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A Review of *Colobura* (Lepidoptera: Nymphalidae) with Comments on Larval and Adult Ecology and Description of a Sibling Species

K. R. WILLMOTT,¹ L. M. CONSTANTINO,² AND J. P. W. HALL³

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ABSTRACT The taxonomy of the genus *Colobura* Billberg, 1820, one of the most common members of the Neotropical lowland forest butterfly fauna, is critically reviewed in light of available information on the morphology of both the immature stages and adults. Although regarded by almost all authors to date as monotypic, *Colobura* contains two species, one of which is described here as *Colobura annulata* sp. n. The immature stages of both the new species and *Colobura dirce* (Linnaeus, 1758) are described, compared, and figured. Both larval and adult phenotypes of the two species may be readily separated, and a key to identification is provided. A review of published and unpublished information on the immature stages, hostplants, and adult behavior of both species reveals a possible case of ecological niche partitioning; larvae of *C. dirce* are solitary or occur in small groups on predominantly young trees or saplings, whereas those of *C. annulata* are highly gregarious on mature canopy trees. There is some evidence to suggest that adult flight height may, in part, be correlated with the height of preferred hostplants.

KEY WORDS *Colobura*, early stages, hostplants, Neotropical, taxonomy

BUTTERFLIES ARE GENERALLY regarded as one of the best taxonomically studied groups of insects (Robbins and Opler 1997), yet even in genera containing very common and widespread species, our understanding of true species diversity may prove to be startlingly below common expectation (Ackery 1987, Willmott et al. 2001). There is perhaps no more outstanding an example of this lack of understanding than in the nymphalid genus *Colobura* Billberg, 1820, a very common member of forest habitats throughout the Neotropical region. The genus has been regarded as monotypic by almost all authors since Linnaeus introduced the first species name in 1758 (Stoll 1787, Godart [1824], Westwood 1850, Kirby 1871, Godman and Salvin 1883, Seitz 1914, DeVries 1987, d'Abreu 1987, Smith et al. 1994, Neild 1996, Constantino 1998), despite the fact that two very distinctive larval phenotypes have been known for at least 200 yr (Stoll 1787, Westwood 1850, Sepp [1852]). Although one author (Sepp [1852]) took the logical step of recognizing and describing a second species based on the larvae, subsequent authors have almost universally regarded the larval phenotypes as individual (Seitz 1914, DeVries 1987) or sexual (Stoll 1787, Westwood 1850, pp. 243–250) forms, in the apparent absence of more than one adult phenotype.

While conducting a long-term systematic and ecological study of Ecuadorian butterflies, K.R.W. and J.P.W.H. identified several adult wing pattern charac-

ters suggesting that *Colobura* contains two species. Almost simultaneously, L.M.C. reared both larval phenotypes to adults in Colombia, presenting an ideal opportunity to study series of both early stages and adults to clarify the species diversity and taxonomy of the genus.

Materials and Methods

Field observations were made on *Colobura dirce* (L.) by L.M.C. during April 1999 at the upper Río Bitaco, Valle del Cauca, Colombia, located on the western slope of the Andes (Cordillera Occidental) at 1,490 m elevation, in secondary forest habitats. Oviposition behavior of two females was observed on *Cecropia peltata* (L.) (Moraceae) trees. Ten recently deposited eggs were collected and the immature stages reared in plastic bags with fresh cuttings of the larval hostplant. Cuttings were replaced every 3 d and sprayed with tap water to prevent dehydration. All observations and rearing were conducted at ambient temperature (typically 21°C, 80% RH).

Field observations for *Colobura annulata* sp. n. (described below) were made by L.M.C. in 1997 during April and May, the first wet season, on the lower Río Anchicayá, Valle del Cauca, Colombia, located in the Pacific coastal region at 70 m elevation, in secondary rain forest habitats. In the town of Sabaletas, at the edge of the Río Anchicayá, several trees of *Cecropia eximia* Cuatrec. and *Cecropia virgusa* Cuatrec. (Moraceae) were observed with heavy aggregations of fifth instars of *C. annulata*, with up to 70–150 larvae per tree during the peak abundance of this species. A total of 150 fifth instars was collected and reared in insect cages to adults, with fresh cuttings of the larval host

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plant. Freshly eclosed adults were introduced to a screened enclosure (10 by 8 by 3 m), with small plantings of *Cecropia eximia*. Adults were fed fermented bananas and kept in captivity for 1 mo. Recently deposited eggs were collected every day and deposited in small plastic containers with fresh cuttings of the larval hostplant. All observations and rearings were conducted at ambient temperature (typically 28°C, 95% RH). In both field sites the immature stages were photographed and measured, and adult voucher specimens were retained by L.M.C.

Series of adult specimens of *Colobura* were studied in the BMNH, KWJH, and USNM, to assess wing pattern variation and geographic ranges. Dissections were made using standard techniques, abdomens being soaked in hot 10% KOH solution for ≈15 min and subsequently stored in glycerol for examination under a binocular microscope. Morphological terms for genitalia largely follow Klots (1956), although venation nomenclature follows Comstock and Needham (1918). Original descriptions were consulted for all published *Colobura* names and attempts made to locate type material. The following collection acronyms are used throughout the text: AMNH American Museum of Natural History, NY, NY, USA; BMNH Natural History Museum, London, UK; KWJH Keith R. Willmott and Jason P. W. Hall collection, Gainesville, FL, USA; LMC Luis M. Constantino collection, Cali, Colombia; MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; RMNH Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; USNM National Museum of Natural History, Washington, DC, USA.

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Colobura Billberg, 1820. Enumeratio Insectorum Museo Gust. Joh. Billberg: 79. Type species by monotypy: *Papilio dirce* Linnaeus, 1758, Systema Naturae, 1: 477.

= *Gynoecia* Doubleday, [1845]. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, 1: 88. Type species by monotypy: *Papilio dirce* Linnaeus, 1758, Systema Naturae, 1: 477.

("-" denotes a subspecies and "-" a synonym)

annulata Willmott, Constantino and Hall, sp. n.

dirce (Linnaeus, 1758)

-*bates* (Linnaeus, 1758)

-*dirceoides* (Sepp, [1852])

-*cassavae* (Fabricius 1938) repl. n.

-*wolcotti* Comstock, 1942

-*avinoffi* Comstock, 1942

-*clementi* Comstock, 1942

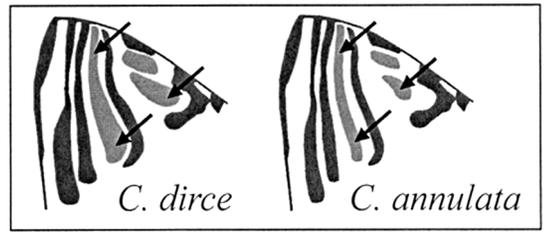


Fig. 1. Schematic drawings of ventral wing apex, illustrating principal pattern differences between the two species of *Colobura*.

