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# *SPEYERIA ATLANTIS* IN COLORADO: REARING STUDIES CONCERNING THE RELATION BETWEEN SILVERED AND UNSILVERED FORMS

JAMES A. SCOTT
60 Estes Street, Lakewood, Colorado 80226

**ABSTRACT.** *Speyeria atlantis* in the SE Rocky Mts. occurs in two forms, silvered and unsilvered, that could be mere forms or separate species. Nine wild females laid eggs and produced adults in the laboratory. Offspring resembled mothers in most cases, except for two mothers about half silvered and one mother about one-third silvered that produced nearly unsilvered offspring. The two forms have the same courtship, without obvious courtship barriers between them, and male pheromones smell the same. Silvered and unsilvered adults have differently colored larvae. The two forms can differ in habitat, and adults actively select different habitats. The two are probably forms of the same species.

**Additional key words:** Nymphalidae, habitat selection, polymorphism, courtship.

The relation between silvered and unsilvered forms of *Speyeria atlantis* (Edw.) has puzzled many people (Scott 1986b). Thus Grey et al. (1963) discussed the two forms in the Black Hills of South Dakota, where the silvered form with chocolate ventral hindwing (*a. atlantis*) predominates in wet meadow areas, and the unsilvered form with reddish-brown ventral hindwing (*a. hesperis* Edw. = *a. lurana* dosP. & G.) prevails in drier areas. From a locality with 44% silvered adults, W. Evans (in Grey et al. 1963:146) reared 3 silvered offspring with chocolate ventral hindwing from silvered mothers with chocolate ventral hindwing, and 26 unsilvered plus at least 1 silvered offspring with a reddish-brown ventral hindwing from unsilvered mothers with a reddish-brown ventral hindwing. The exact number of mothers contributing was not known, but was probably one or two for each form. Evans noted that the double dorsal stripes were light brown on *atlantis* larvae, grayish white on *hesperis* larvae, and that *hesperis* pupae have more light-brown shading on the wing case than do *atlantis*. Grey et al. (1963) suggested that the two could be treated as separate species,

though they retained them in one species because they seem to intergrade in other western U.S. regions.

A similar situation occurs in SW Manitoba where a dark variety of silvered *a. atlantis* (*a. hollandi* F. & R. Cherm.) with chocolate ventral hindwing flies in mountains and forest, whereas a very pale silvered *a. dennisi* dosP. & G. usually with light-brown ventral hindwing flies on tallgrass prairie. They occur near each other. At Duck Mountain, adjacent populations show no intergradation (J. Troubridge pers. comm.). In this area, they behave as separate species, although westward they intergrade at Meadow Lake Park, Saskatchewan (Hooper 1973).

In Colorado E of the continental divide, the unsilvered form (*a. hesperis*) prevails in the mountain foothills, and as one goes higher in the mountains the silvered form (*a. atlantis*, = *a. electa* Edw.) gradually increases in frequency until it predominates in the Canadian Zone. Silvered forms in Colorado's Front Range usually have a chocolate-brown ventral hindwing, whereas unsilvered forms usually have a reddish-brown ventral hindwing, although this association sometimes breaks down; thus some silvered adults have a red-brown ventral hindwing, and some unsilvered ventral hindwing adults have a darker reddish-brown ventral hindwing. Females have a slightly darker ventral hindwing than males; a bilateral gynandromorph from Critchell, for instance, has a very red-brown ventral hindwing on the male side, a darker red-brown ventral hindwing on the female side.

The silvered or unsilvered color is due to light reflection from individual scales. Silver scales appear transparent through a microscope, but their surfaces reflect a white sheen (evidently due to structural interference of light) which causes the silver appearance. Unsilvered scales are cream in color because they appear to be filled with cream pigment, and their surfaces do not reflect light; their scale structure could be the same as silvered scales if the internal pigment blocks transmission of light through the scale to prevent light interference. So the difference between silvered and unsilvered scales could result solely from absence or presence of internal cream pigment. A given wing spot can be entirely cream (unsilvered), or it can be cream with a few silver scales, or the entire spot can be covered with silver scales. Potentially silvered spots occur in four series on the ventral hindwing: basal, postbasal, postmedian, and submarginal. In the basal series, the dot in the discal cell is more likely to have silver scales than the other spots. The postbasal series of spots is less likely to be silvered than the other series, and the basal and marginal series are most likely to be silvered in the mostly unsilvered forms.

