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A SPECTACULAR NEW *DALLA* MABILLE, 1904 FROM VENEZUELA-COLOMBIA (HESPERIIDAE: HETEROPTERINAE)

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ABSTRACT: A remarkable silvery *Dalla* is described and illustrated from high elevations in the Cerro Pintado, Serranía de Valledupar, on the Venezuelan-Colombian border. This species is apparently related to *Dalla semiargentea* (C. Felder & R. Felder, 1867), also redescribed and illustrated, of Colombia. The new species resembles the satyrine *Lymanopoda paramera* Adams & Bernard, 1979, with which it flies and apparently shares a *Chusquea* species as its larval foodplant.

KEY WORDS: Andes, *Chusquea*, genitalia, mimicry, Perijá, Serranía de Valledupar, South America

INTRODUCTION

Dalla Mabille, 1904 (Hesperiidae: Heteropterinae) is a large genus of neotropical skippers, with 95 currently recognized species (Mielke 2005). Most species are small, dark brown to black with large orange macules, and males, along with other members of the Heteropterinae (Warren *et al.*, in press), lack secondary sexual characters. The distribution of *Dalla*, although extending northward into northern Mexico, is centered in the Andes Mountains of South America. The genus occurs nearly exclusively at high elevations, largely above 2500m in South America (Steinhauser 2002), and usually above 900m in Mexico and Central America. Males are often encountered on wet, often vertical surfaces, apparently those enriched with salts, whereas females are seen very

infrequently (Steinhauser 2002). Their flight season appears to be highly seasonal, with the species in Mexico appearing exclusively univoltine (A. Warren, unpubl.). Records from South America, however, indicate that at least some species have more than one generation annually (Steinhauser 1991, 2002). Larval foodplants are virtually unknown (Mielke 2005, Beccaloni *et al.* 2008), but a number of Ecuadorian species feed on bamboo of the genus *Chusquea* Kunth (Poaceae) (H. Greeney, unpubl. pers. comm. to A. D. Warren).

As noted by Steinhauser (2002), phylogenetic relationships within *Dalla*, and between *Dalla* and other genera of Heteropterinae, remain unknown (also see Warren *et al.*, in press), although some characters that may help elucidate relationships were discussed by Warren (2001a,b). Nearly 20% of the species of *Dalla* have been described during the past 50 years, and additional undescribed taxa have been encountered recently (pers. obs., A. Warren), through fieldwork and revision of museum material. Undoubtedly, more species await discovery. Male genitalia have been inadequately illustrated and females of a majority of the known species have not been examined. In an effort to fill another gap in our knowledge, a spectacular species of *Dalla* from the mountains forming the northern portion of the Andes on the east-west border between Colombia and Venezuela, first discovered in the late 1970s by British lepidopterists Michael Adams and George Bernard, and illustrated by Vilorio (2007), is here named and described. It is apparently most closely related to *Dalla semiargentea* (C. Felder & R. Felder, 1867), which is redescribed and its wings and genitalia illustrated for comparative purposes. Full synonymies are given by Mielke (2005).

Dalla semiargentea (C. Felder & R. Felder, 1867)

(Figs. 1, 2, 10)

Eumesia semiargentea C. Felder & R. Felder, 1867

Description. Male (Figs. 1-2) - mean forewing length = 14.7mm (14.1-15.3, n=5) (from Colombia); forewing with termen convex, prominently so at tornus; hindwing slightly produced apically, termen convex, no tornal lobe; dorsal forewing unmarked medium gray-brown (staining to dark brown), overscaled sparsely with pale gray, fringes gray-brown; hindwing iridescent silver-colored, with black basal overscaling extending 1/3 distance to termen in CuA_2-2A and to termen in anal cell; fringes iridescent silver-colored proximad and pale iridescent gold-colored distad. Ventral forewing pale yellow-orange shading to cream-colored at apex and in anal cell; hindwing cream-colored, overscaled with pale red-brown anterior to discal cell and vein R_s , in posterior half of discal cell, anterior half of CuA_2-2A proximad, and along veins M_1 , M_3 , CuA_1 , and CuA_2 to termen; anal cell overscaled with black.