Key to the Species of *Colobura*

Adults

- 1. Ventral forewing with third dark brown submarginal line from dark marginal border thinning from cell M3-M2 toward costa (Fig. 1); ventral forewing with dark brown spot in cell M1-R5 broad, oval shaped, broader than adjacent spot at costa in cell R5-R4 (Fig. 1); typically small; dorsal forewing with distal edge of pale band often "kinked" at vein M3; dorsal forewing with pale band often narrowing at costa *dirce*

Ventral forewing with third dark brown submarginal line from dark marginal border of even thickness throughout (Fig. 1); ventral forewing with dark brown spot in cell M1-R5 small, of equal width to spot adjacent at costa in cell R5-R4 (Fig. 1); typically large; dorsal forewing with distal edge of pale band smooth; dorsal forewing with pale band of even width throughout *annulata*

Larvae

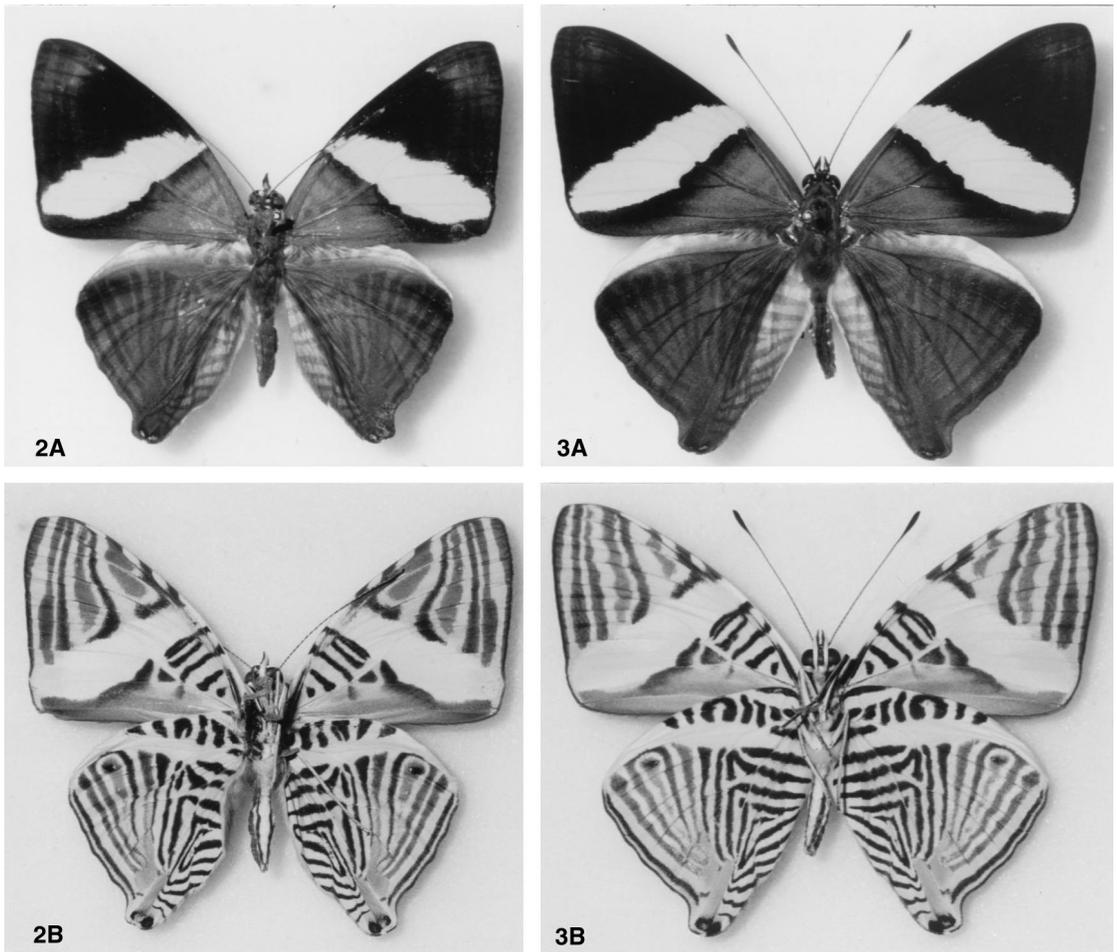
- 1. Later (post third) instar larvae typically solitary or in small groups (<30 individuals); body velvet black, lacking cream-yellow rings between each segment, spiracles yellow; relatively short head horns; head horns and thoracic scoli whitish gray, remaining scoli pale yellow *dirce*

Later (post third) instar larvae typically highly gregarious (>30 individuals); body velvet black with cream-yellow rings between each segment, spiracles cream-yellow; relatively long head horns; head horns and all scoli deep yellow *annulata*

Colobura dirce dirce (Linnaeus, 1758)
(Figs. 2 A and B, 4, 7 A and B)

Papilio dirco (sic) Linnaeus, 1758. Syst. Nat. 1: 477. TL: French Guiana. Neotype male (here designated): "Guyane Française C. Bar/Ex. Oberthür Coll. Brit. Mus. 1927-3." BMNH (examined).

= *Papilio bates* Linnaeus, 1758. Syst. Nat. 1: 485. TL: French Guiana. Neotype male (here designated):



Figs. 2 and 3. (2) Neotype for the names *Colobura dirce*, *C. bates*, and *C. dirceoides*. (A) Dorsal surface; (B) ventral surface. (3) *Colobura annulata* sp. n., holotype. (A) Dorsal surface; (B) ventral surface.

"Guyane Française C. Bar/Ex. Oberthür Coll. Brit. Mus. 1927-3." BMNH (examined).

= *Papilio dirceoides* Sepp, [1852]. Surinam. Vland. 3: 321, pl. 149. TL: French Guiana. Neotype male (here designated): "Guyane Française C. Bar/Ex. Oberthür Coll. Brit. Mus. 1927-3." BMNH (examined).

