AN OVERVIEW OF STRYMON HÜBNER (LYCAENIDAE: THECLINAE: EUMAEINI)

ROBERT K. ROBBINS

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0127, USA

AND

STANLEY S. NICOLAY

1500 Wakefield Drive, Virginia Beach, Virginia 23455, USA

ABSTRACT. North American *Strymon* Hübner was revised about 40 years ago, and the significantly larger Neotropical *Strymon* is now incorporated into this classification. *Strymon* is characterized by anteriorly directed teeth on the posterior dorsal surface of the valvae. These teeth were first noted by Clench and appear to be modifications of the sockets of setae that normally occur on eumaeine valvae. This characterization is most consistent with past usage and appears to represent the best evidence for monophyly. As characterized, *Strymon* contains 48 described species. Variation in morphology of the male genitalia, female genitalia, wings, and head is documented, and male behaviors and larval foodplant records are summarized. We tentatively divide *Strymon* into species groups, one of which is unusual in its use of Bromeliaceae as its sole larval foodplant.

One recently described genus, *Heoda* Johnson, L. Miller & Herrera 1992, and one recently resurrected genus, *Eiseliana* Toledo 1978, are made junior synonyms of *Strymon* Hübner 1818. Six names recently described in *Strymon* are transferred to other genera: *Strymon angulus* Le Crom & Johnson, 1997 to *Thereus* Hübner; *Strymon daplissus* Johnson & Salazar, 1993 to *Ministrymon* Clench 1961; *Strymon carmencitae* Le Crom & Johnson, 1997 and *Strymon cryptogramus* Johnson, Eisele & MacPherson, 1992 to *Nicolaea* Johnson; *Strymon nivnix* Johnson, Eisele & MacPherson, 1990 to *Calycopis* Scudder; and *Strymon additionalis* Le Crom & Johnson, 1997 to *Thecla* F. The hindwings of *Strymon nivnix* are designated a lectotype, and *Strymon anthracaetus* Salazar, Vélez, & Johnson, 1997 is regarded as a *nomen dubium*.

Additional key words: Bromeliaceae, foodplants, territoriality, Heoda, Eiseliana.

Strymon Hübner is possibly the best-known New World hairstreak genus (Lycaenidae: Theclinae: Eumaeini). It occurs from Canada to the temperate parts of Chile and Argentina. Some Strymon are common and well-known, such as S. melinus (Gray Hairstreak), and some are pests on commercial pineapple, such as S. ziba (Hewitson), S. megarus (Godart), and relatives (Harris 1927, Carter 1934, Fonseca 1934, Zikán 1956, Guagliumi 1965, 1967, D'Araujo e Silva et al. 1967-1968, Beutelspacher 1972, Otero & Marigo 1990). The name Strymon has been widely used in North America; the first extensive list of North American Strymon species (Barnes & McDunnough 1917) contained about 40 taxa and was followed by similar listings (Barnes & Benjamin 1926, McDunnough 1938, Klots 1951, Dos Passos 1964). Although Ziegler (1960) and Clench (1961) rather drastically changed the characterization of Strymon, 14 of the 48 described Strymon species currently recognized (Appendix 1) are recorded from North America (Opler & Malikul 1992, Opler & Wright 1999).

"Modern" taxonomic usage of *Strymon* began when the genus was distinguished primarily by genitalic structures (Ziegler 1960, Clench 1961). With increased knowledge of the Neotropical eumaeine fauna, however, it became clear that these characters, as originally proposed, do not delimit *Strymon*. For example, *S. yojoa* (Reakirt) has small anteriorly directed teeth on the dorsal valva tips—a structure

mentioned in Clench's generic diagnosis—but lacks a tightly convoluted spiral of the ductus bursae (Fig. 20)—a structure noted in Ziegler's generic characterization. Alternately, *S. serapio* (G. & S.) has the tightly-convoluted spiral (Fig. 25), but also has a double cornutus, not the single acuminate one described by Clench (1961) (Fig. 16). To complicate matters, the subsequently described genera *Eiseliana* Toledo and *Heoda* Johnson, Miller, & Herrera possess some genitalic structures that Ziegler and Clench used to characterize *Strymon*. Finally, six species described in *Strymon* since 1990 possess none of these characters.

The purposes of this paper are to characterize Strymon, so that it will be clear which species belong to Strymon, and to provide an overview of the comparative morphology and ecology of the genus. Specifically, this paper (1) outlines the nomenclatural history of Strymon, (2) suggests that the best structure for distinguishing Strymon is the unique morphology of the male genitalia valvae, which was first noted by Clench, (3) describes and illustrates morphological variation within the genus, (4) summarizes information on male behavior, larval foodplant specificity, and habitat, (5) preliminarily partitions Strymon species in nine species groups, and (6) transfers six names from Strymon to other genera. This work is intended to set the stage for a species revision, including the description of about five new species, mostly from the dry mountains of Peru and southern Ecuador.

MATERIALS AND METHODS

The results in the this paper were based upon a comparison of adult morphology using the 6,000+ specimens of Strymon in the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA), of which 3,972 are Neotropical, plus many specimens borrowed from other museums. This comparison employed standard entomological techniques (Robbins 1991), including the examination of the male and female genitalia (449 dissections) of all species currently recognized in Strymon (Appendix 1), except that we relied on genitalic figures of two species. For those names that we could not identify from their original descriptions, we examined their types or pictures of the types. For only one species, Strymon anthracaetus Salazar, Vélez, & Johnson, could we not identify the name or find its type (explained below). In preparing a checklist of all Neotropical hairstreaks (Robbins in press), RKR examined the adult morphology of virtually all Neotropical species, although not in the same detail as with Strymon. All genitalic terms follow those in Klots (1970). All specific author names for Strymon are listed in Appendix 1 and thus are omitted from the following text.

Because relationships within the Eumaeini are still poorly known, such as the genera that are most closely related to *Strymon*, we characterize *Strymon* by a complex and conspicuous trait that is unique within the Eumaeini and that is phylogenetically consistent with other traits that are unique within the Eumaeini. We tentatively divide *Strymon* into species group on the basis of many characters, but evidence for their monophyly awaits formal phylogenetic analysis.

NOMENCLATURAL HISTORY

Hübner (1818) described *Strymon* and included two species, *S. melinus* and *Hesperia acaciae* Fabricius. (*Hesperia* currently belongs to the Hesperiidae.) A subsequent list of 13 *Strymon* species (Hübner 1819) caused considerable confusion in the eventual selection of a type species. Scudder (1872) selected *Hesperia titus* F. from the 1819 list as the type (the dates of Hübner's books were uncertain at the time), but Riley (1922) invalidated this selection and replaced it with *Strymon melinus*. Finally, the International Commission on Zoological Nomenclature (1959) placed *Strymon* on the Official List as Name No. 1332 with *Strymon melinus* as type. Hemming (1967) gives a more complete nomenclatural history.

STRYMON HÜBNER

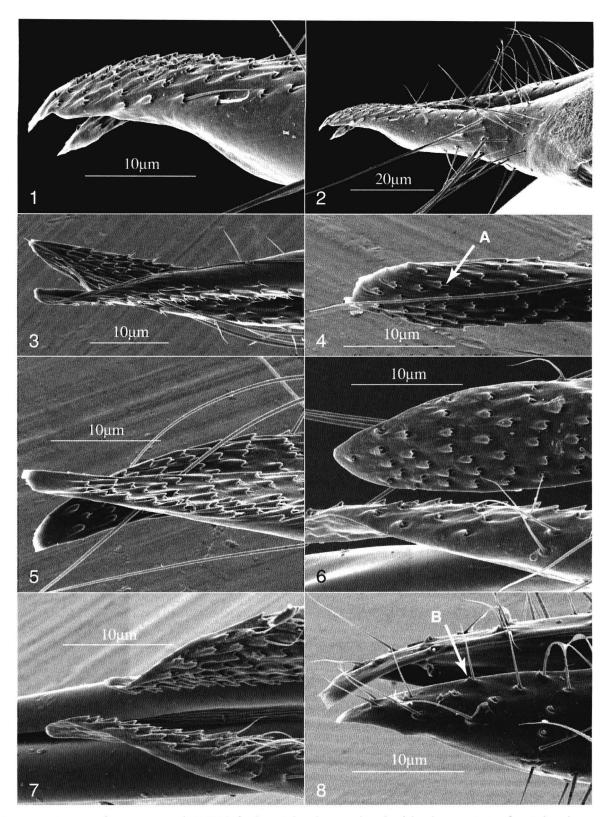
We characterize *Strymon* for the following discussion of comparative morphology by setae on the poste-

rior dorsal surface of the valvae that are modified into anteriorly pointing "teeth" (Clench 1961) (Figs. 1-7). This structure is immediately recognizable; either a species has it or does not. The only exception is S. ziba (Fig. 8), whose valva morphology and systematic position are detailed below. Although the valva structure of Strymon is most easily illustrated using a scanning electron microscope (SEM), Clench discovered it using a light microscope. Almost all species that have been placed in Strymon since 1960 (e.g., Ziegler 1960, Clench 1961, 1964, Johnson et al. 1990, Johnson et al. 1992, Johnson & Kroenlein 1993, Johnson & Salazar 1993, Austin & Johnson 1997) have this valva structure. The only superficially similar valvae in the Eumaeini are those of Allosmaitia Clench, whose valvae are needle-like posteriorly, unlike Strymon, and covered with teeth that are not anteriorly directed (Clench 1964).

