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Author(s): Harold F. Greeney and Andrew D. Warren

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The Natural History, Immature Stages, and Shelter Building Behavior of *Dion carmenta* (Lepidoptera: Hesperiidae: Hesperiinae) in Eastern Ecuador

HAROLD F. GREENEY 1,2 and ANDREW D. WARREN 3

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ABSTRACT We describe the immature stages and shelter building behavior of the skipper butterfly

Dion carmenta (Hewitson) from eastern Ecuador. Adults infrequently are encountered and feed on a variety of flowers, generally at forest edges and clearings. Chusquea c.f. scandens Kunth (Poaceae: Bambusoidea) is the larval food plant. Young larvae have black heads with white, unadorned bodies, changing little as they grow, with the exception of developing a reddish tinge to thoracic segments. Larvae of all stadia construct and dwell in shelters built on the food plant and forcibly eject frass with the aid of an anal comb. Pupation occurs on the food plant in a final structure formed by joining together multiple leaves with silk. Development, from oviposition to eclosion, lasts 128–147 d.

KEY WORDS skipper, bamboo, Poaceae, Chusquea, cloud forest

The Neotropical hesperiid genus Dion Godman (Hesperiinae: Moncini) includes three currently recognized species (Evans 1955, Mielke 2005): D. gemmatus (Butler) of Costa Rica and Panama; D. meda (Hewitson) of southeastern Brazil; and the Andean D. carmenta (Hewitson). Evans (1955) considered D. carmenta to be a polytypic species, comprised of three subspecies differing in details of wing size and markings, D. c. acraea (Plötz) from Colombia (Manizales area, western Cordillera) and Venezuela (Bell 1946); D. c. coma Evans 1955, from Balzapamba, Ecuador; and D. c. carmenta from elsewhere in Colombia, Ecuador, Peru, and Bolivia. No comprehensive taxonomic review of Dion has been made since Evans (1955); thus, the relationships between the subspecies of D. carmenta remain to be elucidated in detail.

Little is known about the genus *Dion*. Rarely encountered, adults of all three species are found in moist forest habitats, usually cloud forest (A.D.W., unpublished data). No details on the life history or larval food plants previously have been presented for any species of *Dion*, other than a recent report of *D. carmenta* (subspecies not indicated) using "*Chusquea* sp." in Colombia (Beccaloni et al. 2008). Below, we provide detailed life history information for *Dion carmenta carmenta*, which we reared on *Chusquea* c.f. scandens Kunth from an eastern Ecuadorian cloud forest.

Materials and Methods

Unless noted otherwise, all rearing and field investigations were conducted at the Yanayacu Biological Station and Center for Creative Studies (00° 35.949' S, 77° 53.403' W) located in Napo Province, in the Andes of northeastern Ecuador. The study site is located approximately 5 km west of the town of Cosanga and includes around 2,000 ha of primary cloud forest bordered by cattle pasture and other disturbed habitats. Dominant trees in the forest canopy include Miconia, Vismia, and Alnus. Daily temperatures range from 50 to 75°F, varying little across the year, with annual rainfall varying generally between 3 and 4 m/yr. See Valencia (1995) for a more complete description of the study area. We collected larvae of Dion carmenta from plants of Chusquea c.f. scandens at elevations ranging from 2,100 to 2,200 m and reared them at the research station located at 2,150 m. Despite ongoing efforts to rear larvae of all Lepidoptera species from all plants encountered at the study site, larvae of D. carmenta were only found on *Chusquea*. We kept larvae in plastic bags or glass jars at ambient temperatures. changing food plant leaves and removing frass semidaily.

We made all observations on larval shelter construction and behavior in the field or with freshly collected larvae still in their shelters. We excluded shelters made in the laboratory from our descriptions and discussions. Terminology for describing larval shelters follows Greeney and Jones (2003) and Greeney (2009). Voucher specimens are deposited in the private collections of both authors.

¹ Biology 0314, University of Nevada, Reno, 1664 N. Virginia St., Reno, Nevada 89557.

² Corresponding author, e-mail: revmmoss@yahoo.com.

³ McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, P.O. Box 112710, Gainesville, Florida 32611.



Fig. 1. Adult $D.\ carmenta$ in Mindo, Pichincha Province, Ecuador, feeding at flower of Rubus sp. (Rosaceae). (Online figure in color.)

