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SPEYERIA HESPERIS AND *SPEYERIA ATLANTIS* ARE DISTINCT SPECIES

by
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Abstract. *S. hesperis* and *S. atlantis* are distinct species; past reports of "intergradation" between them actually represent polymorphism of silvering within *S. hesperis*. *S. atlantis* is always silvered, and has a darker (chocolate-brown to blackish-brown) unh disc; it occurs in eastern North America as *S. a. atlantis*, then ranges as *S. a. hollandi* over the boreal forest/aspen parklands from Man. to Alta., where it is widely sympatric with *S. hesperis helena*; *S. a. hollandi* also occurs in the Rocky Mts. in Alta.-B.C.-NE Wash.-N Ida., where it is sympatric with *S. hesperis beani* and *S. hesperis brico* (B.C., new subspecies). In the Black Hills, *S. atlantis pahasapa* (new subspecies) is sympatric with *S. hesperis lurana*. In S Wyo.-Colo.-N New Mex., *S. atlantis sorocko* (new subspecies) is sympatric with mostly-unsilvered *S. h. hesperis* and mostly-silvered *S. h. electa* (=*cornelia*=*nikias*). *S. hesperis* has a redder unh disc, and ranges from Manitoba and the Black Hills westward to Alaska and the Pacific and south to New Mex.-Calif.; a majority (11 of 19) of its subspecies are usually-silvered, but only the subspecies in the extreme N and NE and S parts of its range are always silvered, and all subspecies across the middle of its range are predominantly unsilvered; silvered/unsilvered intergradation occurs within *S. hesperis* throughout the middle of the range, including the northern Sangre de Cristo Mts. of Colo. where unsilvered *S. hesperis hesperis* intergrades completely with silvered *S. h. electa*. Except in the extreme northern and southern ends of its range, older larvae of *S. hesperis* are blacker than larvae of *S. atlantis*.

INTRODUCTION

Lepidopterists have long known that problems existed in the former concept of *Speyeria atlantis* as defined by dos Passos & Grey (1947), who aggregated numerous former "species" as subspecies of one species *atlantis* (Lionel Paul Grey did the biological work of comparing specimens, while Cyril F. dos Passos handled the nomenclature). For instance Moeck (1957) noted that *S. "atlantis" dennisi* and *S. atlantis hollandi* are very different and yet fly next to each other in Manitoba, and wrote "possibly there has been misdetermination of one or more valid species, now lumped in the complex." Based on this sympatry, Howe (1974) and Klassen et al. (1989) treated the eastern and western populations as two species that meet in Manitoba; then Kondla (1992) showed that the zone of sympatry of those two species extends west to Alberta. Meanwhile in the western mountains, Grey et al. (1963) found that in the Black Hills of South Dakota, two forms *S. atlantis lurana* and *S. a. atlantis* behave essentially as separate species, but they did not formally separate them. And Ferris (1983) stated that *S. a. hesperis* and *S. a. "electa"* behave as sibling species in central Colorado, and *S. a. nikias* and *S. a. "electa"* behave as sibling species in W Colo., but claimed that intergradation occurs in S Wyoming and N New Mex.; Ferris mapped those taxa, based mostly on records in Brown et al. (1957). Hammond (1991) stated that in SW Colo. south of the Gunnison River *S. a. atlantis* and *S. a. nikias* are widely sympatric with strong reproductive isolation. And Scott (1988) documented very conspicuous larval differences and differing habitat selection between *S. a. hesperis* and *S. a. "electa"* (the taxon we name *S. atlantis sorocko* below) in Colo. As long ago as 1926, Barnes and Benjamin (1926) observed that *beani* "may ultimately prove to be a distinct species" from *atlantis*. Thus, good evidence exists to suggest that two species--not one--might be involved, but other evidence (summarized by Scott 1988) suggested that--based mostly on variation of silvering--just one polymorphic species could occur in Colo.

METHODS

The present paper uses the "Paul Grey method" to try to make sense of this situation. Paul Grey used more than 50,000 adult *Speyeria*, collected in series from hundreds of localities, to slowly

move across the continent, from one drainage or mountain range to the next, slowly charting how these butterflies change from one color pattern into the next, thus letting the animals themselves show just what subspecies names belong to what species. In this careful manner he reduced about a hundred "species" names to just 13 in his pioneering paper (dos Passos & Grey 1947) (the number rose to 14 when *S. adiaste* was split from *S. egleis*, and we now increase it to 15). This method has proved to work over and over in numerous animals and plants, in every case in which it has been applied, though considerable work is necessary to assemble the large series required.

The name *electa* is somewhat confusing, because it has been used for several species, and the present paper proves that it belongs to a different taxon than it has been applied to in the past, so it is written in quotes below as "*electa*" when referring to the taxon it was formerly misapplied to, and is written not in parentheses as *electa* when referring to the taxon it correctly applies to.

RESULTS AND DISCUSSION

ADULTS. Newfoundland *canadensis* seems best treated as a synonym, because it differs from *atlantis* only in slightly smaller size. Ssp. *atlantis* varies little in eastern North America, although southern Appalachians populations may be a little paler.

The connection between eastern *S. atlantis atlantis* (Figs. 20-23) and *S. atlantis hollandi* (Figs. 16-19) is rather straightforward, since *hollandi* is very similar and easily treated as a synonym (both have paler grayish areas in the disc and have dark ups margins, wings are about the same size and shape, etc.). Various simple field guides and Klassen et al. (1989) state that *hollandi* is smaller and darker dorsally with more basal suffusion than ssp. *atlantis* (which extends westward into SE Man.); but the opposite is true (Table 1); *hollandi* actually seems to differ only by being slightly paler dorsally with slightly narrower black bars (differences seen by comparing the photos of *hollandi* in Hooper [1973] versus the photos of *atlantis* in Klassen et al. [1989]), and the unh disc is darker on *hollandi*. The unh disc of *hollandi* is dark-brown to blackish-brown (mostly dark-chocolate-brown, with little reddish cast), versus reddish-brown to dark-brown (usually chocolate-brown, thus with a slight reddish cast, the color of a Hershey's Chocolate Kiss) in *atlantis*, based on numerous specimens we have examined (~60 from eastern North America, ~50 from Man., and hundreds from Alta. and B.C.). In SE Man. (Sandilands), the ups also seems paler, so *S. a. hollandi* would seem to occupy all of Man. and extends westward to Alberta and B.C. with little change. However the disc of Sandilands adults is merely chocolate-brown like ssp. *atlantis*, whereas *hollandi* from Riding Mts. in SW Man. to Alta. have a blackish-brown disc, so *atlantis* evidently changes into *hollandi* in SE Man. Kondla has noticed a tendency for Man.-Ont. examples of *atlantis* and *hollandi* phenotypes collected at the same time and place to show different wing wear, suggesting the possibility that they are separate species; but their great similarity and the apparently intermediate Sandilands population suggests that they intergrade.

The other Manitoba taxon, *dennisi*, is very pale, with narrow black dorsal lines, and has a paler (red-brown) unh disc.

Much exploration by Klassen et al. (1989), Jim Troubridge, and others has proved that in the Duck Mtn.-Riding Mts. area of Manitoba, *dennisi* and *hollandi* occur within flight distance of each other yet do not interbreed: *dennisi* flies in drier more open areas (described by Klassen et al. [1989] as forest openings and clearings, dry meadows and scrubby areas near short- or tall- grass prairie), *hollandi* flies in wetter & woods habitat (described as openings in deciduous and coniferous forests, glades, moist meadows, woodland streams and uplands). Hooper (1973) wrote that the two interbreed at Meadow Lake Park Sask., lending hope to the one-species theory. However, N. Kondla recently examined those Meadow Lake Park specimens and found them to represent merely unusually-dark *Speyeria aphrodite manitoba*, thus this was a case of misidentification, not intergradation. Kondla (1992) found that sympatry without interbreeding continues west through most of Alberta (and beyond in NE B.C. as far as Fort Nelson), where *helena* (=*lais*)--the westward representative of *dennisi*--and *hollandi* are still sympatric yet do not interbreed. Over most of the aspen parkland/boreal forest in Canada, *S. hesperis dennisi*/*helena* actually resembles *S. aphrodite manitoba* more than *S. atlantis hollandi*.

(Taxonomic note: no description was needed for publication when Scudder proposed *Argynnis* (*Boloria*) *lais* 1875 in the synonymy of *Argynnis triclaris Hübner*, because standards were incredibly lax at that time (see 1905 Re'gles, Appendix A), so dos Passos & Grey (1955) were correct that *lais* Edwards 1884 is a homonym of *lais* Scudder, and therefore dos Passos & Grey validly replaced *lais* Edwards with *helena*.)

Ssp. *dennisi* extends into Sask., but becomes a little darker westward through Sask., as ssp. *helena*, which is also silvered and is identical to *dennisi* but has the ups black lines often a little wider and the unh disk often a little darker (their variation overlaps considerably so they can be treated as synonyms, though the palest individuals with very narrow black bars and nearly-tan disc are Man. prairie *dennisi*, the darkest individuals with fairly-wide black bars and brown disc are *helena*). Klassen et al. (1989) note that *dennisi* occurs in most of the range in Man. but intergrades with *helena* near the Man.-Sask. border; while Moeck (1957) found *dennisi* on the open prairies of Man., and *helena* in the Turtle Mts. of extreme south-central Man. and adjacent N.D.

It seems best to treat the name *dennisi* as a synonym of *helena*, for the following reasons: They are very similar and their light-to-dark variation overlaps greatly. Kondla suggests that the

variation in darkness/lightness is merely associated with the prairie/forest transition that occurs in an arc around the northern edge of the great plains, with prairie populations being paler in series, and forest populations being darker and redder in series, with individual variation ranging from dark to light extremes in most populations. Beulah Man. (the TL of *dennisi*) is only 35 km E of the Sask. border and thus is in the *dennisi\helena* "intergrade zone" stated by Klassen et al. (1989). And Gunder originally named *dennisi* as an aberration ("transition form"), and *dennisi* was elevated to ssp. rank by dos Passos & Grey (1947) without any statement of how normal specimens vary from other named ssp. At most, *dennisi* is a very weak ssp., so if the slightly-paler prairie populations are to receive any name, they should be called the prairie variety of *helena*.

Kondla (1992) summarized most of the differences between Alberta *helena* and *hollandi* (Table 2): *helena* occurs in poplar forest (drier), and is smaller, flies a bit earlier on average where sympatric, has a paler reddish-brown unh disc with large included tan areas, thinner black ups marks, weaker paler unf tornus spots in cell CuA_2 (the submarginal dash below the dark crescent is only pale-brown, and the oval postmedian spot is smaller), a wider pale unh submarginal band crossed only by narrow dark veins, the unh silver spots are a bit smaller and the marginal silver spots have paler caps, and the ups is paler with pale margins, whereas *hollandi* occurs in coniferous and mixed forest (wetter), and is larger, flies a bit later, has a blackish-brown unh disc with some grayish areas, wider black ups marks, blacker unf tornus spots in cell CuA_2 (the submarginal dash below the dark crescent is blackish, and the oval postmedian spot is larger), a narrower pale unh submarginal band crossed with wide brown edging to the veins, the unh silver spots are a bit larger and the marginal spots have broader darker caps, and the ups is darker with dark-brown margins.

Thus, *hollandi* is sympatric with *helena=dennisi* over a vast region of more than a million square km in Man.-Sask.-Alta.-B.C., where they are obviously separate species. In Alta., *hollandi* occurs throughout the province (as does *S. hesperis*), as far south as the Police Outpost Provincial Park area just N of Montana, and in pine forest in the Cypress Hills.

Klassen et al. (1989), Kondla (1992), and Bird et al. (1995) used the name "*Speyeria electa*" for *dennisi* and *helena*, following Howe (1975). Below we show that *electa* does belong to *S. hesperis*; however the name *electa* cannot be used for the **species** because it was named 14 years after *hesperis*.

In the mountains of Alberta, the unh disc becomes a little darker and the black ups bars become a little wider, as ssp. *beani*, but *beani* still has a reddish-brown unh disc like *helena* and most other traits are similar though often darker, so it is related to *helena* and not to *hollandi*. The unf tornus spots are paler and smaller in *beani* as in *helena* (the submarginal dash near tornus is brownish in these two, versus black in *hollandi*), which helps to identify *beani* even in NW B.C. (Cassiar Mts., Atlin) and Alaska (Gerstle River Wayside, mile 1393 Alaska Hwy.), where adults can be called a blacker-ups variety of *beani*, as they resemble *beani* (including in size) except the ups basal dusting is usually more blackish brown (darker and more contrasting with the orange outer wing color). Hooper (1973) noted *beani* also from Cypress Hills in SW Sask., and *beani* also occurs in the Cypress Hills in Alta. And just south of Alberta in the Sweetgrass Hills of Toole Co. Montana, adults are most like *beani*, but are a little larger.

In the northern part of SE B.C., Kondla has found that a silvered red/cinnamon-disc *S. hesperis brico* (named below, Figs. 24-25, closest to *beani* but with the disc and unh submarginal pale band darker reddish, the blackish ups base more extensive, and slightly larger) flies in mixed and coniferous forest, while the blackish-brown disc *S. a. hollandi* occurs in and near fens/marshes (near Kamloops, Robson Valley, etc.), sometimes in mountainside coniferous forest; these two fly together at several localities in pine forest near fens and sometimes in mountainside coniferous forest (Table 3). Hammond (1991) stated that *S. atlantis atlantis* occurs in SE B.C. and N Ida., but this statement could have referred to some other taxon such as *hutchinsi* since Hammond lumped *hollandi* into *S. a. atlantis* on p. 62 (but not on p. 70); however Hammond (pers. comm. 1995) states that these northwest populations do resemble eastern *atlantis*, and occur west of the continental divide from Bonner and Boundary Cos. in extreme N Idaho and adjacent Pend Oreille Co. in extreme NE Wash., northward through south-central B.C. as far north as Lac La Hache. But Kondla has examined the same specimens Hammond examined in the collection of Jon Shepard, plus many more from SE B.C. etc., and found that NE Wash. specimens are ssp. *hollandi*, not ssp. *atlantis*. Ssp. *hollandi* occurs in Pend Oreille, Stevens, and Okanogan Cos. in the Okanogan Highlands physiographic area of NE Wash., and extends north throughout SE B.C. to Lac La Hache and out onto the Fraser Plateau and onward to central B.C., and probably further north where exploration has been limited. And *hollandi* will probably be found east of Glacier Nat. Park in Montana, since Kondla has found it about a mile north of Montana at the east base of the Rockies. Kondla found that B.C. *hollandi* resemble Alta. *hollandi* except the upperside is a little darker orange with blacker basal dusting, so we will call them *S. a. hollandi*, as these differences do not seem to be great enough to name a new ssp.; B.C. and Wash. adults are not *S. a. atlantis*. Jon Shepard and Jonathan Pelham have also found that *S. atlantis* occurs in colder wetter areas such as spruce bogs in B.C.-Wash., where *S. hesperis* is widely distributed in drier upland forests.

