

EVIDENCE FOR OBLIGATE MONOPHENISM
IN *RELIQUIA SANTAMARTA*,
A NEOTROPICAL-ALPINE PIERINE BUTTERFLY
(LEPIDOPTERA:PIERIDAE)

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INTRODUCTION

The phenomenon of seasonal polyphenism under photoperiodic control is now well established in a variety of butterflies, especially members of the family Pieridae (Shapiro, 1976a). Although it is expressed in nature primarily by multivoltine populations at low to middle altitudes in strongly seasonal mid-latitude climates, polyphenism has been found in a latent form in univoltine species which are ordinarily monophenic. These include species coevolved with vernal-ephemeral host plants (*Pieris virginiensis* Edwards, Shapiro, 1971; *P. napi microstriata* Comstock, Shapiro, 1975a) or facing short growing seasons due to altitude (*Pieris occidentalis calyce* Edwards, Shapiro, 1974) or latitude (*P.o. nelsoni* Edwards, Shapiro, 1975b). To date no population of either the *Pieris callidice* Hübner or *P. napi* Linnaeus complexes has been found to be obligately monophenic, although some *P. napi* (Yukon Territory and central New Mexico, Shapiro, 1976a) produce only more-or-less heavily dark-veined phenotypes. The ability of univoltine Pierines to produce phenotypes analogous to normal seasonal ones produced by their multivoltine relatives, when reared in photoperiod-temperature regimes which do not occur in their natural habitat, has been interpreted (Shapiro, 1976a) as evidence for the derivation of univoltinism/monophenism from multivoltinism/polyphenism in the course of adaptation to new or changing climates.

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Reliquia santamarta Ackery is an unusual Pierine of uncertain affinities which is known only from above 3500 m in the Sierra Nevada de Santa Marta of northeastern Colombia. It was discovered in 1971 and described four years later (Ackery, 1975). Phenotypically, the adult closely resembles high-altitude and -latitude members of the Holarctic *Pieris callidice* complex (figs. 1, 2) and is unlike the distinctive Andean montane and alpine Pierines (*Tatochila*, *Phulia*, *Piercolias*). In those genera the submarginal black chevrons on the hindwing above and below point outward in the interspaces. In Holarctic *Pieris* and in *R. santamarta* they point inward. Morphologically *R. santamarta* is also close to *Pieris*, and indeed would be included therein under the traditional broad concept of the genus, which is beginning to break down (Kudrna, 1974). These facts suggest that *R. santamarta* might represent a relict of a Holarctic stock of the *P. callidice* complex which invaded northern South America during a cold period, presumably in the Pleistocene. The Sierra Nevada de Santa Marta, although only 62 km from the Serrania de Valledupar which connects to the northern Andes, shows a very high degree of faunal and floral endemism. The entomologist who knows it best, Michael Adams, is convinced (1973, 1975, and personal communications) that its butterfly fauna had not begun differentiating before the eastern Andean orogeny — thus precisely contradicting the hypothesis of Todd and Carriker (1922) of an eastern Andean origin for the Sierran alpine avifauna — and that certain groups speciated and underwent character- and altitudinal displacement in the Pleistocene. A.S. Weston (personal communication) has noted a floristic connection between the Sierran páramos and those of Costa Rica. At least one butterfly, *Nathalis iole* Boisduval (Pieridae, Coliadinae) is perhaps a Nearctic relict in the Sierra Nevada de Santa Marta.

R. santamarta has been recorded from both dry seasons, the “verano” (“summer”; actually trade-wind season) in December-March and the shorter and less reliable “veranillo” in July — these being the only times of the year when weather conditions in the high Sierra would make butterfly collecting feasible. No phenotypic differences are apparent among the putative broods. This is perhaps not surprising. Pierines in middle latitudes respond phenotypically to daylength, but the Sierra lies at a latitude of 10°44' N, and the longest and shortest days of the year there differ in length by only about 70 minutes. The literature is devoid of photo-

periodic studies of circumequatorial insects, except for one paper by McLeod (1968) who excluded photoperiod as a factor in the seasonal polyphenism of an African Nymphalid. If, however, *Reliquia santamarta* were a Pleistocene derivative of the *Pieris callidice* complex, it might be expected to show a latent polyphenism when reared under a laboratory regime that induces light phenotypes in that group. Long days, particularly continuous light, coupled with high temperatures are very effective in this regard (Shapiro, 1976a).

