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THE IMMATURE STAGES, LARVAL FOOD PLANTS AND BIOLOGY OF NEOTROPICAL MISTLETOE BUTTERFLIES. I. THE *HESPEROCHARIS* GROUP (PIERIDAE: ANTHOCHARIDINI)

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ABSTRACT. The Neotropical Region contains the highest diversity of the cosmopolitan family Pieridae in terms of generic and species richness, yet the basic natural history of many taxa from Central and South America remains unknown or poorly documented. We provide an overview of the morphology, larval food plants and general biology of the immature stages of the *Hesperocharis* group, one of two distantly related clades of Neotropical pierids that specialize on 'mistletoes' (Santalales). Of the four genera recognized in the group, detailed descriptions are given and compared for two of these, *Hesperocharis* and *Mathania*. Eggs are laid in clusters, the larvae are gregarious or semi-gregarious but pupate singly, and the pupae may undergo winter diapause in temperate latitudes. Only fragmentary information is available for the relict genus *Eroessa*, and the life history of *Cunizza* remains unknown. Optimization of available food plant data in the context of a recent molecular phylogenetic hypothesis for the *Hesperocharis* group suggests the ancestor of *Hesperocharis* + *Mathania* evolved on aerial-stem hemiparasites in the family Loranthaceae. Confirmation of the larval food plant of *Eroessa* (reputedly Asteraceae); however, is required to reconstruct the ancestral food plant of the *Hesperocharis* group and to trace the evolutionary pathway of host shifts within the Anthocharidini.

Additional key words: *Cunizza*, *Eroessa*, Loranthaceae, *Mathania*, Santalales, Viscaceae.

Pierid butterflies occur throughout the world but are not evenly distributed among the major zoogeographic regions. The Neotropical Region, in particular, has a highly distinctive fauna in terms of its composition, richness and endemism—it has by far the highest level of diversity and more than two-thirds of the genera are endemic to the area (Braby *et al.* 2006). The region is also rich in evolutionary radiations, such as the *Tatochila* group of the subtribe Pierina (Pierinae: Pierini) in the Andes of South America (Field & Herrera 1977; Shapiro 1991b and references therein). These butterflies include some of the most speciose and bizarre pierids adapted to extreme high altitudes, and their general ecology and morphology has been well studied in a series of papers by Shapiro (1978a,b, 1979, 1990, 1991a) and Shapiro & Courtney (1986). However, for most Neotropical species, the basic natural history is

poorly documented. Knowledge of the morphology, larval food plants, biology and behavior of the immature stages forms the foundation for more detailed ecological and evolutionary studies, as well as providing an important source of data for systematic work.

As a first step towards documenting characters for phylogenetic analysis, we present here, and in a related paper (Braby and Nishida, unpublished data), an overview of the immature stages, larval food plants and general biology of two distantly related clades of pierids from Central and South America that are intimately associated with mistletoes. Pierids as a whole feed as larvae predominantly on legumes (Fabales), crucifers and allied plants containing mustard oil glucosides (Brassicales), and 'mistletoes' (aerial-stem and root hemiparasites in the order Santalales). Braby and Trueman (2006) showed that mistletoe feeding was a

derived state in the Pieridae, and demonstrated that it evolved at least twice in the subfamily Pierinae. Moreover, they estimated that up to 40% of all species of Pieridae potentially specialize on plants in the Santalales, making the order the most frequently consumed plant taxon for this family of butterflies globally. However, while the immature stages, larval food plants and general biology of mistletoe-feeding pierids from Africa (see Braby 2005 for review) and Indo-Australia (see Braby 2006 for review) have been documented to various extents, the taxa from South America remain very poorly known (Courtney 1986; DeVries 1987).