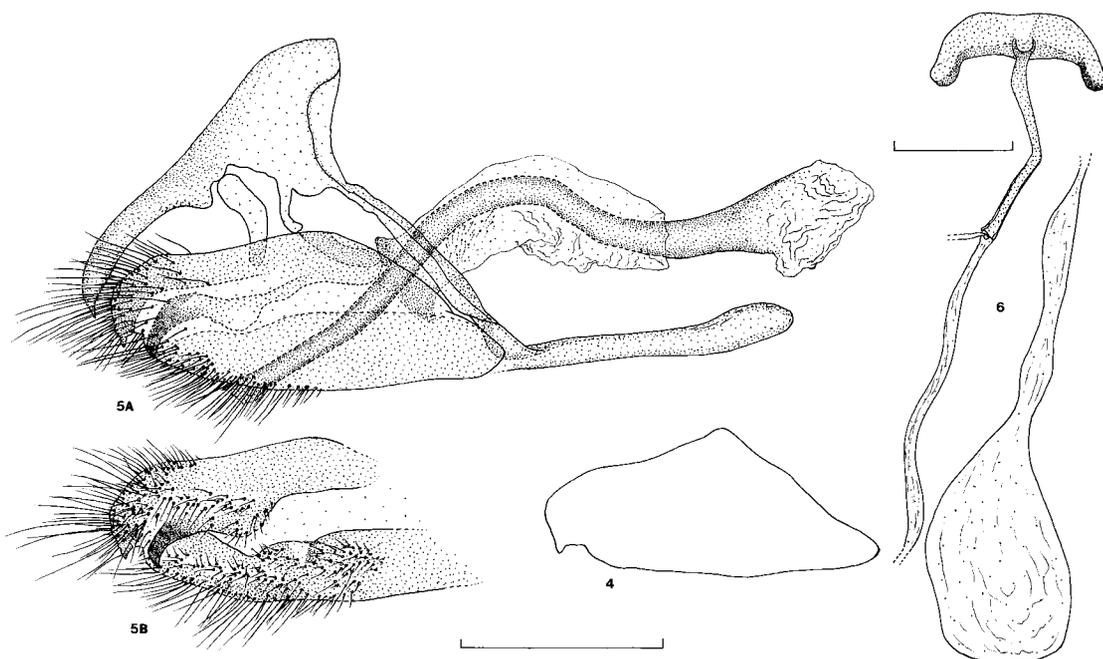
= *Cynthia cassavae* Fabricius, 1938. Syst. Gloss., 105. Unnecessary replacement name for *dirce* Linnaeus, 1758.

Distribution. *Colobura dirce dirce* appears to be more widespread than *C. annulata* (described below), although this may be partly an artifact of differing regional rarity, and occurs throughout the west Andean region from Mexico to western Ecuador, east of the Andes from Venezuela to Bolivia, northern Paraguay and Argentina (Hayward 1964), in south-eastern Brazil, the Amazon basin, the Guianas and Trinidad. To date, *Colobura dirce* is the only *Colobura* species known in the Caribbean (as *C.*

dirce wolcottii), and southern South America outside the Amazon basin.

Biology (Fig. 7 A and B). The early stages of this species have been known since at least the time of Stoll (1787), who figured the fifth instar and pupa in color on plate 2, as Fig. 4 A and B, and they have been described subsequently a number of times (Müller 1886, Dyar 1912, D'Almeida 1922, Beebe 1952, Muysshondt and Muysshondt 1976). Detailed notes on larval behavior were given by Beebe (1952). The immature stages of *C. dirce dirce* in Colombia are very similar to those described by Sepp ([1852]) in Surinam, Beebe (1952) in Trinidad, Muysshondt and Muysshondt (1976) in El Salvador, and DeVries (1987) in Costa Rica, and are summarized here:

Egg. The egg is dark olive-green in color (in *C. annulata* it is pale, whitish green), spherical, and 1 mm in diameter with 11 prominent, whitish-green ribs running vertically from the base, fading at the micropylar zone to leave an empty circular space where the micropyle is clearly visible. The eggs are deposited in



Figs. 4-6. (4) Neotype male for *Colobura dirce*, *C. bates*, and *C. dirceiodes*. Outline of genitalic valva in lateral view. (5) *Colobura annulata* sp. n., holotype. (A) Lateral view of genitalia; (B) inside of genitalic valva. (6) *Colobura annulata* sp. n., paratype female, French Guiana. Genitalia in dorsal view. Scale bars = 1 mm.

small clusters of 2-10 (in *C. annulata*, large clusters of up to 70 eggs are deposited). The egg stage lasts 4 d.

First Instar. The first instar is ≈ 2 mm long just after hatching, and grows to 4 mm before molting. The head is dark brown with fine setae and the body dark green and covered with light brown warts on thoracic segments 2-3 and abdominal segments 2, 4, 6, 8, and 9. The first instar lasts 3 d.

Second Instar. The second instar attains a body length of 7 mm. The head capsule is black with two short, stubby epicranial horns with lateral setae. The body is black with a row of six short scoli on each segment. The thoracic scoli and those on abdominal segments 2, 4, 6, 8, and 9 are white, the remainder dark brown. The second instar lasts 3 d.

Third Instar. The third instar attains a body length of 12 mm. The head capsule is shiny black with two long black horns on the epicranium armed with accessory setae. The body is velvet black with a row of white spots along the spiracular area. Each segment bears a row of six black, rosetted scoli with white tips. The third instar lasts 3 d.

Fourth Instar. The fourth instar attains a body length of 24 mm. The head capsule is shiny black and the epicranium has two prominent, yellowish-white horns with black tips and short accessory short setae. All subdorsal scoli are much longer than in previous instars and pale yellow. The spiracular area of each segment is dark yellow. The fourth instar lasts 6 d.

Fifth Instar (Fig. 7A). The fifth instar attains a body length of 35 mm. The head capsule is shiny black and the epicranium has two short white horns with brown

tips, armed with accessory setae (in *C. annulata* the horns are longer and intense yellow). The larva is velvet black with white thoracic scoli and pale yellow abdominal scoli, which turn completely white before pupation (*C. annulata* has cream-yellow rings encircling the body between each segment, and the abdominal scoli are intense yellow). The spiracular area is dark yellow. The fifth instar lasts 8 d.

Prepupa. In the prepupal stage the abdominal and thoracic scoli become completely white in color. The prepupa hangs vertically with the thorax curved inwards. The prepupal stage lasts 1 d.

Pupa (Fig. 7B). The pupa is cylindrical, 28 mm long and 6 mm wide, elongate and dark brown, resembling a dead twig. The head area is bifid, the thorax has a slight dorsal keel bearing lateral, paired, black warts, and the abdomen has a pair of short, flattened projections on segments 4, 6, and 7. The pupal stage lasts 12-14 d, giving a total life cycle of 35-37 d.