COMPARATIVE MORPHOLOGY

Male genitalia. The setae on the valvae of eumaeine hairstreaks are indistinguishable when viewed with an SEM from those specialized setae that were termed B-type trichoid sensilla (Ma & Schoonhoven 1973). In Strymon, these setae are modified. The anteriorly directed teeth on the posterior dorsal surface of the valvae appear to be modifications of the sockets of these setae. Supporting this interpretation, the setal flagellum is still present, but is short (usually less than 1 μm long) (Figs. 1-7). In S. ziba, some of the setal sockets on the posterior dorsal valva tips are slightly modified into anteriorly pointing teeth with a flagellum that is not reduced in length (Fig. 8). As discussed below, some evidence suggests that this structure is transitional between that in other eumaeines and in Strymon while other evidence suggests that it is a further modification of that which occurs in other Strymon.

We illustrate the male genitalia of nine Strymon species to show the range of morphological variation (Figs. 9-17). The tips of the gnathos in all Strymon species are subterminally expanded and then sharply tapered to a down-curved point (Figs. 9-17), but this structure does not appear to be sufficiently distinct from other eumaeines to distinguish the genus unequivocally. At least one cornutus is present within the shaft of the penis unless the vesica is partially everted (Figs. 12, 14, 15). If there is one cornutus, it is long and slender (slightly wider in S. maritalis and S. christophei) and sometimes barely sclerotized (S. yojoa, Fig. 11). If there are two cornuti, they are usually paired and about the same size (Fig. 16) (first noted and illustrated by Schwartz & Miller 1985). The primary exception is S. ziba, which has one cornutus conVolume 55, Number 3



Figs. 1–8. Scanning electron micrographs (SEMs) of male genitalia valva tips in lateral and dorsal aspects. 1, S. melinus in lateral aspect; 2, S. melinus at lower magnification; 3, S. acis; 4, S. eurytulus in dorsal aspect (Arrow A — setal flagellum); 5, S. bazochii; 6, S. gabatha; 7, S. megarus; 8, and S. ziba (Arrow B — slightly modified setal socket).

siderably larger than the other (Fig. 17). Strymon male genitalia are asymmetrical. For example, the penis is twisted and down turned (Clench 1961) except for S. ziba and S. sylea (Figs. 10, 17). The saccus is generally asymmetrical to the right (Figs. 9b, 12, 14, in ventral aspect, they are on the left side).

Strymon species have paired brush organs (sensu Eliot 1973) that lie on the dorsal vinculum, but we omit them in the figures for clarity. The vinculum is not modified in structure, as it is in some eumaeines (Robbins 1991), except for slight projections of the vinculum in some species, such as S. tyleri and S. crambusa. We are unable to distinguish the structure of the brush organs in Strymon from those that occur in Lamprospilus Hübner, Electrostrymon Clench, Ziegleria Johnson, and Calycopis Scudder. Males of S. istapa in one part of its range (Florida to Puerto Rico) may have or lack brush organs (Robbins & Nicolay 1999), and a similar dimorphism also appears to occur in S. bicolor.

Other than the variation outlined above, the male genitalia of *Strymon* seem to have few good structures for distinguishing species. For example, the male genitalia of *S. istapa*, *S. columella*, *S. limenia*, and *S. toussainti* are essentially indistinguishable except for small differences in size (Robbins & Nicolay 1999) — these species are distinguished by their wing pattern and female genitalia. Except for *S. ziba* and *S. sylea*, few *Strymon* species appear to be authoritatively identifiable solely on the basis of their male genitalic structures.

Female genitalia. The bursa copulatrix of Strymon is asymmetrical, and we illustrate the range of variation (Figs. 18-26). All eumaeines with a sclerotized, looped ductus bursae belong to Strymon, as first noted by Ziegler (1960), but the exact shape of the loop varies greatly interspecifically (Figs. 18-26). It is also highly variable intraspecifically, as in S. cestri, where some individuals lack the sclerotized loop of the ductus bursae, some have it, and others are intermediate between these extremes (Figs. 27-29). A few Strymon species appear to always lack the loop (S. yojoa, S. tegea, S. ohausi, S. sylea, and S. ziba), but the ductus bursae is twisted at the point where the loop would otherwise occur except in S. sylea (Figs. 19, 20, 23). The signa, which are "boat"-shaped, occur in all Strymon species, but may be small in some, such as S. limenia (Hewitson) (Fig. 24), and may lack the anterior pointing spine (S. sylea, Fig. 19). Similar signa are found on occasion in other eumaeines, such as Trichonis Hewitson (Robbins 1987). There are two small teeth inside the anterior ductus bursae (Fig. 18). Similar teeth occur in other eumaeines, such as those illustrated for Rekoa palegon (Cramer) (Robbins 1991).

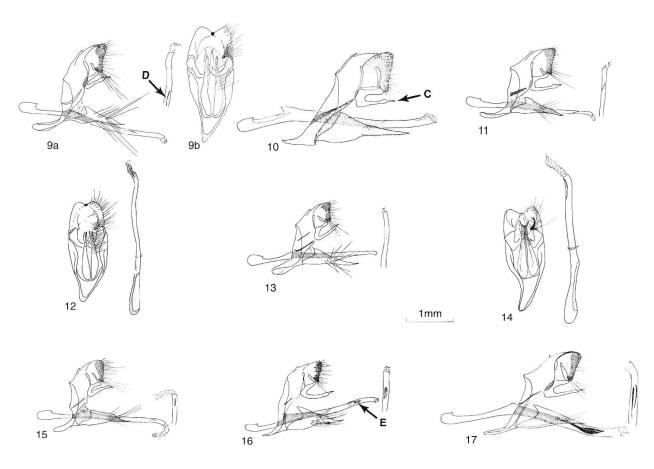
The female 8th abdominal tergum of Eumaeini is sclerotized, the sternum is membranous, and two small circles lacking setae are also membranous (e.g., illustrated by Field 1941). Since spiracles on the 8th abdominal segment of the endoporian Ditrysia, including the butterflies, are absent or vestigial (Dugdale 1974), we presume that these membranous circles are vestigial spiracles. In female Strymon, there are two kinds of 8th abdominal segments. The first, of which S. melinus is an example (Fig. 30), is like many eumaeines with presumed vestigial spiracles at the juncture between the tergum and sternum. The second, of which S. bicolor is an example (Fig. 31), has the presumed vestigial spiracles located within the tergum, whose latero-posterior part has more furrows than the first kind. Johnson et al. (1992) first described the furrowed tergum as "rough" and used it as a distinguishing character of their new genus Heoda. However, this structure is difficult to discern and actually occurs in all members of the S. istapa group (except for S. acis, Appendix 1), including species that Johnson et al. (1992) placed in Eiseliana and Strymon.

When the ductus seminalis does not arise from the posterior tip of the corpus bursae in *Strymon*, such as *S. limenia*, the tip of the corpus bursae, posterior of the ductus seminalis, is lightly sclerotized (Fig. 24). All *Strymon* species with this structure are a subset of those whose females have an 8th tergum with the latero-posterior surface furrowed and with imbedded presumed vestigial spiracles. The posterior end of the corpus bursae of a few other species, such as *S. ziba*, *S. martialis*, and *S. christophei*, is also sclerotized (Figs. 23, 26), but this structure appears to be analogous with the structure in *S. limenia* and relatives because the ductus seminalis arises from the posterior tip of the corpus bursae in these species.

Wings. The wing venation of *Strymon* is typical of the Eumaeini with 10 forewing veins (Eliot 1973). A male scent patch (sensu Robbins 1991) occurs on the dorsal surface of the forewing in the distal part of the discal cell of most species, but is lacking in *S. melinus*, *S. avalona*, *S. sabinus*, *S. tyleri*, *S. rufofusca*, *S. cyanofusca*, *S. ohausi*, *S. christophei*, *S. oribata*, and *S. legota*. Because these species appear to belong to a number of different species groups, as determined below on the basis of many characters, we suspect multiple losses of the forewing scent patch in *Strymon*.

