does not refer to the bromeliad feeders (Honey & Scoble 2001; Robbins 2004b). The name *Thecla basilides* does refer to a pineapple-feeding hairstreak, but is a junior synonym of *S. megarus* (Robbins 2004b). The name *Thecla basalides* is a misspelling of *Thecla basilides* (Robbins 2004b). The 15 other subsequent names that apply to this pineapple-feeding complex were listed by Robbins (2004b) under *S. megarus* (Godart) and *S. ziba* (Hewitson).

No matter which name has been used in the agricultural literature, the pineapple-feeding “species” has been universally treated as one species. However, two pineapple-feeding species with very similar ventral wing patterns (called *S. ziba* and *S. megarus* in Robbins & Nicolay 2002, differentiating characters are given below) are sympatric throughout the Neotropical lowlands. The name *S. megarus* has been used recently for the pineapple-feeding pests (e.g., Pastrana 2004; Inclán et al. 2007, 2008; Faria et al. 2009; Matos & Reinhardt 2009), but these authors did not distinguish *S. megarus* from *S. ziba*. Although the taxonomy of this group is not fully resolved because some of the phenotypes are rare and variable, no more than two species occur at any locality. For this reason, recognizing two co-occurring superspecies (*S. ziba* and *S. megarus*) solves the taxonomic problems sufficiently well to make sense of published work.

The first superspecies is *S. ziba*. Males are distinguished from those of *S. megarus* by a dark-charcoal dorsal wing surface (Figure 1; Mexican and Brazilian individuals sometimes have some submarginal light blue on the dorsal surface of the hindwing), anterior margin of the vinculum usually forming a prominent angle dorso-laterally, a twisted and upturned penis tip, and two heavily sclerotized cornuti (Figure 17). The female anterior ductus bursae is not looped – although twisted and sharply bent – and the posterior part of the corpus bursae is heavily sclerotized (Figure 19, inset). Although this female genitalia morphology differs from most *Strymon*, males have teeth on the distal part of the valves (albeit of different form than in other *Strymon*) and perch with their wings partially open. Both of these characteristics are unique to *Strymon* (Robbins & Nicolay 2002). This species occurs from northern Mexico to southern Brazil, Paraguay, and Argentina with virtually no



Figures 19, 20. Female ductus copulatrix, anterior to left. (19) *Strymon ziba* (Brazil, Rio de Janeiro state) in lateral aspect (top), cervix in dorsal aspect (bottom). (20) *S. megarus* (Brazil, Rio de Janeiro state) in dorsal aspect, arrow points to sclerotized loop of anterior ductus bursae. Scale bar: 1 mm.

geographical variation in genitalia. Geographical wing pattern variation is also slight, with the main variants being darker gray ventral ground color in parts of Argentina and submarginal blue on the dorsal surface of the hindwings in some Mexican and Brazilian specimens. Females oviposit on Bromeliaceae and other monocotyledons, particularly *Heliconia*. Individuals in Panama and Brazil land on orange-red ribbons that are similar in color to the bracts of *Heliconia* flowers and some bromeliad flowers. This species is common virtually everywhere in lowland forest. Males set up mating territories on wooded hilltops from 13:15 to 16:00 h in Panama and Brazil (BA, RJ, SP) (25 vouchers in USNM).

The second superspecies is *S. megarus*. Males are distinguished from males of *S. ziba* by extensive blue on the dorsal surface of the wings (Figures 3, 5, 7), the smooth anterior margin of the male genitalia vinculum, the twisted and downturned penis tip, and two lightly sclerotized cornuti (Figure 18). As in most female *Strymon*, the sclerotized anterior ductus bursae forms a complete loop and the posterior part of the corpus bursae is membranous (Figure 20). One phenotype of *S. megarus* (Figures 3, 4) occurs from Mexico to Trinidad in wet forest (the Transandean Region of Brown 1982) and is uncommon in museums. Males have been recorded setting up mating territories on wooded hilltops from 13:00 to 16:00 h in Panama (nine vouchers in USNM). A second phenotype (Figures 5, 6) occurs in the Amazon Basin and the Guianas in wet forest (the Amazonian Region of Brown 1982). It is rare in collections and variable geographically in phenotype. A third (Figures 7, 8), to which the names *S. megarus* and its synonym *S. basilides* refer, is common from the southern border of Peru (Pampas del Heath area, voucher in MUSM) south and east through Argentina, Paraguay, and Brazil south of the Amazon Basin in dry and wet forest; a distribution similar to the Atlantic Region in Brown (1982). Males have been recorded setting up mating territories on hilltops from 14:24 to 15:25 h in Brazil (BA, SP, SC) (seven vouchers in USNM). It is unclear whether these three phenotypes are distinct species or partially intergrading geographical forms. For example, males from French Guiana have the dorsal wing pattern of those from Panama and a ventral wing pattern similar to those from Amazonian Peru. In this paper, I use the name *S. megarus* for all three phenotypes. Two other very rare species with similar ventral wing patterns, *S. giffordi* Nicolay & Robbins and *S. jacqueline* Nicolay & Robbins, can be differentiated as noted in Nicolay & Robbins (2005). There is also another very rare phenotype in montane Andean forest, but there is insufficient evidence to determine whether this phenotype is an ecotype of the Amazonian *S. megarus* or a distinct taxon. The caterpillars of

S. megarus and relatives have been recorded only from Bromeliaceae, as noted below, with one doubtful exception that needs confirmation.

Food plant records

Strymon ziba (Hewitson)

Bromeliaceae: Aechmea bracteata (Sw.) Griseb.

Mexico, Veracruz, km 15 carretera Paso del Toro to Alvarado. (1♂, 2♀). Leg. C. Beutelspacher. Ex. larvae 14 June 1969 on fruits. Eclosed 8 July 1969. Published in Beutelspacher (1972a) as *Thecla basalides* Geyer with egg and pupa illustrated. Voucher in IBUNAM.

Bromeliaceae: Aechmea nudicaulis (L.) Griseb.

Brazil, Santa Catarina, Santa Catarina Island. Ex. 24 larvae and hatched eggs on inflorescences November 2006 to January 2007. Larval color cryptic, changing from whitish-yellow to reddish-pink. Larvae “fed on the soft nutritive tissues of the ovary and ovules, leaving the rigid coriaceous outer wall of the developing fruit mostly intact.” Development time: egg 5 days, larva 13–15 days, pupa 8–11 days. Antennated in the lab. Published in Schmid et al. (2010). Identification confirmed by dissection. Vouchers in LANUFSC.

Bromeliaceae: Aechmea

Brazil, Rio de Janeiro, Maricá. (1♀). Leg. R. Monteiro. Ex. larva June 1987 on fruits. In USNM.

Brazil, Pará, Carajás. (1♀). Leg. R. Monteiro. Ex. larva July 1987 on fruits. In USNM.

Bromeliaceae: Ananas comosus (L.) Merr. (pineapple)

Mexico, Oaxaca, Loma Bonito. (3♂, 4♀). Leg. Gayden and Alexander. Ex. larvae July 1950 on fruit. Associated larvae in alcohol. In USNM (Lot 50-11265).

Mexico, Oaxaca, Loma Bonito. (1♂). Ex. larva on fruit. Intercepted at El Paso. In USNM (Lot 43-9131).

Mexico. (1♀). Ex. larva on fruit. Intercepted at Laredo. In USNM (Lot 43-9357) with pupal case in alcohol.

Mexico. (1♂, 1♀). Ex. larvae on fruit. In USNM (Lot 52-7492) with larvae and pupae in alcohol.

Mexico. (1♀). Ex. larva on fruit. In USNM.

Honduras, La Ceiba. (3♂, 2♀). Leg. J. Mirenda and R. Lehman. Ex. larvae 28 December 1982 on fruit. In USNM.