Adults are common in a wide variety of forest and secondary growth habitats from sea level to 1,600 m; they are present all year and appear to be generally more abundant than *C. annulata*, at least in drier areas of their range. Males are frequently seen in areas of human habitation in addition to primary forest, and are attracted to a wide range of decomposing organic material. In Ecuador, we once observed a male perching on *Cecropia* tree trunks on an open hilltop in the late afternoon. Females deposit eggs singly or in groups of up to 10 eggs, on the upper or lower side of hostplant leaves, with some preference for young saplings and seedlings (Müller 1886; Hoffmann 1930;

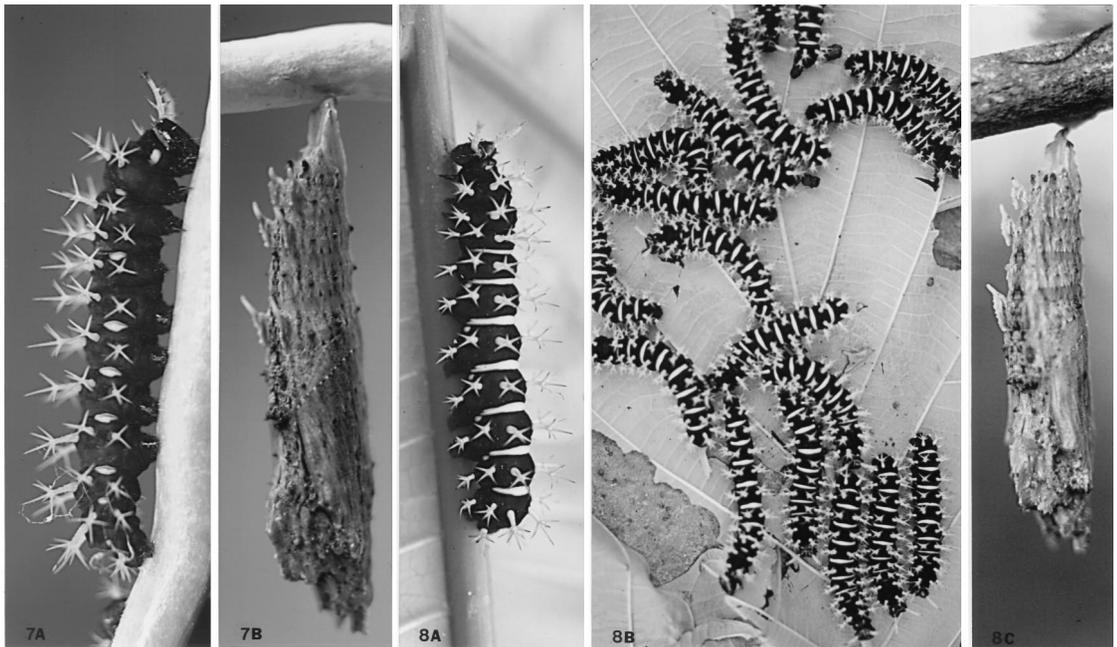


Fig. 7–8. (7) *Colobura dirce*, Colombia, on *Cecropia peltata*. (A) Fifth-instar larva, lateral view; (B) pupa, lateral view. (8) *Colobura annulata* sp. n., Colombia, on *Cecropia eximia*. (A) Fifth-instar larva, dorsolateral view; (B) aggregation of fifth-instar larvae; (C) pupa, lateral view.

Muyshondt and Muyshondt 1976; DeVries 1986, 1987; J. Mallet, personal communication).

Identification and Taxonomy. Adults of *C. dirce* are typically smaller than those of *C. annulata* (described below) and are best distinguished by the configuration of the dark submarginal lines on the ventral forewing, which curve more strongly basally and are more uneven in width, particularly the third submarginal line in from the margin, which always tapers toward the costa (Fig. 1). In addition, the black spot on the ventral forewing distal of the dark postdiscal bar in cell M1-R5 tends to be oval and elongate, and significantly wider than the adjacent spot in cell R5-R4 (Fig. 1). The pale dorsal forewing band frequently narrows at the costa and is often “kinked” at its distal edge at vein M3.

Linnaeus (1758) described *Papilio dirce* with typical brevity, mentioning the dark dorsal surface with yellow forewing band and undulating black ventral lines. The initials MLU following the description indicate that the original material was at that time in the Museum Ludovicae Ulricaе; however, there is now no known type material for *Papilio dirce* (Honey and Scoble 2001). Although the original spelling of the name was “*Papilio dirco*,” Linnaeus (1764) subsequently misspelled it “*dirce*,” and all subsequent authors followed suit. We therefore preserve the name *dirce* as an incorrect subsequent spelling in general usage (ICZN 1999: Art. 33.3.1). Several pages later Linnaeus (1758) described the similar *Papilio bates*, apparently on the basis that it had tailed hindwings (alis subcaudatis), whereas *dirce* did not (alis angulatis), but it can only be assumed that the hindwings were damaged on his *dirce* specimen(s). No type ma-

terial is known for this name either (Honey and Scoble 2001), but both wing surfaces of *P. bates* were figured in color shortly after by Clerck ([1764]), as Fig. 3 on plate 36; this painting shows all the wing pattern characters typical of the species treated here as *C. dirce*. Linnaeus (1764: 287) subsequently not only referred to this figure as representing his name *P. bates* (misprinted *butes*), but also regarded it as conspecific with *P. dirce*, in which he was followed by subsequent authors (Stoll 1787, Westwood 1850, Kirby 1871, Aurivillius 1882).

Sepp ([1852]) figured the fifth instar, pupa, and both adult wing surfaces of *C. dirce* and *C. annulata* (described below), on plates 149 and 145, respectively. The larva illustrated on plate 145 has a black body with yellow rings and spiracles, long, orange head horns, and three pairs of yellow-orange scoli on each segment, and is said to be gregarious (p. 321). The adult has an even, smooth-edged yellow band on the dorsal forewing, while the dark submarginal lines on the ventral forewing, although very similar to those of the specimen figured on plate 149, are slightly narrower and more even. All these larval and adult characters are typical of *C. annulata*, but Sepp appears to have relied on Cramer’s (1779: plate 212, figures C and D) figure of “*Papilio dirce*” as representing Linnaeus’ *P. dirce*, a figure that actually represents typical *C. annulata*. Sepp therefore identified *C. annulata* as *C. dirce* and went on (p. 321) to describe the species figured on plate 149 as a new species, *Papilio dirceoides*, stating that the larvae were solitary and the adults slightly smaller than those of the species figured on plate 145. In addition, the larva figured on plate 149

lacks yellow body rings and has pale gray thoracic scoli and short head horns, while the figured adult has slightly thicker and more uneven submarginal lines on the ventral forewing and the distal edge of the dorsal forewing band slightly kinked at vein M3. The most likely depository for type material of *dirceoides*, the RMNH, contains no potential type specimens, and G. Lamas (personal communication) believes there to be no extant type material for the name. This is not surprising because Sepp's plates and illustrations were based on illustrations made (apparently between 1785 and 1791) by H. J. Scheller for Jean Gerard Wichers, governor of Surinam. Scheller's illustrations were acquired by J. Calkoen from Wichers' family and later edited and published by J. Sepp between 1829–1852; it seems no voucher specimens were kept (G. Lamas, personal communication). However, the larval and adult characters evident in the original description are typical of *C. dirce* treated here; and *dirceoides* must therefore be regarded as a synonym of *dirce*, where it was placed by Kirby (1871) and most subsequent authors (Aurivillius 1882, Godman and Salvin 1883, Seitz 1914, Hayward 1964, DeVries 1987, Neild 1996).

