A tale of two species: detritivory, parapatry, and sexual dimorphism in *Lamprospilus collucia* and *L. orcidia* (Lycaenidae: Theclinae: Eumaeini)

Robert K. Robbins¹, Annete Aiello², Julie Feinstein³, Amy Berkov³, Astrid Caldas⁴, Robert C. Busby⁵ and Marcelo Duarte⁶

Abstract. Lamprospilus collucia (Hewitson) and L. orcidia (Hewitson) are facultatively detritivorous hairstreaks. Females in nature lay eggs on dead twigs and leaves that are on or near the ground. In the lab, females oviposit readily on dead leaves. Caterpillars of both species eat dead plant material in nature and can be reared in the lab to the adult stage on artificial diet to which no plant material has been added. Lamprospilus collucia and L. orcidia have parapatric distributions; the former species is endemic to the Transandean Region and the latter to the Amazonian and Atlantic Regions. Both species have similar male behavior, which is consistent with the hypothesis that their parapatric distributions are maintained by mating interference. The sexes of L. collucia and L. orcidia have been incorrectly associated in compendia of Neotropical butterflies and are associated in this paper by geographic distribution, wing pattern similarity, and rearing data. Although L. collucia and L. orcidia have been considered to be conspecific, an analysis of geographical variation supports the hypothesis that they are distinct biological species.

Key words: Amazonian Region, biogeography, hairstreak systematics, Lecythidaceae, Transandean Region.

Introduction

Lamprospilus collucia (Hewitson) and L. orcidia (Hewitson) are common and widespread lowland Neotropical lycaenids (Theclinae: Eumaeini) that are biologically significant for a number of reasons. First, L. collucia and L. orcidia are ecologically unusual. Larval detritivory occurs rarely in the "Macrolepidoptera" (Powell et al., 1998; Hohn & Wagner, 2002), but has been reported in *Lamprospilus* Geyer (Duarte & Robbins, in press), specifically in L. collucia and L. orcidia. Second, L. collucia and L. orcidia are biogeographically significant because they have been cited as a representative parapatric species pair with a Central/South American distribution (Robbins, 2004a). This biogeographic pattern, while well-known in forest-dwelling aposematic butterfly taxa (Brown, 1982), has not been documented

Received: 15 September 2009 Accepted: 12 October 2009 previously in the Eumaeini. Third, *L. collucia* and *L. orcidia* are of taxonomic interest because they are widely misidentified in publications on Neotropical butterflies (e.g., Godman & Salvin, 1887; Weeks 1911; Draudt, 1919-1920; Kaye, 1921; Barcant, 1970; Robbins & Small, 1981; D'Abrera, 1995). Both species are sexually dimorphic. The males have similar wing patterns (Figs. 1-4, 13-16, 21-22), for which reason they have been considered to be conspecific (Godman & Salvin, 1887-1901; Kaye, 1921). Alternately, the female wing patterns (Figs. 5-12, 17-20, 23) are different from each other and from those of the males, with which they have rarely been associated (e.g., Draudt, 1919-1920).

The purpose of this paper is to address the ecology, biogeography, and taxonomy of *L. collucia* and *L. orcidia* by answering basic questions about them. Where do females oviposit? What do their caterpillars eat? When and where do males set up mating territories? What are the distributions of *L. collucia* and *L. orcidia*? In which habitats do they occur? How are *L. collucia* and *L. orcidia* distinguished? How

¹Department of Entomology, PO Box 37012, NHB Stop 105, Smithsonian Institution, Washington, DC 20013-7012, USA robbinsr@si.edu

²Smithsonian Tropical Research Institute, Smithsonian Institution, Apartado 0843-03092 Balboa, Ancon, Panamá aielloa@si edu

³Department of Biology, City College of New York, City University of New York, Convent Avenue at 138th Street, New York, NY, 10031, USA jfstein@amnh.org, berkov@sci.ccny.cuny.edu

⁴Department of Entomology, PO Box 37012, NHB Stop 105, Smithsonian Institution, Washington, DC 20013-7012 USA astridcaldas@yahoo.com

⁵7 Countryside Way, Andover, MA 01810-6041 USA

rc.busby@comcast.net

⁶Coleção de Lepidoptera, Museu de Zoologia, Universidade de São Paulo, Av. Nazaré 481, 04263-000 São Paulo, SP Brasil mduartes@usp.br

do they vary seasonally and geographically? On what basis are the sexes associated? What is the available evidence that they are different biological species? We add brief notes on nomenclature to confirm that we are using the correct names. The placement of *L. collucia* and *L. orcidia* in *Lamprospilus* Geyer is dealt with elsewhere (Duarte & Robbins, in press).

MATERIALS AND METHODS

Eggs were obtained in the lab following the methods detailed in Duarte *et al.* (2005). Larvae from these eggs were reared on artificial diet to which no vascular plant material was added other than wheat germ and linseed oil (Duarte *et al.*, 2005). Rearing methods for immatures collected in nature generally follow Feinstein *et al.* (2007). Depositories for vouchers are noted.