To determine the relation between the forms in Colorado, I reared the eggs of selected females, especially those females of a form rare in

their population because these would have the greatest likelihood of mating with a male of the opposite form.

## REARING METHODS

To obtain eggs, females were collected from Colorado Front Range localities, brought to the laboratory, and placed in jars with *Viola nephrophylla* Green leaves and fed honey-water once per day. Most females lived about a week and laid several dozen eggs. Eggs hatch readily, but first-stage larvae diapause in nature, so to prevent diapause they were placed under constant light in tiny vials with a slice of green violet leaf. After a few days or weeks some larvae ended diapause and started to feed; these fed steadily until pupation on *V. nephrophylla* leaves. Three months were required to raise offspring of one female. Voucher specimens including larvae, pupal shells, and reared silvered and unsilvered adults are in the National Museum of Natural History, Washington, D.C.

## RESULTS

### Silvering of Mothers and Offspring

A total of 104 adult offspring were reared from 9 mothers from 6 Colorado sites. Each site is described below.

Tinytown (2120 m), Jefferson Co., is a Transition Zone foothills valley bottom with ponderosa pine, douglasfir, willow, alder, honeysuckle, etc., along the creek; the hostplants *Viola canadensis* L. and *V. adunca* Smith (Scott 1986a) are common on the shaded gulch bottom and the base of the N-facing slope. Here 92% of adults had a reddish-brown ventral hindwing with mostly unsilvered spots, 6% were partly silvered (N = 6 half silvered, N = 1 mostly silvered), and 2% were fully silvered with a chocolate-brown ventral hindwing (N = 117). If the fully silvered mother mated at random, the father was probably unsilvered; yet all offspring were silvered (Table 1).

Corwina Park (2120 m), Jefferson Co., is a Transition Zone foothills wooded gulch draining N; the hostplants *V. adunca* and probably *V. canadensis* are in gulch-bottom shade and E-facing shaded slopes. Here 91% of adults were unsilvered with a red-brown ventral hindwing, 9% silvered with a chocolate-brown ventral hindwing (N = 21). If the completely silvered mother mated at random, the father was probably unsilvered; yet all offspring were fully silvered (Table 1).

O'Fallon Park (2100 m), Jefferson Co., is near Corwina Park, and is also a Transition Zone foothills wooded gulch draining N with the hostplants *V. adunca* and *V. canadensis* in gulch-bottom shade and E-facing shaded slopes. Here 83% were unsilvered with a red-brown ventral hindwing, 13% silvered with a chocolate-brown ventral hind-

TABLE 1. Extent of silvering on ventral hindwing spots, and color of basal two-thirds of ventral hindwing, of mothers and offspring. Numbers are proportions: for example, "1" under "base" means all scales on wing base spots are silvered, "1/5" under "postmedian" means 20% of scales of postmedian spots are silvered, "0" under "submarginal" means no scales of submarginal spots are silvered, etc., "gyn" is bilateral gynandromorph, "f" is female, and "m" is male.