The name *Cynthia cassavae* was introduced unnecessarily as a replacement name for *P. dirce* by Fabricius (1938). Fabricius also gave a short description of the larva, stating "Larva nigra, flavo fasciata," which appears to pertain to the yellow-banded larva of *C. annulata*. Notwithstanding this, being proposed as a replacement name the type material of *cassavae* is automatically the same as that of *P. dirce*, and the two names are therefore synonymous.

Because no type specimens are known for any of these names, we believe a neotype designation is warranted for each to ensure future nomenclatural stability. The collection localities of the specimens on which Linnaeus based his names *dirce* and *bates* are unknown, those given in the original description (Linnaeus 1758) being "in Calidis regionibus" and "Indiis," respectively. Both Sepp ([1852]) and Fabricius (1938) gave Surinam as the locality for the specimens on which they based their names, and this is also the most probable locality for the original Linnaean specimens. Because all three names, *dirce*, *bates*, and *dirceoides*, were apparently based on specimens from the same area, we adopt the simplest approach and designate a single specimen as the neotype for all these names. In the absence of male specimens from Surinam in the BMNH, we select as the neotype a specimen from as near that locality as possible, in good condition, otherwise typical of the species and closely resembling Clerck's original figure of *bates*. This specimen bears the data "Guyane Française C. Bar/Ex. Oberthür Coll. Brit. Mus. 1927–3." and is in the main collection of the BMNH (Fig. 2 A and B).

Colobura dirce shows some wing pattern variation throughout its range, most notable being the presence of a yellow dorsal forewing subapical spot in specimens from southern Brazil and Paraguay. However, this is a variable character that also occurs more rarely in specimens from other regions, and as such the phenotype is not worthy of subspecific recognition.

The width of the dark ventral lines is also slightly variable, without any apparent geographic correlation.

Colobura dirce wolcottii Comstock, 1942

Colobura dirce wolcottii Comstock, 1942. J. N.Y. Entomol. Soc. 50: 286. TL: Mayaguez, Puerto Rico. Holotype male: AMNH (examined).

= *Colobura dirce clementi* Comstock, 1942. J. N.Y. Entomol. Soc. 50: 284. TL: Santiago de Cuba, Cuba. Holotype male: AMNH (examined).

= *Colobura dirce avinoffi* Comstock, 1942. J. N.Y. Entomol. Soc. 50: 285. TL: Bath, St. Thomas, Jamaica. Holotype male: AMNH (examined).

Distribution. *Colobura dirce wolcottii* occurs throughout the Greater Antilles (Puerto Rico, Hispaniola, Cuba, Jamaica).

Biology. There are several published field observations on both the early stages, which are similar to those of mainland *C. dirce dirce*, and adults of this subspecies (Brown and Heineman 1972, and see references therein; Riley 1975, Schwartz 1989, Smith et al. 1994). Adults perch head down on trees in open areas in forest, and occur from sea-level to at least 1,150 m (Riley 1975, Schwartz 1989, Smith et al. 1994).

Identification and Taxonomy. Comstock (1942) described populations of *C. dirce* from three of the main islands of the Greater Antilles as distinct subspecies, based on a number of subjective characters of the ground color and extent of ventral markings, most notably the thickened dark lines in the distal half of the wings, which almost coalesce in some specimens. As with the mainland population, there is some variation in all of these characters, although Cuban specimens are particularly heavily marked on the ventral surface and consistently distinguishable. Although some subsequent authors (Brown and Heineman 1972) retained Comstock's three names, with reservations, others (Riley 1975, Smith et al. 1994) regarded them as representing, at best, a single subspecies, for which Riley (1975) selected the name *wolcottii*. We are also skeptical about the status of the Caribbean population, but follow the most recent faunistic work (Smith et al. 1994) in treating it as a single distinct subspecies.

Colobura annulata Willmott, Constantino & Hall, sp. n. (Figs. 3 A and B, 5 A and B, 6, and 8 A-C)

Male (Fig. 3 A and B). Forewing length HT, 34 mm (mean 36 mm, $n = 16$). Forewing triangular with slightly convex distal margin, hindwing triangular with produced tornal lobe. **Dorsal Surface.** Forewing ground color dark blackish brown; cream-colored postdiscal band extending from costa to near tornus, almost to vein 2A, with relatively smooth distal edge; basal third of wing dark brown. Hindwing ground color dark brown, becoming blackish brown in cell M1-Rs; cream-colored costal band distal of vein Rs extending from wing base to apex. **Ventral Surface.**

Forewing ground color cream, except for cell 2A-Cu2, where cream only enters anterior edge adjacent to discal cell; discal cell with four dark brown lines, third line from base extending into cell 2A-Cu2, discocellulars marked with two very close dark brown lines; base of cell Cu2-Cu1 dark brown, followed distally by second dark brown line; slightly paler cream postdiscal band as on dorsal surface; postdiscal band bordered distally from vein M2 to costa by dark brown line; distal of this line two dark brown postdiscal lines, approximately parallel to distal margin, extend respectively from cells M1-R5 and R5-4 to costa; four dark brown submarginal lines, basal-most even in width, extending from vein R3 straight to vein M2, then curving distally to terminate at middle of cell Cu1-M3, third from margin even in width and straight, extending from costa to cell M3-M2, second from margin straight, extending and broadening continuously from costa to cell Cu1-M3, and that closest to margin extending from costa to cell Cu2-Cu1, broadening slightly between veins Cu2-M3; thin, dark brown marginal border, narrowing gradually from apex to tornus. Hindwing ground color cream, becoming yellowish toward distal margin; basal quarter of costa with dark brown stripe; dark brown spot basal of humeral vein; seven dark brown lines in cell Rs-Sc+R1, five most distal extending anterior of vein Sc+R1, fourth and fifth joining distal of vein Sc+R1; dark brown line at base of discal cell extending to anal margin; dark brown streak at discocellular; 10 dark brown lines extending into wing from anal margin, first two entering and crossing discal cell, third reaching base of vein Cu1 then sharply bending toward tornus to meet eighth line from anal margin, fourth extending to vein Cu2 then bending sharply and running parallel to vein to meet seventh line from anal margin, fifth extending to vein 2A then bending sharply basally to run parallel to vein, sixth extending to vein 2A, ninth and tenth extending across posterior half of cell 2A-Cu2; four dark brown postdiscal lines approximately perpendicular to costa extending from base of cell M2-M1 to vein Cu2, mid-cell M1-Rs to mid-cell Cu2-Cu1, and two from vein Rs to vein Cu1, latter two narrowing away from costa; dark brown submarginal band from vein Rs to mid-cell Cu2-Cu1, narrowing to almost vanish away from costa, enclosing blackish spot with blue pupil in cell M1-Rs, blue pupil in cell M2-M1, and pale bluish pupil in cell Cu2-Cu1; three more distal dark brown submarginal lines, basal two from vein Rs to mid-cell Cu2-Cu1, tapering gradually away from costa, distal even in width from mid-cell M1-Rs to vein Cu2; diffuse submarginal patch of orange in posterior half of cell Cu2-Cu1 and anterior half of cell 2A-Cu2; black tornal spot in cell 2A-Cu2 with blue pupil in anterior half; dark brown marginal border from mid-cell M1-Rs to mid-cell 2A-Cu2. *Head*. Labial palpi white, inner and dorsal surfaces black; eyes brown and bare; frons white with central vertical black stripe; antenna brown, ringed with sparse white scales at base of each segment, black clubs, slightly paler at tip. *Body*. Thorax dark blackish brown dorsally, cream ventrally and laterally with four lateral, transverse dark brown