Wing pattern, shape, and size vary greatly among *Strymon* species (Figs. 34–53), and it is difficult to characterize *Strymon* on the basis of these traits. Generally, the pattern on the ventral wing surface is not sexually dimorphic, but males have more sharply produced forewing apices. Seasonal variation of the ven-

Volume 55, Number 3



FIGS. 9–17. Male genitalia of *Strymon*; teeth on valvae are inconspicuous at this magnification. **9**, *S. melinus* in lateral (a) and ventral (b) aspects (Arrow **D** — acuminate cornutus); **10**, *S. sylea* (Arrow **C** — tip of gnathos); **11**, *S. yojoa*; **12**, *S. mulucha*; **13**, *S. albata*; **14**, *S. martialis*; **15**, *S. limenia*; **16**, *S. serapio* (Arrow **E** — paired cornuti); and **17**, *S. ziba*.

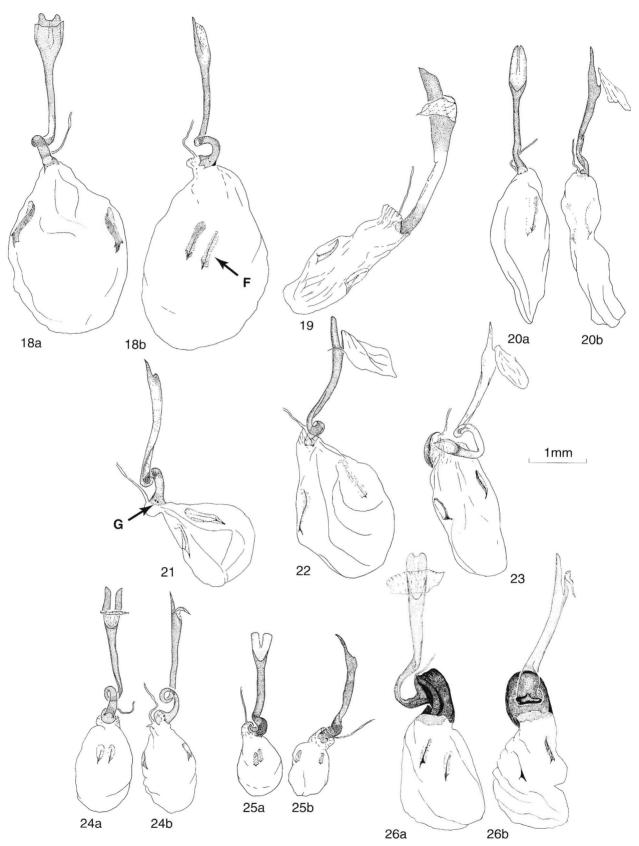
tral wing surface can be marked in some species, such as S. melinus, but virtually absent in others, such as S. bazochii. For example, individuals of S. melinus are smaller and darker on average in early spring in North America than they are in the middle of summer. The dorsal surface of the forewing of most female Strymon has a patch of black scales centered at the end of the discal cell, which is sometimes mistaken for androconia (Figs. 35, 40). Other eumaeines sometimes also have a similar appearing patch of dark scales, such as females of *Tmolus venustus* (Druce). Forewing length varies from more than 2 cm (S. sylea, S. oreala, and S. gabatha) to less than 0.8 cm (S. ohausi, S. ochraceus). And some species, such as S. gabatha and S. serapio, vary greatly in size intraspecifically, which is perhaps related to their bromeliad larval foodplants (flowers of Aechmea and Tillandsia, respectively).

Head. The antennal club of Theclinae, including the Eumaeini, is generally cylindrical and incrassate, but those of most *Strymon* are abrupt and flattened, resembling those of Polyommatinae and Lycaeninae

(Eliot 1973). An antenna with an abrupt and flattened club also occurs in a few other eumaeines, such as *Penaincisalia* Johnson. The frons of *S. melinus* is covered with white and orange scales, and there are also orange scales near the base of the antennae. Most other *Strymon* share this head coloration, but a few lack white or orange scales, such as *S. bazochii* (Godart). However, a hairstreak with orange scales near the base of the antennae, an orange-white frons, and an abrupt, flattened antennal club is almost definitely a *Strymon*, which allows field recognition of this genus in most cases.

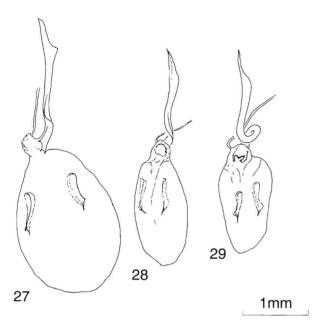
BEHAVIOR AND ECOLOGY

Male behavior. Male Strymon occupy mating territories, usually on hilltops and along forest edges. The males perch in the "territory," fly at other butterflies that enter this area, and then return to a perch very close to the original one unless courtship has ensued (e.g., Powell 1968, Robbins 1978, Alcock 1983, Alcock & O'Neill 1986, 1987, Cordero & Soberón 1990). We



Figs. 18–26. Female genitalia bursa copulatrix of *Strymon*. **18**, *S. melinus* in ventral (a) and lateral (b) aspects (Arrow **F** — signum); **19**, *S. sylea*; **20**, *S. yojoa* in ventral (a) and lateral (b) aspects; **21**, *S. mulucha* (Arrow **G** — teeth inside ductus bursae); **22**, *S. albata*; **23**, *S. martialis*; **24**, *S. limenia* in ventral (a) and lateral (b) aspects; and **26**, *S. ziba* in ventral (a) and lateral (b) aspects.

VOLUME 55, NUMBER 3



FIGS. 27–29. Female genitalia variation of the bursa copulatrix of *S. cestri*. **27**, Peru; **28**, Costa Rica; **29**, Mexico.

have observed this behavior in the United States, Panama, Venezuela, Ecuador, Peru, and Brazil for 15 Strymon species (RKR unpubl.). The males of most species occupy mating territories in the afternoon. A few species do so whenever the weather is favorable (i.e., S. tyleri, S. davara), and one species only in the early morning (males of S. serapio on hilltops in Panama and southern Brazil between 0730 and 1000 hours). The following discussion is based on our unpublished observations.

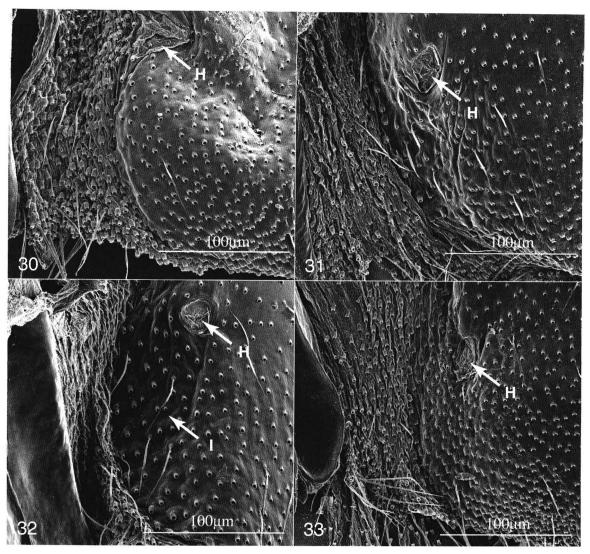
When male Strymon perch in a mating territory, they often open their wings 15-180 degrees, in addition to moving their hindwings back and forth as in all Theclinae (Robbins 1980). We have observed the unusual wing opening behavior (Figs. 54, 55) in S. melinus, S. mulucha, S. yojoa, S. davara, S. cestri, S. bubastus, S. dindus, S. ochraceus, S. ziba, S. megarus, S. azuba, and S. gabatha. Males of other hairstreak genera generally do not open their wings when perching, but we have observed this behavior in some species of Tmolus and Chlorostrymon. Another unusual male Strymon behavior is perching head downwards on tree-trunks, in addition to perching on leaves. This behavior has been recorded in S. ziba, S. gabatha, S. ochraceus, and S. megarus. Only once have we seen a male hairstreak of another genus perch on a tree-trunk (Chalybs janias [Cramer]).