Biogeographic and taxonomic results for L. collucia are based on 96 males (6 genitalic dissections from Mexico, Panama, western Ecuador, and eastern Colombia) and 70 females (6 genitalic dissections from Mexico, Costa Rica, Panama, and Trinidad). Analogous results for L. orcidia are based on 50 males (6 genitalic dissections from Ecuador, Peru, and 3 states in Brazil) and 57 females (6 genitalic dissections from Peru and Brazil). We map the distributions of each species by sex because these distributions are evidence for associating the sexes. Although mitochondrial "barcodes" are reported for L. collucia and L. orcidia (BOLD website, http://www.barcodinglife.org/views/ login.php, accessed 26 Aug 2009), the barcodes are not publically available and the "barcoded specimen" of L. orcidia is misidentified.

Genitalic terms follow Klots (1970), as modified for the Eumaeini (Robbins, 1991). Wing venation follows Comstock (1918), and other morphological terms follow Snodgrass (1935). Geographic distributions are mapped by gender. Months are abbreviated by their first three letters in English.

Vouchers for the distribution maps and other results are deposited in the following collections: (AA) Annette Aiello Collection, Ancon, Panamá; (BMNH) Natural History Museum, London, UK; (DZUP) Universidade Federal do Paraná, Curitiba, Paraná, Brazil; (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge MA, USA; (MECN) Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; (MUSM) Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú; (MZUSP) Museu de Zoologia, Universidade de São Paulo, Brazil; (RCB) Robert C. Busby Collection, Andover, MA, USA; (USNM) National Museum of Natural History, Smithsonian Institution,

Washington, DC, USA.

RESULTS

Ecology and biogeography

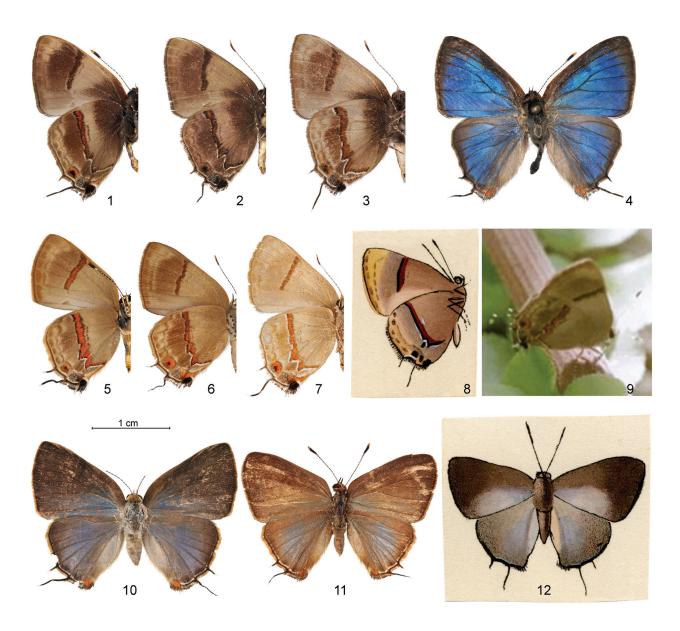
Oviposition and food "plants." As part of a study of plant fungal diseases (Davidson et al., 2000), a "mostly dead" seedling of Anacardium excelsum (wild cashew, Anacardiaceae) was collected by Davidson about 9 Jun 1996 near the Rio Frijoles, Pipeline Road, Canal Area, Panama (see Ridgely, 1976 for information on the Pipeline Road locality). A dark reddish brown larva of L. collucia was found three days later eating the cotyledon of the dead seedling. Aiello fed the caterpillar the peduncle of Anacardium occidentale to complete its development. On 18 Jun 1996, a dark brown pupa with erect setae on the sides of the abdomen was formed. The pupa turned black on 1 Jul 1996, and a male of L. collucia emerged later that day. The reared adult male is deposited in AA (Aiello lot: 1996-10).

A female of *L. collucia* was collected by Robbins and Caldas on 30 Mar 2000 in Ancon, Canal Area, Panama. She laid 22 eggs over 6 days in the lab on dead leaves and on the side of a vial. Aiello reared the hatched larvae on artificial diet without any added plant material. A female emerged on 13 May 2000. The reared female and her mother are deposited in USNM.

Robbins and Caldas observed a female of *L. collucia* ovipositing on a twig on the ground in Ancon on 31 Mar 2000. After capture, the female butterfly laid another 44 eggs over the next 5 days on dead leaves in the lab. Aiello reared the resulting caterpillars on artificial diet without any added plant material, and three males and one female emerged 14-16 May 2000 (Figs. 1, 5). The mother and her reared offspring are deposited in USNM.

Robbins and Caldas observed a female of *L. collucia* ovipositing on a green leaf about 10 cm from the ground on 2 Apr 2000 (Fig. 9). She was not captured and the egg was not collected.