Proceeding southward, in the Highwood Mts. of Choteau Co. in north-central Montana, adults resemble *helena* a little more than *beani*.

The mostly-silvered western Montana *hutchinsi* is best considered a synonym of *beani*, because it seems to represent intergradation of *beani* into *tetonia*, as about half the adults are unsilvered in western Montana. Its TL is Jefferson Co. in southwestern Montana, many unsilvered adults occur

in nearby Granite Co., and Howe (1975) illustrates unsilvered and silvered adults from nearby Beaverhead Co. In extreme SE British Columbia (around Cranbrook) 5-10% of the ssp. *beani* population is unsilvered, and the frequency increases southeastward, so around Missoula in western Montana about half the adults are unsilvered, and at the other end of the cline around Yellowstone Nat. Park in Wyoming most adults are unsilvered. Paul Hammond wrote to Scott: "*hutchinsi* does not constitute a valid biological subspecies in my opinion because it applies to the clinal intergrade zone between *tetonia* and *beani* in Montana, and is not a true evolutionary entity." (The name *hutchinsi* is a "transitional form" name of Jean Gunder, which was elevated to subspecies status by dos Passos & Grey without explanation, but is nevertheless available for use as a ssp./species name) In the easternmost mts. of central Montana (Little Belt Mts.) and south-central Montana (Crazy Mts.), most adults are silvered and pale like *beani* and also have a reddish-brown unh disc, but a third are unsilvered and somewhat resemble *hesperis*. Hammond (1991) stated that populations in the Rocky Mts. of Montana are joined together in a massive three-way hybrid swarm between the northern *beani*, the central [actually SW] *tetonia*, and *helena* [*lais*] of the Canadian prairies. Thus in Mont. intergradation seems to occur between the silvered ssp. *beani* and *helena* to the north, and the unsilvered ssp. to the south, which include *lurana* (which is very similar to *hesperis*) in the Black Hills, and ssp. *tetonia* from NW Wyo. and adjacent Idaho and SW Mont. to the Wasatch Mts. of Utah.

In the Bighorn Mts. of Wyo., the *S. hesperis* population seems to be an intergrade of silvered *beani* to the northwest and *lurana* to the east (Bighorn Mts. adults are mostly unsilvered, the pale submarginal unh band wider than *lurana*, the unh disc redder than *lurana* with more pale tan areas, the black ups bars fairly narrow). Moeck (1957) noted transitions between *helena* (as *lais*) and *hesperis*, including a female intermediate between *beani* and *hesperis* as far north in Montana as Glacier Nat. Park, and adults near *hutchinsi* among Yellowstone region *tetonia*.

In the Paul Grey collection in AMNH are specimens of *S. atlantis* with cryptic/nonspecific data from "Bighorn Mts., Wyo.", which Hammond (pers. comm.) states are similar to Idaho-B.C. *S. atlantis*. However, Scott failed to find true *S. atlantis* in the Bighorn Mts. in 1995 (he did find *S. hesperis*), and Hammond (pers. comm.) failed to find true *S. atlantis* there in several years of searching, and no other *S. atlantis* have been found there by other collectors, so these "Bighorn Mts." specimens must be considered to be mislabeled.

In the Black Hills of South Dakota-Wyoming (Table 4), the pale unsilvered *S. hesperis lurana* has a red-brown unh disc and is similar to *hesperis*, except the ups is a little lighter (evidently because of its proximity to *helena* to the north) with the wing bases a little lighter and the ups black bars narrow, the unh disc is often lighter red-brown, and the unh submarginal band is never suffused as it is sometimes in *hesperis* (and often in *tetonia*); *lurana* mostly flies in aspeny woods. A dark silvered insect there (which we name *S. atlantis pahasapa* below, Figs. 1-9) resembles *hollandi* but has the ups wing margins a little less dark, the upf black bars a little narrower, the unh disc blackish-brown and rather uniform with few paler areas and these not grayish (*atlantis*/*hollandi* have some grayish areas in their paler disc) and flies in wetter areas (including open moist meadows) on granite that does not drain away soil moisture (Grey et al. 1963). These two creatures in the Black Hills look <u>enormously</u> different, often fly together, and few intermediates in coloring or silvering have been found. Essentially everyone who sees them believes they are very distinct species. Grey, Moeck, & Evans (1963) explored this situation, and even did a little rearing (though our research proves that they mistakenly switched the descriptions of larvae of the two taxa, see below). They found a few "intermediates", including red-disc adults with silver spots that were commoner in areas with both taxa, and were rare in the purer *lurana* colonies. But S. Spomer recently reared the offspring of a female apparently intermediate between *lurana* and *pahasapa*, and got only *lurana* offspring, and another partially-silvered *lurana* female produced only *lurana* offspring, which indicates that most or all "intermediates" are just partly-silvered individual variants within a somewhat-variable *lurana* population. Grey et al (1963) attempted to mate reared adults, and managed to get a male *lurana* to mate with a female *lurana*, but could not get a *lurana* male and a *pahasapa* female to mate as the female crawled away and the male never curled his abdomen toward her; they managed to hand-pair a fully-silvered *lurana* male with a *pahasapa* female which produced 80 infertile eggs.

From S-C Wyo. (the Laramie and Medicine Bow Ranges) south along the Front Range of Colorado to the Wet Mts. (and in diluted form in the Sangre de Cristo Mts. of S-C Colo.), ssp. *hesperis* is unsilvered with a red-brown unh disc, and is very similar to Black Hills *lurana* but is a little darker with wider black bars. The other form in the same area, the silvered insect that has been called "*electa*" (which we name *S. atlantis sorocko* below, Figs. 10-15), differs from Black Hills *pahasapa* by having the unh disc chocolate-brown (resembling a Hershey's Chocolate Kiss, a popular candy that has a slight reddish tint to its dark-brown) but not as blackish-brown as in the Black Hills *pahasapa*, the black ups bars are wider, and the male forewing is more convex; "*electa*" is still somewhat similar to *S. atlantis atlantis* from eastern N. Amer. Thus the similarity of the Colorado and Black Hills taxa suggests that "*electa*" is a ssp. of *S. atlantis*; or the differences between *pahasapa* and "*electa*" could also be interpreted to mean that "*electa*" is not *S. atlantis*.

The "*electa*" (*sorocko*) and *hesperis* are sympatric at many localities on the eastern slope of the continental divide in Colo. (where *hesperis* is common in the foothills and Canadian Zone then decreases in abundance higher up, while *sorocko* is scarce in the foothills and predominates in the upper Canadian Zone). The *sorocko* and *hesperis* are about equally common at one Canadian Zone

site in Clear Creek Co., where they show clear differences in habitat selection, as well as differences in larval color (see below, and Figs. 40-41), and where there are few wing-pattern intermediates. A mark-recapture study at this site proved that *sorocko* adults move completely about the habitat including through coniferous woods and sunny open meadows, whereas *hesperis* adults prefer open often-aspeny woods with violets (Scott 1988); both taxa oviposit near violets there, mostly in open woods (Scott 1992). On the eastern slope in southern Colorado, "*electa*" (*sorocko*) occurs in completely-silvered populations (*S. hesperis* absent) in three open wet-meadow enclaves among forest at middle altitudes (near Coaldale in the Arkansas Canyon in Fremont Co., near Westcliffe in the Wet Mtn. Valley in Custer Co., near Stonewall in the upper Purgatoire River Valley in Las Animas Co., Scott & Scott 1980), whereas in the adjacent forested hills both silvered *sorocko* and unsilvered *hesperis* occur. The sympatry and differences in habitat and larval color and adult pattern all suggest they are separate species.

These habitat differences are consistent over much of North America. From Canada to the Black Hills to the Colorado east slope, *S. hesperis* ssp. prefer drier areas such as poplar (mostly aspen) woods, whereas *S. atlantis* ssp. prefer partly-open coniferous forest and open moist meadows within forest. In the rest of the west, *S. hesperis* ssp. generally like aspeny glades as well. In western Colo.-Utah, *S. hesperis* "*nikias*" occupies aspeny places from middle to lower altitudes, so is more widespread than *S. atlantis sorocko*.

Scott (1988) tried to determine whether Colorado "*electa*" (*sorocko*) and *hesperis* were interbreeding by rearing eggs from silvered "*electa*" and unsilvered *hesperis* females, by choosing females of a form rare at each locality in order to maximize the possibility of interbreeding (a female rare in the population would most likely have mated with the common male form if reproductive isolation were absent); but he found that offspring generally resembled their mothers, except that mothers that were nearly half-silvered produced almost-unsilvered *hesperis*. Scott's half-silvered and partly-silvered Colorado females produced only *hesperis* offspring, just as in the Black Hills S. Spomer reared only unsilvered *lurana* from a female apparently intermediate between silvered *pahasapa* and unsilvered *lurana*, and from a part-silvered *lurana*. All these rearings are **fully explained**, even if there is complete reproductive isolation, if we consider that *S. atlantis* is always silvered, whereas *S. hesperis* ssp. in various parts of North America are silvered or unsilvered about equally often, so that some silvering can be expected to remain in the gene pools of mostly-unsilvered ssp. of *S. hesperis* (including *hesperis*, *tetonia*, *lurana*, *wasatchia*, *dodgei*, *viola*, *irene*, etc.) due to past interbreeding with adjacent silvered ssp. (such as *hutchinsi*, *ratonensis*, *nikias*, *chitone*, etc.) (and vice versa, unsilvered males sometimes occur even in normally-silvered *helena* 4 mi. NE Kananaskis Alta.). Thus the partially-silvered "intermediates" found in nature (in the Black Hills and Colo., and elsewhere in Mont., Wyo., New Mex., Ariz., Utah, Ida., Ore., Calif., etc.) evidently always seem to be just individual variants of *S. hesperis*, and are not "intergrades" (thus, Scott's [1988] half-silvered mothers from O'Fallon park and Critchell and his mostly-unsilvered mothers from other sites were *S. hesperis hesperis* and produced *hesperis* offspring, while his fully-silvered mothers from Tinytown and Corwina Park were *S. atlantis* and produced only silvered *atlantis* offspring). This conclusion is also hinted by the fact that most individuals of ssp. *hesperis* have at least a small number of silvered scales at unh base. (Scott [1988] suggested that the silver color in *Speyeria* is due to structural interference of light inside the scale, which can occur only if the scale is transparent because of the lack of the cream pigment that blocks the interference in unsilvered scales; thus the degree of silvering is due to the amount of cream pigment rather than a difference of structure, so simple variation in the amount of pigment would result in variation in silvering, which is no doubt why there is so much variation in silvering in most *Speyeria* species.)

And some anecdotal evidence also suggests that *S. atlantis* "*electa*" (*sorocko*) and *hesperis* are reproductively isolated: at one locality (Scott 1988) six *hesperis* males and only one male and one female *sorocko* were found, but both *sorocko* were in copula; and at another site *hesperis* was common and *sorocko* scarce, yet two *sorocko* females found were dissected (after failing to oviposit) and found to be virgins despite the abundant *hesperis* males, suggesting that the *sorocko* virgins had rejected the common *hesperis* males and were waiting for *sorocko* males.

Scott (1988) found that courtship movements, and the smell (to humans) of male pheromones, are the same in *sorocko* and *hesperis*. However, the ability of humans and insects to detect odors differs so much that the pheromones could still differ as smelled by the insects themselves.

Thus the *S. atlantis* vs. *S. hesperis* theory explains the differences between *sorocko* and *hesperis* found by Scott (1988) including big differences in larval color, nicely explains their sympatry with little apparent interbreeding, and explains the close similarity of the *hesperis*/*sorocko* situation in Colorado, to the *lurana*/*pahasapa* situation in the Black Hills (and to the *helena*/*hollandi* situation in Canada, although both the latter ssp. are silvered). Scott (1988) thought "*electa*" and *hesperis* are probably one species, but his reasoning was based mostly on silvering rather than unh disc color and other traits, and our research has proven that silvering is polymorphic in most *S. hesperis* ssp.

Ssp. *tetonia*/*wasatchia* is similar to *hesperis* but the ups is less ruddy and the submarginal unh band is more suffused with red-brown. More specifically, the northern (W Wyo. and SW Montana) *tetonia* is like *hesperis* but the ups is not quite so reddish-orange, the unh disc is a bit more reddish, the unh submarginal area is more suffused with red-brown (often completely suffused), and it is usually unsilvered (completely unsilvered in the Oquirrh Mts. Utah population which is quite like usually-unsilvered Wyo. *tetonia*). The southern (Wasatch Mts. Utah) *wasatchia* in addition has the

ups more yellowish (like ssp. *chitone*), the unh submarginal band somewhat narrowed with red-brown, and has more rectangular unsilvered unh spots tending toward those of *dodgei*/*irene*. Hammond (pers. comm.) prefers to consider *wasatchia* a synonym of *chitone*, because it is generally very pale with a clear yellow submarginal unh band and is often silvered as far north as Weber Co. Utah (Moeck [1957] noted the presence of *chitone*-like adults even near Salt Lake City), so Weber Co. adults are mostly like *chitone* from Iron and Washington Cos. Utah, while significant intergradation with *tetonia* does not take place until Cache Co. near Logan. However, the original description of *wasatchia* was based on 46 specimens from Utah Co. and stated that both sexes are typically unsilvered like *tetonia*, and stated that the unh verges toward *tetonia* and has a somewhat-narrowed submarginal band. So either of the names *wasatchia* or *tetonia* could be used for Wasatch Mts. adults, as *wasatchia* is somewhat intermediate between *chitone* and *tetonia*. The best way to settle this problem nomenclaturally, is this: we hereby make a first-reviser declaration, that the name *tetonia*--despite being printed after *wasatchia* in the original description in the same paper (dos Passos & Grey 1945; the ICZN code contains no rule regarding page priority), shall hereby take priority over *wasatchia*, so that anyone who treats the two names as synonymous (as did Scott [1986], who cited the name *wasatchia* but not the name *tetonia*) will have to use the name *tetonia*, not *wasatchia*; this action will guarantee that the name *tetonia* will be used by everyone for W Wyo. populations, leaving only the name of the intermediate northern Wasatch Mts. populations to be argued about. (Of course both names will continue to be used by anyone who feels that they are not synonymous, but anyone who believes that they are synonymous must use the name *tetonia* for the combination.)