Larval foodplants. The larvae of *Strymon* eat plants in more than 30 families, ranging from gymnosperms to monocots and dicots, including Alstroe-

meriaceae, Amaranthaceae, Begoniaceae, Boraginaceae, Bromeliaceae, Cactaceae, Cannabidaceae, Chenopodiaceae, Compositae, Convolvulaceae, Crassulaceae, Euphorbiaceae, Flacourtiaceae, Gesneriaceae, Gramineae, Guttiferae, Haemodoraceae, Juglandaceae, Labiatae, Leguminosae, Malvaceae, Melastomataceae, Musaceae, Orchidaceae, Pinaceae, Polygonaceae, Portulacaceae, Rosaceae, Sapindaceae, Sterculiaceae, Strelitziaceae, Surianaceae, Ulmaceae, and Verbenaceae (RKR unpubl., plant family names follow Willis 1973). Some individual Strymon species, such as S. melinus, are exceedingly polyphagous (Ehrlich & Raven 1965, Tietz 1972), eating plant reproductive structures in most of these families. Many of these Strymon species, though, most frequently feed on plants in the Leguminosae and Malvaceae, and some are recorded as pests of beans and cotton (Ehrlich & Raven 1965).

The only Eumaeini with larvae that eat plants in the Bromeliaceae belong to Strymon (RKR unpubl.). Some are serious pests of commercial pineapple (Harris 1927, Carter 1934, Fonseca 1934, Zikán 1956, Guagliumi 1965, 1967, D'Araujo e Silva et al. 1967–1968, Beutelspacher 1972, Otero & Marigo 1990), but the agricultural literature refers to lycaenid pineapple pests as either Thecla echion L. (a misidentification of S. megarus or S. ziba, cf. Honey & Scoble 2001) or Thecla basalides (Geyer), a misspelling of Strymon basilides (Geyer), which, in turn, is a junior synonym of S. megarus (Appendix 1). Consequently, it is unclear exactly how many Strymon species feed on pineapples, but there are records for at least four species. The larvae of S. ziba, unlike those of the others, eat plants in a number of monocot families in addition to those of the Bromeliaceae (e.g., Harris 1927, Robbins & Aiello

Habitat and range. Although Strymon occur in habitats ranging from tropical wet lowland rainforest to temperate climates, they are most diverse in xeric and seasonally very dry tropical areas, which includes most of the Pacific Coast of Mexico and Central America, northern Colombia and northern Venezuela, the mountains of Peru and southern Ecuador (where there are a number of undescribed species), the llanos of central Venezuela and surrounding countries, and eastern Brazil in the cerrado and caatinga life zones west to the Bolivian chaco. Strymon melinus is the only widespread Strymon in temperate North America while S. bicolor ranges from Peru in the Andes to Chile's temperate central valley (Santiago and surroundings), and S. eurytulus occurs from Bolivia and southern Brazil south into Patagonia (Argentina).



FIGS. 30–33. SEMs of female 8th abdominal tergum in dorso-lateral aspect. **30**, S. melinus; **31**, S. bicolor; **32**, S. eurytulus (Arrow I — furrow in tergum); **33**, S. bazochii. Arrows **H** — presumed vestigial spiracles.

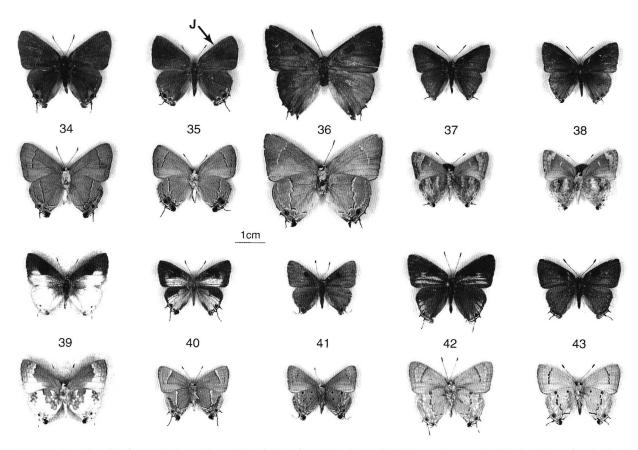
STRYMON AND ITS SPECIES GROUPS

The monophyly of *Strymon*, as we have characterized it, is supported by a complex and conspicuous valva structure that is unique within the Eumaeini and whose presence or absence is unambiguous except for *S. ziba*. Other characters that are unique, or nearly so, within the Eumaeini are restricted to subsets of *Strymon*, adding further support to our characterization of *Strymon* as a monophyletic genus. All species with a scleortized looped ductus bursae belong to *Strymon*, as do all eumaeines with a ventro-lateral surface of the female 8th abdominal tergum that is furrowed with imbedded presumed vestigial spiracles. Behaviorally and ecologically, almost all eumaeine males that perch with their wings open 15–180° belong to *Strymon* (a

behavior that may occur in all *Strymon*), as do all eumaeine males that perch on tree-trunks (one exception noted above), and all species whose larvae eat plants in the Bromeliaceae.

We have divided *Strymon* into nine species groups (listed in Appendix 1) on the basis of many characters, most of which were discussed above. Some of these groups, such as the *S. istapa* and *S. serapio* groups, are reasonably well-characterized while others, such as the *S. mulucha* and *S. albata* groups, lack clear-cut derived distinguishing traits. For example, some characters suggest that *S. cestri* belongs to the *S. yojoa* species group, and others that it belongs to the *S. mulucha* species group. In the following paragraphs we characterize the *S. istapa* and *S. serapio* species groups and discuss the systematic positions of *S. ziba* and *S. sylea*.

Volume 55, Number 3



FIGS. 34–43. Dorsal and ventral wing surfaces. **34**, male *S. melinus* (New Jersey, USA) (Arrow **J** — patch of black scales on female dorsal forewing); **35**, female *S. melinus* (New Jersey, USA); **36**, male *S. sylea* (Loreto, Peru); **37**, male *S. yojoa* (Panama Prov., Panama); **38**, male *S. mulucha* (Canal Area, Panama); **39**, male *S. albata* (Canal Area, Panama); **40**, female *S. martialis* (Florida, USA); **41**, male *S. limenia* (Santiago, Cuba); **42**, male *S. serapio* (Santa Catarina, Brazil); and **43**, male *S. ziba* (Canal Area, Panama).

We characterize those species with paired cornuti that are about the same size as the *Strymon serapio* group (Appendix 1). All recorded larval foodplants in this group are plants in the Bromeliaceae. In fact, except for *S. ziba*, all neotropical lycaenid larvae that use Bromeliaceae, including all pests of commercial pineapple, belong to this group. Except for *S. ziba* and one observation of a male *Chalybs*, all males that are known to perch on tree-trunks belong to the *S. serapio* group.

We characterize the *Strymon istapa* group as those species with a female 8th abdominal tergum whose ventro-lateral surface is furrowed with imbedded presumed vestigial spiracles (Appendix 1). This tergum structure is otherwise unreported in the Eumaeini. Those species with a lightly sclerotized corpus bursae between the origin of the ductus seminalis and the posterior tip of the corpus bursae are a subset of this group. In all other *Strymon*, the ductus seminalis arises at the posterior tip of the corpus bursae. The inclusion of *S. acis* in this species group is provisional, as explained in Appendix 1.

The systematic position of S. ziba is unresolved because of conflicting evidence. On the one hand, S. ziba appears to belong to the S. serapio group. Both have two cornuti, larvae that eat plants in the Bromeliaceae, and males that perch on tree trunks. The ventral wing pattern and male behavior of S. ziba and S. megarus are nearly identical, suggesting that they are sisters. If this systematic position is correct, then the unique valva structure of S. ziba is a modification of the Strymon valva. On the other hand, S. ziba appears to be the sister to the remainder of Strymon. Evidence supporting this systematic position is that the valva structure of S. ziba appears to be intermediate between that of *Strymon* and other eumaeines. And unlike the S. serapio group, S. ziba has paired cornuti of unequal size, and its larvae eat plants in various monocot families, not just Bromeliaceae. This evidence suggests that S. ziba does not belong to the S. serapio group. Hanner and Robbins (in prep.) are trying to resolve this conflicting evidence using mitochondrial DNA sequences.



FIGS. 44-45. Males perching with their wings open. 54, S. melinus (California, USA); 55, S. megarus (Veracruz, Mexico).

The systematic position of *S. sylea* is tentative because its penis is upturned and its ductus bursae is straight, unlike virtually all other *Strymon* species. The male genitalia valvae of *S. sylea* possess the unusual basally directed teeth of *Strymon* when viewed with a light microscope. The tips of the gnathos, scent patch, and antennal club of *S. sylea* are consistent with *Strymon*, and we cannot place *S. sylea* in any other eumaeine genus. Because *S. sylea* is an exceedingly rare species in collections, we have not had the opportunity to examine its valvae using an SEM, which would definitively confirm that the valva teeth are indeed the *Strymon* type. The placement of *S. sylea* in *Strymon* appears to be the best option for now.