MATERIALS AND METHODS

Eight females of *R. santamarta* were collected January 18–22, 1977 at and near the type locality (headwaters of the Río Cambirumeina and south slope of Cerro Icachui, 3950–4400 m). They were induced to oviposit in camp by confining them in sunlight in cylindrical tins 9.5×10.5 cm, covered outside with white glazed paper and topped with gauze, containing fresh sprigs of local Crucifers as oviposition substrates and Composite flowers as nectar sources. One female was a virgin, but all the others laid at least a few eggs. Eggs were placed on the plants, the gauze, and the tins. They were transported by ground to Valledupar, Department of Cesar, on January 26 and thence by air to Cali, Department of Valle del Cauca, the next day, where the first hatch occurred in the afternoon. Rearing was carried out in Cali on continuous light from a 60w bulb in plastic Petri dishes $18 \text{ cm} \times 3 \text{ cm}$ on fresh sprigs of the Crucifer *Lepidium virginicum* L. collected from a vacant lot; this common weed has often been used in experiments with Pierines and is a frequent wild host of North American members of the *callidice* group. The rearing temperature was $26.5^\circ \pm 2^\circ \text{ C}$. These conditions would induce light phenotypes in any Nearctic member of the *callidice* group which has been tested.

Due to electricity rationing in Colombia, it was necessary to substitute a powerful candle for the lamp from 1800 to 1900 hours daily throughout the rearing period. My impression, based on previous work with Pierines, is that this was read as “day” by the animals. Even if it was read as “night,” a 23-hour photophase has always been read as a “long day” by Nearctic species.

R. santamarta proved difficult to rear under the experimental conditions in Cali. The culture started well, but about half the larvae died in the penultimate and ultimate instars of apparent