stripes; abdomen blackish brown dorsally and laterally, cream ventrally, with thin cream-colored lateral line; all legs cream, dorsal surface of tibia and tarsus blackish brown. *Genitalia* (Fig. 5 A and B). Valva terminating posteriorly in a small, ventrally directed point, with a prominent, well sclerotized, ventrally directed spine on the inner edge near the posterior tip; aedeagus heavily sclerotized, strongly curved at mid-point.

Female. Externally similar to male except larger (FW length of topotypic PT, 39 mm) and slightly paler dorsally. *Genitalia* (Fig. 6). Lamella antevaginalis a smooth plate with two heavily sclerotized, anteriorly pointing lobes; ostium bursae elongate, ductus bursae extending almost length of abdomen, corpus bursae lacking signa.

Type Material. HOLOTYPE: 1♂, FRENCH GUIANA: *Cayenne*: "Cayenne/Ex. Oberthür Coll. Brit. Mus. 927-3," BMNH.

PARATYPES. GUATEMALA: 1♂, Forests of N. Vera Paz, BMNH. COSTA RICA: 1♂, Santa Clara Valley, 1,200 feet, F. A. Zurcher, BMNH. COLOMBIA: *Meta*: 1♂, Río Negro, 2,400 feet, 7-II-69, S. S. Nicolay, USNM; *Tolima*: 1♂, State of Tolima, Wheeler, BMNH; *Valle del Cauca*: 3♂, Bajo Anchicayá, Sabaletas, 70 m, 10-IV-97, L. M. Constantino, LMC. ECUADOR: *Morona-Santiago*: 1♂, Macas, 3,500 feet, VI-21, E. W. Rorer coll., USNM; *Esmeraldas*: 1♂, c. km. 15 Lita-San Lorenzo Rd., Anchayacu, 950 m, 1-VII-98, K. R. Willmott, KWJH; *Pastaza*: 1♂, Sarayacu, C. Buckley, BMNH. PERU: *Loreto*: 1♂, 40 km. NE Iquitos, Explorama Lodge, 24-VI-20-VII-90, Menke and Awertschenko, USNM; *Ucayali*: 1♂, Pucallpa, Lago Yarinacocha, 20-IV-46, J. M. Schunke, MUSM; *Pasco*, 1♂, Alto Yurinaqui, nr. Eneas, 1,400 m, 26-IV-66, P. Hocking, MUSM; *Junín*: 1♂, Chanchamayo, 1898, O. Schunke, BMNH; 1♂, La Merced, 2,500 feet, VIII-03, Watkins and Tomlinson, BMNH; *Madre de Dios*, 2♀♀, Boca Rio La Torre, 300 m, 29-XI-79 and 25-VII-80, G. Lamas, MUSM. BRAZIL: *Pará*: 1♂, Pará, BMNH. FRENCH GUIANA: 4♂♂, 1♀, same data as HT, BMNH.

Distribution. *Colobura annulata* is sympatric throughout its range with *C. dirce*. Its range is Mexico to western Ecuador, Venezuela to Bolivia, Amazonian Brazil, the Guianas, and Trinidad.

Etymology. The species name is derived from the Latin adjective "annulatus," meaning ringed, with reference to the diagnostic yellow rings encircling the larvae.

Biology (Fig. 8 A-C). This species occurs from sea-level to at least 1,300 m, typically in association with forested habitats, though it is tolerant of substantial habitat degradation. The early stages have been reported several times (DeVries 1987, Constantino 1998), in some cases with color figures (Stoll 1787, Sepp [1852]). In Colombia, the immature stages appear to be similar to those reported from Surinam (Sepp [1852]) and Costa Rica (DeVries 1987), and are summarized here.

Egg. The egg is pale green in color, spherical, and 1.2 mm in diameter with 11 prominent white ribs running vertically from the base, fading at the micropylar zone

to leave an empty circular space where the micropyle is clearly visible. The eggs are placed in clusters of up to 70–150. The egg stage lasts 4 d.

First Instar. The first instar is ≈ 2 mm long just after hatching and grows to 4.2 mm before molting. The head is dark brown with fine setae, and the body dark green covered with light brown warts on thoracic segments 2–3 and abdominal segments 2, 4, 6, 8, and 9. The first instar lasts 3 d.

Second Instar. The second larva attains a body length of ≈ 8 mm. The head capsule is black with two short, stubby epicranial horns with accessory setae. The body is black with a row of six short scoli on each segment. The thoracic scoli and abdominal scoli on segments 2, 4, 6, 8, and 9 are yellow, the remainder black. The second instar lasts 3 d.

Third Instar. The third instar attains a body length of 13 mm. The head capsule is shiny black with two long black horns on the epicranium armed with accessory setae. The body is velvet black with yellow spiracles and cream-yellow rings encircling the body between each segment. Each segment has a row of six black, rosetted scoli with yellow tipped spines. The third instar lasts 3 d.

Fourth Instar. The fourth instar attains a body length of 28 mm. The head capsule is shiny black and the epicranium has two prominent, intense yellow horns with accessory short setae. The subdorsal rosetted scoli are much longer than the lateral scoli and intense yellow. The body is encircled with cream-yellow rings between each segment. The spiracular area is cream-yellow in color. The fourth instar lasts 5 d.