NOMENCLATURE

Generic synonymy. Using our characterization of *Strymon*, based largely on that of Clench (1961), there are five generic synonyms of *Strymon*, listed with their type species in parentheses. Citations to all original descriptions for this and the following list can be found in Lamas et al. (1995).

Strymon Hübner 1818 (Rusticus melinus Hübner)
Callipareus Scudder 1872 (Strymon melinus Hübner)
Callicista Grote 1873 (Callicista ocellifera Grote)
Uranotes Scudder 1876 (Strymon melinus Hübner)
Eiseliana Toledo 1978 (Eiseliana koehleri Toledo)
Heoda Johnson, L. Miller & Herrera 1992 (Thecla heodes Druce)

Our characterization of *Strymon* appears to be reasonable despite the uncertain systematic position of *S. ziba*. If *S. ziba* belongs to the *S. serapio* group, which is supported by some evidence, then *S. ziba* clearly belongs to *Strymon*. If, on the other hand, *S.*

ziba is the sister to the remainder of Strymon, which is supported by other evidence, then placing S. ziba in Strymon avoids naming a monotypic genus for S. ziba.

The generic names Callicista, Eiseliana, and Heoda could be applied to the S. istapa species group, but we believe that our characterization of Strymon is more reasonable and stable. Recognizing Callicista, Eiseliana, or Heoda would leave the name Strymon for the remainder of species with anteriorly directed teeth on the dorsal valvae, but there is no evidence that this remaining group of species is monophyletic. And if a generic name were also proposed for the S. serapio group, there would still be no evidence for the monophyly of Strymon. Lastly, our characterization of Strymon is consistent with the way that Strymon has been used in North America for the last 40 years (Ziegler 1960, Clench 1961).

Species groups. We list the 183 names that belong to *Strymon* as we have characterized it, partitioned into species groups (Appendix 1). We list the characters for each species group, but many characters are homoplastic, and formal phylogenetic analysis is necessary to establish the monophyly of these groups. The original description of *Strymon anthracaetus* Salazar, Vélez, & Johnson, 1997 was too poor to identify this name or to determine whether it belongs to *Strymon*. In August 2000 G. Lamas could not find the type at the museum in Manizales, Colombia, where it was supposed to be deposited. Consequently, we regard *S. anthracaetus* as a *nomen dubium*.

Names removed from *Strymon*. Many names that were described in *Strymon* do not belong to *Strymon* as we have characterized it. We confirm the previous transfer to other genera (Bridges 1988) of 23

Volume 55, Number 3 95

names that were originally described in *Strymon* (Appendix 2).

We transfer the following six species, which were recently described in *Strymon*, to other genera and give brief reasons for the new generic placement. One is transferred to "*Thecla*" because it belongs to a genus that is yet undescribed.

- 1. Strymon angulus (Le Crom & Johnson, 1997) is transferred to Thereus Hübner, **new combination**. Robbins (1991, 2000) characterized Thereus by a pair of sclerotized invaginations on the membrane attached to the ventro-lateral sides of the papillae anales, a pair of ventro-lateral brush organs in addition to the pair of dorsal ones, and sexual dimorphism in the antennal club (>4 more nudum segments in the female than the male). Although these characters are not mentioned in the original description of S. angulus, the illustrated holotype is a male of Thereus endera Hewitson, which possesses the three synapomorphies of Thereus listed above (Robbins in press).
- 2. Strymon daplissus Johnson & Salazar, 1993 is transferred to Ministrymon Clench, **new combination.** The illustrated holotype of S. daplissus is a male of Thecla clytie Edwards, which Clench (1961) placed in Ministrymon.
- 3. and 4. Strymon carmencitae (Le Crom & Johnson, 1997) and Strymon cryptogramus (Johnson, Eisele & MacPherson, 1992) are transferred to Nicolaea Johnson, **new combinations.** We characterize Nicolaea by its male genitalia vinculum, which is strongly curved anteriorly in lateral aspect and which is flattened dorsally in anterior aspect. These characters cannot be seen in the original descriptions, but the illustrated holotypes of Strymon carmencitae and Strymon cryptogramus are specimens of Nicolaea fabulla (Hewitson, 1868) and N. torris (Druce, 1907), respectively, which possess the vinculum of Nicolaea as described (Robbins in press).
- 5. Strymon nivnix (Johnson, Eisele & MacPherson, 1990) is transferred to Calycopis Scudder, **new combination**. The forewings of the holotype of S. nivnix belong to a different genus than the hindwings (Robbins in press), which appear to be the slightly aberrant hindwings of Calcyopis cecrops F. We designate the hindwings as the lectotype, which is placed in Calycopis as characterized by Clench (1961) and Field (1967).
- 6. Strymon additionalis (Le Crom & Johnson, 1997) is transferred to Thecla F., **new combination.** The holotype is a male of "Thecla" emessa Hewitson, 1867, which is characterized by the form of its scent patch on the dorsal surface of the forewings, a white medial stripe on the frons, and a penis tip with its ventral surface flattened. Because the latter two characters were not illustrated in the original description, our identifi-

cation is based upon the illustrated wing pattern and scent patch.

ACKNOWLEDGMENTS

We dedicate this paper to the memories of J. B. Ziegler and H. K. Clench, who together modernized the generic taxonomy of North American hairstreaks. For the loan or gift of *Strymon* specimens over the years, we are grateful to P. Ackery, C. Brévignon, C. Callaghan, M. Casagrande, J.-Y. Gallard, J. Glassberg, G. Lamas, J. MacDonald, L. Miller, Jacqueline Miller, James Miller, O. Mielke, J. Rawlins, B. Sullivan, R. Vane-Wright, and J. Weintraub. We thank J. Glassberg for allowing us to use his photographs of perching *Strymon* males. We are grateful to V. Malikul for help with photography, S. Braden with the SEM, and G. Venable with digitization and layout of the figures. For detailed comments on the manuscript, we thank J. Brown, J. Burns, P. Gentili-Poole, J. Glassberg, J. Hall, D. Harvey, G. Lamas, C. Penz, B. Sullivan, and the late B. Ziegler.

LITERATURE CITED

- ALCOCK, J. 1983. Territoriality by hilltopping males of the great purple hairstreak, Atlides halesus (Lepidoptera, Lycaenidae): convergent evolution with a pompilid wasp. Behav. Ecol. Sociobiol. 13:57–62.
- ALCOCK, J. & K. M. O'NEILL. 1986. Density-dependent mating tactics in the grey hairstreak, *Strymon melinus* (Lepidoptera: Lycaenidae). J. Zool. Series A 209:105–113.
- 1987. Territory preferences and intensity of competition in the grey hairstreak Strymon melinus (Lepidoptera: Lycaenidae) and the tarantula hawk wasp Hemipepsis ustulata (Hymenoptera, Pompilidae). Am. Midl. Nat. 118:128–138.
- Austin, C. T. & K. Johnson. 1997. Theclinae of Rondônia, Brazil: Strymon Hübner, with descriptions of new species (Lepidoptera: Lycaenidae). Insecta Mundi 11:201–235.
- BARNES, W. & F. H. BENJAMIN. 1926. Notes on diurnal Lepidoptera, with additions and corrections to the recent "List of Diurnal Lepidoptera". Bull. S. Calif. Acad. Sci. 25:88–98.
- Barnes, W. & J. H. McDunnough. 1917. Check list of the Lepidoptera of boreal America. Herald Press, Decatur, Illinois. 392 pp. Beutelspacher, C. R. 1972. Some observations on the Lepidoptera of bromeliads. J. Lepid. Soc. 26:133–137.
- BRIDGES, C. 1988. Catalogue of Lycaenidae & Riodinidae (Lepidoptera: Rhopalocera). Published by the author, Urbana, Illinois. 788 pp.
- CARTER, W. 1934. Notes on two pests of pineapple not known in Hawaii. Proc. Haw. Entomol. Soc. 8:395–397
- CLENCH, H. K. 1961. Tribe Theclini, pp. 177–220. In P. R. Ehrlich & A. H Ehrlich, How to know the butterflies. Brown Co., Dubuque, Iowa.
- 1964. A synopsis of the West Indian Lycaenidae, with remarks on their zoogeography. J. Res. Lepid. 2:247–270.
- CORDERO, C. R. & J. SOBERON. 1990. Non-resource based territoriality in males of the butterfly *Xamia xami* (Lepidoptera: Lycaenidae). J. Insect Behav. 3:719–732.
- D'Araujo e Silva, A. C., C. R. Gonçalves, D. M. Galvão, A. J. L. Gonçalves, J. Gomes, M. do Nascimento Silva & L. De Simoni. 1967–1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil. Ministerio da Agricultura, Rio de Janeiro, Part I, Vol. 1, 422 pp., Vol. 2, 906 pp., Part II, Vol. 1, 622 pp., Vol. 2, 265 pp.
- Dos Passos, C. F. 1964. A synonymic list of the Nearctic Rhopalocera. Mem. Lepid. Soc., No. 1. 145 pp.
- DUGDALE, J. S. 1974. Female genital configuration in the classification of Lepidoptera. N. Zealand J. Zool. 1:127–146.
- EHRLICH, P. R. & P. H. RAVEN. 1965. Butterflies and plants: a study in coevolution. Evolution 18:586–608.