| Material | Sex | Ventral hindwing | Base | Postbasal | Postmed. | Submarg. |
|---|---|---|---|---|---|---|
| Tinytown, Jefferson Co., mother caught 20 July 1984 | | | | | | |
| Mother | 1 f | chocolate | 1 | 1 | 1 | 1 |
| Offspring | 27 m | chocolate | 1 | 1 | 1 | 1 |
| Offspring | 19 f | chocolate | 1 | 1 | 1 | 1 |
| Corwina Park, Jefferson Co., mother caught 13 July 1985 | | | | | | |
| Mother | 1 f | dark choc-brown | 1 | 1 | 1 | 1 |
| Offspring | 2 m | dark red-brown | 1 | 1 | 1 | 1 |
| Offspring | 2 f | choc-brown | 1 | 1 | 1 | 1 |
| Offspring | 1f | dark choc-brown | 1 | 1 | 1 | 1 |
| O'Fallon Park, Jefferson Co., mother caught 12 August 1985 | | | | | | |
| Mother | 1 f | red-brown | 2/3 | 1/5 | 1/2 | 1/2 |
| Offspring | 1 m | very red-brown | 0 | 0 | 1/4 | 1/3 |
| Offspring | 1 f | very red-brown | 0 | 0 | 0 | 1/5 |
| Offspring | 1 f | very red-brown | 2/3 | 0 | 0 | 1/2 |
| Critchell, Jefferson Co., mother caught 3 August 1985 | | | | | | |
| Mother | 1 f | red-brown | 1/2 | 1/10 | 1/2 | 1/2 |
| Offspring | 8 f | very red-brown | 0 | 0 | 0 | 0 |
| Offspring | 6 f | very red-brown | 0 | 0 | 0 | 0 |
| Offspring | 1 gyn | very red-brown | 0 | 0 | 0 | 0 |
| Mt. Judge female B, Clear Creek Co., mother caught 8 August 1985 | | | | | | |
| Mother | 1 f | red-brown | 2/3 | 1/3 | 1/5 | 1/3 |
| Offspring | 1 m | very red-brown | 0 | 0 | 0 | 1/6 |
| Offspring | 6 m | very red-brown | 0 | 0 | 0 | 1/10 |
| Offspring | 1 m | very red-brown | 0 | 0 | 0 | 1/5 |
| Offspring | 1 m | very red-brown | 1/10 | 0 | 0 | 1/5 |
| Offspring | 1 m | very red-brown | 1/5 | 0 | 0 | 1/10 |
| Offspring | 2 f | very red-brown | 0 | 0 | 0 | 1/10 |
| Offspring | 1 f | very red-brown | 0 | 0 | 0 | 0 |
| Cherry Gulch, Jefferson Co., mother caught 17 July 1984 | | | | | | |
| Mother | 1 f | red-brown | 2/3 | 1/5 | 0 | 1/3 |
| Offspring | 1 f | very red-brown | 1/4 | 0 | 0 | 1/3 |
| Mt. Judge female D, Clear Creek Co., mother caught 8 August 1985 | | | | | | |
| Mother | 1 f | dark red-brown | 1/5 | 0 | 0 | 1/2 |
| Offspring | 2 m | very red-brown | 0 | 0 | 0 | 0 |
| Mt. Judge female F, Clear Creek Co., mother caught 8 August 1985 | | | | | | |
| Mother | 1 f | red-brown | 1/5 | 0 | 0 | 1/10 |
| Offspring | 1 m | very red-brown | 0 | 0 | 0 | 1/10 |
| Offspring | 1 m | very red-brown | 1/10 | 0 | 0 | 1/5 |
| Mt. Judge female A, Clear Creek Co., mother caught 8 August 1985 | | | | | | |
| Mother | 1 f | red-brown | 0 | 0 | 0 | 1/5 |
| Offspring | 9 m | very red-brown | 0 | 0 | 0 | 0 |
| Offspring | 3 f | dark red-brown | 0 | 0 | 0 | 1/10 |
| Offspring | 1 f | dark red-brown | 0 | 0 | 0 | 1/6 |
| Offspring | 1 f | red-brown | 0 | 0 | 0 | 0 |
| Offspring | 1 f | red-brown | 0 | 0 | 0 | 1/6 |
| Offspring | 2 f | very red-brown | 0 | 0 | 0 | 0 |

wing, and 4% intermediate (N = 19). If the nearly half-silvered mother mated at random, the father was probably unsilvered; all offspring were nearly unsilvered (Table 1).

Critchell (2370 m), Jefferson Co., is a shaded E–W streamside in the upper Transition Zone foothills, with ponderosa pine, douglasfir, various shrubs, grassy glades, and *V. canadensis* and *V. adunca*. Here 88% were unsilvered with a reddish brown ventral hindwing, 7% fully silvered, and 5% intermediate (N = 2 half silvered, N = 1 mostly silvered) (N = 53). If the nearly half-silvered mother mated at random, the father probably was unsilvered; all offspring were completely unsilvered (Table 1).

Cherry Gulch (2100 m), Jefferson Co., is a Transition Zone foothills gulch at the base of a N-facing slope covered with douglasfir, *Holodiscus, Physocarpus,* other shrubs, and *Viola canadensis.* Here 97% were unsilvered with a reddish brown ventral hindwing, 3% silvered with a brown ventral hindwing (N = 69). If the mostly unsilvered mother mated at random, the father was probably unsilvered; the single offspring was less silvered than the mother (Table 1).