Fifth Instar (Fig. 8 A and B). The fifth instar attains a body length of 37 mm. The head capsule is shiny black and the epicranium has two long, intense yellow horns armed with accessory spines. The body is velvet black with conspicuous yellow-cream rings encircling the body between each segment, with a set of six intense yellow rosetted scoli on each segment. The spiracular area is cream-yellow. The last instar lasts 8 d.

Prepupa. The prepupa resembles the fifth instar and hangs with thorax curved inward. The prepupal stage lasts 1 d.

Pupa (Fig. 8C). The pupa is cylindrical, 30 mm long and 6.3 mm wide, elongate and pale brown, resembling a dead twig. The head area is bifid, the thorax has a slight dorsal keel bearing lateral, paired dark warts, and the abdomen has a pair of short, flattened projections on segments 4, 6, and 7. The pupal stage lasts 12 d, giving a total life cycle of 34–36 d.

The larval hostplants in Colombia include several species of *Cecropia* (Moraceae), mostly *C. eximia*, *C. virgusa*, *C. longipes* Pittier, and *C. peltata*. The larvae feed gregariously in groups of up to 150 individuals and molt synchronously. When larval aggregations on *Cecropia* trees are heavy they may completely defoliate the tree. Although most *Cecropia* trees have hollow internodes inhabited by *Asteca* ants (Dolichoderinae), which protect the trees from insect herbivores, the larvae of both *Colobura* species possess a defensive mechanism in the form of an eversible ventral prothoracic gland. When extruded this gland produces a

very unpleasant strong scent which appears to repel ants. This ventral prothoracic gland has been named the *adenosma* (Muysshondt and Muysshondt 1976), and similar glands are also present in a variety of other nymphalid genera, including *Caligo*, *Opsiphanes*, *Morpho*, *Consul*, *Memphis*, *Taygetis*, *Manataria*, and several moth larvae (Muysshondt and Muysshondt 1976).

Adults exhibit synchronous emergence during the same day. Males are usually one of the first butterflies to be attracted to traps in forest light gaps, and can be found feeding on rotting carrion, fruit and sap flows. Females are more scarce but may also be seen at the latter two food sources. In Ecuador, males perch in groups late in the afternoon (1630–1730 hours) head down on the sides of sunlit tree trunks in forest light-gaps or clearings along ridgetops, from 10 to 20 m above the ground, and engage in very rapid pursuit around the perching tree.

Identification and Taxonomy. Adults of this species may be distinguished from those of *C. dirce* by having more even dark and light submarginal lines on the ventral forewing, particularly the third line from the margin, which does not taper toward the costa. In addition, the black costal spot in cell M1–R5 distal of the black postdiscal line is of similar width compared with the adjacent spot in cell R5–R4, instead of being elongate and oval in shape. Although the yellow dorsal forewing band is variable in width and shape, it is typically more even in width than that of *C. dirce*, which often tapers sharply at the costa, and has smoother distal and basal edges. Adults are typically larger than those of *C. dirce* (mean male forewing length for both species over geographic range of each: *C. annulata* 36 mm [$n = 16$]; *C. dirce* 33 mm [$n = 32$]; t -test, $P < 0.01$). The shape of the male genitalic valvae also appears to differ slightly but consistently between the two species, being more elongate, even in width, and less produced dorsally where connected to the tegumen in *C. annulata* (see Figs. 4 and 5 A and B). The female genitalia of the two species do not differ significantly. The immature stages of the two species exhibit a number of differences as follows: in *C. annulata* the egg is paler and deposited in larger clusters, the larvae are highly gregarious, fourth and fifth larval instars have cream-yellow rings encircling the body between each segment (*C. dirce* lacks these rings), the spiracular area is cream-yellow instead of dark yellow, the head horns are more prominent, and the head horns and scoli are intense yellow (in *C. dirce* the thoracic scoli and head horns are white, and the abdominal scoli pale yellow), and do not fade to white before pupation.

The fact that this species has remained undescribed until now is due to a combination of its great similarity to *C. dirce*, the lack of geographic variation in wing pattern of both species leading to a lack of available, described names, and bad luck on the part of Sepp. Early authors regarded it as representing the female of *C. dirce* (Stoll 1787), despite appearing to have noticed the differences in wing pattern, or at least size, in adult specimens. In their Dutch and German translations of Linnaeus's *Sys-*

Table 1. Hostplant records for *Colobura*

Hostplant	Locality	Hostplant growth and larval feeding behavior	Source and identification
<i>C. dirce</i>			
Moraceae			
<i>Cecropia pachystachia</i>	Brazil (SC)	Saplings; eggs in small groups	Müller (1886) (d,i)
<i>Cecropia peltata</i>	Cuba	—	Dewitz (1879) (l)
<i>Cecropia peltata</i>	Cuba	—	Bruner et al. (1975) (i)
<i>Cecropia peltata</i>	Trinidad	Early instars gregarious	Beebe (1952) (i)
<i>Cecropia peltata</i>	Puerto Rico	—	Martorell (1976) (l)
<i>Cecropia peltata</i>	El Salvador	Seedlings, saplings; solitary or gregarious as early instars	Muyshondt and Muyshondt (1976) (i)
<i>Cecropia peltata</i>	Colombia (west)	See <i>Discussion</i>	This paper
<i>Cecropia mexicana</i>	El Salvador	Seedlings, saplings; solitary or gregarious (<10) as early instars	Muyshondt and Muyshondt (1976) (i)
<i>Cecropia hololeuca</i>	Brazil (SC)	Sapling; small group of larvae	Hoffmann (1930) (d)
<i>Cecropia obtusa</i>	French Guiana	Early instars gregarious	Remillet (1988) (i)
<i>Cecropia</i> sp.	Brazil (RJ)	—	Bönnighausen (1896) (1)
<i>Cecropia</i> sp.	Brazil (SC)	—	Hoffmann (1936) (l)
<i>Cecropia</i> sp.	Argentina	—	Hayward (1940), citing Jörgensen (in litt.) (l)
<i>Cecropia</i> sp.	Brazil (RJ)	—	Zikán and Zikán (1968) (l)
<i>Cecropia</i> sp.	Jamaica	—	Brown and Heineman (1972) (d)
<i>Cecropia</i> sp.	West Indies	Early instars gregarious	Riley (1975) (d)
<i>Cecropia</i> spp.	Costa Rica	Eggs in loose clusters on seedlings to mature trees; larvae semigregarious	DeVries (1986, 1987) (d)
<i>Cecropia</i> sp.	West Indies	Early instars gregarious	Smith et al. (1994) (d)
<i>Cecropia</i> sp.	Costa Rica	Seedling; small groups	J. Mallet (pers. comm.) (d)
<i>Cecropia</i> sp.	Guyana	Seedling	J. Mallet (pers. comm.) (d)
<i>Cecropia</i> sp.	Brazil (southeastern)	Saplings (30–100 cm); 3–17 eggs per group	A. Freitas (pers. comm.) (d)
Caricaceae			
<i>Carica microcarpa</i> ?	Surinam	Solitary larvae	Sepp ([1852]) (i)
Leguminosae			
<i>Cassia fistulosa</i> ?	Puerto Rico	—	Martorell (1976), citing Möschler (l)
<i>Inga</i>	Brazil (SC)	Error-See <i>Discussion</i>	Hayward (1969), citing Hoffmann (l)
Myrtaceae			
<i>Eucalyptus</i>	Brazil (RGS)	Error-See <i>Discussion</i>	Biezanko (1949) (l)
<i>C. annulata</i>			
Moraceae			
<i>Cecropia</i> sp.	Costa Rica	Emergent canopy trees; larvae highly gregarious	Mallet (In DeVries, 1986,
<i>Cecropia virgusa</i>	Colombia (west)	See <i>Discussion</i>	Constantino (1998)
<i>Cecropia eximia</i>	Colombia (west)	See <i>Discussion</i>	Constantino (1998)
<i>Cecropia longipes</i>	Colombia (west)	See <i>Discussion</i>	Constantino (1998)
<i>Cecropia peltata</i>	Colombia (west)	See <i>Discussion</i>	This paper
Caricaceae:			
<i>Carica papaya</i> ?	Surinam	Larvae gregarious	Sepp ([1852]) (i)
Unidentifiable			
Moraceae			
<i>Cecropia peltata</i>	Trinidad	—	Barcant (1970)
<i>Cecropia</i> sp.	Brazil	—	Otero and Marigo (1990)
<i>Cecropia</i> sp.	Brazil	—	Brown (1992)
Rubiaceae:			
<i>Coffea</i> sp. ?	Guyana	—	Bodkin (1915)
<i>Cassia</i> sp. ?	Neotropics	—	Seitz (1914)
Euphorbiaceae			
“Casava” ?	Surinam	—	Stoll (1787), citing Merian (1705)