Honduras, La Ceiba. (2♂, 3♀). Leg. J. Mirenda and R. Lehman. Ex. larvae March 1983 on fruit. In USNM.

Costa Rica, Alajuela, Venecia, San Carlos. 350 m. (2♂). Leg. H.J. Lezama. Ex. larvae 2 June 1990. In USNM.

Costa Rica, Heredia, Chilamate. 450 m. (1♀). Leg. P.J. DeVries. Ex. larva. Eclosed 2 June 1991. Larva produced calls. On loan to USNM with pupal case.

Venezuela, Miranda, Carrizales. (1♂, 1♀). Leg. D. Torrealba. Ex. larvae 20 May 1964 on fruit. Eclosed 19 June 1964. In MIZA (Fusagri Collection).

Venezuela, Aragua, Villa de Cura, Hda. Chaguarama. (3♀). Leg. M. Nieves and Cermeli. Ex. larvae 31 January 1967 on fruit. In MIZA (Fusagri Collection).

Venezuela, Lara, Duaca. (2♂, 2♀). Leg. Quevedo and Geraud. Ex. larvae 22 October 1969 on flowers. In MIZA (Fusagri Collection).

Trinidad. (1♀). Leg. H. A. Ballou. Ex. larva on fruit. In USNM.

Trinidad, Matura. (1♂). Leg. G. Laurence. Ex. larva on fruit. In CIBC.

Venezuela, Trujillo, Valera. (1♂). Leg. P. Guagliumi. Ex. larva 8 August 1953 on fruit. Eclosed 13 September 1953. Published in Guagliumi (1965, 1967) as *Thecla echion*. In MIZA with pupal case.

Peru, Jenaro Herrera, 4°55', 73°40'. (1♀). Leg. G. Couturier. Ex. larva September 1987. In MUSM.

Bromeliaceae

Mexico. (1♂). Ex. larva on flower. Intercepted in San Antonio in shipment from Mexico. In USNM with pupal case.

Brazil, Rio de Janeiro, Maricá (Restinga). (1♀). Leg. A. Lima-Carvalho. Ex. larva June 1986 on inflorescence. In USNM.

Haemodoraceae: Xiphidium coeruleum Aubl.

Panama, Canal Zone, Gamboa. (1♀). Leg. R. Robbins. Ex. three larvae 21 September 1979 which bored into immature fruits. One pupated 8 October and eclosed 17 October 1979. Oviposition observed 21 September 1979. Published in Robbins & Aiello (1982) as *S. basilides*. In USNM with pupal case.

Heliconiaceae: Heliconia densiflora B. Verl.

Peru, Madre de Dios, Manu National Park, Pakitza. Robbins observed oviposition 6 October 1991 at 10:56 h on bract. Ten other eggs found on flower and its bracts as well as six larvae. None reared. Female not collected.

Heliconiaceae: Heliconia latispatha Benth.

Panama, Canal Zone, Gamboa. (2♀). Leg. R. Robbins. Hundreds of eggs found on bracts and flowers

August 1979. Oviposition observed 16 October 1979. Ex. larvae 6 and 8 September 1979 on flowers. Pupa-tion 15 and 19 September 1979. Eclosion 23 and 27 September 1979, respectively. Larvae with dorsal nectary organ, but no ants were tending the larvae. Published in Robbins & Aiello (1982) as *S. basilides*. In USNM with pupal cases.

Heliconiaceae: Heliconia collinsiana Griggs = *Heliconia pendula* Wawra

Panama, Canal Zone, Barro Colorado Island. (2♂). Leg. J. Zetek. Ex. larvae September 1940 on flowers. In USNM (Lot Z-4689).

Heliconiaceae: Heliconia wagneriana Petersen

Panama, Canal Zone, Summit. Leg. R. Robbins. Eggs found on bracts and flowers August 1979. Published in Robbins & Aiello (1982) as *S. basilides*.

Heliconiaceae: Heliconia

Peru, Madre de Dios, Tambopata Reserve. Robbins observed oviposition 25 October 1991 at 14:25 h on bract. Female and egg not collected.

Strelitziaceae: Strelitzia

Colombia. (2♀). Ex. larvae 4 April 1957 on flower. Intercepted in New York in a shipment from Colombia. Associated larvae in alcohol. In USNM (Lot 57-8080) with a larva pickled in alcohol.

Strymon megarus (Godart)

Bromeliaceae: Ananas comosus (L.) Merr. (pineapple)
Brazil, Rio de Janeiro, Itatiaia and Minas Gerais, Passa Quatro. Published in Zikán & Zikán (1968) as *Thecla basalides* and *Thecla echion*. 2♂ in FIOC ex. larvae 5 and 12 September 1925.

Argentina, Misiones. Published in Pastrana (2004), specimens sent for identification in 1958 by A. Turico. A pdf in USNM of Pastrana's notes illustrates *S. megarus* adults and pupae from Misiones (perhaps the ones sent by Turico) where they were attacking pineapple. Malformed pineapples are also illustrated, and there is a note that the butterfly can be controlled with the insecticide Sevin.

Bromeliaceae: Bromelia pinguin L.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National

Park] (10.85827 N, 85.61089 W). (1♂, 1♀). Leg. D.H. Janzen and gusaneros (Lot 90-SRNP-2716.1 and 90-SRNP-2716.2). Ex. larvae 8 December 1990 mining leaves. Pupated 18 December 1990. Eclosed 29 December 1990 (♂), 31 December 1990 (♀). In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.83764 N, 85.61871 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 90-SRNP-2838). Ex. larva 12 December 1990 mining leaves. Pupated 26 December 1990. Eclosed 2 January 1991. Larva came out of leaf and pupated on leaf surface. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-6). Ex. larva 2 January 1992 mining leaves. Pupated 3 January 1992. Eclosed 16 January 1992. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-2). Ex. larva 2 January 1992. Pupated 22 January 1992. Eclosed 2 February 1992. Caterpillar is a "leaf miner, looks like PPU instar, prepupa with rose colored back, growing larvae are clear pale jade green." In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-223). Ex. larva 20 January 1992. Eclosed 16 February 1992. Caterpillar is a "leaf miner in thin leaf of seedling, looks like PU, note that nearly all of these are in the leaves of very young plants." In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.85413 N, 85.61534 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-6217). Ex. larva 30 December 1992. Pupated 3 January 1993. Eclosion not recorded. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 94-SRNP-46). Ex. larva 3 January 1994. Pupated 6 January 1994. Eclosed 20 January 1994. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8359). Ex. larva 6 December 1993. Pupated 15 December 1993. Eclosed 26 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8360). Ex. larva 6 December 1993. Pupated 17 December 1993. Eclosed 29 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8356). Ex. larva 6 December 1993. Pupated 17 December 1993. Eclosed 30 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♂). Leg. Guillermo Pereira (Lot 06-SRNP-12184). Ex. larva 15 January 2006. Pupated 27 January 2006. Eclosed 8 February 2006. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.85827 N, 85.61089 W). (1♂). Leg. Guillermo Pereira (Lot 06-SRNP-12113). Ex. larva 12 January 2006. Pupated 22 January 2006. Eclosed 1 February 2006. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.85827 N, 85.61089 W). (1♂). Leg. Guillermo Pereira (Lot 06-SRNP-12114). Ex. larva 12 January 2006. Pupated 18 January 2006. Eclosed 1 February 2006. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.88268 N, 85.61202 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-135). Ex. larva 16 January 1992 mining leaves. Eclosed 9 February 1992. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.83764 N, 85.61871 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-254). Ex. larva 25 January 1992 mining leaves. Eclosed 13 February 1992. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8364). Ex. larva 6 December 1993 mining leaves. Eclosed 2 January 1994. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8363). Ex. larva 6 December 1993 mining leaves. Pupated 21 December 1993. Eclosed 2 January 1994. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.83764 N, 85.61871 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 97-SRNP-2203). Ex. larva 7 May 1997 mining leaves. Eclosed 21 May 1997. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.85827 N, 85.61089 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 92-SRNP-98). Ex. larva 7 January 1992 mining leaves. Pupated 11 January 1992. Eclosed 22 January 1992. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8357). Ex. larva 6 December 1993 mining leaves. Eclosed 27 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8355). Ex. larva 6 December 1993 mining leaves. Eclosed 25 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8358). Ex. larva 6 December 1993 mining leaves. Pupated 15 December 1993. Eclosed 26 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. D.H. Janzen and gusaneros (Lot 93-SRNP-8362). Ex. larva 6 December 1993 mining leaves. Pupated 17 December 1993. Eclosed 28 December 1993. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.84867 N, 85.63046 W). (1♀). Leg. Eilyn Camacho (Lot 06-SRNP-12182). Ex. larva 15 January 2006. Pupated 27 January 2006. Eclosed 8 February 2006. In USNM.

Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa [Santa Rosa National Park] (10.88268 N, 85.61202 W). (1♀). Leg. Guillermo Pereira (Lot 06-SRNP-12348). Ex. larva 17 January 2006. Pupated 27 January 2006. Eclosed 8 February 2006. In USNM.

Bromeliaceae

Costa Rica: Heredia, La Selva Biological Station, 3 km S Pto. Viejo, 10°26'N, 84°01'W. (1♂). Leg. G.

Gentry (Lot 590). Ex. Larvae 27 May 1995 boring into a bromeliad. On loan to USNM.

Heliconiaceae: Heliconia

Costa Rica, larva intercepted at Atlanta, Georgia, USA. (1♂). 16 May 2005. In USNM with photographic slide of larva from S. Passoa. The adult is positively identified, but there is no direct confirmation that the caterpillar was eating *Heliconia*. This anomalous record needs confirmation.

Strymon megarus or *Strymon ziba*

The following records refer to one or both of these species, but without genitalic dissections, I cannot identify them with certainty.

Bromeliaceae: Aechmea

Trinidad, St. Augustine Experimental Station and other localities at the base of the Northern Range. Published in Harris (1927) as *Tmolus echion*. Extensive information on life history, immature stages, parasitoids, and methods of control. Development time is 3–5 days (ovum), 14–17 days (larva), and 7–11 days (pupa).

Bromeliaceae: Ananas ananassoides (Baker) L.B. Sm.

Brazil, Distrito Federal, Planaltina. (1♂, 2♀). Leg. V.O. Becker. Ex. larvae on fruit. Eclosed 5–21 December 1982. In CPAC (voucher #9531). I did not have the opportunity to identify these specimens.

Bromeliaceae: Ananas comosus (L.) Merr. (pineapple)

Mexico. Larvae enter inflorescence and cause abnormal development and rotting. Published in Beutelspacher (1972a) as *Thecla basalides* Geyer. No vouchers in IBUNAM.

Guatemala, Montufar, Palin, and Escuintla. Found larvae boring into young growing slips at the attachment of slip and fruit, sometimes in the fruit. Published in Carter (1934) as *Thecla echion*. Museum specimens (not necessarily the reared adults) were illustrated.

Trinidad, St. Augustine Experimental Station and other localities at the base of the Northern Range. Published in Harris (1927) as *Tmolus echion*. Extensive information on life history, immature stages, parasitoids, and methods of control. Feeds on both cultivated and wild pineapples. Development time is 3–5 days (ovum), 14–17 days (larva), and 7–11 days (pupa).

Brazil. Larva boring into fruit. Illustrated in Otero & Marigo (1990) as *Strymon basilides*.

Brazil. Nearly 40 records published in D'Araujo e Silva et al. (1967–1968) as *Thecla basilides*, including notes on parasitoids.

An alphabetical sampling of records in the agricultural literature of *Thecla basilides* or *Thecla basilides* eating pineapple are: Anonymous (1960, 1962), Azambuja & Mielitz (1981), Bello (1991), Bello et al. (1997), Chalfoun & da Cunha (1984), Choairy et al. (1984), Choairy & Fernandes (1983), Dolinski & Lacey (2007), Falanghe (1948), Fazolin (2001), Flores (1960), Giannotti et al. (1965), Heinrich (1947, 1955, 1958), Julca & Bello (1994), Leiderman & Vasconcellos (1955), Lima & Guitton (1962), Lorenzato et al. (1997), Maranhão (1962), Mariconi (1953), Marie (1995), Montenegro et al. (1960), Nakano et al. (1968, 1971), Novo (1955–1956), Petty et al. (2002), Py & Tisseau (1965), Reinhardt et al. (2002), Reis (1981), Rhains et al. (1996), Sampaio (1975), Sanches (1981, 1985, 1991, 1993), Sanches et al. (1985), Sifuentes (1971), Silveira (1949), Suplicy et al. (1966), and Zunti & Cardinali (1970).

An alphabetical sampling of records in the agricultural literature of *Tmolus echion* or *Thecla echion* eating pineapple are: Anonymous (1945), Araque (1961), Collins (1960), Johnston (1931), Leal & Avilán (1982), Martinez (1976), Monte (1945), Silva (1934), Squire (1935), and Thorold & Pickles (1940).

An alphabetical listing of records in the agricultural literature of the anomalous name, "*Hypolycaena philippus* Fabricius", eating pineapple are: Bondar (1912, 1915) and Silva (1932, 1934). D'Araujo e Silva et al. (1967–1968) regarded *Hypolycaena philippus* as a misidentification of "*Thecla basilides* Geyer". Accordingly, the figures of the adults in these papers are *S. ziba* or *S. megarus*. The name *Hypolycaena philippus* refers to an Old World genus and species; I have no idea how this misidentification arose.

Heliconiaceae: Heliconia

Trinidad, St. Augustine Experimental Station and other localities at the base of the Northern Range. Published in Harris (1927) as *Tmolus echion*. Extensive information on life history, immature stages, parasitoids, and methods of control. Development time is 3–5 days (ovum), 14–17 days (larva), and 7–11 days (pupa). These records presumably refer to *S. ziba*.

The tangled systematics of Thecla legota and relatives

The names *Strymon dindus* (Fabricius, 1793), *S. lucena* (Hewitson, 1868), *S. cardus* (Hewitson, 1874), *S. legota* (Hewitson, 1877), *S. canitus* (H.H. Druce,

1907), *S. ochraceus* K. Johnson & Salazar, 1993, *S. specialus* K. Johnson, Eisele & MacPherson, 1997, and *S. baricharensis* Le Crom & K. Johnson, 1997 refer to a complex of species. One phenotype occurs rarely in xeric habitats from Panama (Chiriquí) to Argentina (vicinity of Buenos Aires) with relatively minor wing pattern variation (Figures 9, 10). In southern Brazil and adjoining parts of Paraguay, however, the species in this complex are common and exceedingly variable in morphology and habitat, occurring from xeric "restinga" (beach) habitats to wet montane forest at 1800 m. Males in this complex set up mating territories on hilltops from 11:31 to 15:25 h (22 vouchers in USNM).

The number of biological species in this complex is unresolved. For example, the name *S. cardus* is usually applied to males that lack a scent patch on the dorsal surface of the forewing in the discal cell (Robbins 2004b), but of four specimens collected at the same time and place, three lack a scent patch and one has a very small scent patch (vouchers in USNM). Among specimens that refer to the other names (Figures 9–12), the scent patch varies in size from about 20 to 60% of the distal part of the discal cell. Individual size, the extent of blue on the dorsal wings, and details of the ventral wing pattern are all highly variable in southern Brazil. Some large individuals may be difficult to differentiate from *S. oreala* (Figures 12, 13). Finally, none of these names can be differentiated by genitalic structures. A tentative arrangement in Robbins (2004b) recognized *S. dindus* (males with extensive blue on the dorsal surface of the wings and relatively large scent patches; Figure 12), *S. cardus* (males with no scent patch or a very small one), and *S. lucena* (males with less blue than *S. dindus* on the dorsal forewing and a "medium"-sized scent patch; Figures 9–11). Probably no eumaine species complex is more in need of taxonomic characters other than adult morphology.