Head black, posterior margin narrowly whitish, ochreous behind eyes grading to white on venter; palpi black on dorsum, white on sides, pale brown on venter; antennae about 1/2 length of costa, black on dorsum narrowly checked with white proximad, very pale yellow on venter including club, club stout and arcuate, nudum red-brown, 12 (n=2) segments; thorax black on dorsum, white on venter, legs ochreous with rather long cream-colored setiform scales, fore tibiae spined, epiphysis minute; mid- and hind tibiae spined, mid-tibiae with single pair of spurs, hind tibiae with two pairs; dorsal abdomen black with whitish scales caudad, ventral abdomen pale ochreous.



Figures 1-6. *Dalla* adults. 1) *Dalla semiargentea*, male, Colombia, 1931, dorsal surface; 2) *D. semiargentea*, male, same specimen as Fig. 1, ventral surface; 3) *D. superargentea*, holotype male, dorsal surface, data in text; 4) *D. superargentea*, holotype male, ventral surface; 5) *D. superargentea*, paratype female, dorsal surface, data in text; 6) *D. superargentea*, paratype female, same specimen as Fig. 5, ventral surface.

Genitalia (Fig. 10) - uncus in lateral view narrow, concave caudad of middle, strongly hooked caudad; in dorsal view narrow caudad, divided, arms parallel and closely spaced, expanding greatly cephalad to overlap large portion of tegumen as suboval plate possessing white hair tuft; gnathos shorter than uncus, narrow in lateral view, narrowing slightly caudad, interrupted by membranous area before a short sclerotized tip caudad, broad proximad in ventral view, narrowing gradually to undivided caudal end; tegumen broadly curved cephalad; combined ventral arm of tegumen and dorsal arm of saccus nearly straight; cephalic arm of saccus moderately long, thin, and curved dorsad in lateral view, cephalic end blunt in ventral view; valvae slightly asymmetrical, long ($1.3\times$ length of tegumen and uncus), length about $2.6\times$ width, costa concave on dorsal edge toward caudal end, ampulla elongate (longer than costa), and relatively broad (length $2.1\times$ width), right ampulla longer and broader than left, angled dorsad, narrowing caudad to blunt caudal end, setose on both surfaces especially caudad, harpe curved dorsad and slightly inward to blunt caudal end, exceeding caudal extent of ampulla, dorsal edge finely serrate; juxta-transtillia prominent with lobate dorsal edge in lateral view, suboval in ventral view; aedeagus unadorned, moderately sinuate in lateral view, nearly straight in

dorsal view, cephalic end slightly broadened and slightly curved, caudal end not expanded; vesica with single weakly sclerotized chevron-shaped cornutus.

Female - unknown.

Specimens examined. COLOMBIA ('Colombie'): Bogotá, coll. Le Moul't (3 males at McGuire Center for Lepidoptera and Biodiversity); COLOMBIA: (no further locality data), 1931 (2 males at Carnegie Museum of Natural History).

Distribution. As noted by Evans (1955), this species is apparently known only from the region of Bogotá, Colombia. This region includes the high elevations of the Cordillera Oriental de Colombia. However, *D. semiargentea* apparently does not occur in the northernmost portion of that cordillera, the Serranía de El Tamá, on the Colombia-Venezuela border, whose high elevational butterfly fauna has been well prospected (see Pyrcz and Vioria 2007).

Discussion. This species resembles the one to be described next (see discussion for further comparisons).

***Dalla superargentea* Vioria, A. Warren & Austin, new species**

(Figs. 3, 4, 5, 6, 11, 12)

Dalla sp. nov.; Vioria, 2002: 29; 2007: 5, 8, fig. 7.