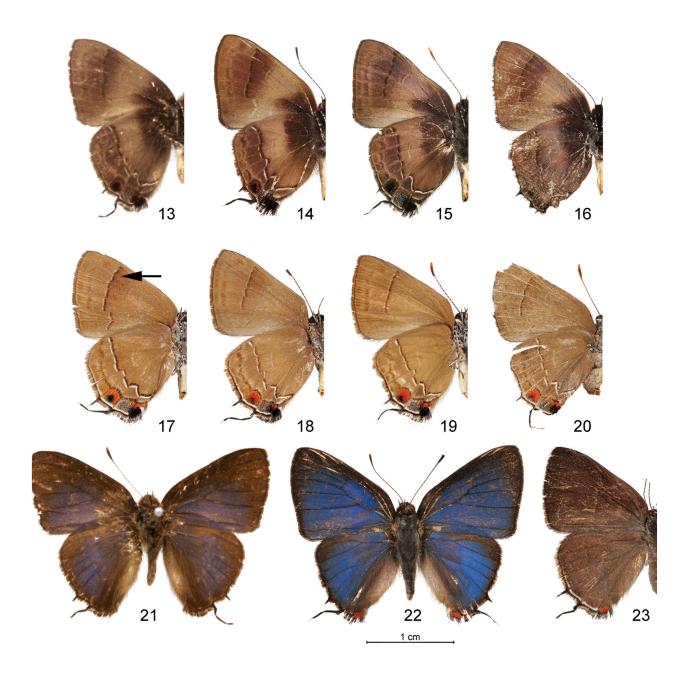
A male of *L. orcidia* was reared from the fallen androecia of *Eschweilera coriacea* (Lecythidaceae, plant vouchers deposited in New York Botanical Garden) from lowland moist forest 7 km north of Saül, French Guiana (3°37' N, 53°12' W). The androecia were collected by Berkov 21 Oct 1995 in the dry season, and the adult male of *L. orcidia* emerged 8 Nov 1995 (voucher deposited in USNM, Fig. 16). Another eight Lycaenidae that belong to another genus were also reared from these androecia (Feinstein, Robbins, & Berkov, in prep.).



Figures 1-12. Lamprospilus collucia adults. 1. \circlearrowleft ventral, Panama, reared, male sibling of 5. 2. \circlearrowleft ventral, Panama, form typically seen in the wet season. 3. \circlearrowleft ventral, Panama, form typically seen in the dry season. 4. \circlearrowleft dorsal of 1. 5. \hookrightarrow ventral, Panama, reared, female sibling of 1. 6. \hookrightarrow ventral, Panama, form typically seen in the wet season. 7. \hookrightarrow ventral, Nicaragua, form typically seen in the dry season. 8. \hookrightarrow ventral, no locality, reproduction of figure from the original description. 9. \hookrightarrow ventral, Panama, female walking on a twig near the ground before laying an egg. 10. \hookrightarrow dorsal, Venezuela. 11. \hookrightarrow dorsal, Venezuela. 12. \hookrightarrow dorsal, no locality, reproduction of figure from the original description.

A male and two females (Fig. 20) of *L. orcidia* (identified as Lycaenidae #2 in Feinstein *et al.* 2007) were reared from larvae found in fallen androecia of *Lecythis corrugata* (Lecythidaceae) during the first three months of 2003 in the wet season at Les Nouragues Research Station in French Guiana (4°05' N, 52°41'W; 110 km south of Cayenne). Although 17 other Lycaenidae were reared, none belong to *Lamprospilus*. Reared adult vouchers are deposited in USNM.

Male behavior. Lamprospilus males display "territorial" behavior that is similar to that reported in other eumaeines (e.g., Alcock & O'Neill, 1986; 1987); males wait for receptive females to fly through the territory and "defend" these areas by flying at other males that enter the territory. Males of *L. collucia* and *L. orcidia* set up mating territories in the morning on hilltops (vouchers below are deposited in USNM, observations are by Robbins; times are standard time



Figures 13-23. Lamprospilus orcidia adults. 13. ♂ ventral, Brazil (Pará), presumed holotype. 14. ♂ ventral, Peru. 15. ♂ ventral, Peru. 16. ♂ ventral, French Guiana, reared from fallen androecia of Lecythidaceae. 17. ♀ ventral, Peru, arrow points to brown scales basal of the postmedian line. 18. ♀ ventral, Peru. 19. ♀ ventral, Peru. 20. ♀ ventral, French Guiana, reared from fallen androecia of Lecythidaceae. 21. ♂ dorsal, Brazil (Pará), presumed holotype. 22. ♂ dorsal, Peru. 23. ♀ dorsal, Peru.

at that locality).

Lamprospilus collucia in Panama, 0730-1045 hours 4 ♂ observed (2 vouchers), 5 Oct 1978, 0730-0745 hours, Canal Area, Paraiso, Cerro Paraíso. 5 ♂ (5 vouchers), 1 Jan 1979, 1000-1030 hours, Canal Area, Paraíso, Cerro Paraíso. 1♂ (1 voucher), 5 Mar 1979, 1045 hours, Canal

Area, Paraíso, Cerro Paraíso. >25♂ observed (2 vouchers), 17 May 1979, 0830-1030 hours, Canal Area, Cerro Galera. 1♂ (1 voucher), 28 Jul 1979, 1000 hours, Canal Area, Paraíso, Cerro Paraíso.

Lamprospilus orcidia in Brazil, 0904-0920 hours

68 J. Res. Lepid.

1 \circlearrowleft (1 voucher), 18 Mar 1991, 0904 hours, São Paulo, 17 km west of Teodoro Sampaio.

1♂ (1 voucher), 24 May 1998, 0920 hours, Rio de Janeiro, Iguaba Grande.