The unsilvered ssp. extend westward to the Pacific coast as *viola* (Idaho, doubtfully distinct from *dodgei*, slightly less reddish than *dodgei* on ups and with slightly paler unh disc), *elko* (a slightly paler *dodgei* from N Nevada), *dodgei* (Oregon and NW Calif. including the Coast Range), and *irene* (Sierra Nevada, postmedian black upf bars narrower). Moeck (1957) notes the presence of *viola*-like adults among the *tetonia* from Targhee Nat. Forest in eastern Idaho, bridging the gap between *hesperis* and *irene*. The four ssp. *viola*, *dodgei*, *elko*, and *irene* are so similar (unh disc red-brown with pale tan streaks, unsilvered spots large and more rectangular, a narrow pale yellowish unh submarginal band) that one name *irene* might suffice; this group of ssp. is rather distinct from other ssp., although even in Ore.-Calif., adults occur that are a third- or half-silvered.

Paul Hammond (pers. comm.) suggests that *Speyeria adiaste* of S California is a geographic representative of *S. atlantis*/*hesperis*. But we fail to see any definite characters to support the connection, and Sims et al. (1979) and Brittnacher et al. (1978) showed that *adiaste* differs electrophoretically from all species of the *callippe*-group including *atlantis*/*hesperis*, and is most similar to *S. hydaspe*. If *adiaste* is a ssp. of any other *Speyeria*, it must be the allopatric *hydaspe*, which shows a slight similarity on the underside, and a strong similarity in the larva (see below).

The silvered ssp. *greyi* (Ruby Mts. in NE Nev.) is rather isolated, with a pale unh disc with fairly large silver spots, though some adults approach *wasatchia* of Utah. An unnamed population in Cassia Co. of south-central Idaho, mostly silvered with a purplish-brown disc, is an intergrade between *tetonia* of eastern Idaho and *greyi*. (A population near *wasatchia* also occurs in Cassia Co. Idaho, at S Fork Sublett Creek in Beaver Dam Can. [coll. Allen Dale].)

The strangest feature of *S. hesperis* is that all the northern ssp. are silvered (*helena-beani-brico*), then a broad blotch of mostly-unsilvered ssp. completely fills the middle part of the range (*lurana-hesperis-tetonia-wasatchia-viola-elko-dodgei-irene*), then southward all ssp. are silvered again (*greyi*, *chitone* [rarely unsilvered]-*schellbachi* [rarely unsilvered]-*nausicaa-dorothea-nikias* [rarely unsilvered]-*ratonensis*). Perhaps the explanation of this peculiar phenomenon is that after one of the Ice Ages the unsilvered ssp. spread out of California or the Great Basin eastward through Idaho-Utah to the south-central Wyoming lowlands, then spread eastward to the Black Hills and south to the Colorado Front Range.

In southern Utah, *chitone* becomes silvered again, though some are unsilvered; the unh disc is reddish-brown like *wasatchia*, but the pale unh submarginal band is not suffused with red-brown, and two traits (fw more pointed, ups wing bases a little darker) trend toward *schellbachi* on the Kaibab Plateau of N Ariz. Ssp. *schellbachi* is usually silvered, quite melanic on ups wing bases, with thick ups black bars and quite pointed fw, and is somewhat intermediate between *chitone* and *nausicaa*.

Ssp. *nausicaa* of the Mogollon Rim from central Arizona to New Mexico, retains the pointed fw but becomes larger and more reddish-brown on ups, with the black marks narrower as usual (but wide on some), while the unh is always silvered, the unh marginal silver spots are lenticular or triangular, and the unh disc is red-brown with included pale-tan or gray areas, the pale unh submarginal band somewhat suffused with tan. Ssp. *nausicaa* is so distinctive that if we did not use the Paul Grey method to trace its apparent intergradation with adjacent ssp., we would have difficulty in assigning it to either *S. hesperis* or *S. atlantis*. The pale-tan or grayish areas in the disc of *nausicaa* are even more extensive than those of *S. atlantis atlantis*/*hollandi*, however the geographically-nearest ssp. of *S. atlantis* (*pahasapa* and *sorocko*) lack these grayish areas in the disc, so this character may not be relevant. The always-silvered spots fit *S. atlantis*, but the nearest ssp. of *S. hesperis* (*chitone*, *schellbachi*, *electa=nikias*) have the spots usually-silvered, so this character does not help either. The *nausicaa* larva is even paler than *S. atlantis atlantis*, as the middorsal yellow-cream lines are enlarged and mostly fused into one stripe (like the 3rd-stage larva of *S. atlantis sorocko* fig. by Scott 1988)(Fig. 35). But various other traits place *nausicaa* into *S.*

hesperis. Most importantly, its red-brown disc matches *S. hesperis*, not *S. atlantis*. Its very-pointed forewing is most like the somewhat-pointed forewing of *S. hesperis electa=nikias* and *S. h. chitone* and especially like *S. h. schellbachi*, and is very unlike the rather rounded forewing margin of the southern Rockies *S. atlantis sorocko*. The large black postmedian oval spot in cell CuA_2 near unf tornus is like *S. hesperis electa=nikias*. And the larva of Abajo Mts. Utah *electa=nikias* often has the two middorsal yellowish lines fused as in *nausicaa*, demonstrating intergradation in this trait, as larvae of *electa* (especially northward) resemble larvae of *S. h. hesperis* (see below). The final arbiter, the Paul Grey method, seems to indicate that *nausicaa* belongs to *S. hesperis* based on two independent geographic transitions: the transition through Wyo.-Utah-Ariz. from *hesperis* to *tetonia* to *wasatchia* to *chitone* to *schellbachi* to *nausicaa*, plus the transition through N.M.-Colo. from *nausicaa* to *dorothea* to *electa=nikias* to *hesperis*.

Kilian Roever (pers. comm.) has collected very-dark disc adults at higher altitudes in the White Mts. of Arizona, which are presumably variant *S. h. nausicaa*. Paul Grey described them as "Appalachian phenotype" in some correspondence, suggesting that they might possibly be a remnant population of true *S. atlantis*; if they are *S. atlantis sorocko*, then of course *nausicaa* would have to be related to *S. hesperis*. But ssp. *nausicaa* is quite variable: the amount of reddish on ups varies considerably, the amount of brown ups suffusion varies somewhat and a few males have little suffusion, the black fw bars are usually rather wide but are sometimes narrow, the unh disc usually contains many tan patches but some specimens (esp. males) have the disc nearly entirely light-brown (and some males have the disc more uniform dark-reddish-brown with only a few paler patches), the unh submarginal pale area is usually narrow and suffused with a little brownish beyond the postmedian silver spots but a few adults have a wider little-suffused yellowish band, a few males have the fw margin straight instead of concave as usual, size varies a little, a few males have a violet sheen on the basal silver unh spots, etc. Dr. Frederick Rindge picked out the six darkest-disc specimens out of 454 *nausicaa* adults from the White Mts. in AMNH, and the darkest-disc male has a dark unh that resembles *S. zerene bremneri* (but its other characters clearly show that it is *nausicaa* and not mislabeled *bremneri*). One female *nausicaa* Scott has seen could pass for *electa*. However, in all this variation there is no indication of a discontinuity in the variation, thus all these variable specimens seem to belong to one taxon *nausicaa*, and not to several sympatric species.

Ssp. *dorothea* (in central New Mex. and the Chuska Mts. of Ariz.-New Mex.) seems to be an intergrade between *nausicaa* and northern New Mex. *electa=nikias*, as it resembles *nausicaa* somewhat and is almost as large with almost-as-pointed forewings and has a similar larva, but the unh disc is uniform reddish-brown with tan areas (lacking the grayish streaks of *nausicaa*), and the upf has wide black bars and a dark base. Ssp. *capitanensis* from Capitan Mts. of south-central N.M. is a smaller variety of *dorothea* with darker ups wing bases.

In the Rocky Mts. of north-central New Mex., adults are nearly always silvered, but most adults have a reddish-brown unh disc, and some (about 25%) have a chocolate-brown disc. These variants have been interpreted--as in Colorado--as mere polymorphic forms (*nikias* and "*electa*") of one species. But the simplest and evidently correct explanation is that the red-brown disc adults in N New Mex. are *S. hesperis electa* (=*nikias*)(Figs. 26-29), while the chocolate-brown disc adults are *S. atlantis sorocko* ("*electa*")(Figs. 10-15), as noted above.

The connection between *hesperis* and *nikias* in Colorado has been rather muddled (by the presence of *sorocko*), so the connection is most clear in a roundabout trip through nearby states, as *hesperis* becomes *tetonia* which becomes *wasatchia* which becomes *chitone* (which resembles *nikias* but is paler) which becomes *schellbachi* which becomes *nausicaa* which becomes *dorothea* which becomes *nikias*. So the subspecies scheme we propose works out best if *nikias* is a ssp. of *S. hesperis*, and if "*electa*" (*sorocko*) is a ssp. of *S. atlantis*; with that scheme, "*electa*" could be expected to be widely sympatric with both *nikias* and *hesperis*, as happens in the records of Brown et al. (1957) and on the map of Ferris (1983); and with that scheme, *hesperis* and *nikias* would be expected to mostly replace each other geographically, as also happens in those records/map. *S. hesperis hesperis* occurs on the east slope of the continental divide, in the Medicine Bow Range and Laramie Range of Wyo. and the Front Range and Wet Mts. of Colo., whereas *S. hesperis nikias* occurs on the west slope, in Colo. north to Carbon Co. Wyo., westward into the Uintah, La Sal, and Abajo Mts. of Utah, and occurs on both slopes of the continental divide in N New Mex.

Unsilvered *hesperis* and silvered *nikias* intergrade in several areas: In the northern Sangre de Cristo Mts. in southern Colo. (Fremont and Custer Counties, south to Medano Pass in Huerfano/Saguache Co.) *hesperis* and *nikias* intergrade fully, and silvered and unsilvered adults are about equally common (28 adults mostly or completely silvered, 30 mostly or completely unsilvered) along with numerous partially-silvered adults; all have a red-brown disc, but some (uncommon) adults have a paler disc partially tending toward *ratonensis*. In the Wet Mts., most adults are unsilvered *hesperis*, but the population is less pure than in the Front Range so about one-sixth of adults are silvered like *nikias*, including one male and one female at Oak Creek Cgd. that are 2/3 silvered, one male fully silvered and one female 2/3 silvered at Greenhill Divide, and at Ophir Creek 10300' an unsilvered male *hesperis* was found in copula with a female *nikias* that was mostly silvered (completely silvered at unh base, mostly silvered elsewhere), while the only other adult found there was an 80%-silvered *nikias* male. This mating pair helps prove that *hesperis* and *nikias* belong to the same species (all the other mating pairs Scott has found involved both-unsilvered *S. hesperis* or both-silvered *S. atlantis*).

Additional proof that both *hesperis* and *nikias* are ssp. of *S. hesperis* is the larva of *nikias*, which is identical to *hesperis* (see below).

Farther south in the Sangre de Cristo Mts., at Cuchara Creek in Huerfano Co., *nikias* predominates (89%) so only 11% are partly- or completely unsilvered, and 31% have a slightly-paler unh disc slightly tending toward the very pale disc of *ratonensis* (Figs. 30-33) to the southeast. In the Sangre de Cristo Mts. in New Mex., and westward in the Rocky Mts. of New Mex. and on the western slope in Colo., *nikias* predominates and unsilvered adults like *hesperis* are rare.

S. hesperis hesperis is usually unsilvered, so silvered adults are scarce in the Front Range of northern Colo. in general, but are a bit more common at the eastern end of the Moffat Tunnel through the continental divide in Gilpin Co., where most adults are unsilvered *hesperis*, but about half the adults have a slightly-silvered unh base and margin, and 14% are 2/3-3/4 silvered and thus resemble *nikias* (this site is barely on the eastern slope, but has other western slope species such as *Speyeria zerene*, *Lycaena nivalis*, *L. xanthoides editha*, and *Oeneis jutta*, so the population has evidently been influenced by immigrating *nikias*). In the foothills of the Front Range, silvered adults resembling *nikias* occur but are rare, approximately 1% (among many hundred adults of mostly-unsilvered ssp. *hesperis*, Scott has found one male and six females that are mostly silvered, from Tucker Gulch, Critchell, Cherry Gulch, Indian Gulch, and Shingle Creek all in Jefferson Co., and from Williams Can. in El Paso Co., plus many others that are half-silvered). And *hesperis* adults resembling *tetonia* (with the unh submarginal band nearly completely suffused with red-brown) are also rare in the Front Range (Scott found 7 males 6 females from Jefferson & Boulder Cos). One male from Mt. Judge in Clear Creek Co. has a red-brown disc and is completely silvered like *nikias*, but has a pale ups and looks like it might possibly be a hybrid with *S. atlantis sorocko*.

In W Colo., many people note that *nikias* and "*electa*" are distinct. In SW Colo. both *nikias* and "*electa*" (*sorocko*) occur, and Hammond (1991) stated that these two are widely sympatric with strong reproductive isolation south of the Gunnison River, but interbreed northward in NW Colo. Also, Ray Stanford (pers. comm.) states that he can tell the difference between "*electa*" and *nikias* in W Colo., and Scott L. Ellis (as stated by Ferris 1983) found that field observations of pairs in copula in W Colo. indicate the absence of matings between "*electa*" and *nikias*.