The nomenclature of this complex also needs resolution. For example, the oldest name, *S. dindus*, is identified from a very poor illustration in Jones' *Icones* (cf. Robbins & Lamas 2006). At such a point that it is clearer what is and what is not a species, the best option may be to declare this name a *nomen dubium*. As a second example, *Thecla lucena* was named from Venezuela, but the wing pattern of the type does not otherwise occur in Venezuela, so far as I am aware.

The reared specimens in this species complex are phenotypically homogeneous (similar to Figure 9) except possibly for the record in Fonseca (1934), for which I have not seen a voucher. Following the tentative arrangement in Robbins (2004b), I refer these foodplant records to *S. lucena* with the realization that this name may change in the future.

Strymon lucena (Hewitson)

Bromeliaceae: *Ananas comosus* (L.) Merr. (pineapple)
Brazil, São Paulo. Leg. J.P. Fonseca. Ex. larvae on new fruits. Published in Fonseca (1934) as *Thecla legota*. I have not seen a voucher specimen.

Brazil, Rio Grande do Sul. Ex. larvae. From an unpublished manuscript in DZUP by C.M. de Biezanko as *Thecla legota*. An individual from Argentina that Biezanko identified as this species is deposited in USNM.

Bromeliaceae: *Bromelia fastuosa* Lindl. = *Bromelia antiacantha* Bertol.

Brazil, Rio Grande do Sul. Ex. larvae. From an unpublished manuscript in DZUP by C.M. de Biezanko as *Thecla legota*. An individual from Argentina that Biezanko identified as this species is deposited in USNM.

Bromeliaceae: *Tillandsia aeranthos* (Loisel.) L.B. Sm.

Argentina, Buenos Aires. Ex. eggs on leaves (off-white color). Leg. N.R. Vannucci. Larva green, bores into center of the rosette. Non-reared vouchers in USNM (Figure 9), which are the same phenotype as the Argentine male that Biezanko identified as *Thecla legota*.

Bromeliaceae: *Tillandsia*

Brazil. Intercepted at Miami customs 16 September 1988. In USNM.

Strymon oreala (Hewitson)

Identification. *Strymon oreala* is distinguished from *S. dindus* primarily by its large size (male forewing length typically 1.5 cm and larger) and slightly darker blue dorsal color, but larger individuals of “*S. dindus*” (male forewing length typically 1.1–1.2 cm) may be similar (Figures 12, 13). However, eight males of “*S. dindus*” collected over three days on one hilltop were consistently smaller than males of *S. oreala* and consistently had lighter blue dorsal coloration (vouchers in USNM).

Biology. *Strymon oreala* occurs commonly in wet and dry forest in lowland and montane habitats in Brazil’s Mata Atlântica. Male mating behavior has not been recorded.

Bromeliaceae: *Aechmea caudata* Lindm.

Brazil, Santa Catarina, Santa Catarina Island. Ex. Seven larvae on inflorescences April 2008. Larvae same reddish pink color as the inflorescence stem and

fed on developing fruits. Development time of pupa 15–16 days. Ant-tended on occasion. Published in Schmid et al. (2010). Identification confirmed by image of adult. Vouchers in LANUFSC.

Bromeliaceae: *Aechmea lindenii* (E. Morren) Baker

Brazil, Santa Catarina, Santa Catarina Island. Ex. two larvae on inflorescences August to September 2007. Larvae same reddish pink color as the inflorescence stem and fed on developing fruits. Development time of pupa 15–16 days. Ant-tended on occasion. Published in Schmid et al. (2010). Identification confirmed by image of adult. Vouchers in LANUFSC.

Bromeliaceae: *Ananas comosus* (L.) Merr. (pineapple)

Brazil, Rio de Janeiro, Parque Nacional do Itatiaia. 700 m. (1♀, 1♂). Leg. J. Zikán. Ex. larva 13 November 1936 emerging from fruit. Pupated 16 November 1936 and eclosed 2 December 1936. Ant-tended. Published in Zikán (1956) as *Thecla oreala* with description of immature stages. Also published in Lima (1947). There are four reared adults in FIOC, one from December 1936.

Brazil, Rio de Janeiro, Parque Nacional do Itatiaia; Minas Gerais, Passa Quatro and Fazenda dos Campos. (1♂). Leg. J. Zikán. Ex. 14 larvae and five pupae 16 January 1937 on fruit. Ant-tended. Published in Zikán (1956) as *Thecla oreala* with description of immature stages. There are four reared adults in FIOC, but none from 1937.

Brazil, Rio Grande do Sul. Ex. larvae. From an unpublished manuscript in DZUP by C.M. de Biezanko as *Thecla oreala*. Specimens that Biezanko identified as this species are deposited in USNM.

Bromeliaceae: *Ananas silvestris* (Vell.) F.J. Müll.

Brazil. Larvae bore into the fruit. Published in D’Araujo e Silva et al. (1967–1968) as *Thecla oreala*. I have not seen vouchers.

Bromeliaceae: *Bromelia fastuosa* Lindl. = *Bromelia antiacantha* Bertol.

Brazil, Rio Grande do Sul. Ex. larvae. From an unpublished manuscript in DZUP by C.M. de Biezanko as *Thecla oreala*. Specimens that Biezanko identified as this species are deposited in USNM.

Bromeliaceae: *Quesnelia lateralis* Wawra

Brazil, Rio de Janeiro, Serra Macaé de Cima. 1550 m. (2♂). Leg. V. Harris and V. Hunter. Ex. larvae 30 March

1991 on flowers. Pupated 9 April 1991. Emerged 23 April 1991. Larvae and frass pink, matching the pale centers of the flowers. I have seen photographs of the adults. Published in Bland (1994). In RSME with pupal cases.

Bromeliaceae

Brazil, Minas Gerais, Sapucaí-Mirim. 1400 m. (4♂, 3♀). Leg. A. Ramalho. Ex. larvae 6–15 November 1959 on inflorescence. In DZUP with one pupal case.

***Strymon serapio* (Godman & Salvin)**

Identification. Males of *S. serapio* are differentiated from males of other described species in the *S. serapio* species group by blue “rays” on the dorsal surface of the wings and no basal spots on the ventral surface of the wings (Figure 14). However, the ventral wing pattern varies geographically and with elevation, and it is possible that more than one species is represented by this name. However, I have seen no evidence to suggest that more than one species occurs at any locality.

Biology. *Strymon serapio* occurs in wet and dry forest from Mexico to southern Brazil, but is a rare species in museum collections. Males set up mating territories on hilltops in Panama and southern Brazil (RJ, SC) from 07:30 to 10:03 h (eight vouchers in USNM). This early morning behavior has not been recorded in any other *Strymon*.

Bromeliaceae: Tillandsia caput-medusae E. Morren

Mexico, Guerrero, Acahuizotla. (1♂). Leg. C. Beutelspacher. Ex. larva 28 May 1970 on leaves. Eclosed 20 June 1970. Published in Beutelspacher (1972a, 1972b) as *Thecla hesperitis*. In IBUNAM with Beutelspacher determination label *Thecla hesperitis*. This record was listed as *Ziegleria hesperitis* in Frank & Lounibos (2009).

Bromeliaceae: Tillandsia

Mexico, Chiapas and San Luis Potosí. (1♂). Leg. S. Gardner. Ex. larvae on inflorescences. One reared to adult. In TAMU. I have not seen the reared male, but there are black and white photographs of the larva and adult in USNM.