Habitat. Lamprospilus collucia and L. orcidia occur in wet and dry lowland forest, ranging from "relatively virgin" forest (e.g., Parque Manu, Peru) to mature secondary forest (e.g., Gamboa, Canal Area, Panama) to patchy disturbed forest in urban areas (e.g., Ancon, Canal Area, Panama). We have seen no specimens of L. collucia collected above 1,000 m elevation in Central America, but in western Ecuador they have been found in wet forest at 1,500 m and on a ridge with dry forest at 2,100 m where there is often a strong westerly wind. Most individuals of L. orcidia are recorded from lowland forest, but some have been recorded from 1,000 m elevation in southern Brazil. Adults of L. collucia and L. orcidia are most abundant at the end of the dry season and beginning of the wet season in Panama and southeastern Peru, a pattern typical of the Lamprospilus Section (Duarte & Robbins, in press).

Distribution. Males of *L. collucia* are recorded from northeastern Mexico to Ecuador west of the Andes and to Trinidad, northern Venezuela, and central Colombia east of the Andes (circles in Fig. 24) while males of *L. orcidia* are known east of the Andes from central Venezuela to southern Brazil and Bolivia (squares in Fig. 24). Males of *L. collucia* and *L. orcidia* are not sympatric.

Females of *L. collucia* are recorded from northeastern Mexico to the northwestern tip of Peru west of the Andes and to Trinidad, and central Venezuela east of the Andes (circles in Fig. 25) while females of *L. orcidia* are known from east of the Andes from the Guianas and southern Venezuela and southern Colombia to southern Brazil (squares in Fig. 25). Females of *L. collucia* and *L. orcidia* are not sympatric.

There is one male of *L. orcidia* and one female of L. collucia from the Rio Suapure, Venezuela (MCZ), a tributary of the Rio Orinoco in central Venezuela (Bolivar state) that flows through llanos (savannah) and Amazonian forest habitats (arrows in Figs. 24-25). These specimens lack collection date or more specific locality data. Weeks (1911) noted only that they were collected in "the neighborhood of the Suapure River in Venezuela." It is unknown if both were collected at the same locality along the Rio Suapure, but if so, it is the only locality where both species have been found. The female from Rio Suapure was listed and illustrated as Thecla madie Weeks, but the male was apparently misidentified as Thecla xenata (a misspelling of Thecla xeneta Hewitson, see taxonomy section below) (Weeks, 1911). There are no males of Calycopis xeneta from the

Rio Suapure in the Weeks Collection (MCZ).

Taxonomy

Distinguishing male characters. Location of the charcoal-black patch on the ventral forewing is the most consistent and easy way to distinguish males of *L. collucia* and *L. orcidia* (Figs. 1-3, 13-16). In *L. collucia*, this patch is distal of the postmedian line whereas in *L. orcidia*, it is distal and basal with the basal part darker in some individuals. We have not seen a male with an intermediate wing pattern. Godman and Salvin (1887-1901) and Kaye (1921) apparently considered this difference to be intraspecific variation, but Comstock and Huntington (1962) noted that the two wing patterns were distinct.

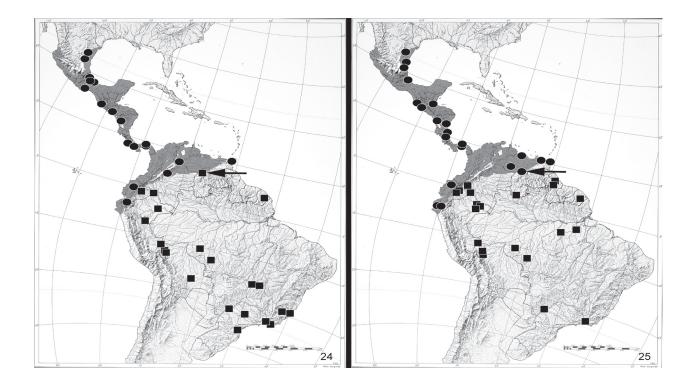
The ventral wing patterns of these males are similar to those of other species with charcoal-black patches. Males of some other *Lamprospilus* species, such as *L. coelicolor* (Butler & Druce) and *L. aunus* (Cramer), are easily distinguished by the better defined and more triangular shape of the dark brown patch on the ventral forewing (Fig. 42 in Duarte & Robbins, in press). Males of *Calycopis xeneta* (Hewitson) have a brown spot in ventral hindwing cell Cu₂-2A just distal of the postmedian line (Fig. 58 in Duarte & Robbins, in press) that is lacking in *Lamprospilus*.

Variation of male wing pattern. Wing pattern variation in male *L. collucia* is most evident on the ventral wings (Figs. 1-3). The width and exact shape of the postmedian line on both wings is perhaps the most variable element. The darkness and extent of the charcoal-black patches is also variable. Those individuals with a ventral wing pattern which is a bit lighter than average (Fig. 3) are more prevalent in the dry season, but we find no evidence for geographical variation.

Wing pattern variation in male *L. orcidia* is also most evident on the ventral wings (Figs. 13-16). Again, the shape of the postmedian line and the extent and darkness of the charcoal-black patches on both wings are the most variable elements. We do not have sufficient data to assess seasonal wing pattern variation, but find no evidence of geographical variation.