Description. Male (Figs. 3-4) - forewing length = 14.8mm (holotype), 14.9mm (paratype); forewing with termen convex, prominently so at tornus; hindwing produced apically, termen convex, then slightly concave before slight tornal lobe; dorsum unmarked iridescent silver-colored; forewing with black overscaling at base, largely confined to basal 1/8 of wing but extending 1/4 distance to termen between vein Sc and anterior vein of discal cell; hindwing also with black basal overscaling extending 1/3 distance to termen in CuA₂-2A and to termen in anal cell; fringes iridescent silver-colored proximad and iridescent gold-colored distad. Ventral forewing yellow-orange; some tan scaling along entire costal margin grading to a scattering of tan scales apically; hindwing with a mixture of pale orange and tan scales imparting a nearly olive hue; anal area blackish, overscaled with ochreous especially heavily in 2A-3A and ochreous setiform scales, especially in base of 2A-3A, along vein 3A, and in anal cell; pale streaks and macules as follows: pale ochreous nearly in base of costal cell along vein Sc+R₁ (extending to costa proximad on one paratype), narrowing distad; dull white in Sc+R₁-Rs, wedge-shaped narrowing proximad, along caudal edge of vein Sc+R₁ just proximad of termen; shining white in anterior half of discal cell, continued in anterior half of M₁-M₃ to termen where it narrows by about 1/2 its proximal width (partially divided by sliver of ground color along vein M₁-M₂ on one paratype), shining white in posterior half of M₁-M₃, narrow bar just distad of end of discal cell; shining white elongate chevrons extending from termen in M₃-CuA₁ and CuA₁-CuA₂; shining white oval macule near base of CuA₁-CuA₂; shining white irregular macule in middle of anterior cell CuA₂-2A adjacent to macule in CuA₁-CuA₂; long ochreous wedge in posterior CuA₂-2A along vein 2A extending from termen nearly to base of wing. It should be noted that some of the silvery color on the dorsum apparently was stained (this asymmetrical) during the relaxing process, with some of the yellow ventral color bleeding through, especially along the costa and veins of the forewing and whitish along the veins of the hindwing.

Head black with small white spots posterior to antennae, posterior margin narrowly pale red-brown, red-brown behind eyes grading to ochreous and then white on venter;

palpi black on dorsum, white on sides, pale brown on venter, covered with long setiform scales, with black dorsad and grading to red-brown on sides and ochreous on venter; 3rd segment stout, porrect, hidden among setiform scales of 2nd segment; antennae about half length of costa, black on dorsum narrowly checked with very pale yellow, very pale yellow on venter including club, club stout and arcuate, nudum red-brown, 12 (holotype), 13 (paratype) segments; dorsal thorax black with pale red-brown setiform scales along anterior edge and white setiform scales caudad; ventral thorax rubbed but apparently whitish, pectus ochreous, legs ochreous with rather long cream-colored setiform scales, fore tibiae spined, epiphysis very short, mid- and hind tibiae spined, mid-tibiae with single pair of spurs, hind tibiae with two pairs; dorsal abdomen black with scattered ochreous setiform scales, especially dense on last two segments, ventral abdomen ochreous.

Genitalia (Fig. 11) - uncus in lateral view narrow, concave caudad of middle, strongly hooked caudad; in dorsal view narrow caudad, divided, arms parallel and closely spaced, expanding greatly cephalad to overlap large portion of tegumen as oval plate possessing dense pale brown hair tuft; gnathos shorter than uncus, relatively broad in lateral view, narrowing caudad, sclerotized for proximal 2/3, then interrupted by membranous area before a short sclerotized tip caudad, broad proximad in ventral view, narrowing gradually to undivided caudal end; tegumen broadly curved cephalad; combined ventral arm of tegumen and dorsal arm of saccus strongly curved; cephalic arm of saccus short, thin, and angled slightly above horizontal in lateral view, cephalic end pointed in ventral view; valvae more or less symmetrical, long ($1.4 \times$ length of tegumen and uncus), length about $2.8 \times$ width, costa concave on dorsal edge toward caudal end, ampulla elongate (about length of costa), and relatively broad (length $2.3 \times$ width), angled slightly dorsad, caudal end rounded, setose on both surfaces, especially caudad, harpe curved dorsad and slightly inward to blunt caudal end, exceeding caudal extent of ampulla, dorsal edge weakly grooved; juxta-transtilla prominent with pointed dorsal edge in lateral view, subquadrate in ventral view; aedeagus unadorned, weakly sinuate in lateral view, straight in dorsal view, cephalic end slightly broadened and slightly curved, caudal end slightly expanded; vesica with single weakly sclerotized chevron-shaped cornutus.