But what about the intergradation between "*electa*" (*sorocko*) and *nikias* said to occur by some authors including Ferris (1983) and Hammond (1991)? Intergradation could be real, or bogus, because identifications in the past unfortunately have been based on little more than one character: silvered adults with wider black ups bars were generally called *nikias*, those with narrow bars "*electa*", and all unsilvered adults were called *hesperis*. But seldom can we trust that single characters correlate with actual biological entities, and by comparison with Black Hills taxa and Front Range *sorocko*/*hesperis*, a better character would be to call the red-disc adults *nikias*, the brown-disc adults *sorocko*.

After examining many specimens from all over Colorado and New Mexico, Scott has become convinced that the color of the unh disc--not the silvering emphasized by Scott (1988)--is the key feature separating the two sympatric species in the southern Rockies, for numerous reasons. First, *S. atlantis* has a browner disc and *S. hesperis* a redder disc everywhere else where they are obviously-distinct sympatric species (Man. to B.C., and the Black Hills), so this is the most obvious character to use in the southern Rockies as well. Second, the disc color also works in the Colo. Front Range to separate the brown-disc *S. a.* "*electa*" (*sorocko*) from the sympatric red-brown-disc *S. h. hesperis*. Third, the brown-disc *sorocko* populates the three wet-meadow enclaves in southern Colorado noted above, surrounded by combined populations of *sorocko* and *hesperis* in nearby hills. Fourth, when adults are sorted by brown disc versus red-brown disc, numerous other characters are highly correlated as well (Table 5), including forewing shape. And applying the "Paul Grey" method, we jump from the Black Hills to the Colorado Front Range and find that both taxa are changed but still recognizable; then we jump over the mountains to the western slope of the continental divide and find that *S. a. sorocko* is unchanged from the Front Range, while *S. hesperis* is still recognizable but has become silvered (*nikias*).

The two southern Rockies species on the western slope seem to be properly sorted as follows (Table 5). *S. atlantis sorocko* ("*electa*") is the same on both east and west slopes, and is the same from the Front Range to New Mexico: it is <u>always</u> silvered, and has a chocolate-brown (the color of a Hershey's Chocolate Kiss, thus with a slightly reddish tint to the dark-brown) disc (browner than the red-brown disc of *nikias-hesperis*) that is uniform or has only small paler areas within it (the disc is redder than *S. a. pahasapa*, but is similar to *pahasapa* in lacking grayish pale areas), the unh cream submargin is usually narrow, the male forewing margin is generally convex (not indented at veins M_3-CuA_1, thus the tip not pointed) or straight, the upperside tends to be slightly creamier-orange with a lighter upf wing base, the upf postmedian black bars tend to be narrower neat rectangles, and the ups margin is a little darker. In addition, the silver spots are often smaller than those of *nikias*, and the marginal unh silver spots are most often triangular (fewer are lenticular). The convex fw margin--clearly shown on the "*electa*" (*sorocko*) figures of Brown et al. (1957) and Ferris & Brown eds. (1981)--is especially interesting, because all other taxa of both *S. hesperis* and *S. atlantis* (*nikias*, *hesperis*, *lurana*, *hollandi*, *atlantis*, *canadensis*, etc.) all have concave or straight margins.

In contrast, the silvered (sometimes unsilvered) *S. hesperis nikias* has a red-brown disc (females have the disc slightly darker and the ups a little paler, which is clearly proven by comparing the left versus right wings of several bilateral gynandromorphs of ssp. *hesperis*) that usually has rather large

tan areas within it, the unh cream submarginal band is usually wide (sometimes narrow), the male forewing margin is generally concave (at the end of veins M_3-CuA_1, making the wingtip rather pointed) or straight, the upperside tends to be redder-orange with a darker ups base and the upf median-postmedian black bars tend to be wider and more irregular (in particular the black bar in cell CuA_1 usually seems to be more splayed-out where it contacts the wing veins, and sometimes it does not contact the black median bar in cell CuA_2), and the postmedian-submarginal black ovals on fw are larger (esp. the one in unf cell CuA_2). In addition, the silver spots of *nikias* are often larger than those of *sorocko*, and the marginal unh silver spots are most often lenticular (fewer are triangular) especially in New Mex. where most seem to be lenticular. The unsilvered *S. hesperis hesperis* is similar to *nikias* but is usually unsilvered, the unh submarginal cream band is mostly narrow (and rarely suffused with red-brown like *tetonia*), and the unh marginal spots are quite often triangular. *S. h. nikias* and *S. h. hesperis* seem to interbreed extensively in the northern Sangre de Cristo Mts. of southern Colo. as noted above, where silvered and unsilvered adults are about equally common in a polymorphic population; *S. a. sorocko* ("*electa*") also occurs less commonly, but occurs in pure populations in the three wet meadow enclaves already noted.

(Using these criteria [Table 2], the lectotype of *nikias* in the Carnegie Museum seems to belong to *S. hesperis* instead of *S. atlantis*. These traits of the lectotype are like W Colo. *S. hesperis*: the unh disc has large paler light-brown areas within it; it has silvered spots; the silver spots are rather large, and the marginal ones are lenticular; the fw margin is slightly concave; the upperside is the usual *nikias* shade of orangish (the same shade as the *electa* lectotype discussed below, and a little darker than the *cornelia* lectotype); the ups margins are pale (orangish); and the black bar in fw cell CuA_1 does not contact the black postmedian bar in cell CuA_2. But one trait is like Colo. *S. atlantis*: the disc is chocolate-brown (not red-brown like most *S. hesperis*), darker than that of the *electa* lectotype (thus the dark dashes distal to unh postmedian silver spots are chocolate-brown). And some traits are rather intermediate in assigning it to species: the unh cream submarginal band is fairly wide posteriorly (like Colo. W-slope *S. hesperis*) but fairly narrow anteriorly (the width of *S. atlantis*), and the veins through this band are moderate in width (a bit wider than most W-slope *S. hesperis*, and narrower than *S. atlantis*); the ups bases are not very dark; the black median bars are not very wide (a somewhat variable trait) and the bar in cell CuA_1 is not splayed-out (also variable); and the postmedian black oval in unf cell CuA_2 is only moderate in size and covers only 1/3 the area of the same spot in cell CuA_1. Thus this *nikias* lectotype is not at either of the two extremes of variation, but most characters suggest that it is *S. hesperis*, and in overall appearance it looks like W slope *S. hesperis*, not *S. atlantis*. In the past this specimen would have been considered to be somewhat intermediate due to introgression or hybridization, but hybridization has proven to be absent in the rest of the shared range of these two species, so is somewhat doubtful here also, so we will consider the specimen just a variant of W slope *S. hesperis*. For nomenclatural purposes, this lectotype has to be considered to belong to *S. hesperis*. This lectotype has four labels: "Jemez Springs J. Woodgate Col. 7/9 1914 New Mexico", and "Ehrman [spelled with one n on label even though other authors spell it Ehrmann] coll. Carn. Mus. Acc. 7815", and "A. *nikias* Ehrm. Male. Type", and a red "type" label.)

Sorting the Southern Rocky Mts. SPECIMENS using the above characters to separate *S. hesperis nikias* from *S. atlantis sorocko* seems to work well to reveal the true BIOLOGICAL SPECIES in nature (except occasional males and many females refuse to be sorted by humans), as these correlated characters--including the structural difference in wing shape--add confidence to the scheme. And many other authors sort them similarly, judging by their figured adults of "*electa*" (*sorocko*) and *nikias* (Brown et al. 1957, Ferris & Brown eds. 1981).

However, sorting the TYPES of the named subspecies this way requires some shifting of the application of the names, because the *cornelia* lectotype has all the traits of *nikias* (we have nice color slides, and Brown 1965 figured black and white ups and uns of male lectotype; Holland 1931 pl. XI fig. 8 figured another male, a specimen Brown states is now lost). The lectotype resembles *nikias* in these traits: the disc is rather light red-brown (as also noted by by Holland 1931) full of large tan streaks, the spots are silvered and fairly-large, the dashes distal to postmedian silver spots are light-reddish-brown, the unh submarginal pale band is wide with light-reddish-brown veins, the fw margin is concave, the unf black oval spot near tornus in cell CuA_2 is fairly large (almost half the area of the spot anterior to it), the ups is the usual orangish shade (as is Holland's fig.), the marginal silver spots are mostly lenticular, and the ups wing margin is quite pale (orangish); several traits of the lectotype are ambiguous: the upf base is moderately dark (Brown's b/w photo is too dark), and the black postmedian upf bars are moderate in width. This lectotype has three labels: 1) "*cornelia* male WHE", 2) "lectotype *Argynnis cornelia* male, W. H. Edwards, designated by dos Passos & Grey 1947", and 3) "Ouray Col. Aug" (this last label is written very faintly and was not illustrated by Brown 1965). Obviously *cornelia* belongs to *S. hesperis nikias* and not to *S. atlantis sorocko*, and was named 25 years before *nikias*, thus the name *cornelia* (type loc. Ouray on the western slope of SW Colo.) must be used instead of *nikias*.

Furthermore, the type of *electa* (a lectotype in Carnegie Museum) also seems to be *S. hesperis*. We have fine color slides of the lectotype (the black and white figure of it in Brown 1965 p. 307 is too dark [underexposed compared to the photo of *cornelia* type on p. 311--compare the darkness of print on the labels]). The lectotype *electa* has a red-brown unh disc with large paler-red-brown areas, both traits of *S. hesperis*. And many more traits definitely match *S. hesperis cornelia=nikias* (Table 5): its forewing postmedian black bars are very wide, the black postmedian oval spot near

tornus in unf cell CuA_2 is wide, the upf base is somewhat dark, the unh cream submarginal band is very wide, the silvered spots are fairly large, the marginal silver spots are lenticular, the unh has red-brown dashes distal to the unh postmedian silver spots, the ups margin is somewhat-pale, and the ups is the usual shade of orange. Scott has never seen a true *S. atlantis* from the southern Rockies with black bars as wide as this lectotype, or with unh submarginal band as wide. The only trait that tends slightly toward *S. atlantis* is the very-slightly-convex forewing margin. The labels on the *electa* lectotype are: “type *electa* male Colo. Mead ‘71”, and “Collection W. H. Edwards”, and “*Argynnis cornelia* male. Fide W. J. Holland.”, and “lectotype *Argynnis electa* male W. H. Edwards designated by dos Passos & Grey 1947” (this label not shown by Brown 1965). The *electa* lectotype clearly belongs to *S. hesperis*, and fits the Colo. western slope silvered phenotype *S. hesperis nikias*. This conclusion leaves the S Rockies ssp. of *S. atlantis* without a name. Furthermore, dos Passos & Grey (1947) synonymized *cornelia* to *electa*, as did W. J. Holland who attached an *Argynnis cornelia* label to the *electa* specimen. Paul Hammond (pers. comm.) agrees that "The lectotype of *cornelia* is very definitely a *nikias*. Likewise, the lectotype of *electa* also shows the characteristics of *nikias*." The oldest name for *nikias* is thus *electa* (=*cornelia*=*nikias*).

But the *electa* type locality must be fixed. The current (Miller & Brown 1981) type localities of both *electa* and *hesperis* are the same locality, Turkey Creek Junction, Jefferson Co. Colo., which is only 1/2 mile from Tinytown where Scott has found both *S. atlantis* (scarce) and *S. hesperis hesperis* (common) for many years, and where Scott (1988) reared only *S. atlantis* offspring from a *S. atlantis* mother. The problem is that *electa* (*S. hesperis nikias*) does not occur at Turkey Creek (Tinytown); all the completely-silvered adults there are *S. atlantis sorocko*, though a rare fully-silvered *S. hesperis hesperis* may eventually turn up there. But Turkey Creek in Jefferson Co. is doubtfully the true *electa* type locality. The only locality listed in the original description or on the specimen is “Colorado”, then dos Passos & Grey (1947) restricted it (without reason) to “Rocky Mountain National Park, Colo.”, but Brown (1955) disagreed and suggested that Mead collected it at Turkey Creek. But June 20-30 is generally too early for these *Speyeria* (though Scott has found a few *S. h. hesperis* then), and in addition *hesperis* is common at Turkey Creek (all unsilvered) but silvered *S. atlantis* are scarce (and were not seen in 1993-1995, so evidently breed there only in some years following dispersal of a few km from higher altitude). Brown (1965, 1955) and Brown & Brown (1996) noted that in 1871 (the date on the lectotype) Theodore Mead collected "*S. atlantis*" in the Front Range (but not in Middle Park Aug. 6-14); Mead's itinerary in Brown (1955) and Brown & Brown (1996) indicates Mead could have collected the *electa* lectotype at Twin Lakes in Lake Co. July 9-20, or near Georgetown in Clear Creek Co. Aug. 3, or Idaho Springs in Clear Creek Co. Aug. 19, or Bailey in Park Co. Aug. 26. Mead visited Middle Park in Summit Co. Colo., but “In the Middle Park there was but little to be found.” (Brown & Brown 1996). Only ssp. *nikias* was listed from Lake Co. by Brown et al. (1957) (though *S. atlantis sorocko* no doubt also occurs there), whereas *S. atlantis* and *S. h. hesperis* but not *nikias* occur in Clear Creek and Park and Jefferson Cos. Therefore, as the lectotype is synonymous with *cornelia* and *nikias*, the type locality must be corrected to Twin Lakes, Lake Co., the only locality in Mead’s itinerary where Mead collected specimens and where *nikias* actually occurs. Brown designated the type locality of Turkey Creek Jct. based only on Mead's itinerary; we hereby correct the TL to Twin Lakes, based on both its wing pattern and the itinerary.

To conclude, the southern Rockies *S. atlantis* ssp. is unnamed, since all the available names, *electa*, *cornelia*, and *nikias*, belong to *S. hesperis*. It is named *S. atlantis sorocko* below. And the Colo. western slope silvered ssp. of *S. hesperis* must be called *S. hesperis electa* (=*cornelia*=*nikias*).