Distinguishing female characters. Shape and color of the ventral forewing postmedian line is the most consistent way to distinguish females of *L. collucia* and *L. orcidia*. This line is relatively thick and reddish to dark maroon in *L. collucia* (Figs. 5-9) and is a relatively thin black and white line with diffuse light brown scaling basally in *L. orcidia* (Figs. 17-20, arrow points to brown scaling).

The ventral wing pattern of female *L. collucia* could be confused with that of female *L. lanckena* (Schaus),



Figures 24-25. Distribution of *L. collucia* (circles) and *L. orcidia* (squares). Arrows point to possible sympatry on the Rio Suapure (Venezuela). The shaded area is an extremely close approximation to the Transandean Region of Brown (1982: 456); this area of endemism was proposed without exact borders. **24.** Males. **25.** Females.

but the later has the ventral forewing postmedian line of L. collucia in cell $\mathrm{Cu_2}\text{-}2\mathrm{A}$ and more rounded hindwings. The black and white forewing postmedian line with brown basal scaling is the best way to distinguish L. orcidia from other hairstreak species, but this character is sometimes inconspicuous (Fig. 19). Even with genitalic dissection, some females of L. orcidia may be difficult to identify definitively.

Variation of female wing pattern. Wing pattern in female L. collucia is quite variable. Dorsal ground color has variable amounts of blue scaling (Figs. 10-11), which varies in hue from shining blue to chalky gray. The ventral brownish-black patch of scales distal of the postmedian line varies from absent (Fig. 7) to conspicuous (Figs. 5-6). The color of the ventral postmedian line varies from reddish to dark maroon, but the thick forewing line from the costa to vein Cu_2 is a constant feature. As in the male, individuals with a lighter ventral wing pattern (Fig. 7) tend to be most frequent in the dry season.

Wing pattern variation in female *L. orcidia* is similarly variable. Dorsal ground color varies from blue to chalky gray. The ventral wing pattern is rather "non-descript", but the black and white postmedian line with basal brownish scaling appears to be constant,

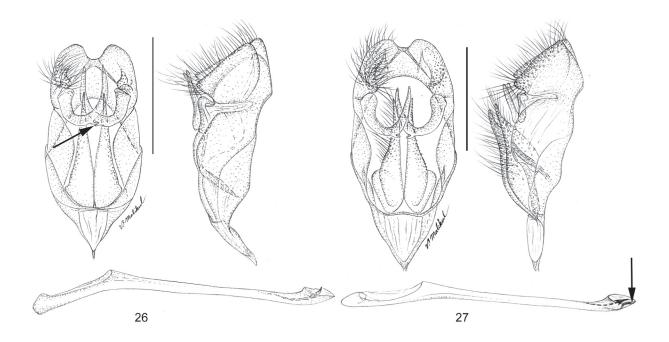
even if its expression is variable (Figs. 17-20).

Male genitalia and their variation. The male genitalia of *L. collucia* and *L. orcidia* are typical of *Lamprospilus* (Duarte & Robbins, in press) with a single medium sized tooth on each gnathos arm (arrow in Fig. 26). The only evident genitalic difference between the two species is that the penis of *L. orcidia* consistently has a small second cornutus (arrow in Fig. 27) while that of *L. collucia* may or may not (Fig. 26) have the second cornutus. Otherwise, the illustrated differences in the saccus, penis, and valvae (Figs. 26-27) fall within the range of intraspecific variation.

Female genitalia and their variation. The female genitalia of *L. collucia* are typical of *Lamprospilus* with "fan-shaped" signa (Figs. 28-29) and an inwardly curved sclerotized ridge on the distal end of the 8th abdominal tergum (illustrated in Duarte & Robbins, in press). The shape of the ductus bursae, especially the posterior end, varies intraspecifically, but does not distinguish the species. The signa of the two species differ in the sample (Figs. 28-29), but are structurally quite variable, for which reason we suspect that this difference might not be confirmed by a larger sample size.

Nomenclature. Thecla collucia Hewitson was

70 J. Res. Lepid.



Figures 26-27. Male genitalia, ventral aspect (left), lateral aspect (right), penis in lateral aspect (bottom). **26.** *L. collucia*, Panama (Canal Area), arrow points to single "tooth" on the gnathos. **27.** *L. orcidia*, Brazil (Minas Gerais), arrow points to small second terminal cornutus. Scale 1 mm.

described from at least one pair in the Hewitson Collection (now in BMNH), but only the female was illustrated (Figs. 8, 12). No type locality was given. Johnson (1993: 22) designated a female lectotype (B.M. Type Rh 1010) from Esp. Santo (presumably Espírito Santo, Brazil) that fits the original illustration very well even though it is missing most of its forewings. However, there was no type locality in the original description, and a photograph of the lectotype and its labels from the 1970s shows that this specimen lacked a locality label at that time. Johnson (1993: 22) did not list Brazil as part of the South American distribution of collucia, so his "Esp. Santo" citation is difficult to interpret. Primary types of Thecla collucia's junior synonyms have been examined: madie Weeks (\mathcal{Q}, MCZ) , amphrade Schaus $(\mathcal{Q}, USNM)$, the original description erroneously listed the BMNH), iodinus Kaye (\circlearrowleft , BMNH), posetta Dyar (\updownarrow , USNM), and shueyi Johnson (\circlearrowleft , AMNH).