Female (Figs. 5-6) - forewing length = 15.3mm (paratype); dorsum iridescent silver-colored; forewing with gray-brown along costa anterior to discal cell, extending distad to apex and outside of discal cell to vein M_3 , also as thin line in distal end of discal cell, and distal 1/2 of M_3 - CuA_1 and CuA_1 - CuA_2 ; black overscaling at base of wing, largely confined to basal 1/8 of wing; silver-colored subapical macules in R_3 - R_4 , R_4 - R_5 , and R_5 - M_1 , increasing in size caudad; hindwing as on male; fringes iridescent silver-colored proximad and iridescent gold-colored distad. Venter as on male; hindwing with additional white chevron distad in CuA_2 -2A.

Head as on male; palpi and antennae missing; dorsal thorax black with pale red-brown setiform scales along anterior edge and white to greenish setiform scales caudad; ventral thorax rubbed but apparently largely white, pectus pale ochreous, legs ochreous with rather long cream-colored setiform scales, fore tibiae spined, epiphysis very short, mid- and hind tibiae spined, mid-tibiae with single pair of spurs, hind tibiae with two pairs of spurs; dorsal abdomen black, greased but apparent scattered pale setiform scales, ventral abdomen pale ochreous.

Genitalia (Fig. 12) - lamella postvaginalis broad, central 1/2 of excavated caudal edge lightly sclerotized; lamella antevaginalis narrow, lobate, spiculate, deeply divided on caudal margin in U-shape; antrum sclerotized, short, but longer than broad, narrowing cephalad; ductus bursae narrower than cephalic end of antrum, relatively short, somewhat sinuate; corpus bursae globular, narrowing cephalad to broad connection to short cephalic appendix bursae, barely broader than long and breadth of connection to corpus bursae; no apparent internal sclerotization within ductus bursae, corpus bursae, or appendix bursae.