Mt. Judge (2 km NE, 2770 m), Clear Creek Co., is a Canadian Zone valley bottom, with forest (spruce, pine, douglasfir, some aspen) beside grassy meadows, a tiny creek on the valley bottom, and *V. canadensis* and *V. nephrophylla*. Silvered adults with a chocolate ventral hindwing were most common, with a few silvered adults with a reddish brown ventral hindwing; but unsilvered adults with a red-brown ventral hindwing were also found, a few unsilvered adults with a brown ventral hindwing, and a few variably silvered intermediates. The upperside black lines vary from narrow to wide independent of ventral hindwing variation. Shape of silver spots varies between individuals, as does amount of black at the base of each silver spot, but this variation is also independent of degree of silvering. Four females from this site labeled A, B, D, and F, produced offspring (Table 1). If the Mt. Judge mothers mated at random, they probably mated with silvered males because 74% of males here were silvered (Table 2). However, because of habitat selection at this site (described in next section), and because all four mothers were found in mixed woods away from the creek where only 38% of males were silvered (Table 2), the mothers probably mated with unsilvered fathers. Mother B was about one-third silvered; her offspring were almost completely unsilvered. Mothers A, D, and F, and their offspring, were almost completely unsilvered.

## Habitat Selection and Movements

The Mt. Judge site displayed habitat selection by the forms (Table 2). In several meadows along the tiny creek 90% of adults were silvered,

TABLE 2. Frequency of color forms at Mt. Judge site, based on nine visits 1984 to 1987.

| Silvering | Mixed woods away from creek | | Meadows along creek | |
|---|---|---|---|---|
| | No. male | No. female | No. male | No. female |
| Mostly unsilvered | 24 | 13 | 11 | 2 |
| Half silvered | 1 | 0 | 1 | 0 |
| Completely silvered | 15 | 8 | 72 | 53 |

10% unsilvered. In contrast, at the habitat edge near the head of the valley, away from the creek in mixed woods–tiny meadows edging the large meadow and in the adjacent meadow-edge, one-third (38%) of adults were silvered, and two-thirds (62%) unsilvered.

A small mark-recapture study was conducted at Mt. Judge in 1987 (31 July, 5, 9 Aug.), in which 33 adults were marked and 16 recaptured. Six unsilvered adults were marked (2 male, 4 female), and 3 females recaptured, all in the mixed woods, one after 5 days. Twenty-seven silvered adults were marked (14 male, 13 female), and 13 recaptured (7 male, 6 female), after up to 9 days, including 5 moves completely across the habitat, and 6 halfway across it. I conclude that silvered adults move completely about the habitat, and females probably oviposit in the mixed woods where host violets grow under conifers. But judging from the restricted distribution of unsilvered adults (Table 2), these are more local, and their restricted movement causes the habitat selection difference. In general, unsilvered Colorado adults prefer open woods with violets (N-facing slopes and gulch bottoms in the foothills), whereas silvered adults also occupy more open wet valley bottoms.

### *Pheromones*

Male odor of both forms from Mt. Judge was compared by the author. Males of silvered and unsilvered forms smelled the same: the odor is sweet but has a "hot" or "peppery" sensation, sweet but slightly peppery pungent. Virtually every male had this odor, a few weaker than others. Females lacked an odor. The description of odor is subjective, and different observers might use different words to describe it, but it was the same for both forms. Thus, the male pheromone is probably the same in both forms, although the human nose certainly cannot match the precision of laboratory instruments.

The pheromone system is complex. Males have androconial scales on dorsal wing veins (Scott 1986b:fig. 37) which evidently produce the pheromone odor; pheromone from these scales in the closely related European *Argynnis paphia* L. causes the female to land and accept the male (Magnus 1958). Females have a dorsal gland between abdomen segments 7 and 8 (Scott 1986b:fig. 37). This gland in *A. paphia* produces

a pheromone that attracts males: femalelike dummies attract males but do not elicit complete courtship, and freshly killed females are more attractive to males than dried females (Magnus 1958); virgins respond to nearby males by exposing the abdomen gland and aiming the abdomen tip toward the male (Treusch 1967). Males have a paired gland on the abdomen tip (Arnold & Fischer 1977, Scott 1986b) which, by comparison with Heliconiini (Scott 1986b), could possibly transfer pheromone to the female during mating to enable mated females to produce a third pheromone that repels males.