Results

Adult Behavior. Adults of D. carmenta (Fig. 1) rarely are observed in our area. We occasionally have found them in the early morning in disturbed areas along the forest edge, perching on the underside of a leaf, presumably in the position in which they spent the night. On one occasion, an adult was observed visiting the flowers of a common roadside Erato DC. (Asteraceae). At a site in western Ecuador (Mindo, Pichincha Province), we observed adults of D. carmenta visiting flowers of Impatiens L. (Balsaminaceae; n+2), $Streptosolen\ jamesonii$ (Benth) Miers (Solanaceae; n+1), and Rubus L. (Rosaceae; n+1; Fig. 1).

We witnessed only a single oviposition event. At 1130 hours, the senior author observed a female *D. carmenta* flying rapidly over a large patch of *Chusquea* c.f. *scandens* in a disturbed area along the roadside at our study site. She touched down very briefly on the upper side of several leaves, but otherwise maintained a rapid and erratic flight over *Chusquea* for several minutes before landing on the underside of a mature leaf near the end of an isolated shoot, hanging over the road. She remained on the underside of the leaf for 3–4 s, where she laid a single egg (Fig. 2a–b).

General Immature Biology. Larvae of all instars were observed to forcibly eject frass from the anus by using an anal comb (Fig. 4b). Larvae backed to the edge of their shelter and extruded their terminal abdominal segments to accomplish this, and no frass was observed to accumulate inside larval shelters.

Egg. (Figs. 2a-2b; n+1; \approx 1.25 mm diameter by 0.5 mm tall; 15 d). Egg flattened dome-shaped, appear-

ing smooth but with minute, irregular, vertical striations visible under dissecting microscope, pale yellow to cream-colored (Figs. 1a-b). Based on egg scars near recently hatched first instars in the field, larvae consume most or all of the chorion upon emergence.

First Instar. (Figs. 2c-2f; n + 8; 3–6 mm; 17–18 d). Head round to roundly triangular, smooth, shining black to dark brown with sparse minute pitting and sparse short pale setae, epicranial crease very weak; body at hatching widest around A6-7, abdominal segments A3-7 slightly projected laterally, giving a "lumpy" appearance; later in the stadium these projections less noticeable and body more elongate. Upon hatching, body clear pale yellow-white, becoming greenish after feeding commences; T1 deep maroon colored, fading onto anterior margin of T2. Entire body with sparse, short, pale setae except for a few long pale setae in a fringe on A10; true legs weakly sclerotized and same color as body; pronotal shield strongly scleritized, black, laterally elongated, extending to subdorsal area.

Second Instar. (Fig. 2g; n+11; to 9 mm; 17–19 d). Head and body as described for first instar, but epicranial crease slightly more pronounced, and prothoracic shield well developed, black, and extending to spiracular area; maroon coloration on thorax now extending weekly as far as T3.

Third Instar. (Figs. 2h-2k; n+16; to 14 mm; 13-16 d). Head as described for second instar; body similar to previous instar but maroon coloration on thorax slightly reduced, still prominent on T1.

Fourth Instar. (Figs. 3a-3b; n+24; to 22 mm; 14-17 d). Immediately after molting, appearance as described for third instar, but maroon coloration on thorax further reduced on all segments, skin chalkier white, becoming more pronounced during development; appearance late in instar more like fifth instar (described below).

Fifth Instar. (Figs. 3c-3f, 4a-4b; n+39; to 34 mm; 27–33 d including prepupa). Head black, roundly triangular (narrowing slightly dorsally), slight epicranial crease densely pitted and sparsely covered with short, pale setae; setae slightly longer around stemmata and mouthparts. Body whitish, dark green of gut sometimes showing through in middle abdominal segments, becoming chalkier white later in instar; prothoracic shield prominent, shining black, extending to spiracular area; reddish cast to T1 faint, disappearing later in instar; entire body sparsely covered with short, pale setae, longest in a fringe around anal plate.

Prepupa. (n + 27; 20-25 mm; 3-5 d). Soon after (or during) completion of their pupal shelter, fifth instars develop a white, powdery flocculence on the ventral areas of A4-A7. Once the pupal shelter is complete, this substance is smeared over the surface of the inner chamber, along with silk, and the larva turns dull yellow.