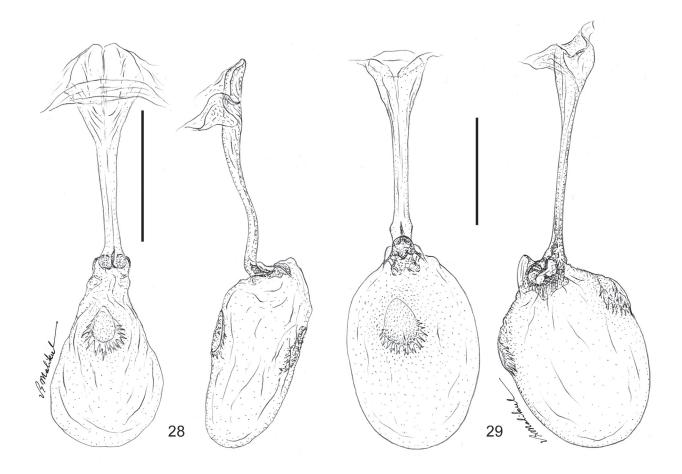
Thecla orcidia Hewitson was described from at least one male in the H. W. Bates collection (now in BMNH) from the Amazon. There is one male in the BMNH that fits this description (Figs. 13, 21, B.M. Type Rh 872) and is presumed to be a holotype. Illustrations of the holotypes (by original designation) of junior synonyms tafiensis Johnson (AMNH), mossi Johnson & Kroenlein (BMNH), silva Austin & K. Johnson (DZUP), rondonia Austin & K. Johnson (DZUP),

obscura Austin & K. Johnson (DZUP), perplexa Austin & K. Johnson (DZUP), and purpura Austin & K. Johnson (DZUP) can be found in the original descriptions (Johnson, 1993; Johnson & Kroenlein, 1993; Austin & Johnson, 1997).

The wing pattern of female *L. orcidia* is non-descript, as noted. Perhaps for that reason, a female of *L. orcidia* was included in the type series of the unrelated *Thecla ceromia* Hewitson. However, Johnson and Kroenlein (1993: 4) designated another specimen as the lectotype, which is the reason that *Thecla ceromia* is now placed in *Ziegleria* (Robbins, 2004b; Duarte & Robbins, in press).

DISCUSSION

Detritivory. Females of *L. collucia* have been recorded in nature ovipositing on dead twigs on the ground and on a leaf near the ground. In the lab, females oviposit readily on dead leaves. Caterpillars of *L. collucia* and *L. orcidia* in nature have been found eating a "nearly" dead seedling and the androecia of Lecythidaceae flowers on the ground. In the lab, larvae complete development on live and dead organic matter. Although many butterflies, including Lycaenidae, can be reared on an artificial diet to which dried, ground leaves of the food plant are added (Morton, 1981; Mark, 1993; 1995), larvae of



Figures 28-29. Female genitalia, dorsal (left) and lateral aspects. 28. L. collucia, Panama (Canal Area). 29. L. orcidia, Peru (Madre de Dios). Scale 1 mm.

L. collucia and L. orcidia readily ate and completed development on an agar-based artificial diet without the addition of leaves. These results are very similar to those reported for Calycopis (S. Johnson, 1985; Robbins et al., 1996; Duarte et al., 2005), and are consistent with the hypothesis that L. collucia and L. orcidia are facultative detritivores.

Different kinds of detritus provide different kinds of nutrition for a caterpillar. A preliminary analysis of some Lecythidaceae androecia showed that they have higher sugar and phosphorus content than "leaf litter" (nitrogen levels were variable), but a lower content of other minerals and fiber (A. Whigham pers. comm.). Detritivores may also eat micro-organisms living on detritus (Findlay & Tenore, 1982; Hohn & Wagner, 2002), but to date, the nutrition that lycaenid detritivorous caterpillars derive from different food objects is an unexplored subject.

Maximal adult abundance of *L. collucia* and *L. orcidia* at the end of the dry season and beginning of the wet season suggests that larvae find more suitable

food or suffer lower mortality during the dry season. Many trees are deciduous during the dry season, but whether fungi and other caterpillar pathogens and predators are less abundant at that time is an open question.

Parapatry. Brown (1982) partitioned the distribution of Neotropical forest butterflies into four slightly overlapping "fuzzy-edged" biogeographic regions of endemism, three of which (Transandean, Amazonian, and Atlantic) consist primarily of areas under 1,500 m elevation. The biogeographic distribution of L. collucia is a "textbook" example of Brown's Transandean Region; this species occupies virtually the entire Transandean Region (shaded part of Figs. 24-25). The distribution of L. orcidia is a combination of Brown's Amazonian and Atlantic Regions. So far as we are aware, this is the first time that a clear-cut Transandean/Amazonian parapatric distribution has been documented in the Eumaeini. In most other potential cases, such as Lamasina draudti (Lathy) and L. ganimedes (Cramer) (Robbins & Lamas,

72 J. Res. Lepid.

2008), species are not sufficiently well-represented in museum collections to determine whether distributions are allopatric or parapatric.