### *Courtship*

Courtship of *Speyeria atlantis*, which is nearly identical to that of *Argynnis paphia* (Magnus 1950), was described by Scott (1986b) based mainly on unsilvered form courtships in Jefferson Co., Colorado. In addition, a completed courtship between silvered male and female forms was seen at Mt. Judge: female on flower when male sighted her and landed; she fluttered her mostly spread wings with small amplitude for 1 s, he flicked his nearly closed wings behind her for 1–2 s; she rotated around flower top 1 revolution with her wings still spread while he rotated after her and flicked his nearly closed wings once during turn; she stopped, closed her wings, tilted forward so that her abdomen was raised slightly but lowered from between hindwings; he spread his wings partway; they joined.

Four courtships were seen at Mt. Judge between unsilvered males and silvered females, as follows.

1) Male patrolled near female (prior mating status unknown) on flower, landed, flicked wings (wingtips vibrating 0 to 1 cm apart about twice per s) for 10 s, curved abdomen laterally to attempt joining (meanwhile female, wings closed, leaned forward with abdomen lowered from between closed hindwings and abdomen raised above horizontal about 60°); wind blew them and he flew, fluttered over her for 1 s, landed, flicked beside her 10 s, curved his abdomen but was too close and his abdomen tip missed (during his bending she kept abdomen exposed), then he flew away. Female was evidently receptive because she exposed her abdomen and did not perform rejection dance (fluttering wings vigorously).

2) Male patrolled near silvered virgin (later found to have no spermatophores) on flower, landed, flicked his wings, she crawled away with closed wings, he crawled after her for 5 min while flicking and bending his abdomen, she stopped and spread wings partly while he flicked and curved abdomen to attempt mating for 5 min, he flew away (evidently she did not extrude genitalia, so he could not join). She was unreceptive even though she did not flutter her wings, perhaps because, as judged from weak flight, she was too young.

3) He pursued her in flight, they landed, she fluttered slightly and crawled away while he flicked his wings and crawled behind, she got farther away, he flew up a short distance but did not find her and flew away.

4) She raised her wings and slightly lowered and partly extruded her abdomen while he flicked his nearly closed wings behind her, he flew away after about 30 s.

Data on courtship between forms are too few to be conclusive, but no obvious courtship barriers to mating occur. Releases of reared virgins are needed. Grey et al. (1963) inconclusively report abnormal courtship of a few laboratory adults.

## *Larval Differences* (Figs. 1–14)

Color photographic slides were made of larvae and pupae from each study site except larvae from Corwina, and some larvae and pupae were preserved to correlate their color pattern with adult appearance.

From a distance, older larvae producing silvered adults (Figs. 5, 7–9) appear mottled black with orangish tan spines and two middorsal white lines, whereas older larvae producing unsilvered adults (Figs. 10–14) appear solid black with orange spines. Viewed more closely, larvae of both forms are basically black, with a pair of middorsal whitish lines 1 mm apart, and three rows of scoli (lateral to middorsal lines, supraspiracular, and subspiracular) which are tan or orange with black tips. The head of both forms is black with the dorsal half of the rear half of the head orangish.

Larvae of the silvered form (based on larvae from Tinytown, Figs. 5, 7–9) have the middorsal whitish lines conspicuous and mostly continuous, though alternately wider and narrower. Because Corwina pupae had less conspicuous lines than Tinytown pupae, Corwina larvae may not have had the lines this conspicuous. Scoli of the silvered form are orangish tan with black tips. Ground color is not as black as in the unsilvered form so three rows of black bands with very sinuous narrowly white edges are recognizable: along the dorsalmost scoli (edging middorsal white lines), along the supraspiracular scoli, and in between these (Figs. 8, 9). A light gray-brown transverse band circles the rear of each segment except middorsally, a remnant of the pale transverse stripes of *Speyeria nokomis* (Edw.) larvae (Scott & Mattoon 1981).