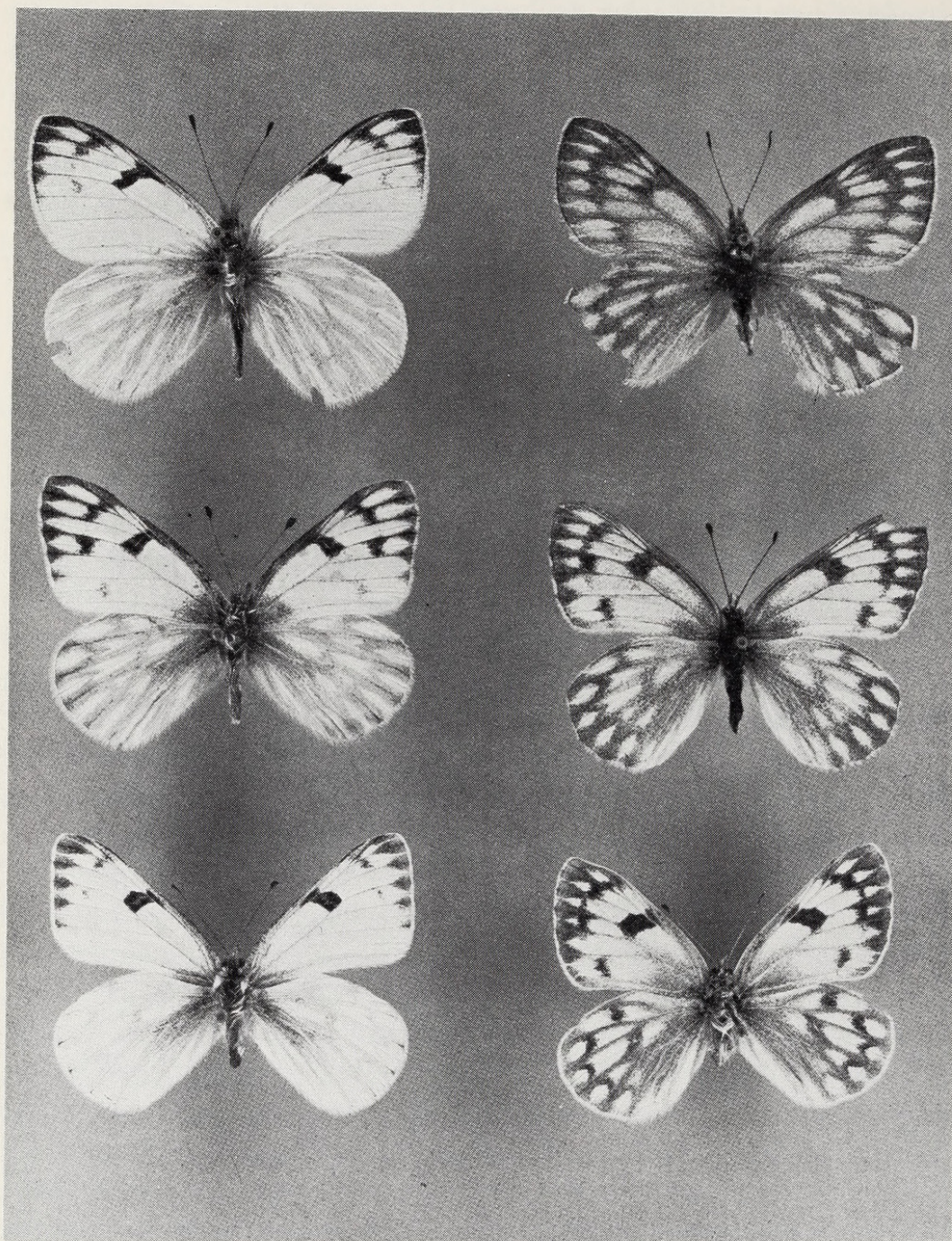


Figure 1. Dorsal surfaces of three Pierines from extreme climates, males at left. Top row: *Reliquia santamarta*, 4200 m, Sierra Nevada de Santa Marta, Colombia, 10°44' N. Centre: *Pieris occidentalis* "calyce," 3640 m, Colorado front range, USA, 40°01' N. Bottom: *Pieris occidentalis nelsoni*, Fairbanks, Alaska, 64°51' N.

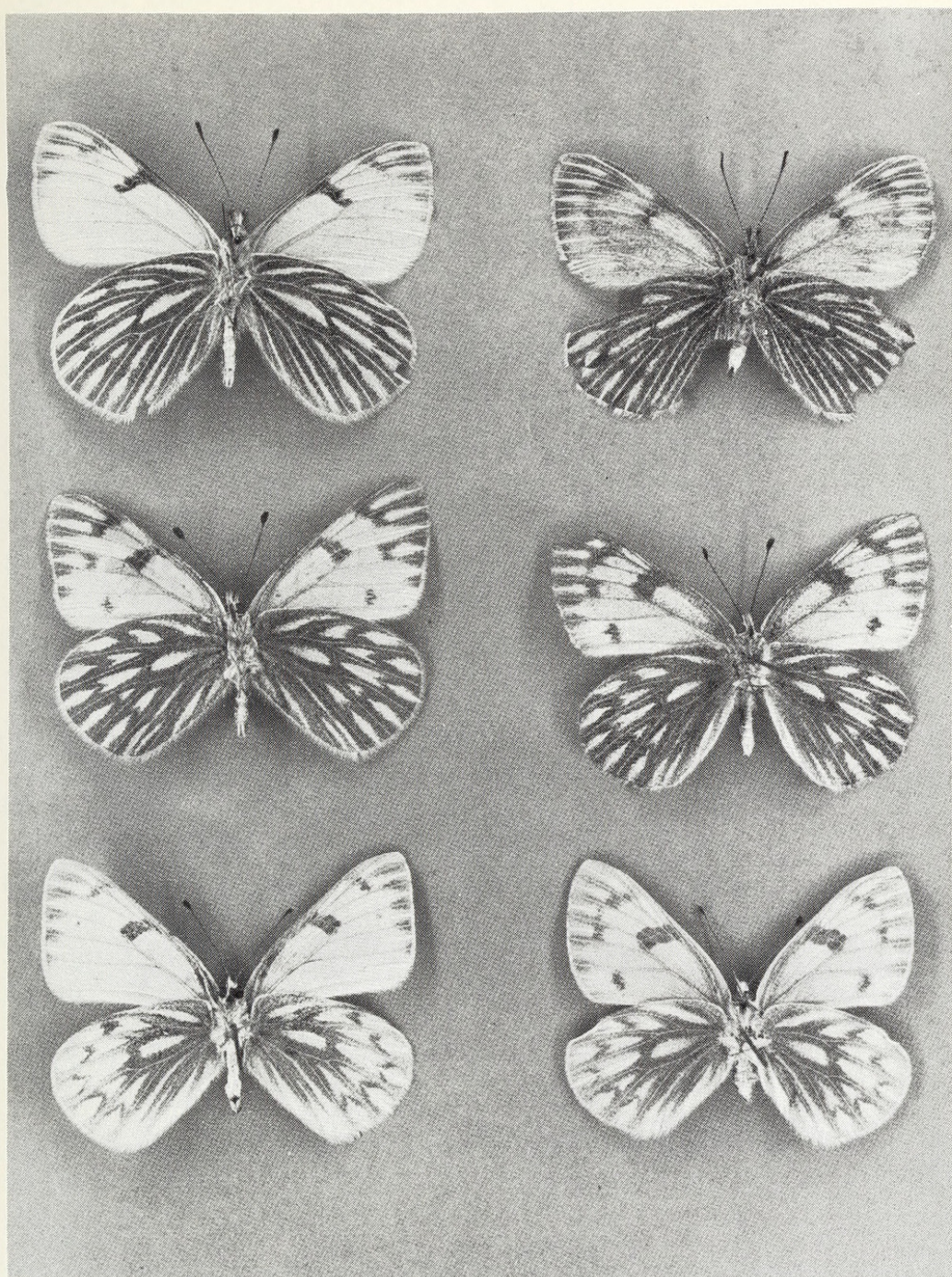


Figure 2. Same as figure 1, ventral surfaces.