Ferris (1983) stated that "*electa*" (*S. atlantis*) and *nikias* intergrade in the southern part of the southern Rockies in Taos Co. New Mex., and claimed that a cline runs from *hesperis* through “*electa*” to *nikias* in the Sierra Madre Mts. of Wyo. But this impression of intergradation may have resulted in part from a slight influx of *dorothea* into New Mex. *nikias*, and in part from misidentifying variants of a polymorphic (silvered/unsilvered) *S. hesperis* population with *S. atlantis sorocko* (confusion that is understandable because the types of all four of the previously-named taxa in the S Rockies all belong to *S. hesperis*). However Scott's specimens show no intergradation. Scott's 2 males 2 females from Santa Fe Ski Area (Santa Fe Co. N.M.) are typical *nikias* except 1 male has a more-uniform red-brown disc like most *dorothea* (and could possibly be a redder *S. atlantis sorocko*), and his 13 specimens from Taos Ski Area (Taos Co. N.M.) are typical *nikias* (one unsilvered) except one female has a darker disc and could be *S. a. sorocko* or possibly another influx of *dorothea*. And at Rabbit Ears Pass in the Sierra Madre Range (Park Range) of Routt Co. Colo., little or no intergradation occurs: about two-thirds of Scott's very many specimens are ordinary *S. h. electa*=*cornelia*=*nikias* (about 4% of these are mostly-unsilvered *hesperis*, and rare adults are silvered but have the unh submarginal area suffused like *tetonia*)(there is no "*dorothea*" here contrary to Brown et al. 1957), while one-third of adults are ordinary *S. a. sorocko*. And in the San Juan Mts. near Tierra Amarilla New Mex., *S. a. sorocko* is distinct and identical to Front Range *sorocko*, and is not hybridized. Thus, reports of “intergradation” in the southern Rockies between *S. atlantis* and *S. hesperis* seem to be misinterpretations of the polymorphism in silvering within the commoner species *S. hesperis*.

However, it is still possible that some past hybridization (introgression) may have occurred between *S. hesperis* and *S. atlantis sorocko* in the southern Rockies, causing them to resemble each other a little more closely than they do in the Black Hills and Canada. Or, genes may have been

transferred between these species by viruses, which have been proven to be capable of transferring genes between various animals and plants, even between rodents. Virus transmission of genes has probably been enormously important in the evolution of life on earth, because without it, individual species could evolve advances in one or two structures or in one or two biochemicals, but these advances could not be brought together in one species (because separate species could not mate and transfer genes); with virus transfer of genes, unique advances made by many **different** species can be brought together into **one** species, enormously speeding evolution. In *Spyeria*, there are many areas in western U.S. where sympatric species resemble each other closely (converge) in wing pattern traits that are doubtfully adaptive, which may be explained best by virus transmission of genes.

Continuing the geographic survey, on the relatively isolated Mesa de Maya mesas along the eastern part of the New Mexico-Colorado border, the extremely pale ssp. *ratonensis* (Figs. 30-33) is almost identical to Manitoba *S. hesperis helena*/*dennisi*, suggesting it is a ssp. of *S. hesperis*; its unh disc is just as pale and sometimes even paler, and the only major difference is its slightly wider black ups bars. Ssp. *ratonensis* is <u>always</u> silvered, which might suggest a relationship to the silvered *S. atlantis sorocko*; however the nearest population of *S. hesperis* is "*nikias*" to the west, which is nearly always silvered, so the silvered spots of *ratonensis* evidently come from "*nikias*". The light reddish-brown tint of the disc of *ratonensis* is like *S. hesperis*, not *S. atlantis*; actually, among the traits in Table 5, *ratonensis* resembles *S. hesperis electa* and not *S. atlantis sorocko* in all traits except those involving the pallidity of *ratonensis*. Ssp. *ratonensis* also closely resembles *S. hesperis greyi* of NE Nevada, which is always silvered with a pale somewhat-reddish brown unh, though the silver spots of *greyi* are larger than those of *ratonensis*; *greyi* is isolated among unsilvered populations, but a mostly-silvered purplish-brown-disc intergrade population to the north in Cassia Co. Idaho connects it to unsilvered *S. hesperis tetonia* in eastern Idaho, and the *lurana*-like larva of *greyi* clearly suggests *greyi* is a ssp. of *hesperis*. These similarities of *ratonensis* to *helena* and *greyi* support the *S. hesperis ratonensis* assignment. Ssp. *ratonensis* does not intergrade much with adjacent ssp. as Ferris (1983) claimed (it seems mostly isolated from both ssp. *hesperis* and ssp. "*nikias*"), for instance W of Spanish Peaks (Cuchara Creek) nearly all adults are silvered with a darker disc (a third have a slightly-paler disc) so do not resemble *ratonensis*; the only "intergradation" is the occasional pale-reddish-disc *S. hesperis* adults--both silvered and unsilvered--in the Sangre de Cristo Mts. from east of Great Sand Dunes southward (Medano Pass, Cuchara Creek, etc.; only one paler-disc male was found as far north as Hermit Pass Road W of Westcliffe; one silvered male from Medano Creek resembles *hesperis* X *ratonensis*).

LARVAE. Most ssp. of *Speyeria* have been reared, but unfortunately nothing of value--no photos or drawings or written descriptions--was recorded during most of these rearings. Scott (1988) documented many differences between larvae of *S. a. sorocko* (as *atlantis* "*electa*") and *S. hesperis hesperis* in Colorado, and illustrated b/w photos (b/w photos are also shown in the current paper on Figs. 40-41, and color photos are shown by Scott 1997 on CD-ROM format, specifically ssp. *hesperis* mature larva on photo 1691113, and ssp. *sorocko* mature larva on photo 1691117 as ssp. "*atlantis*"). The *hesperis* larva is almost solid black (with weak pattern, thus the two middorsal lines are brown and not very noticeable) with black-tipped orange scoli (branching spines)(Fig. 40), whereas *sorocko* has more of a pattern (mottled black & brown) with two middorsal creamy lines and black-tipped orange-tan scoli (Fig. 41). Edwards' (1888b) description of *hesperis* larva was identical to Scott's. And larvae of *hesperis* and *sorocko* reared by Spomer (from eggs laid by females collected from Rampart Range, Route 67, Douglas Co. Colo., July 19, 1996, coll. Paul C. Hammond) were identical to Scott's larvae of these (showing the same differences between them, Figs. 40-41), except the photo of *hesperis* larva has the scoli only orangish-tan.

But W. Evans in Grey et al. (1963) gave different descriptions from Scott's, describing the unsilvered Black Hills *S. h. lurana* larvae as black with two middorsal grayish-white lines and orange scoli, and describing the silvered Black Hills "*atlantis*" (*S. a. pahasapa*) larvae as black (the middorsal lines light-brown thus not very noticeable) with orange scoli. However, Spomer reared Black Hills *lurana* and his photos (Fig. 39) prove that it is identical to Colorado *hesperis*, although the scoli may be a bit paler (orange-tan). Therefore Evans (in Grey et al. 1963) must have mistakenly reversed his descriptions of *lurana* and "*atlantis*" (*S. a. pahasapa*); if we reverse his descriptions, they fit the known correct descriptions.

The larva of Manitoba ssp. *hollandi* (photos by Spomer, Fig. 42) has two pale (orangish-cream) middorsal lines (interrupted at segment joints) on a blackish body with black-tipped orangish scoli, and thus is closer to Colorado *sorocko* larva. Edwards (1888a) described ssp. *atlantis* larvae in Vermont as similar to *sorocko* with the same bands, but even paler: two greenish-yellow middorsal lines, then a brown-black area, an area between the top two rows of scoli that is greenish-gray with white edges, then a gray supralateral area with rust-red tint in middle, underside more brown-gray, the uppermost scoli gray, second row gray tipped with rust-yellow, lateral row dark rust; head dark-brown with dull-yellow rear. But the ssp. *atlantis* larva may not be quite that gray, as Paul Hammond (letters to J. Scott, 1995-1996) described Pennsylvania *atlantis* as similar to Man. *hollandi* and Colorado *sorocko*, mottled black and brown with yellowish spines, and two separated bright yellow middorsal lines.

All other reared ssp. of *S. hesperis* have very dark larvae like ssp. *hesperis* and *lurana*. The larva of ssp. *electa* (=*nikias*) looks like typical ssp. *hesperis* (from Rabbit Ears Pass, Routt Co. Colo., reared by Spomer) (*S. egleis secreta* larvae from there look completely different even though

adults are somewhat similar). The larva of ssp. *greyi* resembles *lurana*; and an intermediate population in Cassia Co. in S Idaho (with adults that are transitional from *tetonia* to *greyi*, the ups light, a purplish-brown unh disc and mostly silvered spots) has larvae that are almost identical to *lurana* (S. Spomer). Ssp. *tetonia* is also similar to *hesperis* and *lurana*, by having very black larvae with little trace of paler dorsal lines, and dark scoli (Paul Hammond, pers. comm.). Ssp. *dodgei* larvae (reared by Spomer) are also very similar to *lurana*, except perhaps darker (they are identical to *S. hydaspe* (Bdv.) larvae, which are always very blackish), with little trace of the two middorsal lines, but (Paul Hammond, pers. comm.) have reddish lateral scoli as in *Speyeria cybele*.

Larvae of *S. adiaste adiaste* (W. Edw.) and *S. a. clemencei* (J. Comstock) reared by Spomer are also dark, and look closest to the dark *S. hydaspe* larvae; *adiaste* larvae are distinguished by having the top row of scoli black, and by having the posterior paler head "cap" (present on nearly all *Speyeria*) (if present) dark brown and thin.

Ssp. *beani* larvae are also rather dark and resemble *lurana*, at least in some areas. In Cypress Hills Sask. the "*beani*" larva (the mother was evidently not misidentified *hollandi*) reared by Spomer is more similar to *hollandi* than *lurana*, thus has fairly-noticeable twin middorsal paler lines, and has black scoli bases bordered with some white scaling above and below like *hollandi*, which *lurana* lacks. However *beani* larvae from SE B.C. (near Wilmer, and Fort Steele, reared by Spomer, Figs. 37-38) are darker like *lurana*: a Wilmer larva (Fig. 37) is blackish with twin tan middorsal lines, a Ft. Steele larva (Fig. 38) is black with very faint twin tan middorsal lines; both have black-tipped orangish scoli. Thus the Sask. larva of "*beani*" may possibly show considerable influence from ssp. *helena* populations that surround the Cypress Hills.

But the extreme southernmost ssp. of *S. hesperis* have brightly-colored larvae. Larvae of Ariz. *nausicaa* (reared by Spomer, Fig. 35) and southern New Mex. *capitanensis* (reared by Spomer, Fig. 36) and central New Mex. *dorothea* (Paul Hammond, pers. comm.) not only have the two ochre middorsal lines of *S. atlantis*, these lines are broadened and mostly fused together (about 60-70% fused in *nausicaa*, 40% in *capitanensis*) into a yellowish-cream middorsal band (this fusion is a unique trait among larvae of the *Speyeria callippe*-group). Some ssp. *nausicaa* larvae are rather light, with the usual black patches and some orange-tan areas, the middorsal band of two partly-fused lines is yellowish-cream, the dorsolateral paler areas (and the ~four intersegmental folds at each segmental joint) are mottled with orangish, ochre, and yellowish-cream (the orangest spots are at base of scoli and in notches of the large black patches), the uppermost scoli are brown with black tips, the middle scoli ochre with orange-brown more distally then black tips, the lowermost scoli are ochre with brown tips; the head is black as usual with orange-brown posterior portions except for the middorsal black valley. Other *nausicaa* larvae are darker, except for the yellow-cream middorsal band; the body has large black patches and large dorsolateral areas of ochre and yellow-cream; all three rows of scoli are orange-brown with black tips. Larvae of ssp. *capitanensis* are very similar to the pale *nausicaa* larva described above except are a little darker, so the dorsolateral areas are mostly brownish-orange (with some smaller yellow-cream areas), and the middle row of scoli is orangish-brown with black tips. Thus the larvae of these three Ariz.-New Mex. ssp. resemble *S. atlantis* more than other ssp. of *S. hesperis* (but actually are quite different from both), yet these three ssp. evidently belong to *S. hesperis* rather than *S. atlantis* if we apply the Paul Grey method. *S. atlantis* does not occur within the range of these three ssp. (it doubtfully occurs in the White Mts. Ariz. as noted above), whereas northward in western N.A. where the two species do occur together, "character displacement" may have occurred such that their larvae differ.

But the larvae of some adjacent ssp. to the north suggest that the southernmost ssp. (*nausicaa* etc.) do belong to *S. hesperis*. First, the older larva of *S. h. schellbachi* (reared by Spomer, Fig. 34) shows definite intermediate traits between the blackish *lurana*/*hesperis* type larva and the pale *nausicaa* larva. The middorsal pale band of *schellbachi* is like that of *nausicaa*, yellow-cream and formed of two lines that are very close together and 30-40% fused (the dark heart-band weak [very narrow] and 30-40% absent). But the body is rather dark, consisting of the usual black patches and a ground color that is a little darker than medium-gray. The scoli are fairly dark also, the uppermost row being blackish, the middle row brown or blackish with black tips, the lateral row ochre with black tips and some brownish-red at base. The head is blackish on front, brown-red on sides and on each side of top, ochre on the middorsal valley. Thus, intermediate traits of both larvae and adults of *schellbachi* definitely suggest that *nausicaa* belongs to *S. hesperis*.

Furthermore, mature larvae of *S. h. electa* (=*nikias*) from SE Utah (Abajo Mts., San Juan Co.) also show a link to *nausicaa* (Paul Hammond, pers. comm.): One adult female laid eggs that produced black larvae with dark scoli and little trace of the two middorsal lines, while a second female produced larvae with the same dark body appearance, except they had a very narrow yellowish middorsal band in which the usual two middorsal lines were mostly fused as in *nausicaa*/*dorothea*. Thus the traits of SE Utah *S. h. electa* (=*nikias*) suggest that *electa* is a ssp. of *hesperis* because their larvae are similarly dark (this conclusion is confirmed by the larvae of *nikias* from northern Colo. which are identical to *hesperis* as noted above), and also suggest that *nausicaa* is a ssp. of *S. hesperis* because the SE Utah middorsal band intergrades toward *nausicaa*. Adults from the Abajo Mts. resemble Colorado *electa* (=*nikias*) in wing pattern, but are often larger as in *nausicaa*.

Evidently, what has happened is that the original progenitor larva of *S. hesperis* was similar to *S. atlantis*, because that type occurs in most *Speyeria* (for instance *S. callippe* is similar, see figs. in Emmel & Emmel 1973) so is evidently primitive, and then that larval type persisted in some ssp.

such as *beani*, but the larva became blacker in the ssp. in the middle of the range of *S. hesperis* (where greater melanism is evidently simultaneously responsible for blacker larvae and unsilvered adults, Scott 1988), and the larva became a little yellower in Ariz.-N.M.