In this paper we focus on the morphology, larval food plants and biology of the immature stages of the *Hesperocharis* group of the tribe Anthocharidini (Pierinae), one of two distantly related clades of Neotropical pierids that specialize on mistletoes in the families Loranthaceae, Viscaceae and/or Santalaceae (Braby & Trueman 2006; Braby and Nishida unpublished data). The *Hesperocharis* group is restricted to the Neotropical region and comprises a well-supported monophyletic group of four genera: *Eroessa* Doubleday, 1847, *Cunizza* Grote, 1900, *Hesperocharis* C. Felder, 1862, and *Mathania* Oberthür, 1890 (Braby *et al.* 2006). These four genera currently embrace a total of 17 species, although at least a further two species await description (Lamas 2004). Phylogenetic relationships of the *Hesperocharis* group (Fig. 1), based on combined analysis of four genes (*EF-1 α* , *wingless*, *COI*, *28S*) (Braby *et al.* 2006), indicate that *Eroessa* is sister to the three other genera, which comprise a monophyletic group and which Klots (1933) originally treated as subgenera of *Hesperocharis* *sensu lato*. The butterflies (Figs 2–7) occur in a range of habitats, from tropical lowland and mid-elevation forest to cool temperate rainforest and temperate arid xerophytic woodland (Figs 8, 9, 11, 14). The most species-rich area is in the eastern slopes of the Andes and edge of the Amazon Basin (Fig. 14), where males may be commonly observed puddling from moist sand (Fig. 5) along creeks (Fig. 15) or banks of rivers.

MATERIALS AND METHODS

The immature stages and general biology of the *Hesperocharis* group were studied in the field in Costa Rica, Peru and Chile in 2000, with additional observations made in Costa Rica in 2004–06. In Costa Rica, most observations were made in the vicinity of San José in the central valley (around 10°N, 84°W) at altitudes between 950–1200 m. In Peru, the areas of San Ramón (11°10'S, 75°23–25'W; 1100–1800 m a.s.l.) and Satipo (11°18'S,

74°42'W; 800 m), Chanchamayo District, and Tingo María (9°22'S, 75°58'W; 750 m), all on the eastern slopes of the Andes and edge of the Amazon Basin, were visited during November 2000. In Chile, we sampled the areas of Farellones on the western slopes of the Andes east of Santiago, Región Metropolitana (33°20'S, 70°19–21'W; 1600–1850 m), and Parque Nacional Puyehue east of Osorno, Región de Los Lagos (40°45'S, 72°18'W; 600 m), in December 2000.

Concentrated searches for the immature stages were made on mistletoes in these areas. Samples of the eggs and early instar larvae were initially reared on single leaves placed in small plastic vials (65 mm \times 40 mm diam.); older larvae were subsequently transferred to large clear plastic bags, the top of which was tied in a twisted fold and clamped with a close-peg, and supplied with fresh branches of the larval food plant. In some cases, a branch of the host tree supporting the mistletoe clump was removed and placed inside the plastic bag; the base of the branch was secured with moistened tissue to minimize desiccation. All rearing containers were checked at least twice daily and cleaned of frass or replaced. Cohorts from Costa Rica were reared either in plastic bags or netted cages, several of which were placed in an entomological laboratory maintained at constant room temperature of around 23–24°C in the Escuela de Biología, Universidad de Costa Rica.

Larval food plant data were reviewed, as far as possible, from records published in the primary scientific literature, drawing particularly on the recent compilation of Beccaloni *et al.* (2008).

Abbreviations. The following standard codes refer to museums where voucher specimens of the immature stages have been deposited or where preserved material was examined:

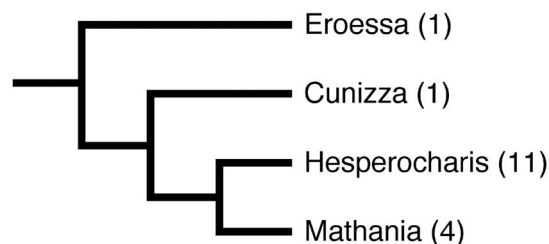


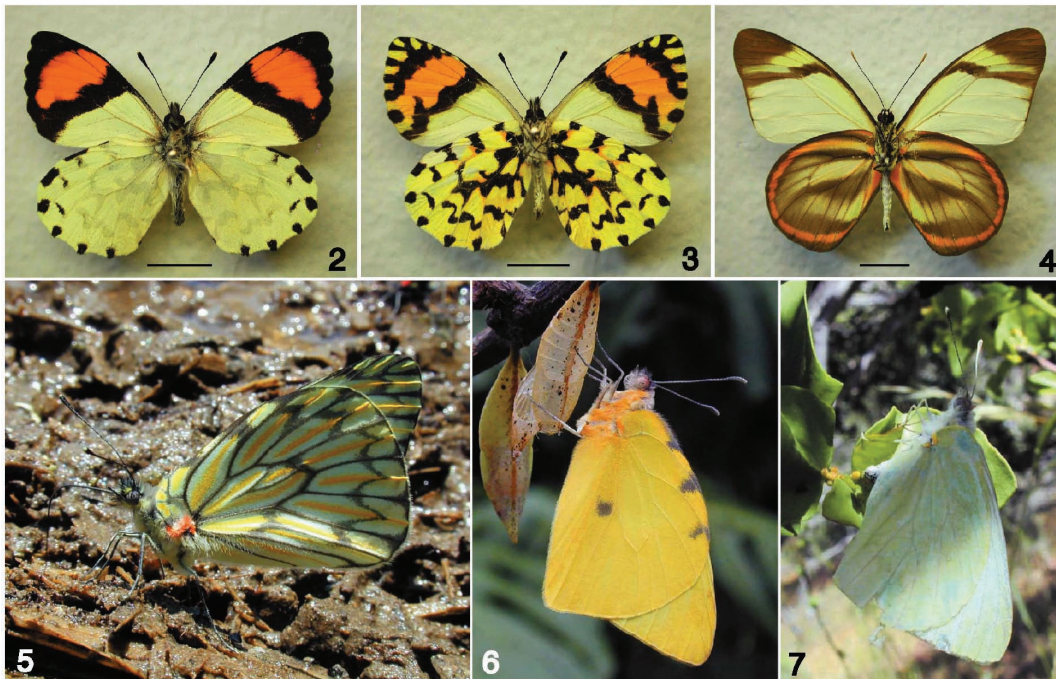
Fig. 1. Phylogeny of the *Hesperocharis* group, showing systematic relationships at the generic level. Phylogenetic hypothesis is based on combined analysis of four genes (*EF-1 α* , *wingless*, *COI*, *28S*) (3675 bp, 1091 parsimony informative characters, consistency index 0.265) for the family Pieridae (Braby *et al.* 2006). All nodes are well supported (bootstrap 85–100%). Numbers in parentheses indicate number of species currently assigned to taxa (from Lamas, 2004).

BMNH: The Natural History Museum, London, England
 INBio: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
 MCZ: Museum of Comparative Zoology, Boston, USA
 UCR: Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica
 USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA

Eroessa Doubleday, 1847

This monotypic genus, containing the species *E. chiliensis* (Guérin-Méneville, [1830]) (Figs 2, 3), is endemic to southern South America. It occurs largely in the temperate areas of central Chile, formerly from coastal areas of the Región del Maule south and inland to the foothills and lower mountains of the Andes (up to 1000 m) in the Provinces of Osorno and Llanquihue (Peña & Ugarte 1996). It also extends across the Andean border into Argentina in the Provinces of Neuquén and Río Negro where it occurs in Nahuel Huapí and Lanín National Parks of Patagonia (Shapiro 1991b). The butterfly is restricted to cool temperate evergreen rainforest (valdivian forest) (Fig. 8); however, much of the natural habitat has been eliminated and fragmented, largely as a result of rapid expansion of commercial

forest plantations (Echeverría *et al.* 2006). Consequently, the extent of occurrence of *E. chiliensis* is now substantially reduced and the species is considered threatened (A. Ugarte, pers. comm.). Angulo and Weigert (1974) described and illustrated in detail the final instar larva and pupa from material collected from Concepción, Chile, in October. However, they did not report the larval food plant or provide any information on the biology or life cycle. Oliver (1926) reported *E. chiliensis* ovipositing on the underside of leaves of 'palo mato', *Dasyphyllum diacanthoides* (Less.) Cabrera (Asterales: Asteraceae), in the coast of San Vicente, Concepción, during January. This record appears to have been repeated by Peña (1975) and Peña and Ugarte (1996) who listed the same food plant (as *Flotovia diacanthoides*), although A. Ugarte (pers. comm. 2000) noted that he once observed a female ovipositing on this plant growing along a creek crossing in Parque Nacional Puyehue. *D. diacanthoides* grows as a shrub or small rainforest tree and further observations are needed to confirm that it is the usual food plant. We believe it unlikely that the larval food plant will prove to be mistletoes (Loranthaceae) that parasitize *Dasyphyllum* and/or other trees in the canopy because extensive searches for early stages on these parasitic plants at Puyehue, which preserves a