bacterial septicemia, despite stringent sanitation and daily replacement of the host plant. Ultimately 16 pupae were obtained, but 9 of these died without showing development. The remaining 7 pupae proceeded rapidly to the pharate adult, but failed to eclose. On February 15 they were all dissected to determine the phenotypes of the pharate adults — an easy and reliable procedure. Examples of the early stages were preserved and the life-history will be described elsewhere.

RESULTS AND CONCLUSIONS

All of the pharate adults (5 males, 2 females) were in good enough condition for the ventral hindwing phenotype to be determined (one female had to be degreased). All were completely normal, with the dark ventral pattern precisely as it occurs on wild specimens from the mountains.

Despite the small sample size, the use of the candle, and the overall logistical difficulty of the experiment, this is a definitive result since the phenotypes were so consistent and because no known Nearctic Pierine reared under the same conditions would have given the same result. Obviously we cannot exclude the possibility of a latent polyphenism, but it is made much less probable by the demonstration that it cannot be exposed under the most effective rearing regime known for that purpose. Since no Nearctic species yet tested has so canalized its phenotype, the likelihood that *R. santamarta* is a close relative of the species it most resembles is diminished.

Why lose the potential for polyphenism? There is no obvious selective advantage in doing so. In Holarctic populations it is merely submerged when selection for an appropriate phenology alters photoperiodic thresholds. This is especially easy in taxa in which phenotype is somehow coupled to pupal diapause, since all diapaused pupae will yield dark adults. We do not know if *R. santamarta* is capable of diapause; certainly it would make sense during the wettest months (October and November), but we do not know what the environmental cues might be. At any rate, the animals collected in January 1977 were in very mixed condition, suggesting overlapping broods during the "verano." As noted before no sign of seasonal phenotypes has been detected even though

some of these adults would have been from diapause pupae if there are any such. We know from the experiment what non-diapause animals look like.

The dark-veined phenotype is undoubtedly optimal at all seasons at Cambirumeina. In the two dry seasons the normal weather is clear in the morning and foggy in the afternoon. Night temperatures drop below freezing; before the fog asserts itself the temperature may climb to 18° C, but then it drops to 5–7° C and remains there until after nightfall, when clearing occurs. During my stay fog set in from 1000 to 1400 hours on different days, i.e. from 2 to 6 hours after the initiation of flight activity. This was at the sunniest time of the year; during the rainy seasons the temperature probably hovers between 2° and 6° C most of the time, and sunshine occurs only fleetingly. The *R. santamarta* phenotype is of a sort known to be thermoregulatorily used by Nearctic Pierines (Shapiro, 1975c, 1976a) and the behavior of *R. santamarta* afield precisely matches theirs (Shapiro, 1977). *Pieris occidentalis* "calyce" Edwards in the Colorado front range has the same kind of weather during its flight season in August and matches *R. santamarta* in pattern, almost scale for scale. However, it retains a latent polyphenism (Shapiro, 1974, 1976b).

It is, of course, possible that the phenotype of *R. santamarta* is merely convergent to *Pieris*, and that no polyphenism has ever existed in its ancestry. If this is the case, the phylogeny of the Pierini is more confused than ever, and *R. santamarta* has no known close relatives.

SUMMARY

Reliquia santamarta is a multivoltine Pierine butterfly from above 3500 m in the Sierra Nevada de Santa Marta, Colombia, latitude 10°44' N. Its single natural phenotype is extremely similar to the high-altitude and -latitude members of the Holarctic *Pieris callidice* complex. When reared on continuous light at 26.5° ± 2° C, *R. santamarta* produced only its usual dark-veined, presumably thermoregulatory phenotype. In this regard it differs from all previously tested, Holarctic Pierines, which display latent polyphenism attributable to their evolution from multivoltine, phenotypically plastic ancestors. The seeming lack of a latent polyphenism in *R. santamarta* casts doubt on the close affinity of that animal to the *P. callidice* complex. Its relationships remain important for understanding the biogeography of the unusual endemic group of Andean Pierini.

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