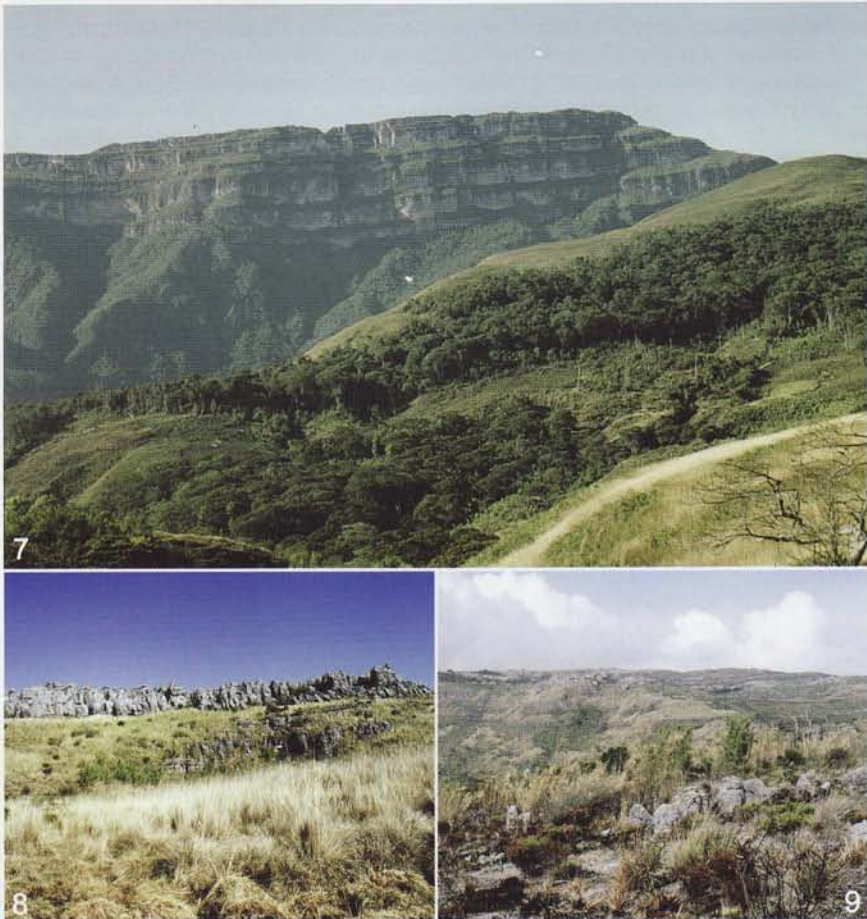
Types. HOLOTYPE male with the following labels: white, handprinted - / Front. Colombo.-Vzlana. / Sierra de Valledupar. / Cerro Pintado. 3020- / 3100 m. / 15/17-III-1993. /; white, handprinted - / J. Camacho / A. Viloría. / Colectores /; red, printed - HOLOTYPE / *Dalla superargentea* / Viloría, A. Warren & Austin /. PARATYPES: one male (GTA #14098) and one female (GTA #14099) with same data as holotype; one male from VENEZUELA: Estado Zulia; Serranía de Valledupar, east above Manaure, 3050m, 26 August 1977, M. J. Adams, G. I. Bernard (983) (forewing length=14.30mm); one male with same data except 28 August 1977, M. J. Adams, G. I. Bernard (985) (forewing length=13.05mm). The holotype is deposited in the Museo de Artrópodos, Facultad de Agronomía, La Universidad del Zulia (MALUZ), Maracaibo, Venezuela; a pair of paratypes is deposited at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida; and the remaining paratypes are deposited at The Natural History Museum, London, UK.

Type locality (Figs. 7-9). VENEZUELA/COLOMBIA border: Serranía de Valledupar, summit of Cerro Pintado (3020-3100m) (locally called "Cerro Pintao"), a prominent limestone table mountain situated in the Serranía de Valledupar. This serranía (Fig. 7) forms the main and higher ridge of the greater Sierra de Perijá, a mountain range in the northernmost extreme of the Andes, along which runs the borderline between Colombia (in the departments of Norte de Santander, Cesar and Guajira) and Venezuela (in the state of Zulia). The type specimens were collected between 3020 and 3100m (Figs. 8-9), in close association with a shrubby *Chusquea* (subgenus *Swallenochloa* McClure). At this elevation, most of the land is covered by open, paramo vegetation, with scattered patches of cloud forest, especially in lower and more humid areas.

Etymology. This species is named for the silvery dorsal color occurring across both the forewing and hindwing.

Distribution and Phenology. *Dalla superargentea* is currently known only from the immediate vicinity of the Venezuelan-Colombian border in the Serranía de Valledupar between 3020 and 3100m where it flies in close association with bamboos of the genus *Chusquea*. It is certainly endemic to the high elevational habitats (paramos) of the Sierra de Perijá, as are nearly all butterflies known from this isolated region (see Viloría 1990). The summit of Cerro Pintado is in fact the northernmost paramo of the entire Cordillera de los Andes (ca. 8000km long). It represents an important portion of the paramos of the Perijá mountains, whose total area above 3000m has been estimated to cover less than 500km² (Rodríguez and Rojas-Suárez, in press), and is considerably isolated from other paramos in the Andes and the neighboring Sierra Nevada de Santa Marta (in Colombia). As an ecosystem that only develops in high Andean lands north of the Marañon Depression (Peru), the paramo is fragmented in small, insular units in the northernmost Andes (Colombia and mainly Venezuela). This spatial disposition has been considered biogeographically equivalent to an archipelago (Simpson 1971). The paramo unit of the Sierra de Perijá is not only one of the most isolated, but also one of the least known biologically. It comprises the summit of Cerro Pintado and the Sabana Rubia (the