Pupa. (Figs. 4c-4 g; n + 23; 24-27 mm; 23-27 d). Pupa elongate, nearly cylindrical, broadest at thorax, tapering abruptly at head and at A9; head with a stout,

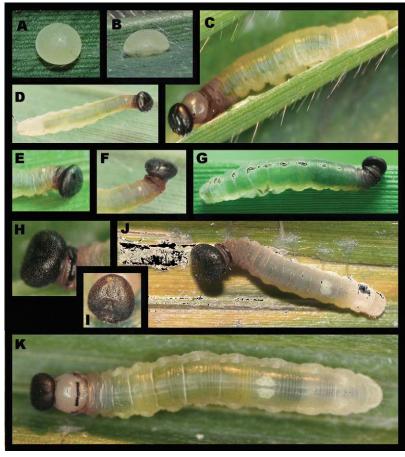


Fig. 2. Immature stages of *D. carmenta* at Yanayacu Biological Station, Napo Province, 2,100 m, Ecuador. (A) dorsal view of recently laid egg. (B) lateral view of recently laid egg. (C) premolt first instar. (D–F) first instar. (G) second instar. (H–I) detail of head of third instar. (J) recently molted third instar consuming its shed skin. (K) premolt third instar. (Online figure in color.)

rounded, conical forward-oriented projection; proboscis sheath attached until posterior margin of wing pads, then detached and extending to about A7; entire pupa dull, translucent yellow, cremaster and head projection red-brown, prothoracic spiracular covers with vague light brown hue; setae lacking except for a few sparse patches of pale setae near the eyes. During development, pupae dark brown, beginning with dark highlights, and finally become black with sharply contrasting prothoracic spiracular covers.

Larval Shelters. (Fig. 5). First-instar shelters are constructed by rolling a small portion of the leaf margin onto the upper surface of the leaf, forming a loose, tubular "group I, type 2, no-cut fold shelter". Once the shelter is complete, larvae begin feeding at one end, and the loose tube is soon silked into a triangularly shaped pocket (Fig. 5a). At this stage, the shelter no longer resembles its original form, and if the ontogeny of shelter construction is not known, it would mistakenly be called a "type 4, one-cut shelter". Most individuals remain in this first shelter until molting to the third instar. As feeding contin-

ues, however, the shelter becomes more tightly sealed with silk and flattened. Because of feeding damage at both ends combined with continued silking, the shelter gradually takes on a long, rectangular shape (Fig. 5c); often, the distal end of the leaf is eaten completely. When first or second instars are forced to abandon their shelters, they quickly make a second shelter that is larger but otherwise identical to the first. Most larvae, either in late third or early fourth instar, build a second shelter by rolling a leaf and silking it tightly closed, then feeding around the shelter it until its final form resembles the rectangular shelter described above. From this shelter, during fourth instar, larvae begin to tie adjacent leaves together around the shelter; by the time they molt to fifth instar, they have created a "type 2, multileaf shelter" (Fig. 5b). Usually, this shelter is outgrown during the fifth instar, and the larva builds a second multileaf shelter. This shelter is slowly eaten from the outside and silk is constantly applied to the inner chamber. Before pupation, larvae build a final shelter like those built by fifth

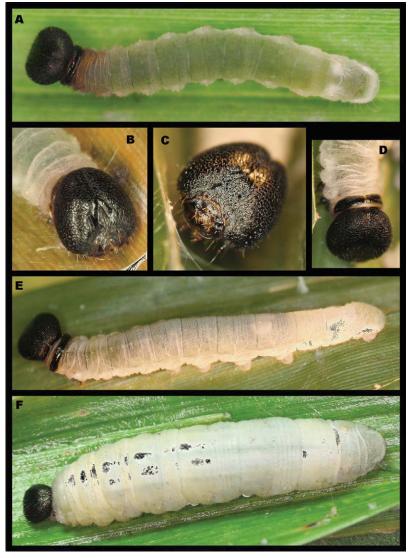


Fig. 3. Immature stages of *D. carmenta* at Yanayacu Biological Station, Napo Province, 2,100 m, Ecuador. (A) recently molted fourth instar. (B) detail of fourth instar head. (C–D) details of fifth instar head. (E) fifth instar. (F) mature (prepupal) fifth instar, dorsal view. (Online figure in color.)

instars (Figs. 5d-e). This shelter differs from the final larval shelter only in that copious silk is spun around the outside (Fig. 5d), binding the leaves tightly together. Pupae often remain in this shelter after the included leaves have died, and this extra silking likely helps prevent the shelter from falling off the plant.