Bromeliaceae: Vriesea friburgensis Mez

Brazil, Santa Catarina, Santa Catarina Island. Ex. four brownish-yellow larvae on inflorescences December 2007. Larvae fed on seeds in the fruits.

Development time of pupa 11 days. Published in Schmid et al. (2010). Identification confirmed by image of adult. Voucher in LANUFSC.

Bromeliaceae

Trinidad, Curepe. (1♂). Leg. M.J.W. Cock. Ex. larva January 1981 in seed pods. In MJWC with pupal case.

***Strymon azuba* (Hewitson)**

Identification. *Strymon azuba* can be distinguished from others in the *S. serapio* species group by blue restricted to the posterior half of the dorsal hindwings in both sexes coupled with no basal spots on the ventral surface of the hindwings (Figure 15). It can be distinguished from *S. cyanofusca* in the *S. melinus* species group by possessing a scent patch on the dorsal surface of the forewings (lacking in *S. cyanofusca*).

Biology. *Strymon azuba* occurs primarily in xeric areas throughout the Atlantic Biogeographic Region as delimited in Brown (1982), including the cerrado, but is uncommon in museum collections. Males set up mating territories on hilltops in southern Brazil (BA, MG) from 14:41 to 16:00 h (eight vouchers in USNM).

Bromeliaceae: Bromelia fastuosa Lindl. = *Bromelia antiacantha* Bertol. (gravatá)

Brazil, Rio Grande do Sul. Ex. larvae, oviposition observed. This record is from an unpublished manuscript in DZUP by C.M. de Biezanko as *Thecla valentina* Berg. Specimens in USNM and in MCZ that were identified by Biezanko as *T. valentina* are *S. azuba*.

Uruguay or Brazil. Published in Biezanko et al. (1974) as *Thecla valentina*.

***Strymon gabatha* (Hewitson)**

Identification. The mainland *Strymon gabatha* (Figure 16) and Hispaniolan *S. monopeteinus* Schwartz & J.Y. Miller can be distinguished from others in the *S. serapio* species group by two minute cornuti in the male genitalia penis (figure 9 in Schwartz & Miller 1985). Whether *S. monopeteinus* is considered a distinct species, as in Robbins (2004b), or an allopatric population of *S. gabatha* depends upon the species concept being used.

Biology. On the mainland, *S. gabatha* occurs in wet lowland and montane forest from Mexico to northern Peru in the Amazon Basin (Loreto) and is frequent in museum collections. Males set up mating

territories on hilltops from 13:00 to 13:30 h in Panama (four vouchers in USNM).

Bromeliaceae: Aechmea rubiginosa Mez = *Aechmea magdalenae* (André) André ex Baker

Costa Rica, Puntarenas, Parque Nacional Corcovado, Sirena. (1♀). Leg. L. Gilbert and M. Odum. Ovipositing on red bracts on 21 July 1983. Larvae bore into buds and young fruit. In USNM.

Costa Rica, Puntarenas, Parque Nacional Corcovado, Sirena. (1♂). Leg. L. Gilbert and M. Odum. Ex. pupa 21 July 1983 on bracts. Eclosed 31 July 1983. In USNM with pupal case.

Costa Rica, Puntarenas, Parque Nacional Corcovado, Sirena. (1♀). Leg. L. Gilbert and M. Odum. Ex. pupa 21 July 1983 on flower head. Eclosed 26 July 1983. In USNM with pupal case.

Costa Rica, Puntarenas, Parque Nacional Corcovado, Sirena. (1♂, 1♀). Leg. P.J. DeVries. Ex. ova 1 September 1984. Female pupated 22 September 1984, eclosed 2 October 1984. Male eclosed 9 October 1984. Larvae bored into fruits. (No Lot numbers). In USNM with female pupal case.

Bromeliaceae: Chevaliera veitchii (Baker) E. Morren = *Aechmea veitchii* Baker

Panama, Darien, Serrania de Pirre, Cana. 1500 m. Leg. G.B. Small. Ex. one ovum and one larva 19 April 1983. Flat white egg, laid on white part of flower. Larvae ate seeds. Both larvae pickled. Descriptions of larvae in Small's notes. In USNM (Lot GS83-26).

Panama, Darien, Serrania de Pirre, Cana. 1500 m. (1♀). Leg. G.B. Small. Ex. larva 20 May 1983. Pupated 24 May and eclosed 4 June 1983. In USNM (Lot GS83-60) with pupal case and last instar head capsule.

Panama, Darien, Serrania de Pirre, Cana. 1500 m. Leg. G.B. Small. Ex. larva 24 May 1983. Pickled 11 June 1983. Description of larva in Small's notes. In USNM (Lot GS83-66).

Discussion

Systematics

Members of the *S. ziba* and *S. serapio* species groups are the only Lycaenidae associated with Bromeliaceae. All records in the literature of *Thecla basalides*, *Thecla basilides*, *Thecla echion*, *Tmolus echion*, and *Hypolycaena philippus* feeding on bromeliads are based on misidentifications of *Strymon ziba* and/or *S. megarus*. The records of *Thecla hesperitis* and *Ziegleria*

hesperitis eating *Tillandsia* are based on a misidentification of *S. serapio*. The record of *T. valentina* eating *Bromelia* is a misidentification of *S. azuba*.

Guagliumi (1967) recorded *Pseudolycaena marsyas* (Linnaeus) from pineapple fruit, but this record appears to be an error because there are no vouchers for this rearing in MIZA. He reported that *P. marsyas* eats plants in five families besides Bromeliaceae, and there are vouchers in MIZA of specimens that he reared from Combretaceae, Meliaceae, Polygonaceae, Rosaceae, and Sterculiaceae. There is also a voucher of *T. echion* (actually *S. ziba*), which he reared from Bromeliaceae. The record of *P. marsyas* on Bromeliaceae, if correct, needs confirmation.

Adults of *S. ziba* and *S. megarus* have distinctly different male and female genitalia (Figures 17–20), so identification is definitive if there is an adult abdomen. Ventral wing pattern characters have been suggested that differentiate many specimens (Glassberg 2007, p. 47), and a more complex scheme might be devised that would work in all cases. There has been no attempt to differentiate larvae, and the ability to do so would seem to be a high priority task for agricultural workers.

Robbins & Nicolay (2002) presented an overview of *Strymon*, but were unable to analyze phylogenetic relations within the *S. serapio* species group because they found few phylogenetically informative characters in the external morphology. A phylogenetic analysis based on DNA sequences is needed. To date, however, most barcode sequences for *Strymon* have unconfirmed identifications and are not publically available (www.boldsystems.org, accessed 27 October 2009).

Ecology and evolution

The phenology of a butterfly specialist on flowers and fruits is dependent upon the flowering and fruiting phenology of its hosts. One possibility for the bromeliad-feeding butterflies is to utilize a variety of bromeliad species with complementary flowering and fruiting seasons, as suggested in Schmid et al. (2010). Most butterflies noted in this paper eat more than one bromeliad species, suggesting that this strategy is widely utilized. A second possibility is for a butterfly to attune its phenology strictly to that of its host. This strategy would be expected in extreme habitats where only one bromeliad species might be sufficiently abundant to support a butterfly population. A third possibility is to feed on leaves when flowers and fruits are unavailable. This strategy has apparently been adopted by *S. megarus* and *S. ziba* (e.g., Carter 1949; Sanches et al. 1985; Janzen & Hallwachs 2009). According to Faria et al. (2009, p. 221), "The borer preferentially attacks the inflorescences, but its attack

on crowns, slips, suckers, peduncles and leaves, especially in [the] absence of inflorescences, has been reported by different authors.” Specifically, when flowers and fruits are unavailable, larvae bore into leaves, so that they appear to be leaf miners (images in Janzen & Hallwachs 2009). Boring into food objects by larvae is a widespread trait in Eumaeini (e.g., Ziegler & Escalante 1964; Kendall 1975) and would appear to be a reason that *S. ziba* and *S. megarus* were able to “evolve” as facultative leaf miners. Whether this strategy is employed by other members of the *S. serapio* species group is yet unknown.