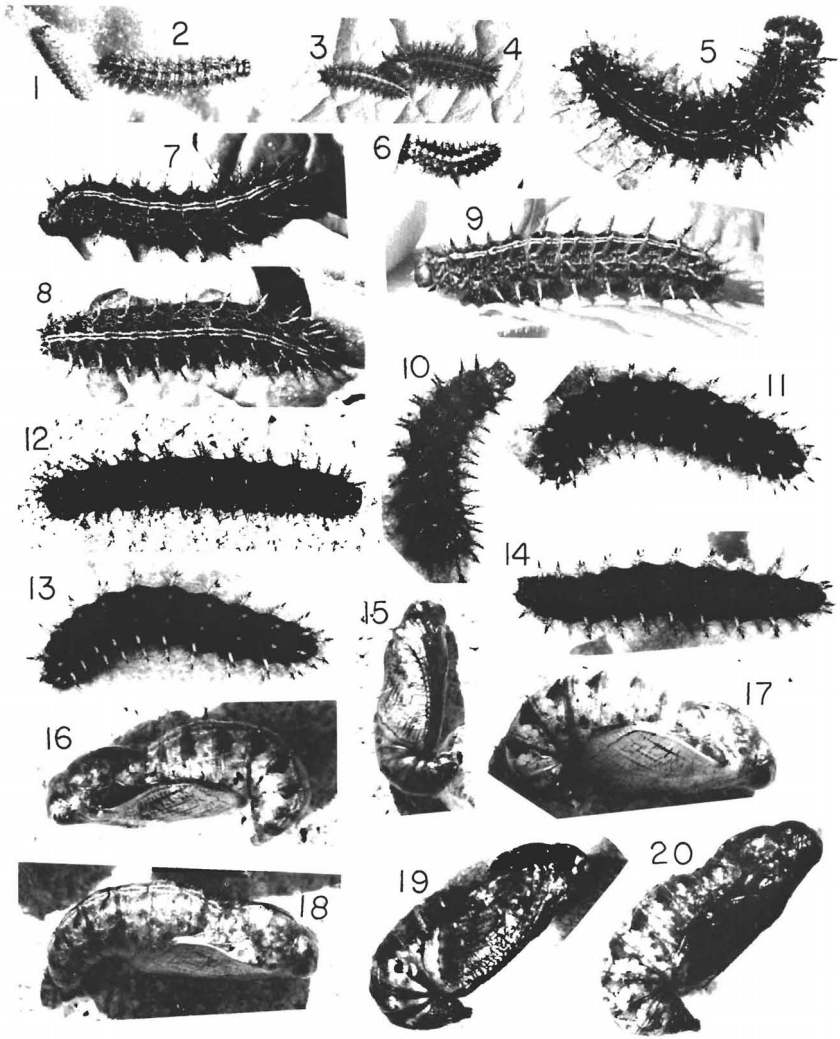
Larvae of the unsilvered form (from O'Fallon, Critchell, Cherry Gulch, Mt. Judge) are a little darker black and the pattern is obscured, so the black sinuous bands are unrecognizable without a microscope, and the middorsal two lines are fainter and broken into two dashed lines (Figs. 10–14). Scoli are orange with black tips. The only variation between localities among unsilvered larvae involves the single Cherry Creek larva which had slightly less orangish scoli. Edwards' (1888b) description of the unsilvered form is very similar.

The above descriptions of larvae do not correspond with descriptions of larvae of the silvered and unsilvered forms in the Black Hills of South Dakota (Grey et al. 1963). Both are described as identically black with orange spine shafts, the two middorsal lines grayish white in the unsilvered form, light brown in the silvered form. Thus the two middorsal lines are described as whiter in the unsilvered form in South Dakota, whereas they are whiter in the silvered form in Colorado. My descriptions are based on 104 larvae and dozens of color slides from many sites, whereas the South Dakota data are fewer.

Width of the two pale middorsal lines of the larva is apparently not closely linked to degree of silvering of the adult; among larvae producing silvered adults, the whiteness differed somewhat between the Tinytown and Corwina sites in Colorado as noted above, and differed between Colorado and South Dakota adults.

Thus, both larvae and adults of the unsilvered form have more pigment—more cream in adult scales, more orange on larval spines, more black on larval body—so one can guess that the gene responsible for the unsilvered form causes an increased deposition of some dark pigment such as melanin.