Discussion

At our study site, *D. carmenta* appears to specialize on *Chusquea* c.f. *scandens*, as larvae were not found on any other plants studied during our comprehensive surveys for immature Lepidoptera (see www.caterpillars.org). Although food plant information is lacking for other *Dion* taxa, they occur in

habitats rich in bamboos (A. D.Warren, unpublished data), including *Chusquea* in Costa Rica, and those plants should be the subjects of initial searches for immature stages.

Dion joins a number of lepidopteran genera using Chusquea as larval food plants, including other hesperiine and heteropterine skippers (Steinhauser 1974, Beccaloni et al. 2008, Viloria et al. 2008, Austin and Warren 2009, Greeney and Warren 2009a); a large number of satyrine nymphalids (Schultze-Rhonhoff 1930; Biezanko 1960; Silva et al. 1968; Hayward 1969; Heimlich 1972; DeVries 1986, 1987; Acosta 1999; Beccaloni et al. 2008); and dioptine notodontids (Miller 2009), among others. The fact that some groups using Chusquea have evolved into super-diverse assemblages (e.g., Adams 1985, Pyrcz and Viloria 1999, Pyrcz

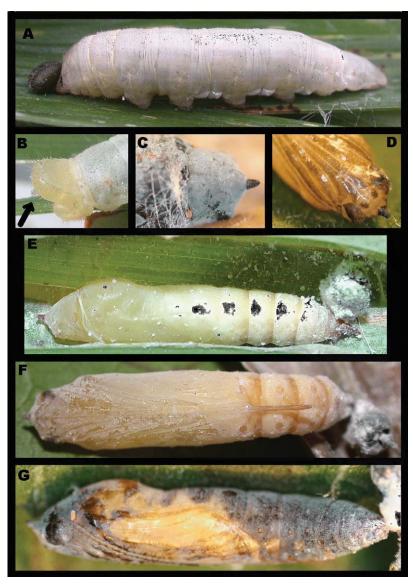


Fig. 4. Immature stages of *D. carmenta* at Yanayacu Biological Station, Napo Province, 2,100 m, Ecuador. (A) mature (prepupal) fifth instar, lateral view. (B) posterior segments of fifth instar immediately after throwing a frass pellet, notice the extended anal comb (arrow). (C–D) details of pupal head. (E) lateral view of recently pupated individual. (F) ventral view of pupa. (G) lateral view of pupa 4–5 d before eclosion. (Online figure in color.)

2004, Viloria 2007) reinforces the need for a taxonomic reassessment of *D. carmenta*. Given patterns seen in other *Chusquea*-feeding taxa, we would not be surprised if more than one species-level taxon is present among the described subspecies of *D. carmenta* in the Andes.

Like other hesperiine skippers, *D. carmenta* builds fairly simple shelters, likely constrained by the relatively uniform leaf architecture found within their monocotyledonous food plants (Greeney 2009). It is interesting to note that, like the sympatric *Falga jeconia* Evans 1955, Greeney and Warren 2009a), *D. carmenta* begins the construction of its first shelter with a simple leaf curl and subsequently alters the

form of the shelter with feeding damage and further silking. Whereas *F. jeconia* creates a roughly rectangular refuge, *D. carmenta* larvae form a triangular-shaped retreat, a trait shared with another hesperine, *Vettius coryna* Hewitson 1866 (Greeney and Warren 2009b). Although our understanding of the importance of such architectural variation is hindered by a dearth of detailed studies (but see Greeney and Sheldon 2008), we feel that such variation may provide phylogenetically informative characters, and we encourage others to carefully describe the shelters of further species, even those considered "well studied", to make these characters available for future phylogenetic analyses.

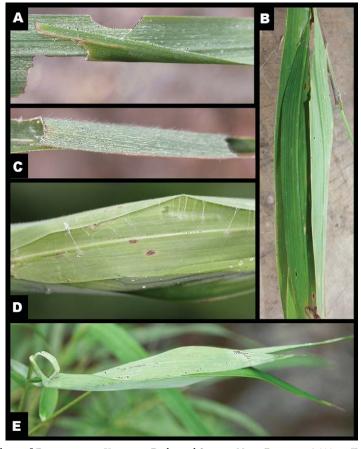


Fig. 5. Larval shelters of *D. carmenta* at Yanayacu Biological Station, Napo Province, 2,100 m, Ecuador. (A) first-instar shelter after commencement of feeding, note triangular shape. (B) fifth instar shelter. (C) second shelter built by third or fourth instar showing feeding damage which leads to elongate rectangular shape. (D) details of silking on outside of pupal shelter. (E) in situ pupal shelter. (Online figure in color.)

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