The parapatric distributions of *L. collucia* and *L. orcidia* (Figs. 24-25) are unlikely to be maintained by competition for larval food; it is difficult to visualize the dead organic matter that the caterpillars eat as a limiting resource. However, males of both species set up mating territories in the morning on hilltops and occur in similar habitats. These findings suggest the testable hypothesis that mating interference is responsible for maintaining parapatry between the two species.

Associating males and females. The evidence that males and females of L. collucia are correctly associated is that the distribution of each sex is almost identical (Figs. 24-25), both sexes have a dark brown patch on the ventral forewing distal of the postmedian line (Figs. 1-3, 5-9), and both sexes have been reared from eggs laid by the same mother (Figs. 1, 5). The evidence that the male and female of L. orcidia are the same species is that the distribution of males and females is almost identical (Figs. 24-25), both sexes have darker scales (albeit, much reduced in the female) basal of the ventral forewing postmedian line (Figs. 13-20), and both have been reared from fallen flowers of Lecythidaceae (Figs. 16, 20; no other Lamprospilus species were reared from these flowers). Finally, no other "unassociated" Lamprospilus male or female has the same distribution as either species.

Biological species. With the possible exception of the old Rio Suapure specimens mentioned above from Weeks (1911), the distributions of *L. collucia* and *L. orcidia* are parapatric (Fig. 24-25). Distinguishing characters are consistent throughout the range of each species and do not vary in the areas where the distributions meet. This evidence is consistent with the hypothesis that the two taxa do not interbreed.

Lamprospilus collucia and L. orcidia are likely to be phylogenetic sisters. In a phylogenetic analysis intended to determine relations among the genera of the "Lamprospilus Section" (Duarte & Robbins, in press), the morphological character coding for L. collucia and L. orcidia was identical. However, the coding was also very similar to that for L. coelicolor and L. aunus. For this reason, an analysis of phylogenetically informative characters among Lamprospilus species is needed to test whether L. collucia and L. orcidia are indeed sister species.

ACKNOWLEDGEMENTS

We are grateful to Karie Darrow for preparing the plates of adults, to Vichai Malikul for preparing the genitalic illustrations, to Brian Harris for help with technical aspects of this project, to Gerardo Lamas for providing data on *L. collucia* in Peru, and to Amie Whigham for allowing us to cite her preliminary unpublished information. For supporting travel by both Duarte and Robbins and for substantial funds, we thank Fundação de Amparo à Pesquisa do Estado de São Paulo/FAPESP (as part of the project "Systematics, Bionomy, and Evolution of Neotropical Lepidoptera"; process numbers 02/13898-0 and 03/13985-3) and Pró-Reitoria de Pesquisa da Universidade de São Paulo/USP/Projeto 1. For excellent suggestions on the manuscript, we thank Paul Goldstein, André Freitas, and Rudi Mattoni.

LITERATURE CITED

- ALCOCK J. & K. M. O'NEILL. 1986. Density-dependent mating tactics in the gray hairstreak, *Strymon melinus* (Lepidoptera, Lycaenidae). Journal of Zoology 209: 105–113.
- Alcock, J. & K. M. O'Neill. 1987. Territory preferences and intensity of competition in the grey hairstreak *Strymon melinus* (Lepidoptera: Lycaenidae) and the tarantula hawk wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae). American Midland Naturalist 11: 120–138.
- Austin, G. T. & K. Johnson. 1997. Theclinae of Rondônia, Brazil: Gigantorubra and Angulopis, with descriptions of new species (Lepidoptera: Lycaenidae). Insecta Mundi 11(3/4): 255-272.
- Barcant, M. 1970. Butterflies of Trinidad and Tobago. London, Collins. 314 pp., 28 pls.
- Brown, K. S. 1982. Historical and ecological factors in the biogeography of aposematic neotropical butterflies. American Zoologist 22(2): 453-471.
- Comstock, J. H. 1918. The wings of insects. The Comstock Publishing Company, Ithaca. 430 pp.
- COMSTOCK, W. P. & E. I. HUNTINGTON. 1962. An annotated list of the Lycaenidae (Lepidoptera: Rhopalocera) of the Western Hemisphere. Journal of the New York Entomological Society 70: 39 46.
- D'ABRERA, B. L. 1995. Butterflies of the Neotropical region. Part VII. Lycaenidae. Black Rock, Hill House, i-xi + 1098-1270 pp.
- DAVIDSON, J. M., S. A. REHNER, M. SANTANA & E. LASSO. 2000. First report of *Phytophthora heveae* and *Pythium* spp. on tropical tree seedlings in Panama. Plant Disease 84(6): 706.
- DRAUDT, M. 1919-1920. Theclini F., pp. 744-812, *In*: A. Seitz (Ed.).
 Die Gross-Schmetterlinge der Erde, vol. 5. Die amerikanischen Tagfalter. Stuttgart, Alfred Kernen.
- DUARTE, M. & R. K. ROBBINS. IN PRESS. Description and phylogenetic analysis of the Calycopidina (Lycaenidae, Theclinae, Eumaeini): a subtribe of detritivores. Revista Brasileira de Entomologia.
- DUARTE, M., R. K. ROBBINS, & O. H. H. MIELKE. 2005. Immature stages of *Calycopis caulonia* (Hewitson, 1877) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), with notes on rearing detritivorous hairstreaks on artificial diet. Zootaxa 1063: 1-31.
- ELIOT, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bulletin of the British Museum (Natural History) Entomology 28(6): 371-505.
- FEINSTEIN, J., S. MORI, & A. BERKOV. 2007. Saproflorivory: a diverse insect community in fallen flowers of Lecythidaceae in French Guiana. Biotropica 39(4): 549–554.
- FINDLAY, S. & K. TENORE. 1982. Nitrogen source for a detritivore: detritus substrate versus associated microbes. Science 218: 371–373.
- GODMAN, F. D. & O. SALVIN. 1887-1901. Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera. Fam. Lycaenidae. 2: 1-112.
- HOHN, F. M. & D. L. WAGNER. 2002. Larval substrates of herminiine