Larvae and pupae of silvered ventral-hindwing *S. atlantis* from NE




FIGS. 1–20. **1,** First-stage larva, silvered form, Tinytown; **2,** Second-stage larva, silvered form, Tinytown; **3,** Third-stage larva, silvered form, Tinytown; **4,** Fourth-stage larva, silvered form, Tinytown; **5,** Fourth-stage larva, silvered form, Tinytown; **6,** Third-stage larva, silvered form, Tinytown; **7,** Mature larva, silvered form, Tinytown; **8,** Mature larva, silvered form, Tinytown; **9,** Mature larva, silvered form, Tinytown; **10,** Third-stage larva, unsilvered form, O'Fallon female C; **11,** Mature larva, unsilvered form, O'Fallon female C; **12,** Mature larva, unsilvered form, Cherry Gulch; **13,** Mature larva, unsilvered form, Mt. Judge female F; **14,** Mature larva, unsilvered form, Mt. Judge female A; **15,** Pupa (orange-brown wings), silvered form, Tinytown; **16,** Pupa (orange-brown wings), silvered form, Tinytown; **17,** Pupa (orange-brown wings), silvered form, Tinytown; **18,** Pupa (orange-brown wings), silvered form, Tinytown; **19,** Pupa (partly orange-brown wings), unsilvered form, O'Fallon female C; **20,** Pupa (black wings), unsilvered form, Mt. Judge female F.

U.S. (Edwards 1888a) are grayer than Colorado-South Dakota *S. atlantis*; larvae and pupae evidently show geographic variation as do adults.

### *Pupal Differences*
(Figs. 15–20)

Pupae from localities with sufficient numbers show great individual variation, but there is no obvious important difference between silvered and unsilvered forms. The pupa resembles *S. nokomis* (Scott & Mattoon 1981) in general, but is darker (orange-brown), and the posterior half of each abdominal segment is darker because it is mottled with tiny black dots and dashes. The anterior half of each abdominal segment is not uniformly black as in *nokomis*: some pupae have a broad black irregular band, but most have the black areas broken into spots, including triangular spots just beside the anterior-pointing orange-brown middorsal triangles on segments 5–7. Pupae from Tinytown have two sinuous tan middorsal abdominal lines, but pupae from Corwina (both sites produced silvered adults) and the other sites had weak tan middorsal lines. Pupal wing color varies from mostly black to almost wholly orange-brown, but most are mostly orange-brown, a few black-winged.

Grey et al. (1963) describe the pupal wing cases of silvered forms as darker with less light brown mottling than those of unsilvered forms in the Black Hills. However, they reared only three silvered adults, so the difference is probably due to small sample size because all Colorado sites with large samples show considerable variation in pupal wing color. Pupae producing silvered adults are not darker in Colorado.

## DISCUSSION

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as distinct species: they often fly together, they prefer different microhabitats, amount of silvering seems usually linked with ventral hindwing color, mothers usually produce offspring resembling themselves, and their larvae differ. If scientists were aware only of Black Hills populations, the two would certainly be treated as separate species because they are so distinct there. Some anecdotes (coincidences?) also fit the two-species theory. For instance, six unsilvered males and one silvered pair were found in the Mt. Judge mixed woods 28 July 1987, the silvered pair in copula.

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as one species:

1) Silvered and unsilvered forms are linked by a complete series of intermediate adults, from slightly to partly to half to mostly silvered, although only slightly silvered intermediates are common.

2) Unsilvered mothers sometimes produce silvered offspring (Grey et al. 1963:146), and half-silvered mothers often produce unsilvered offspring (Table 1).

3) In many populations, silvered forms are rare (<5%) as in the lower foothills of the Colorado Front Range, rarity a true species might have difficulty surviving. The reverse is also true, in which unsilvered forms are rare within silvered populations, as in the wet center of the Black Hills (Grey et al. 1963). However, *S. coronis* (Behr) is just as rare and it survives.

4) Frequencies of the forms show clinal trends, both altitudinally in the Colorado Front Range, and along habitat gradients. For instance, in the Black Hills (Grey et al. 1963), *atlantis* is common in wet meadow habitats on poorly drained granite, and is rarer away from these areas. Similarly, in S Colorado (Scott & Scott 1980) *hesperis* predominates in the lower foothills, both forms occur in dry areas at higher altitude, and *atlantis* predominates in three wet meadow enclave habitats at middle altitudes: Coaldale in Arkansas Canyon, Fremont Co.; SW of Westcliffe on Wet Mountain Valley floor, Custer Co.; Stonewall in upper Purgatoire River valley, Las Animas Co. Such enclaves have not been found in the Front Range W of Denver, where silvered forms are rare in the foothills and increase in frequency with altitude until they predominate in the upper Canadian Zone.