Figs. 2–7. Adults of the *Hesperocharis* group. 2, *Eroessa chiliensis* male upperside, Parque Nacional Puyehue, Chile. 3, *E. chiliensis* male underside, showing 'yellow from' in which the underside ground color of the hindwing is rich yellow instead of white, Parque Nacional Puyehue, Chile. 4, *Cunizza hirlanda* male underside, showing aposematic pattern on hindwing, Satipo, Peru. 5, *Hesperocharis nereina* male puddling, Chanchamayo district, Peru. 6, *Hesperocharis crocea* freshly emerged from pupa, San José, Costa Rica. 7, *Mathania leucothea* female ovipositing on *Tristerix corymbosus*, Farellones, Chile. Scale bars for Figures 2–4 = 10 mm.

significant remnant population of *E. chiliensis*, by us and A. Ugarte (pers. comm. 2005) were unsuccessful. The species appears to be univoltine and protandrous, with adults emerging in November; they are most abundant in December and January, and continue into February (Wagenknecht 1968a,b), but by late March only a few adults in worn condition are on the wing (A. Ugarte, pers. comm. 2000). Wagenknecht (1968a) noted that the adults fly during the afternoon (up to 1900 h in January) and high above the ground, typically at or above the forest canopy some 6–12 m from ground level. He also noted that the adults readily feed from flowers, especially those colored red such as *Fuchsia magellanica* Lam. (Onagraceae), *Tropaeolum speciosum* Poepp. & Endl. (Tropaeolaceae), *Escallonia rubra* (Ruiz & Pav.) Pers. (Saxifragaceae), *Mutisia ilicifolia* Cav. (Asteraceae) but also *Corynabutilon vitifolium* (Cav.) Kearney (Malvaceae). During our observations at Parque Nacional Puyehue (600 m) 6–7 December 2000 we found that males greatly outnumbered females by about 50:1. Males typically flew rapidly in sunlit areas, such as along the edge of the forest, often high up in the canopy. Flight activity continued throughout the day (up to 1810 h) but was less pronounced after 1730 h. Adults devoted considerable part of the day searching for flowers on which to feed, especially those colored red (e.g. *Fuchsia magellanica*, *Embothrium coccineum* Forster & Forster f. (Proteaceae)) growing in sunlit patches, although nectar feeding was less intense during the early afternoon (1300–1430 h). Males occasionally settled on foliage, several metres above the ground, in sunlit patches to bask for short periods; when settled the wings were opened at about 90° towards the afternoon sun.

***Cunizza* Grote, 1900**

Cunizza is monobasic, containing the single polytypic species *C. hirlanda* (Stoll, 1790) (Fig. 4). The genus occurs in Ecuador, Colombia, Peru, Bolivia, Venezuela, Guyana, Surinam, and Brazil (Lamas 2004). It has also been collected from Bocas del Toro and Darién, Panama, by G. Small (G. Lamas, pers. comm.), and there is a single specimen from Estación Biológica La Selva on the Atlantic coast of Costa Rica in INBio (1♂ labelled “Est. Magsasay, 200 m P N Braulio Carrillo, Prov Here., Costa Rica, Junio 1991. R. Aguilar | L_N264600, 531000, CB: 1302229”): these records provide a substantial northern range extension of the genus to Central America. *Cunizza* appears to be restricted to wet lowland tropical forest below 800 m, but the larval food plant, immature stages and general biology have not been reported. Salazar (2004)