- ELIOT, J N 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bull. Brit. Mus. (Nat. Hist.) Entomol. 28:371–505.
- FIELD, W. D. 1941. Notes on Erora laeta (Edwards) and Erora quaderna (Hewitson) (Lepidoptera, Lycaenidae). Ann. Entomol. Soc. Amer. 34:303–316.
- FONSECA, J. P. 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. (S. Paulo) 5:263–189.
- GUAGLIUMI, P. 1965. Contributo all conoscenza dell'entomofuana nociva del Venezuela (coninuazione e fine). Riv. Agricol. Subtrop. Trop. 59:447–472.
- . 1967. Insetti e arachnidi delle piante comuni del Venezuela segnalati nel periodo 1938–1963. Relaz. Monogr. Agraria Subtrop. Trop. (N.S.) 86:391 pp.
- HARRIS, W. V. 1927 On a lycaenid butterfly attacking pineapples in Trinidad, B.W.I. Bull. Entomol. Res. 18:183–188.
- Hemming, F. 1967 The generic names of the butterflies and their type-species (Lepidoptera: Rhopalocera). Bul. Brit. Mus. (Nat. Hist.) Entomol., suppl. 9. 509 pp.
- HONEY, M. R. & M. J. SCOBLE. 2001. Linanaeus's butterflies (Lepidoptera: Papilionoidea and Hesperioidea). Zool. J. Linn. Soc. 132:277–399.
- HÜBNER, J. 1818. Zuträge zur Sammlung Exotischer Schmettlinge [sic], bestehend in Bekundigung einzelner Fliegmuster neuer oder rarer nichteuropäischer Gattungen. Jacob Hübner, Augsburg 1:1–49.
- . 1819. Verzeichniss bekannter Schmettlinge [sic|. Jacob Hübner, Augsburg. 2–8:17–128.
- International Commission on Zoological Nomenclature. 1959. Opinion 541. Suppression under the plenary powers of the generic names *Chrysophanus* Hübner, 1818, and *Bithys* Hübner, 1818 (Class Insecta, Order Lepidoptera) (Opinion supplementary to Opinion 165). Opin. Internat. Comm. Zool. Nomen. 20:87–101.
- JOHNSON, K., R. C. EISELE & B. N. MACPHERSON. 1990. The "hair-streak butterflies" (Lycaenidae, Theclinae) of northwestern Argentina. II. Strymon, sensu stricto. Bull. Allyn Mus. 130:1–77.
- JOHNSON, K. & K. R. KROENLEIN. 1993. Three remarkable new species of Strymon Hübner from Brazil and Ecuador (Lepidoptera, Lycaenidae, Theclinae). Rep. Mus. Nat. Hist., Univ. Wisc. (Stevens Point). 35:1–8.
- JOHNSON, K., L. D. MILLER & J. V. HERRERA. 1992. Eiseliana and Heoda, high Andean and austral genera of neotropical Eumaeini (Lepidoptera: Lycaenidae). Acta Entomol. Chilena 17:107–146.
- JOHNSON, K. & J. A. SALAZAR. 1993. New species, statuses and combinations in northern South American Strynnon (Lycaenidae, Theclinae). Rep. Mus. Nat. Hist., Univ. Wisc. (Stevens Point). 26:1–13.
- KLOTS, A. B. 1951 A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin, Boston, 349 pp.
- . 1970. Lepidoptera, pp. Ĭ15–130. *In* S. L. Tuxen (ed.), Taxonomist's glossary of genitalia in insects. Munksgaard, Copenhagen.
- Lamas, G., R. G. Robbins & W. D. Field. 1995. Bibliography of butterflies. An annotated bibliography of the neotropical butterflies and skippers (Lepidoptera: Papilionoidea and Hesperioidea). Atlas Neotr. Lepid. 124, 463 pp.

- MA, W. C. & L. M. SCHOONHOVEN. 1973. Tarsal contact chemosensory hairs of the large white butterfly *Pieris brassicae* and their possible role in oviposition behaviour. Entomol. Exp. & Appl. 16:343–357.
- McDunnough, J. H. 1938. Check list of the Lepidoptera of Canada and the United States of America Part 1. Macrolepidoptera. Mem. 5th Calif. Acad. Sci. 1:3–272 (1–3 [corrigenda]).
- OPLER, P. & V. MALIKUL. 1992. A field guide to eastern butterflies. Houghton Mifflin, Boston. 396 pp.
- OPLER, P. & A. B. WRIGHT. 1999. A field guide to western butterflies. Houghton Mifflin, Boston. 540 pp.
- OTERO, L. S. & L. C. MARIGO. 1990. Butterflies: beauty and behavior of Brazilian species. Marigo Comunicação Visual, Rio de Janeiro. 128 pp.
- POWELL, J. 1968. A study of area occupation and mating behavior in *Incisalia iroides* (Lepidoptera: Lycaenidae). J. N. Y. Entomol. Soc. 76:47–57.
- RILEY, N. D. 1922. Notes on the generic names of Indian Theclinae and Amblypodiinae (Lep. Rhop.). J. Bombay Natur. Hist. Soc. 28:465–473.
- ROBBINS, R. K. 1978. Behavioral ecology and evolution of hairstreak butterflies (Lepidoptera: Lycaenidae). Ph.D. Dissertation, Tufts University. 146 pp.
- ——. 1980. The lycaenid "false head" hypothesis: historical review and quantitative analysis. J. Lepid. Soc. 34:194–208.
- ——. 1987. Evolution and identification of the New World hairstreak butterflies (Lycaenidae: Eumaeini): Eliot's *Trichonis* Section and *Trichonis* Hewitson. J. Lepid. Soc. 40:138–157.
- ——. 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). Smith. Contr. Zool. #498. 64 pp.
- 2000. The New World Hairstreak Genus Arawacus Kaye (Lepidoptera: Lycaenidae: Theclinae: Eumaeini). Proc. Wash. Entomol. Soc. 102:162–169.
- In Press. Eumaeini. In G. Lamas (ed.), Checklist: Part 4A. Papilionoidea—Hesperioidea. In J. B. Heppner (ed.), Atlas of Neotropical Lepidoptera. Scientific Publishers, Gainesville.
- ROBBINS, R. K. & A. AIELLO. 1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. J. Lepid. Soc. 36:65–75.
- ROBBINS, R. K. & S. S. NICOLAY. 1999. Taxonomy and nomenclature of *Strymon istapa* and S. *columella* (Lycaenidae: Theclinae). J. Lepid. Soc. 52:318–327.
- SCHWARTZ, A. & J. Y. MILLER. 1985. A new species of hairstreak (Lycaenidae) from Hispaniola. Bull. Allyn Mus. 99:1–6.
- SCUDDER, S. H. 1872. A systematic revision of some of the American butterflies, with brief notes on those known to occur in Essex County, Massachusetts. Report, Peabody Acad. Sci. 4:24–83.
- Tietz, H. M. 1972. An index to the described life histories, early states and host of the Macrolepidoptera of the continental United States and Canada. Vol. 1. Allyn Museum of Entomology, Sarasota. 536 pp.
- WILLIS, J. C. 1973. A dictionary of the flowering plants and ferns. 8th ed. revised by H. K. Airy Shaw. University Press, Cambridge, 1945 pp.
- bridge. 1245 pp.
 ZIECLER, J. B. 1960. Preliminary contribution to a redefinition of the genera of North American hairstreaks (Lycaenidae) north of Mexico. J. Lepid. Soc. 14:19–23.
- ZIKÁN, J F. 1956. Beiträg zur Biologie von 12 Theclinen-arten. Duscnia 7:139–148.

VOLUME 55, NUMBER 3 97

APPENDIX 1. Species groups, their characters, and remarks. Character states in **bold** are especially useful in delimiting that species group. Species synonymies follow Robbins (in press). The subspecies concept was not used in Robbins (in press), so we have designated geographically variable species as Synonyms and Subspecies.

STRYMON MELINUS GROUP. Characters: Male lacking a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW (except S. tyleri), penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: Some members, such as S. melinus, S. tyleri, and S. rufofusca, can be exceedingly common where they occur.