5) When attempts are made to divide *S. atlantis* into silvered and unsilvered "species", their distributions are incongruous because unsilvered forms cut an E–W swath through the range of silvered forms, replacing them in the process (Scott 1986b).

The silvered-unsilvered division also fails to solve the problem of sympatry of *S. a. dennisi* and *S. a. atlantis* (*hollandi*), both of which are silvered, in Manitoba. A species *S. dennisi* could include *S. atlantis ratonensis* Scott from NE New Mexico and *S. a. greyi* from NE Nevada, but *dennisi* is said to intergrade W to *atlantis* in Saskatchewan-Alberta, and *greyi* intergrades with *dodgei* in S Idaho (P. C. Hammond pers. comm.), and at least *greyi* seems independently evolved toward similar pallidity.

6) Other *S. atlantis* subspecies have polymorphisms of silvered-unsilvered adults: *wasatchia* dosP. & G. (=*tetonia* dosP. & G.) in W Wyoming-Utah is usually unsilvered, *chitone* (Edw.) in S Utah and *schellbachi* Garth in N Arizona are usually silvered.

7) Other species of *Speyeria* have silvered-unsilvered polymorphisms: *zerene* (Bdv.) in California and S Oregon, *callippe* (Bdv.) in N California and the Sierra Nevada, *egleis* (Behr) in the Sierra and Utah, *hydaspe* (Bdv.) in British Columbia. These polymorphisms are accepted by lepidopterists. Boggs (1987) hypothesized that rare unsilvered *S. mormonia* are homozygous recessives that fail to reproduce, which is dubious because *S. mormonia artonis* (Edw.) are nearly always unsilvered.

8) Association between ventral hindwing color and silvering and larval color pattern breaks down geographically. In the Black Hills and E of the continental divide in the Colorado mountains, silvered adults have a chocolate-brown ventral hindwing (darker in the Black Hills), and unsilvered adults usually have a reddish brown ventral hindwing. However, in N-central New Mexico, 98% of adults (N = 60) are silvered but the ventral hindwing varies from chocolate- to reddish brown. In SW Manitoba *S. atlantis dennisi* and *S. a. atlantis* (*a. hollandi*) are 100% silvered but the ventral hindwing is usually light brown in the former and chocolate-brown in the latter. And silvered adults have the ventral hindwing browner in the Black Hills than in the Colorado Front Range. Larval differences in Colorado are partially reversed in the Black Hills, and larvae are grayer in E North America.

The conclusion that silvered and unsilvered adults are polymorphic forms of one species seems preferable.

## Paleogeography

The current geographic distribution of wing characters suggests that the dark silvered form (*S. a. atlantis*) occupied the coniferous forest in N U.S. and the Rocky Mountain foothills during the Ice Age; afterwards

it moved higher in altitude and latitude. The unsilvered form with reddish brown ventral hindwing (now *S. a. hesperis, a. wasatchia, a. irene* [Bdv.]) occupied open forest in the southern Great Basin lowlands; after the Ice Age it spread N into the mountains, E through lowland S Wyoming to the Black Hills, and S along the Colorado mountain foothills. The silvered form with narrower black lines and a pale brown ventral hindwing (now *S. atlantis dennisi* and *a. ratonensis*) occupied aspen parkland in the current S Great Plains or central Texas; after the Ice Age it spread, respectively, N to Canada, and upward to a mountain mesa. The forms became sympatric after the Ice Age.

## Mechanism of Inheritance

The inheritance mechanism of silvering is unknown. Rarity of half-silvered adults suggests dominance, but some broods with half the offspring silvered and half unsilvered should occur but did not. If half-silvered adults were heterozygotes, they would not produce all-unsilvered broods as at Critchell. If silvered is dominant, rare silvered mothers would be likely to produce silvered offspring, as at Tinytown and Corwina. O'Fallon and Cherry Gulch broods perhaps suggest modifier genes that cause part-silvering.

Maternal inheritance seems the best guess now, and fits all the reared broods; offspring would resemble the mother, the father having no effect or perhaps merely modifying partly silvered offspring. Sterling O. Mattoon (pers. comm.) states that *Speyeria* offspring generally resemble their mother very closely, although some silvered offspring have been reared from unsilvered mothers and vice versa.

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