Many Eumaeini are polyphagous, with their caterpillars primarily eating flowers, fruits, and other rapidly developing tissue (Chew & Robbins 1984). For example, *Strymon melinus* is recorded eating the flowers and fruits of more than 20 families of dicotyledons and monocotyledons (Ehrlich & Raven 1965; Tietz 1972; Robbins & Nicolay 2002). Adult females of *Strymon* land on a taxonomically wide array of flowers to “drink” floral nectar, and this chronic contact may be a factor in expanding the taxonomic range of the flowers on which females will lay eggs (Chew & Robbins 1984). This idea is consistent with the hypothesis that a polyphagous ancestor of the *S. ziba* and *S. serapio* species groups added Bromeliaceae flowers to the plants on which it would nectar, followed eventually by oviposition, which was followed later by specialization on Bromeliaceae.

Agricultural pest status

Although four *Strymon* species are recorded eating pineapple, “*Thecla basilides*” is the “species” of concern in the agricultural literature. A biogeographic perspective best summarizes the situation. In the Transandean Region of Brown (1982) – essentially Mexico south to the Pacific slope of the Peruvian Andes and to Trinidad north of the Andes – *S. ziba* is common to abundant and *S. megarus* is uncommon. Accordingly, the records in this paper suggest that *S. ziba* is the primary pineapple pest in the Transandean Region. In the Amazonian Region – essentially the Guianas and Amazon Basin – *S. ziba* is sometimes common and *S. megarus* is rare. Except for one Peruvian record for *S. ziba*, I have seen no vouchers of either species on pineapple in this area. In the Atlantic Region – essentially coastal Brazil to Bolivia – both *S. ziba* and *S. megarus* are common to abundant butterflies. Unfortunately, there are almost no vouchers of pineapple-eating *Strymon* in Brazilian museums. It is yet an open question whether both species are greatly injurious to commercial pineapple in the Atlantic Region, but this question can be answered easily using the identification characters given in this paper.

The flowers of all plants used as larval hosts by the *S. ziba* and *S. megarus* species groups have orange-red coloration except for *Xiphidium coeruleum*, which has white flowers and rusty orange-red fruits. Accordingly, female oviposition by *S. ziba* was noted only on the fruits of *Xiphidium*, not on the flowers. Hummingbird-pollinated flowers are often red – and hummingbirds appear to be the predominate pollinator of bromeliads (Benzing 2000; Dziedziuch et al. 2003) – although there may be a complex hierarchy of factors influencing visitation by hummingbird pollinators (Stiles 1976). I have twice seen individuals of *S. ziba* landed on orange-red ribbons (the ribbons marked experimental plots unrelated to the butterflies), a behavior that has not been reported for any other eumaeine. These ribbons were very similar in color to many bromeliad flowers and *Heliconia* bracts. It seems likely that bromeliad-feeding butterflies use long wavelength colors as a cue in finding suitable oviposition substrates, but as with hummingbirds, it is probably one of a hierarchy of factors. However, if these preliminary observations are correct, “sticky traps” that are the same reddish-purple color as pineapple flowers might be a non-toxic, inexpensive means of ameliorating damage to fruits from *Strymon* in commercial pineapple fields.

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References

- Anonymous. 1945. A cultura do abacaxi. AgricPecuária (Rio J). 16(264):22–24.
- Anonymous. 1960. Combate à broca do abacaxi. Bol Agric (Belo Horizonte). 9(5–6):73.
- Anonymous. 1962. La piña, reina de las frutas tropicales. La Vida Agric (Lima). 39(469):649–652.
- Araque R. 1961. El cultivo de la piña en Venezuela. Caracas, Consejo de Bienestar Rural. 36 p. [reprinted in Agric Américas. 11(3):26–28, 30, 34, 36 and in Serie de Cultivos. Consejo de Bienestar Rural (Caracas). 5:1–36.]
- Azambuja MD, Mielitz LR. 1981. Comportamento de cinco inseticidas no controle da “broca do abacaxi” – *Thecla basilides* Geyer, 1837 – Lepidoptera – Lycaenidae. Agron Sulriograndense 17:341–346.
- Beccaloni GW, Vilorio AL, Hall SK, Robinson GS. 2008. Catalogue of the hostplants of the neotropical butterflies. Zaragoza (Spain): Soc Entomol Aragonesa. 536 p.
- Bello S. 1991. Cultivo de la piña en la selva central del Perú. Informe Técnico INIAA-PICT (Lima). 15:1–46.
- Bello S, Villachica H, Julca A. 1997. Resistencia de cultivares de piña a la “broca de la fruta” *Thecla basilides* Geyer en Chanchamayo – Perú. Acta Hort. 425:187–192.
- Benzing DH. 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge (UK): Cambridge University Press. 690 p.
- Beutelspacher CR. 1972a. Some observations on the Lepidoptera of bromeliads. J Lepid Soc. 26:133–137.
- Beutelspacher CR. 1972b. Fauna de *Tillandsia caput-medusae* F. Morren, 1880 (Bromeliaceae). Anal Inst Biol. Univ Nac Autón México (Zool). 43(1):25–30.
- Biezanko CM de, Ruffinelli A, Link D. 1974. Plantas y otras sustancias alimenticias de las orugas de los lepidopteros Uruguayos. Rev Centro Ciênc Rurais (Santa Maria, Rio Grande do Sul). 4(2):107–147.
- Bland KP. 1994. *Strymon oreala* (Hewitson, 1868) (Lepidoptera: Lycaenidae) reared from flower of the bromeliad, *Quesnelia lateralis* in southern Brazil. News Lepid Soc. 1994(1):5.
- Bondar GG. 1912. Uma praga do abacaxi. Bol Minist Agric, Ind Comm (Rio J). 1(4):103–104.
- Bondar GG. 1915. Bichos damninhos da fruticultura e arboricultura. São Paulo: Editora Chácaras e Quintaes. 52 p. (Biblioteca Agrícola Popular Brasileira; 22).
- Brown KS. 1982. Historical and ecological factors in the biogeography of aposematic neotropical butterflies. Am Zool. 22(2):453–471.
- Carter W. 1934. Notes on two pests of pineapple not known in Hawaii. Proc Hawaii Entomol Soc. 8(3):395–397.
- Carter W. 1949. Insect notes from South America with special reference to *Pseudococcus brevipes* and mealybug wilt. J Econ Entomol. 42(5):761–766.
- Chalfoun SM, Cunha GAP da. 1984. Relação entre a incidência da broca-do-fruto e a fusariose do abacaxi. Pesq Agropec Brasil. 19:423–426.
- Chew FS, Robbins RK. 1984. Egg-laying in butterflies. In: Vane-Wright RI, Ackery PR, editors. The biology of butterflies. London: Academic Press. p. 65–79. (Symposium of the Royal Entomological Society of London; 11).
- Choairy SA, Fernandes PD. 1983. Densidades de plantio na cultura do abacaxi. Pesq Agropec Brasil. 18:985–988.
- Choairy SA, Santos ES dos, Sanches NF. 1984. Incidência de broca e fusariose em fruto de abacaxizeiro. Agropec Técnica (Aréia, Paraíba). 5(1–2):1–7.
- Collins JL. 1960. The pineapple. Botany, cultivation, and utilization. London: Leonard Hill. xvii+294 p.
- D’Araujo e Silva AG, Gonçalves CR, Galvão DM, Gonçalves AJL, Gomes J, Silva M do Nascimento, Simoni L de. 1967–1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil. Rio de Janeiro: Ministério da Agricultura. Part I, vol. 1, p. 422, vol. 2, p. 906; Part II, vol. 1, p. 622, vol. 2, p. 265.
- Dolinski C, Lacey LA. 2007. Microbial control of arthropod pests of tropical tree fruits. Neotrop Entomol. 36(2):161–179.
- Dziedzioch C, Stevens A-D, Gottsberger G. 2003. The hummingbird plant community of a tropical montane rain forest in southern Ecuador. Plant Biol (Stuttgart). 5:331–337.
- Ehrlich PR, Raven PH. 1965. Butterflies and plants: a study in coevolution. Evolution. 18:586–608.
- Falanghe O. 1948. Constatação de uma coleobroca como praga do abacaxi. O Biológico (São Paulo). 14(7):165–167.
- Faria DC de, Carvalho AJC de, Coelho RI, Oliveira Filho JC de. 2009. Bud moth {*Strymon megarus* (Godart, 1824)} causes severe losses in young plants of pineapple cultivars Perola and Smooth Cayenne in Rio de Janeiro, Brazil. Acta Hort. 822:219–224.
- Fazolin M. 2001. Reconhecimento e manejo integrado das principais pragas da cultura do abacaxi no Estado do Acre. Docum Embrapa Acre. 62:1–26.
- Flores FG. 1960. Noções preliminares sobre a cultura do abacaxizeiro. In: Fruticultura gaucha – Abacaxi, banana, citrus. Porto Alegre: Secretaria da Agricultura, Indústria e Comercio. p. 5–20.
- Fonseca JP. 1934. Relação das principais pragas observadas nos anos de 1931, 1932 e 1933, nas plantas de maior cultivo no Estado de S. Paulo. Arq Inst Biol. (São Paulo) 5:263–189.