- 1. Strymon melinus (Hübner, 1813)
 - SYNONYMS AND SUBSPECIES: Thecla hyperici (Boisduval & Leconte, 1835), Thecla humuli (Harris, 1841), Thecla pudica (H. Edwards, 1877), Strymon atrofasciata McDunnough, 1921, Strymon setonia McDunnough, 1927, Strymon meinersi Gunder, 1927, Thecla clarionensis (Heid, 1933), Strymon youngi Field, 1936, Strymon franki Field, 1938, Strymon caldasensis Salazar, Vélez & K. Johnson, 1997
- 2. Strymon avalona (W.G. Wright, 1906)
- 3. Strymon tyleri (Dyar, 1913)
- 4. Strymon sabinus (C. Felder & R. Felder, 1865) SYNONYM: Thecla promissa (Möschler, 1883)
- Strymon rufofusca (Hewitson, 1877)
 SYNONYMS AND SUBSPECIES: Thecla (Uranotes) valentina (Berg, 1896), Thecla lucaris (A.G. Weeks, 1901), Thecla grisea (Dufrane, 1939), Thecla nigriplaga (Dufrane, 1939), Strymon guanensis Le Crom & K. Johnson, 1997
- 6. Strymon cyanofusca K. Johnson, Eisele & MacPherson, 1990

STRYMON ALBATA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW (except S. albata), penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The only consistent difference with the previous group is that the males have a scent patch.

7. Strymon albata (C. Felder & R. Felder, 1865) SYNONYM: Thecla sedecia (Hewitson, 1874)

- 8. Strymon alea (Godman & Salvin, 1887) SYNONYM: Callicista laceyi (Barnes & McDunnough, 1910)
- 9. Strymon bebrycia (Hewitson, 1868) SYNONYMS: Thecla chonida (Hewitson, 1874), Strymon buchholzi H.A. Freeman, 1950

STRYMON YOJOA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW (except S. ohausi), no basal patch of white scales on the ventral surface of the HW (except S. yojoa), penis tip downturned with a single slender cornutus that is barely sclerotized, ductus bursae with a twist, but lacking a sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: Johnson et al. (1992) noted that Thecla tegea Hewitson does not belong to Strymon, but its male genitalia have anterior pointing teeth on the valvae, and its male and female genitalia are exceedingly similar to those of S. yojoa.

- Strymon yojoa (Reakirt, 1867)
 SYNONYMS AND SUBSPECIES: Thecla daraba (Hewitson, 1867), Thecla beroea (Hewitson, 1868)
- 11. Strymon tegaea (Hewitson, 1868) SYNONYM: Thecla seitzi (Spitz, 1931)
- 12. Strymon ohausi (Spitz, 1933)

STRYMON MULUCHA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, with basal patch of white scales on the ventral surface of the HW, penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop (except for some individuals of *S. cestri*), ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: This species group is probably paraphyletic with respect to the previous group.

- 13. Strymon mulucha (Hewitson, 1867)
 - SYNONYMS: Tmolus invisus (Butler & H. Druce, 1872), Strymon necjebus Le Crom & K. Johnson, 1997, Strymon necjabus Le Crom & K. Johnson (missp.), 1997, Strymon novasignum Austin & K. Johnson, 1997, Strymon implexus Austin & K. Johnson, 1997, Strymon implexus Austin & K. Johnson, 1997, Strymon inmirum Austin & K. Johnson, 1997, Strymon incanus Austin & K. Johnson, 1997
- 14. Strymon cestri (Reakirt, 1867)
 - SYNONYMS AND SUBSPECIES: Thecla cydia (Hewitson, 1874), Thecla crossoea (Hewitson, 1874), Strymon chamiensis Salazar, Vélez & K.

- Johnson, 1997, Strymon germana Austin & K. Johnson, 1997
- 15. Strymon davara (Hewitson, 1868) SYNONYMS: Thecla joannisi (Dufrane, 1939), Thecla pallida (Dufrane, 1939)
- 16. Strymon crambusa (Hewitson, 1874)
- 17. Strymon astiocha (Prittwitz, 1865)

SYNONYMS: Thecla faunalia (Hewitson, 1868), Thecla deborrei (Capronnier, 1874), Strymon halos Austin & K. Johnson, 1997, Strymon conspergus Austin & K. Johnson, 1997

STRYMON MARTIALIS GROUP. Characters: Male with or without a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the, penis tip down-turned with a single "wide" cornutus, ductus bursae with sclerotized loop complex, especially in S. martalis (Fig. 23), ductus seminalis arises from the posterior end of the corpus bursae which is sclerotized dorsally, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: A sister species relationship between the two included species is a new hypothesis, but one that appears to be reasonably strongly supported by the shape of the cornutus and by the sclerotized patch on the corpus bursae. This species group may be more closely related to the S. *melinus* species group than its position here indicates.

- 18. Strymon martialis (Herrich-Schäffer, 1865)
- 19. Strymon christophei (W.P. Comstock & Huntington, 1943)

STRYMON ISTAPA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW (except for S. oribata), no basal patch of white scales on the ventral surface of the HW, penis tip down-turned with a single slender cornutus, ductus bursae with sclerotized loop simple except in S. acis, ductus seminalis arises either from the unsclerotized posterior end of the corpus bursae or from a point anterior of a sclerotized patch on the dorsal surface of the corpus bursae, female with 8th tergum furrowed (except in S. acis) and with imbedded presumed vestigial spiracles. Remarks: The inclusion of S. bazochii and S. acis in this group are new hypotheses. The latter species is included because it has imbedded presumed vestigial spiracles and basal spots on the ventral surface of the HW, which most of the species in this group share. Its inclusion is highly tentative because its female 8th abdominal tergum lacks furrows and the sclerotized loop of its ductus bursae is exceedingly complex, unlike any other Strymon species.

20. Strymon istapa (Reakirt, 1867)

- SYNONYMS AND SUBSPECIES: Lycaena modesta (Maynard, 1873), Callicista ocellifera (Grote, 1873), Thecla cybira (Hewitson, 1874), Thecla arecibo (W.P. Comstock & Huntington, 1943), Thecla clarionica (Vázquez, 1958), Thecla socorroica (Vázquez, 1958), Strymon clenchi Austin & J.F. Emmel, 1998
- 21. Strymon bazochii (Godart, 1824) SYNONYMS: Hyreus thius (Geyer, 1832), Thecla agra (Hewitson, 1868), hecla infrequens (A.G. Weeks, 1901), Strymon gundlachianus M. Bates, 1935, Strymon diagonalis Austin & K. Johnson,
- 22. Strymon acis (Drury, 1773) SYNONYMS AND SUBSPECIES: Papilio mars (Fabricius, 1776), Thecla gossei (W.P. Comstock & Huntington, 1943), Thecla bartrami (W.P. Comstock & Huntington, 1943), Thecla casasi (W.P. Comstock & Huntington, 1943), Thecla petioni (W.P. Comstock & Huntington, 1943), Strymon armouri Clench, 1943, Strymon leucosticha Clench, 1992
- 23. Strymon columella (Fabricius, 1793) SYNONYMS: Papilio dion (Schaller, 1788), Tmolus erytalus (Butler, 1870), Thecla antigua (W.P. Comstock & Huntington, 1943)
- 24. Strymon limenia (Hewitson, 1868)
- 25. Strymon toussainti (W.P. Comstock & Huntington, 1943)
 - SYNONYMS: Strymon andrewi K. Johnson & Matusik, 1988, Strymon rhaptos K. Johnson, Eisele & MacPherson, 1990, Strymon amonensis D.S. Smith, K. Johnson, J.Y. Miller & McKenzie, 1991
- 26. Strymon bubastus (Stoll, 1780) SYNONYMS AND SUBSPECIES: Papilio minereus (Fabricius, 1787), Thecla salona (Hewitson, 1868), Thecla sapota (Hewitson, 1877), Thecla peruensis (Dufrane, 1939), Thecla ponce (W.P. Comstock & Huntington, 1943), Strymon vividus Le Crom & K. Johnson, 1997
- Strymon eurytulus (Hübner, 1819)
 SYNONYMS AND SUBSPECIES: Thecla americensis (Blanchard, 1852), Thecla argona (Hewitson, 1874), Thecla rana (Schaus, 1902, Thecla tucumana (H.H. Druce, 1907), Thecla nigra (Lathy, 1926), Strymon peristictos K. Johnson, Eisele & MacPherson, 1990, Heoda nivea (K. Johnson, L.D. Miller & Herrera, 1992)
- 28. Strymon flavaria (Ureta, 1956) SYNONYM: Heoda erani (Benyamini & K. Johnson, 1996)
- 29. Strymon ollantaitamba (K. Johnson, L.D. Miller & Herrera, 1992)