- noctuids (Lepidoptera): macrodecomposers of temperate leaf litter. Environmental Entomology 29: 207–212.
- JOHNSON, K. 1993. Neotropical hairstreak butterflies: new sister genera of the "Electrostrymon/Angulopis" grade of Eumaeini (Lepidoptera, Lycaenidae, Theclinae). Reports of the Museum of Natural History. University of Wisconsin (Stevens Point) 32: 1-76.
- JOHNSON, K. & K. R. KROENLEIN. 1993. Revision of Angulopis (Lepidoptera, Lycaenidae, Theclinae). Reports of the Museum of Natural History. University of Wisconsin (Stevens Point) 33: 1-38.
- JOHNSON, S. A. 1985. Culturing a detritivore, Calycopis isobeon (Butler & Druce). News of the Lepidopterists' Society 3: 41–42.
- KAYE, W. J. 1921. A catalogue of the Trinidad Lepidoptera Rhopalocera. Memoirs of the Department of Agriculture of Trinidad and Tobago 2: i-xii, 13-163.
- KLOTS, A. B. 1970. Lepidoptera, pp. 115-130, In: S.L. Tuxen (Ed.), Taxonomist's glossary of genitalia in insects. Munksgaard, Copenhagen.
- LAMAS, G., R. K. ROBBINS & D. J. HARVEY. 1997. Mariposas del alto Rio Napo, Loreto, Peru (Lepidoptera: Papilionoidea y Hesperioidea). Revista Peruana de Entomología 39: 63-74.
- MARK, H. -G. 1993. Erste Mitteilung über Tagfalter- und Zygänenzuchten mit semisynthetischem Kunstfutter. Nachrichten des Entomologischen Vereins Apollo, N.F., 14: 275–280.
- MARK, H. -G. 1995. Tagfalter- und Zygaenenzuchten mit semisynthetischem Kunstfutter, zweite Mitteilung: Lepidoptera, Lycaenidae. Nachrichten des Entomologischen Vereins Apollo, N.F., 16: 263–274.
- MORTON, R. S. 1981. Rearing butterflies on artificial diet. Journal of Research on the Lepidoptera 18: 221–227.
- Powell, J., C. Mitter & B. D. Farrell. 1998. Evolution of larval food preference in Lepidoptera, pp. 403–422, *In*: N. P. Kristensen (Ed.). Band/ Volume IV Arthropoda: Insecta. Lepidoptera, Moths and Butterflies: Evolution, Systematics, and

- Biogeography. *In*: M. Fischer (Ed.). Handbuch der Zoologie. Handbook of Zoology. Berlin, Walter de Gruyter.
- RIDGELY, R. S. 1976. A guide to the birds of Panama. Princeton Univ. Press, Princeton, NJ. 394 pp.
- ROBBINS, R. K. 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). Smithsonian Contribution to Zoology 498, 64 pp.
- ROBBINS, R. K. 2004a. Introduction to the checklist of Eumaeini (Lycaenidae), pp. xxiv-xxx, *in*: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea Papilionoidea. *In*: Heppner, J. B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- ROBBINS, R. K. 2004b. Lycaenidae. Theclinae. Tribe Eumaeini, pp. 118-137, *In*: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea Papilionoidea. *In*: Heppner, J. B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- ROBBINS, R. K. & G. LAMAS. 2008. Nomenclature, variation, and the biological species concept in *Lamasina* (Lycaenidae: Theclinae: Eumaeini). Revista Brasileira de Zoologia 25(1): 116-127.
- ROBBINS, R. K., G. LAMAS, O. H. H. MIELKE, D. J. HARVEY & M. CASAGRANDE. 1996. Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Peru, pp. 217-252, *In*: Manu: The biodiversity of Southeastern Peru (D. E. Wilson and A. Sandoval, (Eds.). Smithsonian Institution Press, Washington DC. 679 pp.
- ROBBINS, R. K. & G. B. SMALL. 1981. Wind dispersal of Panamanian hairstreak butterflies (Lepidoptera: Lycaenidae) and its evolutionary significance. Biotropica: 13(4): 308-315.
- Snodgrass, R. E. 1935. Principles of insect morphology. McGraw-Hill Book Co., New York, 667 pp.
- Weeks, A. G. 1911. Illustrations of diurnal Lepidoptera. With descriptions. Boston, The University Press. 2: xvi + 37 p.