larger paramo of the region, south of Cerro Pintado and only separated from it by a deep canyon formed by the headwaters of the Guasare and Apón rivers), and the paramo del Tetari, which is located 22km to the south (Viloria 1990, 1991). There appears to be some degree of ecological continuity among these paramos, and *Dalla superargentea* might occur in all of them, ranging in the area indicated above. The known dates of flight for this species (March, August) are too few to generalize except to observe that there are at least two annual generations, as suggested for other *Dalla* in South America (e.g., Steinhauser 2002). Pulido and Andrade (2007), however, did not encounter the species in January and February.



Figures 7-9. Cerro Pintado on the Colombian-Venezuelan border. 7) View of the Colombian slopes of the Cerro Pintado, a monumental limestone table that reaches 3300m in the Sierra de Perijá; 8) view of the paramo of Cerro Pintado with limestone blocks emerging on top (2-10m in height); yellow grasses are conspicuous during the dry season, but *Chusquea* remains green; 9) type locality of *Dalla superargentea* in the paramo of Cerro Pintado (3000-3300m); some clumps of green *Chusquea* can be seen to the right.

Ecology. *Dalla superargentea* shares its habitat with the endemic satyrines *Dangond dangondi* Adams & Bernard, 1979, *Lymanopoda paramera* Adams & Bernard, 1979, and *Manerebia quinterae* (Adams & Bernard, 1979). Three pierids, a species of *Tatochila* Butler, 1870 (probably undescribed), *Catasticta tricolor* Butler, 1897 (new subspecies), and *Nathalis iole* (probably a new subspecies) also fly in the same paramo; the first two seem to be less common. *Vanessa virginiensis* (Drury, 1773) and *Dione glycera* (C. Felder & R. Felder, 1861) (Nymphalidae), have also been detected in the paramo of Cerro Pintado. Some satyrines endemic to the uppermost cloud forest are also occasionally found flying around the bamboos in the cloud forest-paramo ecotone, where *D. superargentea* was also observed (*Pedaliodes cesareense* Adams & Bernard, 1979; *P. vallenata* Adams & Bernard, 1979; *Lymanopoda altaselva* Adams & Bernard, 1979; and *Eretris apuleja altamira* Adams & Bernard, 1979).

As noted by Viloría (2007), *Dalla superargentea* appears to be involved in a mimicry complex with *Lymanopoda paramera* Adams & Bernard, 1979, and the species of *Tatochila* mentioned above. Adults of *D. superargentea* were encountered flying in the canopy of the tallest clumps of *Chusquea*, which were growing mostly in more humid places, usually adjacent to rock faces (and therefore partly sheltered from the wind; pers. obs., A. Viloría). *Dalla superargentea* flies rapidly, several meters above the ground, especially during sunny periods, and in flight is not easily distinguished in appearance or behavior from *Lymanopoda* (even though they are of different size).

Diagnosis. *Dalla superargentea* and *D. semiargentea* are the only known members of the genus that have silver-colored dorsa. The dorsum is nearly entirely silvery on *D. superargentea* while *D. semiargentea* has a brown forewing with silver color only on the hindwing. The ventral forewing of *D. superargentea* is similar to that of *D. semiargentea* but is a richer yellow-orange. The ventral hindwings of the two species are substantially different in appearance, with *D. superargentea* exhibiting a dark ground color crossed by strongly contrasting pale stripes and macules. The ventral hindwing of *D. semiargentea* is considerably paler with a subdued pattern of weakly contrasting central and caudal rays.