Volume 55, Number 3 99

- Strymon colombiana (K. Johnson, L.D. Miller & Herrera, 1992)
 SYNONYM: Heoda lecromi (K. Johnson & Lugo, 1997)
- 31. Strymon bicolor (Philippi, 1859)
 - SYNONYMS AND SUBSPECIES: Thecla quadrimaculata (Hewitson, 1874), Thecla heodes (H. H. Druce, 1909), Thecla leptocosma (Hayward, 1949), Thecla tricolor (Ureta, 1949), Heoda atacama (K. Johnson & L.D. Miller, 1992), Eiseliana probabila (K. Johnson, L.D. Miller & Herrera, 1992), Heoda suprema (K. Johnson, L.D. Miller & Herrera, 1992), Heoda shapiroi (K. Johnson, L.D. Miller & Herrera, 1992)
- 32. Strymon wagenknechti (Ureta, 1947)
- 33. Strymon oribata (Weymer, 1890)

SYNONYMS AND SUBSPECIES: Thecla arenicola (Jörgensen, 1934), Thecla punona (Clench, 1944), Thecla rojasi (Ureta, 1956), Eiseliana koehleri (Toledo, 1978), Eiseliana patagoniensis (K. Johnson, L.D. Miller & Herrera, 1992)

STRYMON SYLEA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal markings on the ventral surface of the HW, penis tip up-turned with a single slender cornutus, ductus bursae straight without a loop or twist, ductus seminalis arises either from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The upturned penis tip and straight ductus bursae, which is like most Eumaeini other than Strymon, suggest that the single species in this group may be sister to the remainder of the genus.

34. Strymon sylea (Hewitson, 1867)

STRYMON SERAPIO GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW, penis tip down-turned with paired cornuti, ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: All larval foodplant records in this groups are Bromeliaceae, as noted.

35. Strymon serapio (Godman & Salvin, 1887)

SYNONYMS AND SUBSPECIES: Thecla lemnos (H.H. Druce, 1890), Thecla mesca (Dyar, 1914), Thecla inconspicua (Lathy, 1930), Strymon golbachi K. Johnson, Eisele & MacPherson, 1990, Strymon trunctogen K. Johnson & Salazar, 1993, Strymon altamiraensis K. Johnson & Kroenlein,

- 1993, Strymon henaoi Salazar, Vélez & K. Johnson, 1997, Strymon hurtadoi K. Johnson, 1997, Strymon rosari Torres & K. Johnson, 1997, Strymon originatus K. Johnson, Hernández & Cock, 1997
- 36. Strymon glorissima K. Johnson & Salazar, 1993 SYNONYM: Strymon campbelli K. Johnson & Salazar, 1993
- 37. Strymon gabatha (Hewitson, 1870) SYNONYMS: Thecla balius (Godman & Salvin, 1887), Strymon alexandra K. Johnson & Kroenlein, 1993, Strymon alicia Salazar, Vélez & K. Johnson, 1997
- 38. Strymon monopeteinus Schwartz & J.Y. Miller, 1985
- 39. Strymon veterator (H.H. Druce, 1907) SYNONYMS: Strymon lorrainea K. Johnson, Eisele & MacPherson, 1990, Strymon coronos K. Johnson, Eisele & MacPherson, 1990
- 40. Strymon oreala (Hewitson, 1868)
- 41. Strymon dindus (Fabricius, 1793)
- 42. Strymon ochraceus K. Johnson & Salazar, 1993 SYNONYM: Strymon baricharensis Le Crom & K. Johnson, 1997
- 43. Strymon lucena (Hewitson, 1868) SYNONYMS: Thecla cardus (Hewitson, 1874), Thecla canitus (H.H. Druce, 1907), Strymon specialus K. Johnson, Eisele & MacPherson, 1997
- 44. Strymon legota (Hewitson, 1877)
- 45. Strymon azuba (Hewitson, 1874) SYNONYMS: Strymon montevagus K. Johnson, Eisele & MacPherson, 1990, Strymon rojos K. Johnson & Kroenlein, 1993
- 46. Strymon eremica (Hayward, 1949) SYNONYMS AND SUBSPECIES: Strymon lariyojoa K. Johnson, Eisele & MacPherson, 1990, Strymon barbara K. Johnson, Eisele & MacPherson, 1990, Strymon nicolayi K. Johnson, Eisele & MacPherson, 1990
- 47. Strymon megarus (Godart, 1824)
 SYNONYMS AND SUBSPECIES: Tmolus basilides (Geyer, 1837), Thecla basalides (W.F. Kirby, 1871) (missp.), Thecla tigonia (Schaus, 1902), Strymon amphyporphyra K. Johnson, Eisele & MacPherson, 1990, Strymon rotundum Austin & K. Johnson, 1997, Strymon gallardi Faynel & K. Johnson, 2000

STRYMON ZIBA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW, penis tip up-turned with two large unpaired cornuti, ductus bursae slightly twisted without a sclerotized loop, ductus seminalis arises from the sclerotized posterior end of the corpus bursae, female with 8th ter-

gum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The single included species is widespread and common. It is the only *Strymon* lacking the clear-cut anterior pointing teeth on the valvae.

48. Strymon ziba (Hewitson, 1868)

SYNONYMS AND SUBSPECIES: Thecla thulia (Hewitson, 1868), Thecla diaguita (Hayward, 1949), Strymon baptistorum K. Johnson, Eisele & MacPherson, 1990, Strymon dondiego K. Johnson & Adams, 1997, Strymon profusorubrus Le Crom & K. Johnson, 1997, Strymon spinatus Austin & K. Johnson, 1997, Strymon latamaculus Austin & K. Johnson, 1997, Strymon pallidulus Austin & K. Johnson, 1997, Strymon tholus Austin & K. Johnson, 1997, Strymon tholus Austin & K. Johnson, 1997

APPENDIX 2. Alphabetical list of specific names that were originally described in *Strymon* and that have been transferred to other genera (Bridges 1988). For those names that are junior synonyms, we note its senior synonym.

- 1. Cyanophrys agricolor (Butler & Druce, 1872)
- 2. Satyrium aliparops (Michener & dos Passos, 1942), a junior synonym of Satyrium liparops (Leconte)
- 3. Satyrium borealis (Lafontaine, 1969), a junior synonym of Satyrium calanus (Hübner)
- 4. Satyrium caryaevorus (McDunnough, 1942)
- 5. Satyrium chlorophora (Watson & Comstock, 1920), a junior synonym of Satyrium saepium (Boisduval)
- 6. Lamprospilus coelicolor (Butler & Druce, 1872)
- 7. Satyrium coolinensis (Watson & Comstock, 1920), a junior synonym of Satyrium acadica (Edwards)
- 8. Satyrium desertorum (Grinnell, 1917), a junior synonym of Satyrium sylvinus (Boisduval)

- 9. Electrostrymon dowi (Clench, 1941), a junior synonym of Electrostrymon angelia (Hewitson)
- 10. Satyrium fletcheri (Michener & dos Passos, 1942), a junior synonym of Satyrium liparops (Leconte)
- 11. Satyrium godarti (Field, 1938), a junior synonym of Satyrium calanus (Hübner)
- 12. Calycopis gottschalki (Clark & Clark, 1938), a junior synonym of Calycopis cecrops (Fabricius)
- 13. Satyrium immaculosus (Comstock, 1913), a junior synonym of Satyrium titus (Fabricius)
- 14. Satyrium kingi (Klots & Clench, 1952)
- 15. Satyrium montanensis (Watson & Comstock, 1920), a junior synonym of Satyrium acadica (Edwards)
- 16. *Satyrium muskoka* (Watson & Comstock, 1920), a junior synonym of *Satyrium acadica* (Edwards)
- 17. Satyrium okanagana (McDunnough, 1944), a junior synonym of Satyrium saepium (Boisduval)
- 18. Cyanophrys pastor (Butler & Druce, 1872), a junior synonym of Cyanophrys longula (Hewitson)
- 19. Satyrium polingi (Barnes & Benjamin, 1926)
- 20. Satyrium provo (Watson & Comstock, 1920), a junior synonym of Satyrium saepium (Boisduval)
- 21. Satyrium swetti (Watson & Comstock, 1920), a junior synonym of Satyrium acadica (Edwards)
- 22. Satyrium violae (Stallings & Turner, 1947), a junior synonym of Satyrium favonius (Smith)
- 23. Satyrium watsoni (Barnes & Benjamin, 1926), a junior synonym of Satyrium titus (Fabricius)