Therefore, we conclude that larvae of all *S. atlantis* ssp. are very similar (paler, with twin pale middorsal lines), and are similar to some *S. hesperis* ssp. in the northern part of its range, but are much different from the dark larvae of most *S. hesperis* ssp. in the middle of its range, and are different from the yellower larvae of several southern *S. hesperis* ssp. In larvae as in adults, *S. atlantis* is a rather uniform species, compared to the highly variable polymorphic and polytypic *S. hesperis*.

HOSTPLANTS. *S. atlantis* hosts: ssp. *sorocko* eats *Viola sororia affinis* (which was called *V. nephrophylla*, but is now called *V. s. affinis* by the new Jepson Manual of California plants and by the floras of botanists such as William Weber etc., though the recent Great Plains Flora merely states that *nephrophylla* may be a ssp. of *V. pratincola*, and both may be ssp. of *sororia*) in the Colo. Front Range (Scott 1992), where *sorocko* probably (based on association) also eats *Viola scopulorum* (often called *V. canadensis* var. *scopulorum*, although the names within the *Viola canadensis* species group are not settled), and where *sorocko* probably also eats *Viola rydbergi*. (which was formerly also confused with *V. canadensis*). Ssp. *atlantis* is found near *Viola canadensis* in W. Va. or N.Y. (W. Edwards, Butt. North America) and near *Viola septentrionalis* in N.Y. (A. Shapiro, Butt. New York).

S. hesperis hosts: ssp. *hesperis* eats *Viola rydbergii* (formerly lumped into *Viola canadensis* var. *scopulorum)* (Scott 1992, and Scott's 1997 data) and *V. adunca* (Scott 1992, and Scott's 1997 data) in the Colorado Front Range, where it may also eat *Viola scopulorum* by association; ssp. *dorothea* eats *Viola sororia affinis* (=*nephrophylla*) in San Juan Co. New Mex. (Scott 1992); ssp. *dodgei* eats *V. adunca bellidifolia* in Ore. (O. Shields et al., J. Res. Lepid. 8:32) and *Viola nuttallii* var. *linguaefolia* in Ore. (P. Hammond, J. Res. Lepid. 20:179-191); ssp. *irene* eats *Viola purpurea* in Calif. (T. Emmel et al., J. Res. Lepid. 9:239, and O. Shields & J. Emmel, J. Res. Lepid. 18:94); ssp. *ratonensis* is assoc. with *V. rydbergii* ("*canadensis* var. *scopulorum")* in N.M.-Colo. (Scott).

NEW SUBSPECIES. Our researches prove that three subspecies are unnamed in the area of overlap of the two species. They were not recognized in the past because their characteristics were lost in the great specimen variation caused by lumping both *S. atlantis* and *S. hesperis* into one species. They are:

Speyeria atlantis pahasapa Spomer, Scott, & Kondla, NEW SUBSPECIES (Figs. 1-9)

This is the fully-silvered portion of the hodgepodge formerly called *S.* "*atlantis*" in the Black Hills. It is similar to ssp. *hollandi*, but the unh disc is much darker (blackish-brown, which can also be described as very-dark-chocolate-brown), the ups margin (between the true margin and the submarginal black line) is more orangish, versus mostly blackish in ssp. *hollandi* and *atlantis*, and the black ups bars are a little narrower (Table 1). Some traits are convergent with sympatric *S. hesperis lurana* (the narrow black bars, light ups base, triangular marginal silver spots, and small size), but other characters greatly differ between the two (Table 4). Grey et al.(1963) detailed its distribution in the Black Hills (as the "*atlantis*-form"), and tried to deduce its relationship with *lurana*, though they inadvertently reversed descriptions of mature larvae. **NAME**: *pahasapa* is the Sioux name for the Black Hills ("Hills of the Shadows"). The name is unrelated to pahaska (as in *Hesperia pahaska*, Hesperiidae), which is the Sioux name for "Yellow Chief" (Buffalo Bill Cody). **TYPE LOCALITY**: Deerfield Reservoir, Pennington Co., S.D. **TYPES** (all from Black Hills in South Dakota): Holotype male (AMNH) Deerfield Res. July 13, 1990, S. M. Spomer. Allotype female (AMNH) S Castle Creek Road, Deerfield Lake, July 14, Jim M. Reiser. 15 male 5 female paratypes (in collection of collector except as noted): Pennington Co.: 1 male, Deerfield Res., July 13, 1990, S. Spomer; 1 male, Deerfield Lake, July 13, 1990, Jim Reiser; 4 males, S Castle Creek Rd. near Deerfield Res., July 14, 1990, S. Spomer; 1 female, same site July 15, 1994, S. Spomer; 1 male, same site, July 14, 1990, Jim Reiser; 6 males, 3 females,same site, July 20, 1991, Jim Reiser; 1 female, Castle Creek, 2 mi. E of Deerfield, Aug. 5, 1961, [Arthur] "Moeck 1962" (O. D. Spencer collection); 3 males Castle Creek T2NR1E, July 18, 1970, John S. Nordin (in Scott coll.); 4 males Ditch Creek S of Deerfield Res., July 19, 1970, J. Nordin (in Scott coll.); 3 males Willow Creek, July 16, 1986, J. Scott; Custer Co.: 1 male, Iron Creek near Lakota Lake, July 8, 1989, Gary M. Marrone; Lawrence Co.: 1 male, 2 miles SW Dumont, July 14, 1984, G. Marrone; 1 male Long Draw, 6000 feet, July 21, 1968, J. Nordin (in Scott coll.). **RANGE**: thus far known only from Custer, Pennington, and Lawrence Cos. in the Black Hills of South Dakota.

Speyeria atlantis sorocko Scott, Kondla, & Spomer, NEW SUBSPECIES (Figs. 10-15, 41)

Found in the southern Rockies, it is distinguished from *S. a. pahasapa* (Table 1) by having wider ups black bars, a more rounded male forewing, a lighter disc, and slightly darker upf margin and base. It is distinguished from *S. a. hollandi* and *S. a. atlantis* by rounder male forewings, no pale-

grayish areas in the disc, paler ups base and margin, and smaller size; also, it has a paler disc than *hollandi*, and has narrower ups black bars and paler ups than *atlantis*. It is distinguished from *S. hesperis electa* (=*nikias*) (Table 5) by having a darker reddish-brown disc with smaller or absent pale areas within it, a more convex male forewing, narrower unh submarginal cream band, neater narrower black upf bars, mostly-triangular marginal silver unh spots, silver spots that are often smaller, and slightly paler ups including base but a slightly darker ups margin. **NAME** is from SOuthern ROCK-y mOuntains. **TYPE LOCALITY**: several km NE of Mt. Judge, 9100 feet altitude, Clear Creek Co., Colo. (the site described by Scott 1988). **TYPES**: all from type loc., July 23-Aug. 18, 1984-1990, holotype and allotype in AMNH, most paratypes in Scott coll. **RANGE**: Scott has examined definite *sorocko* specimens from Montezuma, San Juan, Conejos, Rio Blanco, Garfield, Eagle, Park, Grand, Summit, Routt, Gilpin, Clear Creek, Jefferson, Teller, Saguache, Fremont, Custer, and Las Animas Cos. Colo., and from the San Juan Mts. of Rio Arriba Co. New Mex. Spomer has seen *sorocko* from Douglas Co. Colo. (Scott has examined definite *S. hesperis electa=nikias* specimens from Sandoval, Rio Arriba, Santa Fe, San Miguel, Taos, and Colfax Cos. New Mex., from La Plata, San Juan, Archuleta, Hinsdale, Montrose, Gunnison, Saguache, Mesa, Rio Blanco, Moffat, Pitkin, Eagle, Grand, Summit, Jackson, and Routt Cos. Colo., from the Abajo Mts. in San Juan Co. Utah, and from Carbon Co. Wyo. In addition, Spomer found *electa=nikias* in Costilla Co. Colo. Scott has examined *S. hesperis electa*/*hesperis* intergrades from the Sangre de Cristo Mts. in Fremont, Custer, Saguache, and Huerfano [near *electa*] Cos. Colo.; and *S. hesperis hesperis* from Pueblo, Custer, El Paso, Teller, Douglas, Jefferson, Clear Creek, Gilpin, Boulder, and Larimer Cos. Colo., and Albany & Carbon Cos. Wyo.)

Speyeria hesperis brico Kondla, Scott, & Spomer, NEW SUBSPECIES (Figs. 24-25)

This subspecies resembles *S. hesperis beani*, but the disc is darker-red, with smaller tan areas, and the disc extends farther into the pale submarginal unh band (thus the pale submarginal band is narrower and slighly suffused with reddish-buff, and at unh tornus the disc usually extends across the pale submarginal band so is mostly connected to the reddish cap of the tornal marginal silver spot). The blackish ups base is more extensive than in *beani*, and forewing length is slightly larger (27-29 mm *brico*, 26-27 mm *beani*). It is often sympatric with *S. atlantis hollandi* (Table 3). **NAME** is from BRI-tish CO-lumbia. **TYPE LOCALITY**: Castle Creek Forest Service Rd. km 23.5, Cariboo Mts. (25 air km due S of McBride), B.C. **TYPES**: holotype and allotype (deposited in CNC) from type locality June 18, 1995, and numerous paratypes from there and km 18, all coll. N. Kondla, most in Kondla coll., some in Scott coll. **RANGE**: It occurs in the northern part of SE British Columbia, specifically the Interior Plateau (Lac La Hache etc.), the Rocky Mtn. Trench (near McBride, Tete Jaune Cache), the west slope of the main Rocky Mtn. chain (on the Alta. border), and the northern part of the Monashee Mts. Ssp. *brico* occurs in the Interior Cedar/Hemlock biogeoclimatic zone, and the zone just above it, the Englemann Spruce/Subalpine Fir zone (zones defined by Meidinger & Pojar 1991); this habitat is a little wetter than adjacent forest, with more cedars, and is commonly called the “interior wet belt”, which extends in a swath from the U.S. border noth to the west slope of the Rockies NW of McBride B.C. (Ssp. *beani* occurs in extreme SE B.C. at Ft. Steele and Wilmer etc.) Of three males in the adjacent mts. of Alta (near Jasper), one resembles *brico*, a second resembles *brico* X *beani*, and a third resembles *beani*, suggesting that *brico* extends across the low pass in the continental divide from B.C. into Jasper and intergrades with *beani* there. Extreme NW B.C. populations are ssp. *beani* with increased dorsal melanism; extreme NE B.C. populations are *helena* blending into *beani*; finally, populations in the remainder of B.C. (except for *brico*) are *beani* with a slightly more reddish disk and a tendency for reddish intrusion into the ventral submarginal pale band (thus have a slight tendency toward *brico*).

CONCLUSION

When Moeck (1957) wrote his fine paper on geographic variation in *Speyeria*, it was thought that *S. atlantis* was an example of a circle of races, overlapping only in Manitoba, or was an ordinary species with just one small unexplained anomaly in Man. But we now know that these butterflies form two completely distinct species that are sympatric without interbreeding over vast areas from Man. to B.C.-Wash.-Ida. and the Black Hills and southern Rockies, except interbreeding is perhaps occasional in the southern Rockies from Wyo. to New Mex. (although the "perhaps" may be only our current flawed perception, as a result of our inadequate ability to separate all adults of two species in the southern Rockies, two species that may be reproductively isolated using pheromones that the human nose cannot smell instead of the visible wing characters that are our only clues). The ssp. should be placed among the two species according to the following list. Strict synonyms are listed after an = sign, while less-distinctive ssp. or almost-synonyms are indented farther to the right below the ssp. they most resemble, and the farther they are indented the weaker they are (this indenting scheme is an advance, because it more-realistically shows the continuum of distinctiveness of various populations in nature). Attempts have been made to reduce the number of subspecies accepted as valid in *Speyeria*, but as Paul Grey (1989) noted, when there is greater difference between subspecies than between sympatric species, due to local convergence of color

pattern between species, then we are forced to look for and call attention to rather fine differences within each species, and name these differences as subspecies, in order to be able to properly define and identify even the species themselves.

Speyeria atlantis (Edw.) 1862
ssp. *atlantis* (Edw.) 1862, TL Hunter, Greene Co., N.Y., =*canadensis* (dos Passos) 1935, TL Doyles Station, Nfld.
ssp. *hollandi* (F. & R. Chermock) 1940, TL Riding Mts., Man.
ssp. *pahasapa* Spomer, Scott, & Kondla 1998, new ssp. (this paper) (Black Hills), TL Deerfield Res., Pennington Co. S.D.
ssp. *sorocko* Scott, Kondla, & Spomer 1998, new ssp. (this paper) (southern Rockies), TL NE Mt. Judge, Clear Creek Co. Colo.

Speyeria hesperis (Edw.) 1864
ssp. *helena* dos Passos & Grey (1955), TL Edmonton, Alta., =*lais* (Edw.) 1884, TL Edmonton, Alta., =*dennisi* dos Passos & Grey 1947, TL Beulah, SW Man.
ssp. *beani* (Barnes & Benjamin) 1926, TL Banff, Alta., =*hutchinsi* dos Passos & Grey 1947, TL T2N R1W, Jefferson Co. Mont.
ssp. *brico* Kondla, Scott, & Spomer 1998, new ssp. (this paper) (east-central B.C.), TL Castle Creek Rd. S of McBride, B.C.
ssp. *ratonensis* Scott 1981, TL Raton Mesa, Colfax Co. New Mex.
ssp. *greyi* (Moeck) 1950, TL Lamoille Can., Ruby Mts., Elko Co. Nev.
intergrade population (*greyi* X *tetonia*) Cassia Co. Ida.
ssp. *lurana* dos Passos & Grey 1945, TL Harney Peak, Black Hills, S.D.
ssp. *hesperis* (Edw.) 1864, TL Turkey Creek Jct., Jefferson Co. Colo.
ssp. *irene* (Bdv.) 1869, TL Massack, Plumas Co. Calif.
ssp. *dodgei* (Gunder) 1931, TL Diamond Lake, Douglas Co. Ore.
ssp. *viola* dos Passos & Grey 1945, TL Trail Creek, Sawtooth Mts., Idaho
ssp. *elko* Austin 1983, TL Owyhee Valley, Elko Co. Nev.
ssp. *tetonia* dos Passos & Grey 1945, TL Teton Mts., Wyo. (declared in this paper--as first reviser--to have priority over *wasatchia*)
ssp. *wasatchia* dos Passos & Grey 1945, TL Payson Can., Utah Co. Utah
ssp. *chitone* (Edw.) 1879, TL Cedar Breaks Nat. Mon., Iron Co. Utah
ssp. *electa* (Edw.) 1878, TL Twin Lakes, Lake Co. Colo. (corrected herein from Turkey Creek Junction, Jefferson Co. Colo.), =*cornelia* (Edw.) 1892, TL Ouray, Ouray Co. Colo., =*nikias* (Ehrmann) 1917, TL Jemez Springs, Sandoval Co., New Mex.
ssp. *schellbachi* Garth 1949, TL Neal Springs, North Rim Kaibab Plateau, Coconino Co. Ariz.
ssp. *nausicaa* (Edw.) 1874, TL Rock Can., Graham Co. Ariz.
ssp. *dorothea* Moeck 1947, TL Sandia Mts., Sandoval Co., New Mex.
ssp. *capitanensis* Holland 1988, TL Capitan Mts., Lincoln Co. New Mex.