- Frank JH, Lounibos LP. 2009. Insects and allies associated with bromeliads: a review. *Terrestrial Arthropod Rev.* 1:125–153.
- Giannotti O, Orlando A, Duzzi D. 1965. Noções fundamentais sobre as pragas da lavoura no Estado de São Paulo e como combatê-las. *O Biológico (São Paulo)*. 31(11):231–273.
- Glassberg J. 2007. A swift guide to the butterflies of Mexico and Central America. Morristown (NJ): Sunstreakbooks.com. 266 p.
- González JM, Jaffe K, Michelangeli F. 1991. Competition for prey between the carnivorous Bromeliaceae *Brocchinia reducta* and Sarraceneacea [sic] *Heliamphora nutans*. *Biotropica*. 23:602–604.
- Guagliumi P. 1965. Contributo all conoscenza dell'entomofauna nociva del Venezuela (coninuazione e fine). *Riv Agric Subtrop Trop.* 59:447–472.
- Guagliumi P. 1967. Insetti e arachnidi delle piante comuni del Venezuela segnalati nel periodo 1938–1963. *Relaz Monogr Agraria Subtrop Trop.* (N.S.) 86:1–391.
- Harris WV. 1927. On a lycaenid butterfly attacking pineapples in Trinidad. *Bull Entomol Res.* 18(2):183–188.
- Heinrich WO. 1947. Resinose do fruto do abacaxi. *O Biológico (São Paulo)*. 13(7):119–122.
- Heinrich WO. 1955. O Rhodiatox no combate às pragas do abacaxi. Resinose do abacaxi. Sítios Fazendas (São Paulo). 21(10):25–26.
- Heinrich WO. 1958. Experiências para combate à *Thecla basilides* (Geyer, 1837), broca do abacaxi (Lepid. Lycaenidae). *Arq Inst Biol (São Paulo)*. 25(12):109–119.
- Honey MR, Scoble MJ. 2001. Linnaeus' butterflies (Lepidoptera: Papilionoidea and Hesperioidea). *Zool J Linn Soc.* 132(3):277–399.
- Inclán DJ, Alvarado E, Williams RN. 2007. Evaluación de cuatro insecticidas naturales para el control de *Thecla, Strymon megarus* (Godart) (Lepidoptera: Lycaenidae), en el cultivo de piña. *Tierra Trop.* 3(2):199–210.
- Inclán DJ, Bermúdez FJ, Alvarado E, Ellis M, Williams RN, Acosta N. 2008. Comparison of biological and conventional insecticide treatments for the management of the pineapple fruit borer, *Strymon megarus* (Lepidoptera: Lycaenidae) in Costa Rica. *Ecol Engin.* 34(4):328–331.
- Janzen DH, Hallwachs W. 2009. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservación Guanacaste (ACG), northwestern Costa Rica; [cited 2009 Nov 6]. Available from: <http://janzen.sas.upenn.edu>
- Johnston JR. 1931. Enfermedades y plagas de la piña en la América tropical. *Rev Agric Puerto Rico*. 26(7):4–11. [Also in *Bol Unión Panamer (Agricul)* (Washington DC). 65:88–103].
- Julca A, Bello S. 1994. La “broca de la piña” *Thecla basilides* Gey. en la selva central del Perú. *Rev Per Entomol.* 36:61–62.
- Kendall RO. 1975. Larval foodplants for seven species of hairstreaks (Lycaenidae) from Mexico. *Bul Allyn Mus.* 24:1–4.
- Lamas G. 2008. Bibliography of butterflies. An annotated bibliography of the neotropical butterflies and skippers (Lepidoptera: Papilionoidea and Hesperioidea). Revised electronic edition. 580 p.; [cited 2009 Nov 6]. Available from: <http://muse-oh.nmms.edu.pe/divisiones/zoologia/entomologia/ento-publicaciones.html>
- Leal FJ, Avilán L. 1982. Areas potenciales para el desarrollo de diferentes especies frutícolas en el país. III La piña. *Rev Facul Agron (Maracay)*. 12(3/4):283–300.
- Leiderman L, Vasconcellos FTC. 1955. Combate à “resinose” do abacaxi com modernos inseticidas orgânicos. *O Biológico (São Paulo)*. 21(6):97–103.
- Lima AMC. 1947. Sobre endoparasitos de *Thecla basilides* (Lep., Lycaenidae). *Anais Acad Brasil Ciênc.* 19(3):277–281.
- Lima AM da C, Guitton N. 1962. *Tetrastichus gahani* sp. n. (Hym., Chalcidoidea, Tetrastichidae). *Mem Inst Oswaldo Cruz (Rio J)*. 60(2):253–255.
- Lorenzato D, Chouêne EC, Medeiros J, Rodrigues AEC, Pederzoli RCC. 1997. Ocorrência e controle da broca-do-fruto-do-abacaxi. *Pesq Agropec Gaúcha*. 3(1):15–19.
- Maranhão ZC. 1962. Brocas. *Bol. Didático Escola Super Agricul. “Luiz de Queiroz” (Piracicaba)*. 1:1–17.
- Mariconi F de AM. 1953. Broca do abacaxi. *O Biológico (São Paulo)*. 19(2):37.
- Marie F. 1995. Survey on pineapple pests and diseases on the Caribbean. *Trop Fruits Newsl (Port-of-Spain)*. 14:3–4.
- Martinez NB de. 1976. Estudio preliminar en el control de los insectos causantes de la gomosis en pina. *Agron Trop.* 26:3–7.
- Matos AP de, Reinhardt DH. 2009. Pineapple in Brazil: characteristics, research and perspectives. *Acta Hort.* 822:25–36.
- Monte O. 1945. A broca do abacaxi. *Chácaras Quintais (São Paulo)*. 71(6):700.
- Montenegro HWS, Gallo D, Rocha J de M. 1960. Novos inseticidas no controle da broca do abacaxi (*Thecla [sic] basilides*, Geyer). *Bol Escola Sup Agric “Luiz de Queiroz” (Piracicaba)*. 16:1–7.
- Nakano O, Assis-Machado C de, Kinoshita K, Campos-Penteado LA de. 1971. Teste de novos inseticidas no controle da broca do abacaxi (*Thecla basilides* Geyer). *O Solo (Piracicaba)*. 63(1):17–19.
- Nakano O, Parra JRP, Filho JM. 1968. Ensaio de campo visando o controle da broca do abacaxi (*Thecla basilides* Geyer). *O Solo (Piracicaba)*. 60(2):29–31.
- Nicolay SS, Robbins RK. 2005. Five new dry-area South American *Strymon* species (Lycaenidae: Theclinae) and their biogeographic significance. *J Res Lepid.* 38:35–49.
- Novo E da S. 1955–1956. Identificação e combate de pragas. *Bol Flumin Agric (Niterói)*. 4(46):18–19, 36, (59):32–33.
- Otero LS, Marigo LC. 1990. Butterflies: beauty and behavior of Brazilian species. Rio de Janeiro: Marigo Comunicação Visual. 128 p.
- Pastrana JA. 2004. Los lepidópteros argentinos: sus plantas hospedadoras y otros sustratos alimenticios. Buenos Aires: Sociedad Entomológica Argentina. xvi + 334 p.
- Petty GJ, Stirling GR, Bartholomew DP. 2002. Pests of pineapple. In: Peña J, Sharp JL, Wysoki M, editors. *Tropical fruit pests and pollinators. Biology, economic importance, natural enemies and control*. Wallingford, UK: CABI Publishing. p. 157–195.
- Py C, Tisseau M-A. 1965. *L'ananas*. Paris: G.-P- Maisonneuve & Larose. 300 p.
- Reinhardt DHRC, editor. 2009. VI International Pineapple Symposium. Leuven (Belgium): International Society for Horticultural Science. 328 p. (Acta Horticulturae; 822).
- Reinhardt DH, Cabral JRS, Souza LF da S, Sanches NF, Matos AP de. 2002. Pérola and smooth cayenne pineapple cultivars in the state of Bahia, Brazil: growth, flowering, pests, diseases, yield and fruit quality aspects. *Fruits*. 57(1):43–53.
- Reis PR. 1981. Pragas do abacaxizeiro. *Informe Agropecuário (Belo Horizonte)*. 7(74):29–32.
- Rhainds M, Gries G, Morales JL. 1996. Oviposition deterrence in pineapple borer females, *Thecla basilides* (Lepidoptera: Lycaenidae). *Ecol Entomol.* 21(1):105–106.
- Robbins RK. 2004a. Introduction to the checklist of Eumaeini (Lycaenidae). In: Lamas G, editor. *Checklist: Part 4A. Hesperioidea – Papilionoidea*. In: Heppner JB, editor. *Atlas of Neotropical Lepidoptera*. Vol. 5A. Gainesville (FL): Association for Tropical Lepidoptera; Scientific Publishers. p. xxiv–xxx.
- Robbins RK. 2004b. Lycaenidae. Theclinae. Tribe Eumaeini. In: Lamas G, editor. *Checklist: Part 4A. Hesperioidea – Papilionoidea*. In: Heppner JB, editor. *Atlas of Neotropical Lepidoptera*. Vol. 5A. Gainesville (FL): Association for Tropical Lepidoptera; Scientific Publishers. p. 118–137.
- Robbins RK, Aiello A. 1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *J Lepid Soc.* 36:65–75.