Male genitalia of the two species, while grossly similar, exhibit a number of differences. The narrow arms of the caudally divided uncus are shorter on *D. superargentea* than on *D. semiargentea* and the portion of the uncus overlapping the tegumen is more expansive. The gnathos of *D. superargentea* is broader than on *D. semiargentea*, the combined ventral arm of the tegumen and dorsal arm of the saccus is more prominently curved, and the anterior arm of the saccus is shorter and more pointed cephalad. The valvae of the two, although of the same ground plan, differ in detail. The valvae of *D. superargentea* are relatively symmetrical, but those of *D. semiargentea* are somewhat asymmetrical, especially the ampullae. The valva of *D. superargentea* is proportionally longer and narrower than that of *D. semiargentea*, the harpe is less upcurved caudad, and the ampulla is less angled dorsad. The aedeagus of *D. superargentea* is less sinuate and the juxta-transtilla is broader and has a narrower and more pointed dorsal process.

DISCUSSION

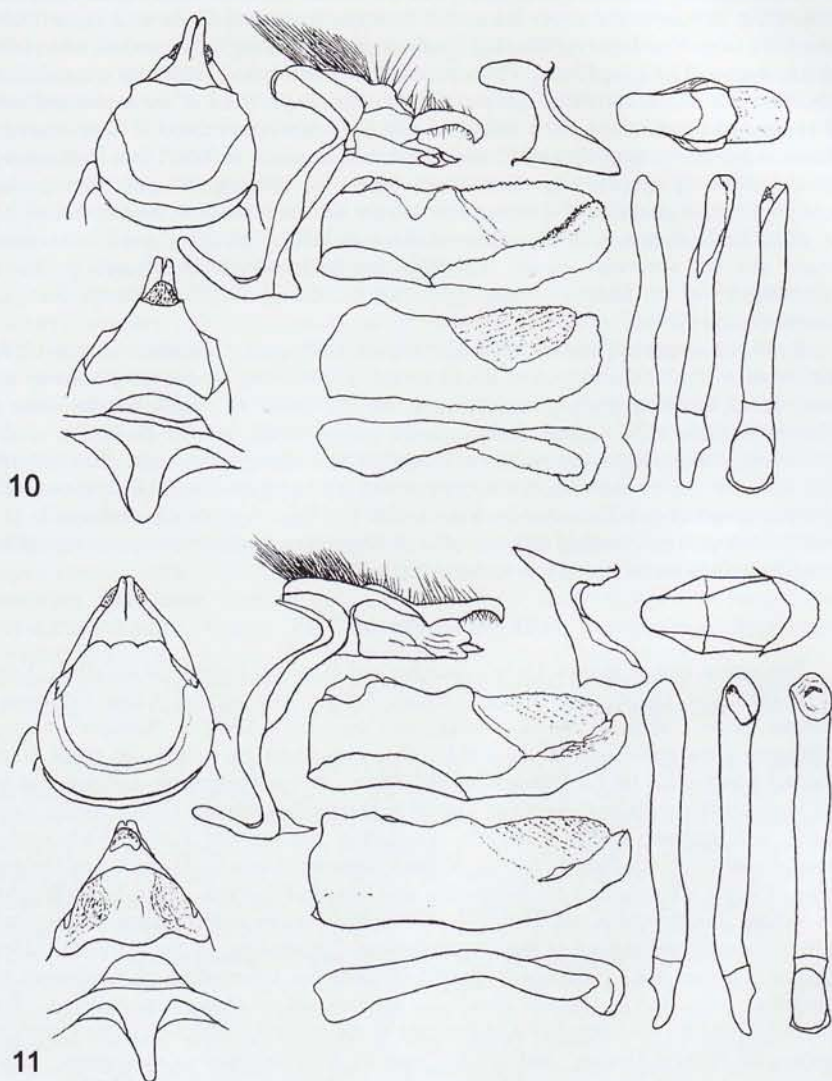
Dalla superargentea is yet another endemic species of butterfly at the higher elevations within the Sierra de Perijá on the Venezuelan-Colombian border (Adams and Bernard 1979, Viloría 1990, Pulido and Andrade 2007). *Dalla superargentea* and *D. semiargentea* are quite similar in their color, pattern and genital morphology, and thus