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Table 1. Diagnostic features of *Speyeria atlantis* ssp. (All ssp. have always-silvered spots, the unh disc is always some shade of chocolate-brown or dark-chocolate-(blackish)-brown (not red-brown), the submarginal silver spots tend to be fairly triangular, the unh creamy submargin is nearly always narrow.)

Trait	*atlantis*	*hollandi*	*pahasapa*	*sorocko*
fw length (mm)	male 31, female 31 (Nfld. male 29, fem. 30, Sandilands m 32, f33)	male 31 Man. male 30 Alta. fem. 32.5 Alta.	male 29 female 31	male 29.5 female 31
unh disc color	chocolate-brown	blackish-brown	darker blackish-brown	chocolate-brown
gray areas in unh disc	present	present	absent or weak	absent or weak
male fore-wing margin	concave	concave	concave	more convex
ups black bars	wider	narrower	narrowest	narrower
black spot in base upf cell CuA_2	usually large, some tiny	usually absent, some tiny	tiny	tiny
ups margin	thick, mostly blackish	thick, mostly blackish	thinnest, palest	thinner, slightly paler
ups orange color	slightly darker	slightly paler	slightly paler	slightly paler
upf base darkness	somewhat dark	somewhat dark	pale (palest)	slightly paler

Table 2. Differences between *Speyeria atlantis hollandi* and *Speyeria hesperis helena*/*dennisi* from British Columbia to Manitoba. Both have similar silver unh spots on the disc. Grayish unh areas on *hollandi* (disc, and beyond postmedian silver spots) may have a greenish tint on fresh specimens.

Character	*S. atlantis hollandi*	*S. hesperis helena*/*dennisi*
fw length (Alta.)	male 30 mm female 32.5 mm	male 27 mm female 28 mm
fw length (Man.)	male 31 mm -----	male 27 mm female 28 mm
unh disc	blackish-brown, with some grayish paler areas	red-brown, with large tan areas
dark dash distal to unh postmedian silver spots	blackish-brown (many partly grayish)	dark-red-brown, some pale-brown in *helena*, pale-brown *dennisi*
unh submarginal pale band	narrow, with dark veins	wide, with paler veins
unh marginal silver spot shape	mostly triangular, slightly larger, with broader blackish-brown caps	mostly triangular (some lenticular), slightly smaller, more thinly capped with red-brown
ups black bar width and male androconia veins	wider	narrow *helena*, very narrow *dennisi*
unf tornus spots	strong, dash black	weak, dash light-brown
upperside color	darker-orange	paler-orange
upperside margin	dark	pale
habitat and flight period	mesic to wet mixed coniferous forest & mixed forest including bogs	dry to mesic mostly poplar forest, earlier peak flight where sympatric

Table 3. Differences between *Speyeria atlantis hollandi* and *Speyeria hesperis brico* in Robson Valley area of east-central B.C.

Character	*S. atlantis hollandi*	*S. hesperis brico*
unh disc	dark-brown with gray pale areas	dark reddish-brown, pale areas limited (tan)
unf apical area	brown	reddish-brown
dark dash distal to unh postmedian silver spots	dark-brown	reddish-brown
unh submarginal pale band	very narrow, pale-tan	slightly wider, slightly reddish-buff
unh marginal silver triangles	capped with dark-brown to blackish-brown	capped with reddish-brown
unf tornus spots	strong, black	weak to moderate
upperside margin	mostly black, orange only on rear of uph	more orange, less black
habitat	local, marsh & moist forest	general, forests

Table 4. Differences between *Speyeria atlantis pahasapa* and *Speyeria hesperis lurana* in the Black Hills of South Dakota-Wyoming.

Character	*S. atlantis pahasapa*	*S. hesperis lurana*
unh disc silver spots	silvered, small or larger	unsilvered (occasionally part-silvered esp. distally), small or larger
unh disc	dark blackish-brown, with smaller pale (not gray) areas	red-brown, usually with very large tan areas
dark dash distal to unh postmedian silver spots	blackish-brown	dark red-brown
male forewing margin shape	usually concave or straight	usually concave or straight
upf base darkness	lighter than *hesperis*	same, lighter than *hesperis*
ups postmedian black bars	usually more rectangular and narrower	usually more rectangular and narrower
ups color of males	slightly darker-orange	slightly paler-orange (females same)
unh submarginal pale band	narrow	narrow, never suffused with brown
ups wing margin of males	mostly orangish, slightly darker esp. uph anterior	mostly orangish, paler esp. uph
marginal silver spot shape	triangular, some lenticular	triangular, some lenticular
habitat	wetter areas incl. moist meadows	aspeny woods (usually fairly dry, seldom wet)

Table 5. Differences between *Speyeria atlantis sorocko* and *Speyeria hesperis electa* and *Speyeria hesperis hesperis* from southern Wyoming to northern New Mexico.

Character	*S. atlantis sorocko*	*S. hesperis electa =cornelia=nikias*	*S. hesperis hesperis*
silvered or unsilvered spots on unh disc	always silvered, sl. smaller, fairly round	almost always silvered, sl. larger & rounder	almost always unsilvered, sl. larger, sl. pointier
unh disc (slightly darker in females)	chocolate-brown, with absent or smaller pale (not gray) areas	red-brown, usually with large pale areas	red-brown, usually with large pale areas
dark dash distal to unh postmedian silver spots	blackish-brown	dark red-brown	dark red-brown
unh submarginal pale band and its dark veins	narrow, wider in some, veins darker (wider)	wide, some narrow, veins paler (narrower)	narrow, some brownish, veins paler
male forewing margin shape	usually convex or straight	usually concave or straight	usu. concave or straight
upf wing base	slightly less dark	usually darker	usually darker
fw postmedian black bars	usually more rectangular and narrower	usually more splayed out on veins, usually thicker	usually more splayed out on veins, some thicker
unf black oval spot near tornus in cell CuA_2	1/4 the area of spot above (tiny to 2/3 its width)	1/2 the area of spot above (small to 3/4 its width)	same as *electa*
usual ups color	slightly creamier-orange	slightly redder-orange	slightly redder-orange
unh marginal silver spot shape	triangular, some lenticular	lenticular, some triangular (esp. lenticular N.M.)	triangular, some lenticular
ups wing margin	somewhat blacker esp. upf	pale (oranger)	pale (oranger)
habitat	wetter areas incl. moist meadows/conifer woods	aspeny woods	aspeny woods

Figures 1-2. *Speyeria atlantis pahasapa* holotype male, Deerfield Res., Pennington Co. S.D., July 13, 1990, coll. S. M. Spomer.

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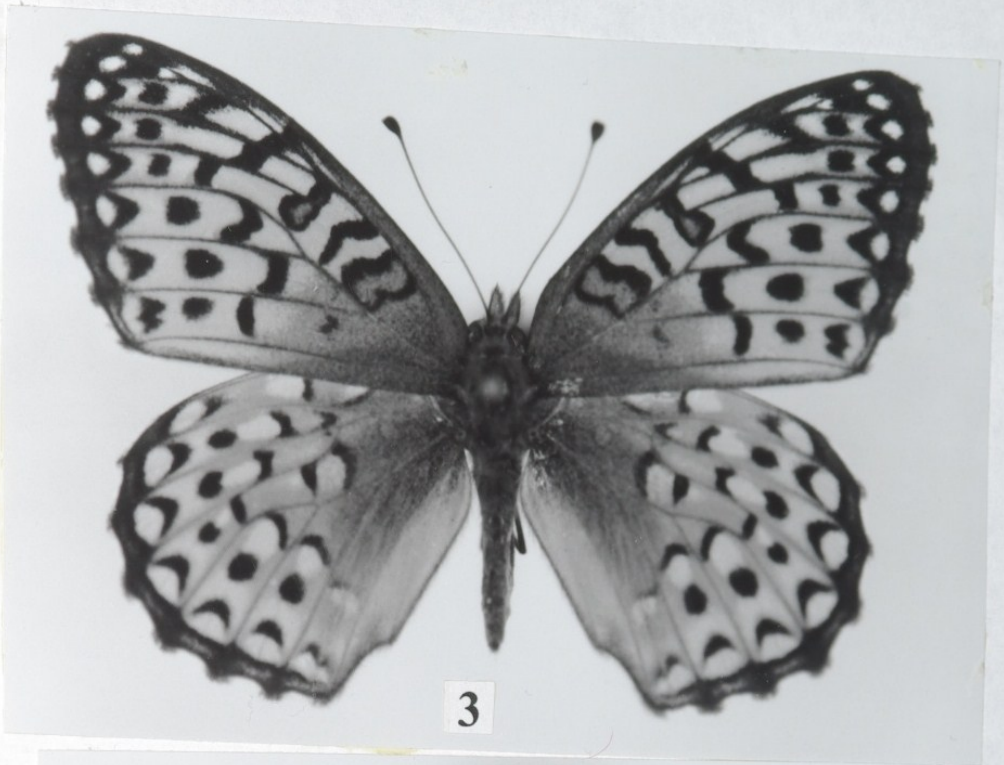
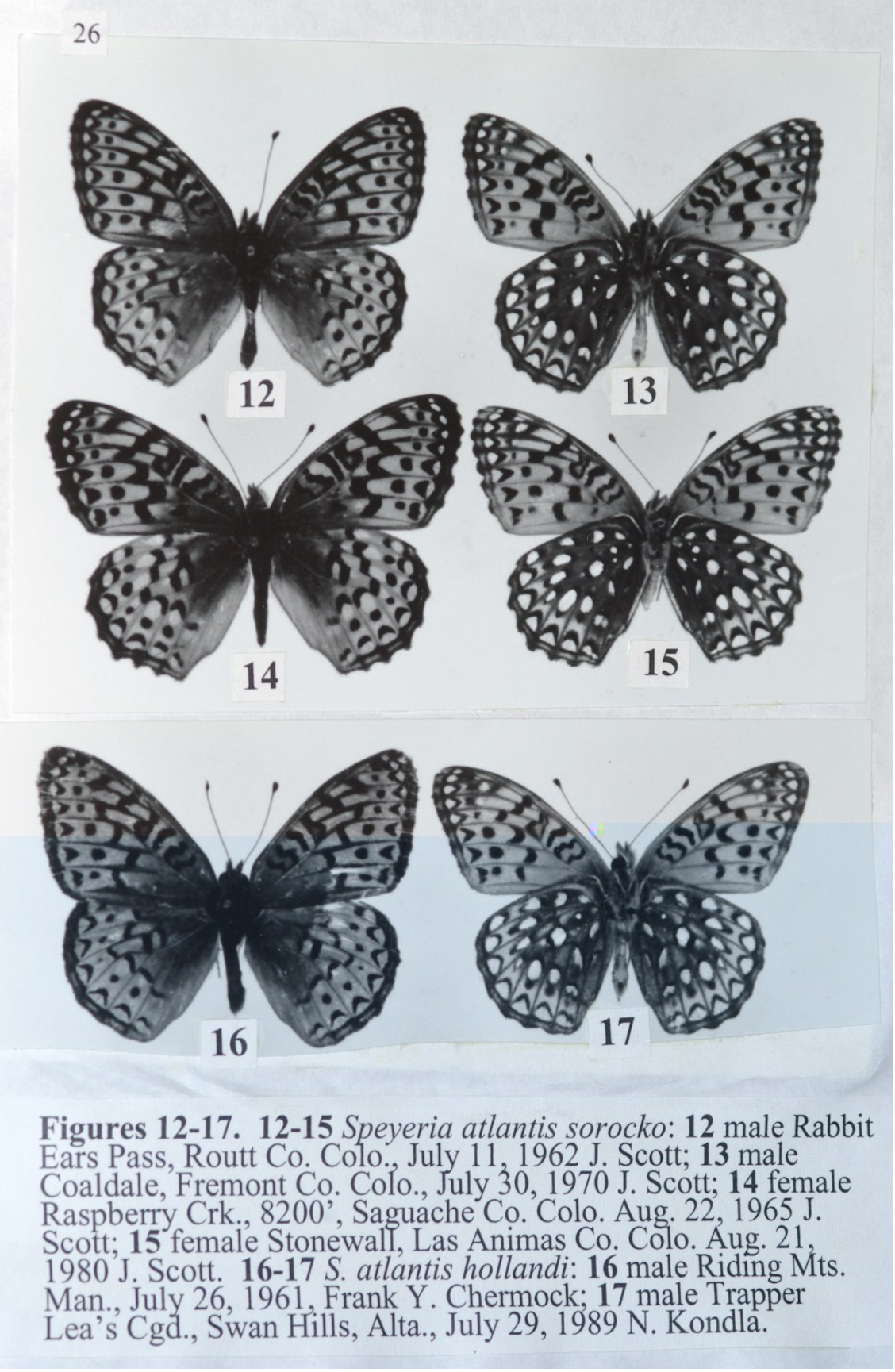
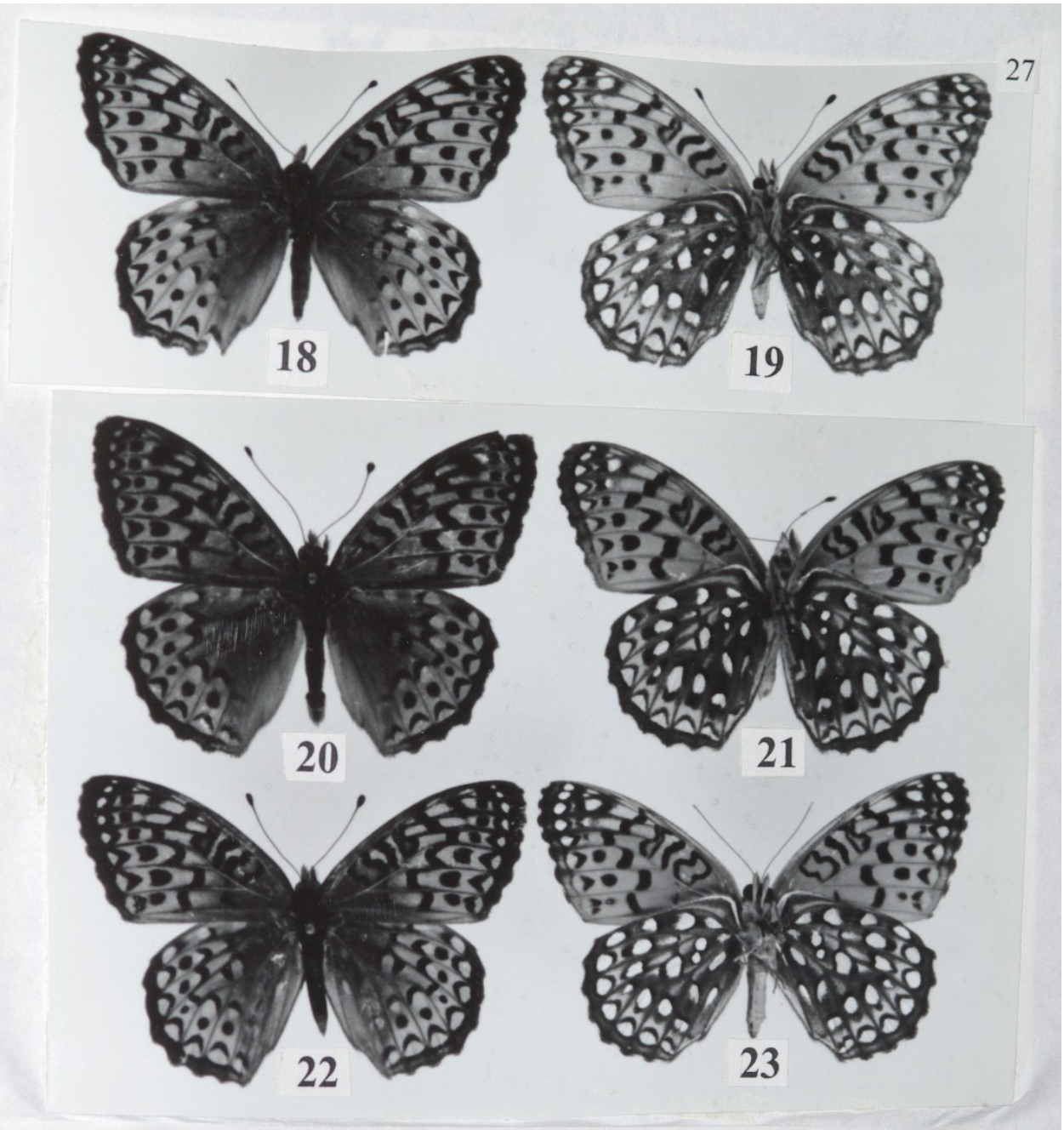