- Robbins RK, Lamas G. 2006. Stabilizing the nomenclature of Fabrician names of North American hairstreaks (Lycaenidae: Theclinae: Eumaeini). *J Lepid Soc.* 60(2):86–91.
- Robbins RK, Nicolay SS. 2002. An overview of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini). *J Lepid Soc.* 55:85–100.
- Sampaio AS. 1975. A broca dos frutos ou resinose do abacaxi. *A Lavoura (Rio J)*. 78:9.
- Sanches NF. 1981. Entomofauna do abacaxizeiro no Brasil. Documentos. Centro Nac Pesq Mandioca Fruticult (Cruz das Almas). 10:[v]+1–68.
- Sanches NF. 1985. A broca-do-fruto do abacaxi. Informe Agropecuário. 11:43–46.
- Sanches NF. 1991. Frequência de ataque da broca do fruto do abacaxi (*Thecla basilides*) na região de Coração de Maria-BA. *Rev Bras Fruticult.* 13(4):179–185.
- Sanches NF. 1993. A broca-do-fruto do abacaxi e seu controle. *Abacaxi em Foco.* 77:[1]–[2].
- Sanches NF, Choairy SA, Vilardebo A. 1985. Ataque de *Thecla basilides* (Geyer, 1837) (Lepidoptera: Lycaenidae) em folhas de abacaxi na Paraíba, Brasil. *Anais Soc Entomol Bras.* 14(1):167–169.
- Schmid S, Schmid VS, Kamke R, Steiner J, Zillikens A. 2010. Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil. *J Res Lepid.* 42:50–55.
- Schwartz A, Miller JY. 1985. A new species of hairstreak (Lycaenidae) from Hispaniola. *Bull Allyn Mus.* 99:1–6.
- Sifuentes JA. 1971. Pérdidas causadas por algunas plagas de importancia económica en México. *AgricTécnica México.* 3(3):86–88.
- Silva RF e. 1932. Cultura racional do abacaxi. Recife (Brazil): Publ Secret Agricul, Viação Obras Públicas. 75 p.
- Silva RF e. 1934. Doenças e pragas do abacaxi. Rio de Janeiro: Typographia Carmo. 36 p.
- Silveira GG da. 1949. Alguns processos para combater a “resinose” do abacaxizeiro. *Chácaras Quintais (São Paulo)*. 80(1): 47–48.
- Squire FA. 1935. Recent entomological investigations. *Agric J Br Guiana.* 6(2–3):84–90.
- Stiles FG. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *Condor.* 78(1):10–26.
- Suplicy Filho N, Giacomelli EJ, Sampaio AS, Orlando A. 1966. Experiências sobre o controle químico da broca do fruto do abacaxizeiro – *Thecla basilides* (Geyer). *Lepidoptera – Lycaenidae. O Biológico (São Paulo)*. 32(6):122–126.
- Thorold CA, Pickles A. 1940. Control of pineapple caterpillar. *Trop Agric.* 17(11):215–216.
- Tietz HM. 1972. An index to the described life histories, early states and host of the Macrolepidoptera of the continental United States and Canada. Vol. 1. Sarasota (FL): Allyn Museum of Entomology. 536 p.
- Velasco PH. 1972. Fluctuación del daño del barrenador de la piña *Thecla* sp. y su control con insecticidas. *Folia Entomol Mex.* 23–24:62–63.
- Ward DB, Fish D. 1979. Powdery *Catopsis*. In: Ward DB, editor. Rare and endangered biota of Florida. Vol. 5, Plants. Gainesville: University Presses of Florida. p. 74–75.
- Ziegler JB, Escalante T. 1964. Observations on the life history of *Callophrys xami* (Lycaenidae). *J Lepid Soc.* 18(2):85–89
- Zikán JF. 1956. Beitrag zur Biologie von 12 Theclinen-Arten. *Dusenía.* 7:139–148.
- Zikán JF, Zikán W. 1968. Inseto-fauna do Itatiaia e da Mantiqueira. III. Lepidoptera. *Pesq Agropec Brasil (Agron)*. 3:45–109.
- Zunti AC, Cardinali LR. 1970. Controle à broca do fruto (*Thecla basilides*) do abacaxizeiro (*Ananas comosus*) com inseticidas clorados, fosforados e carbamatos. *Pesq Agropec Brasil.* 5:29–33.