appear to be each other's closest relative. No other known congener possesses the dorsal silvery coloration. Although their superficial gestalt differs from other members of the genus, other structural characters are well within the concept of *Dalla* as it is currently understood (e.g., Steinhäuser 1991, 2002). Their antennae have robust and arcuate clubs and a nudum of 12-13 segments. The uncus of the genitalia is cephalically expanded as seen to various degrees on other species of *Dalla* and the presence of the associated hair tuft appears to be universal. The valvae of both *D. superargentea* and *D. semiargentea* includes a prominent dorsally angled ampulla that is also seen in most other *Dalla* along with the relatively simple, and often sinuate aedeagus, and the well-developed juxta-transtillia. Female genitalia of *D. superargentea* are similar to those of the females of the few other *Dalla* examined. Characters of these include a relatively small sclerotized antrum and an appendix bursae, although the latter character appears to be a synapomorphy of the Heteroptera, apparently present in all genera except *Butleria* (Warren *et al.*, in press).

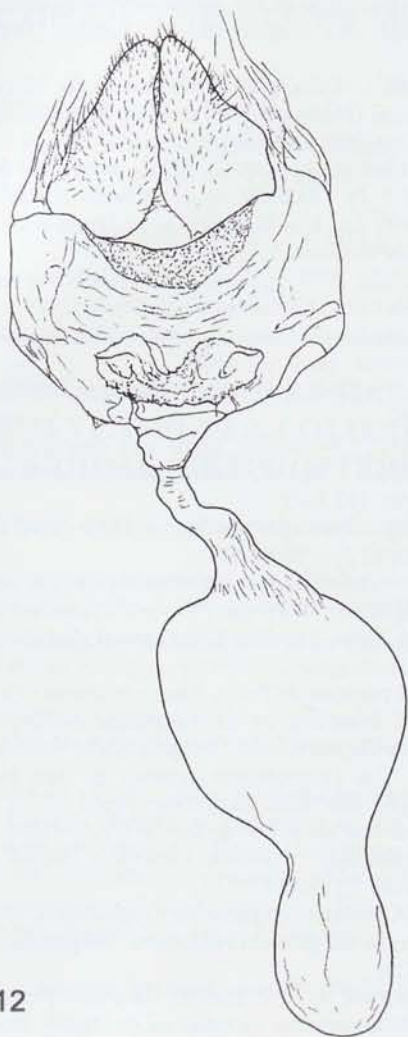
Dalla semiargentea, known from the region of Bogotá, Colombia (Evans 1955; Steinhäuser 1991, 2002; Warren *et al.*, in press), differs from *D. superargentea* by its brown dorsal forewing with silver-color only on the hindwing. Both species share a yellowish venter. The ventral forewings are very similar, but the hindwing of *D. superargentea* has a distinctive pattern of pale rays on a dark ground color. This pattern, along with the silvery dorsum, is convergent with the sympatric satyrine *Lymanopoda paramera* as noted and illustrated by Vilorio (2007). This suggests a potential of a yet unstudied mimetic relationship that may also exist among a number of satyrine and other butterflies at high elevations in the Andes (Vilorio 2007).

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Figures 10-11. Male genitalia of *Dalla*. Shown are dorsal view of uncus, gnathos, and tegumen; ventral view of uncus and gnathos; left lateral view of uncus, tegumen, and saccus; internal lateral view of right valva; external lateral view of left valva; dorsal view of valva; lateral and dorsal views of juxta-transtilla; and left, right and dorsal views of aedeagus. 10) *D. semiargentea*, Colombia, Bogotá (GTA #14097); 11) *D. superargentea*, paratype (GTA #14098).



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Figure 12. Female genitalia of *Dalla superargentea*, paratype, ventral view (GTA #14099).

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