Figures 3-4. *Speyeria atlantis pahasapa* allotype female, S of Castle Creek Rd., Deerfield Lake, Pennington Co. S.D., July 14, 1990, coll. Jim M. Reiser.

Figures 5-11. **5-9** *Speyeria atlantis pahasapa*: **5-6** males Castle Crk., Pennington Co. S.D. July 18, 1970 J. Nordin; **7-9** males Willow Crk. Trailhead, Pennington Co. S.D. July 16, 1986, J. Scott. **10-11** *S. atlantis sorocko*: **10** holotype male NE Mt. Judge, Clear Creek Co. Colo., Aug. 5, 1987, J. Scott; **11** allotype female NE Mt. Judge, Aug. 2, 1989, J. Scott

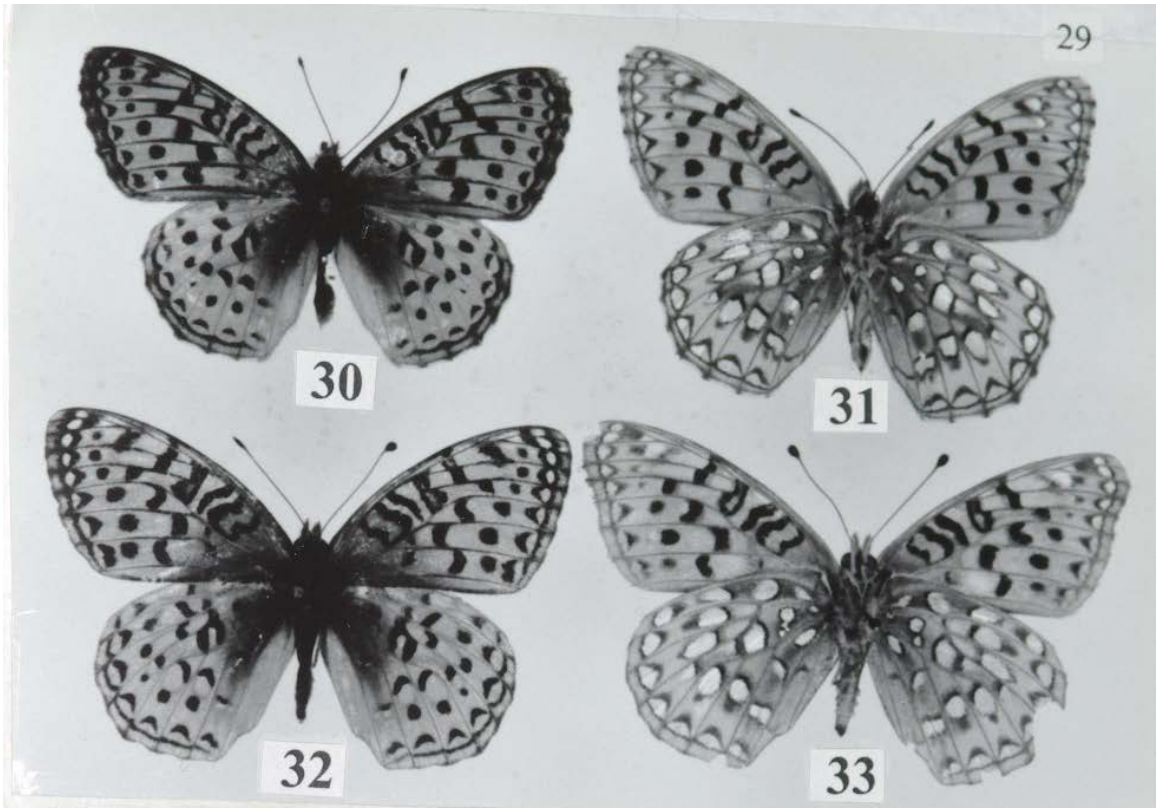


Figures 12-17. 12-15 *Speyeria atlantis sorocko*: **12** male Rabbit Ears Pass, Routt Co. Colo., July 11, 1962 J. Scott; **13** male Coaldale, Fremont Co. Colo., July 30, 1970 J. Scott; **14** female Raspberry Crk., 8200', Saguache Co. Colo. Aug. 22, 1965 J. Scott; **15** female Stonewall, Las Animas Co. Colo. Aug. 21, 1980 J. Scott. **16-17** *S. atlantis hollandi*: **16** male Riding Mts. Man., July 26, 1961, Frank Y. Chermock; **17** male Trapper Lea's Cgd., Swan Hills, Alta., July 29, 1989 N. Kondla.



Figures 18-23. 18-19 *S. atlantis hollandi* females Trapper Lea's Cgd., Swan Hills, Alta., July 29, 1989, N. Kondla. **20-23** *S. atlantis atlantis*: **20** male Algonquin Prov. Park, Ont. July 21, 1965 J. Riotte, P. Hebert; **21** male Doyles, Nfld. July 14, 1983 L. P. Grey; **22** female Kettle Lake Ont. Aug. 1, 1972 W. Gregory; **23** female Oscoda Co. Mich. July 12, 1944 D Eff.

Figures 24-29. 24-25 *S. hesperis brico*: **24** holotype male **25** allotype female, both Castle Creek Forest Service Rd. km 23.5, Cariboo Mts. (25 air km due S of McBride), B.C, June 18, 1995, coll. N. Kondla. **26-29** *S. hesperis electa* ("*nikias*"): **26** male Rabbit Ears Pass, Routt Co. Colo. July 7, 1989 J. Scott; **27** male 5 mi. N Chama, Rio Arriba Co. New Mex., July 23, 1979 G. Scott; **28** female NW Minturn, Eagle Co. Colo. Aug. 22, 1964 J. Scott; **29** female Peñasco Amarillo, 10600', Rio Arriba Co. New Mex. July 24, 1979 G. Scott.



Figures 30-33 *S. hesperis ratonensis*, Raton Mesa, Colfax Co.
New Mex. J. Scott: **30** July 21, 1972; **31** July 4 1973; **32-33** Aug. 24 1979.

Figure 34, *S. hesperis schellbachi* mature larva, Saddle Mtn.
area, Coconino Co. Ariz., S. Spomer.

Fig. 35, *S. hesperis nausicaa* 6th-stage Arizona, S. Spomer: Oak Creek Can., Coconino Co. Ariz. (left), 1995; White Mts., Ariz. (right), 1996 [right photo added in 2014]).

Fig. 36 *S. hesperis capitanensis* mature larva (two photos), N Ruidoso, Monjou Lookout Rd., Lincoln Co. New Mex., S. Spomer (right photo added in 2014).

Fig. 36a *S. hesperis dorothea/ nausicaa* mature larva, Tsaile Creek, Chuska Mts. Ariz., 1999, S. Spomer. (photo added in 2014)

Fig. 37, *S. hesperis beani* 6th-stage larva, 3.4 mi W Wilmer, SE BC, S. Spomer.

Fig. 38, *S. hesperis beani* 6th-stage larva, between Ft. Steele and Bull River, near Fernie, B.C., S. Spomer.

Fig. 39, *S. hesperis lurana* mature larva, Pennington Co. S. D., 1994, S. Spomer.

Fig. 40a, *S. h. hesperis* mature larva, Rampart Range, Route 67, Douglas Co. CO, female July 19, 1996 by P. C. Hammond laid eggs in lab, reared by S. Spomer.

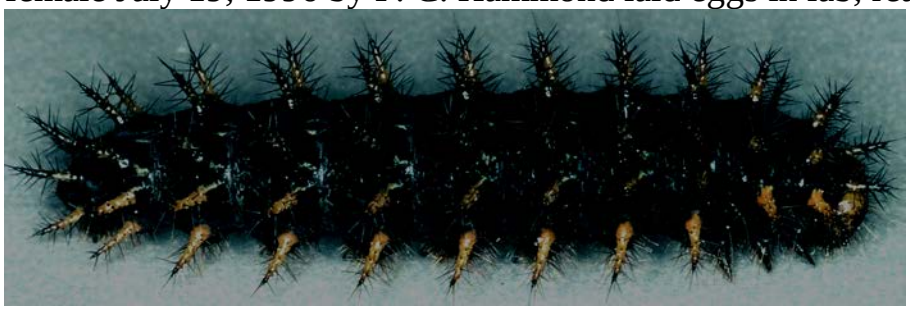


Fig. 40 b, *S. hesperis hesperis* mature larva, Tinytown, Jefferson Co. Colo., 1993, J. Scott (photo added in 2014).

Fig. 41a, *S. atlantis sorocko* mature larva, Rampart Range, Route 67, Douglas Co. Colo., female coll. July 19, 1996 by P. C. Hammond laid eggs in lab, reared by S. Spomer.

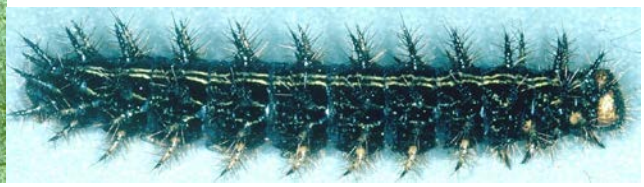


Fig. 41b, *S. atlantis sorocko*, N fork Clear Crk., Gilpin Co. Colo. June 14, 1989 J. Scott (photo added in 2014).

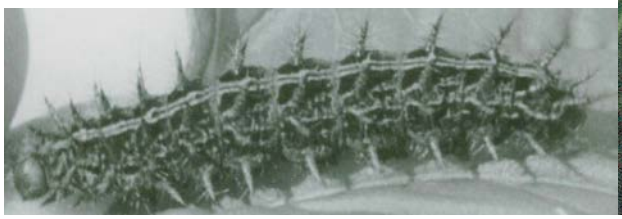


Fig. 41c, *S. atlantis sorocko* mature larva, Tinytown, Jefferson Co. Colo., July 1984 J. Scott (photo added in 2014).

Fig. 42a, *S. atlantis hollandii* 6th-stage larva, Duck Mtn. Provincial Park, Manitoba, 1994.

Fig. 42b, *S. atlantis hollandii* mature, Bonaparte Meadows,. Okanogan Co Wash., S Spomer (photo added in 2014).

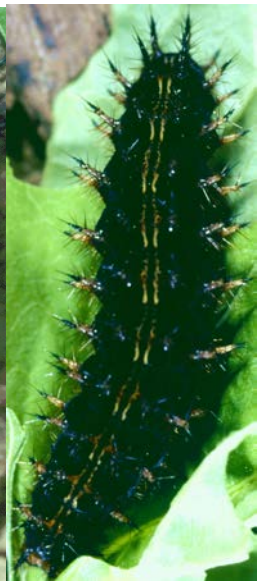


Fig. 43. *S. atlantis pahasapa* mature (darker), S.D., S. Spomer (photo added in 2014).

(Figs. 34-42 of larvae were re-scanned and improved in 2014, because the original 1998 figures were bad. The extra photos added one page, so there are 32 pages in this version, 31 in the original.)