Doubtful records are followed by a “?”; Species have been identified through illustrations or descriptions of adults or larvae (i/d), or by records originating from localities where only a single species is known to occur (l).

tema Naturae, Houttuyn (1767, plate 89, figure 9) and Müller (1774, plate 19, figure 9), respectively, figured the ventral surface of what is probably a specimen of *C. annulata* as *Papilio bates*. Several later authors have quoted Sepp’s work while speculating on the possibility of sibling species in *Colobura*, including DeVries (1987), who also reported the larvae of both species in Costa Rica. However, Brévignon and Brévignon (1997) appear

to have been the only authors since Sepp to actually fully recognize two species, figuring both but incorrectly applying the names *dirce* and *dirceoides* to them.

Discussion

The unusually marked differences in coloration and gregariousness between later instar larvae of the two

Colobura species suggests the possibility that ecological differences may have been of some importance in initially promoting speciation. We therefore reviewed the literature on *Colobura* hostplant choice and adult behavior to investigate whether any additional general patterns might be apparent.

Although a number of different plant taxa have been cited as hostplants of *Colobura* (Table 1), all credible records are in the genus *Cecropia* (although *Pourouma* [Moraceae] is also accepted, with slower development, in captivity in Colombia [LMC]). Stoll's (1787) citation of "Cassava" is almost certainly erroneous, as suggested by Müller (1886), whereas records of *Carica*, *Coffea*, and *Cassia* are also historical and dubious. Sepp's ([1852]) records of *Carica* probably stem from original purely decorative illustrations of the plant to accompany those of the early stages; Sepp did not actually rear either species himself (see identification and taxonomy section of *C. dirce*). Two other certainly erroneous records are *Eucalyptus* and *Inga*. Both of these taxa were given by Hoffmann (1930) as plants on whose fermenting sap adult *Colobura* fed, but subsequent authors seem to have regarded them as larval hostplant records (Biezanko 1949, Hayward 1969). However, although there appear to be no significant differences in hostplant taxon choice, there is a reasonable body of evidence to suggest that ovipositing female *Colobura* discriminate between young and mature plants. In primary forests, both J. Mallet and P. DeVries (personal communication) reported that larvae of *C. dirce* are most frequently found on seedlings to saplings, whereas *C. annulata* occurs most often on mature canopy trees. Our observations in secondary forest and artificial environments in Colombia (LMC) have not demonstrated this dichotomy so convincingly, but literature records (Table 1) suggest that selection of young plants by ovipositing females is a general trait of *C. dirce* throughout its range. Although there are much less data for *C. annulata*, this is perhaps partially indicative of the reduced apparency of its early stages to biologists, because the adults appear to be almost as common as those of *C. dirce*, at least throughout the range of the former species in South America.

The greater food resources of a mature canopy tree clearly permit the larger aggregations of larvae that are typical of *C. annulata*, whereas small saplings restrict the number of later instar *C. dirce* to much smaller groups, or even solitary individuals. Because qualitative secondary chemicals are often mobilized toward sources of feeding damage, and quantitative secondary chemicals (such as tannins) are more concentrated in mature leaves and trees, greater levels of tolerance of both might allow *C. dirce* larvae their gregarious lifestyle on canopy trees. Feeding tests in captivity could test both of these hypotheses. Specialization by *C. dirce* on young, early successional plants perhaps also helps explain its wider geographic distribution.

The differences in hostplant maturity and height may also influence flight height in adult *Colobura*. Beccaloni (1997) demonstrated a correlation between

adult flight height and hostplant height in Neotropical ithomiine butterflies, and P. DeVries (personal communication) based on reanalysis of data presented by DeVries et al. (1999) reported statistically significant differences in flight height of both sexes between the two *Colobura* species in lowland primary forest in eastern Ecuador. Paired canopy and understory traps reveal a tendency for *C. annulata* to occur in the canopy, and for *C. dirce* to occur in the understory.

That interspecific flight height differences apply to both males and females is interesting, because it suggests the possibility that the height at which males perch may correlate with hostplant height and female flight height. Perching behavior is exhibited by many Neotropical butterflies and involves males waiting for females at particular sites, such as a ridgetop or riverside. Such behavior is thought to allow females to locate males more easily (Scott 1968, 1975) and has been suggested to provide a premating isolating mechanism (Callaghan 1983). Our observations in Ecuador (see *Biology* section for each species) suggest that *C. annulata* perches high in the canopy, whereas *C. dirce* perches lower to the ground, but more data are clearly needed on male perching height for these two species and other perching butterflies before any firm conclusions may be drawn on relationships between female hostplant choice and male perching behavior.

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