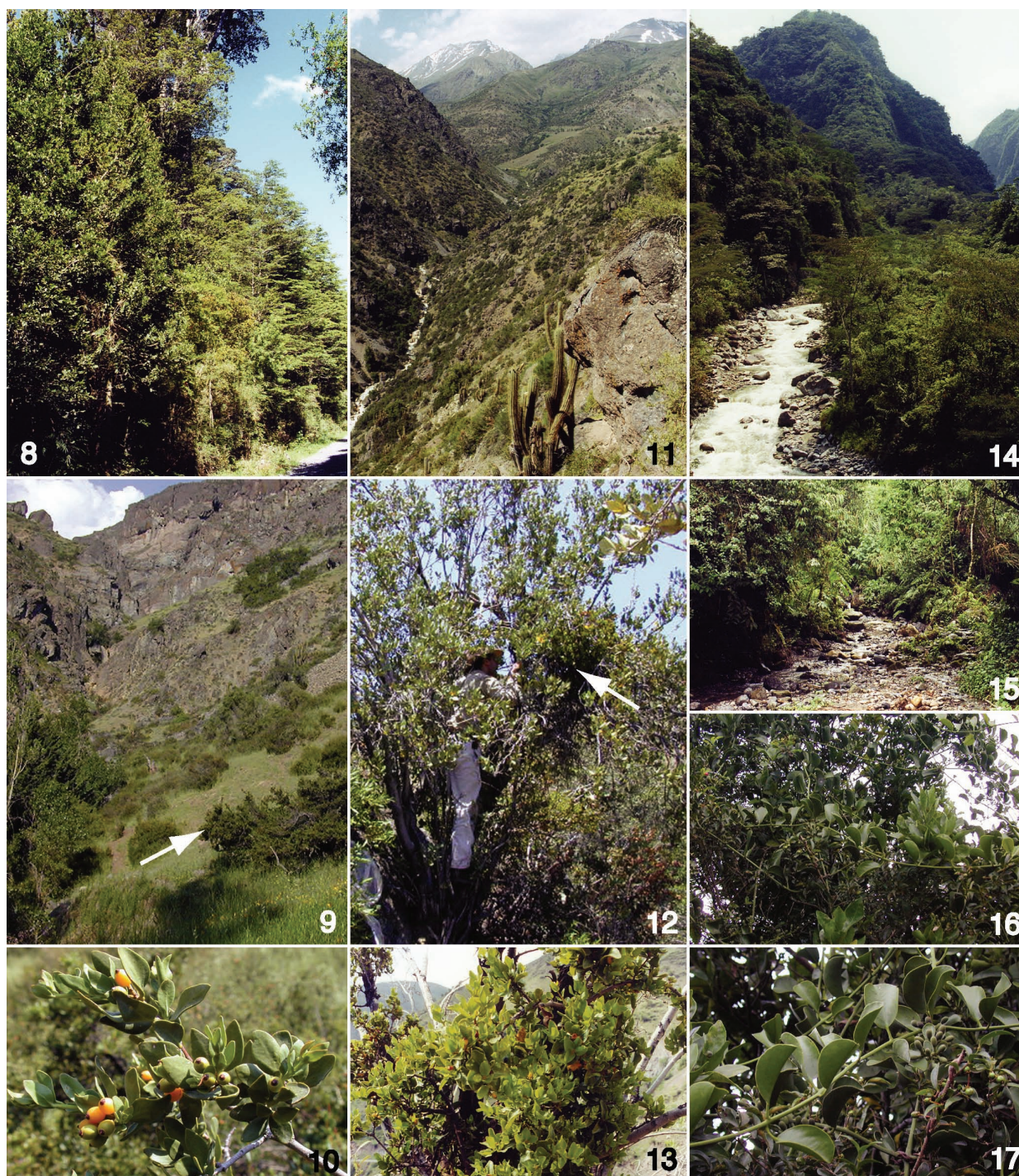
suggested the larval food plants most likely comprise Loranthaceae on account of the close relationship of the genus with *Hesperocharis*. In Colombia, males are observed seasonally and locally in congregations drinking from water puddles or moist sand along borders of rivers or streams (Salazar 2004). In Peru, we encountered a few males puddling in damp sand along the banks of watercourses or flying rapidly along trails in humid tropical forest 9 km south of Tingo Maria on 19 November 2000, but were not successful in locating the immature stages. Local entomological dealers recorded numerous males exhibiting similar habits at Río Shimá, 45 km ENE of Satipo (11°08'S, 74°13'W; 300 m a.s.l.).

***Hesperocharis* C. Felder, 1862**

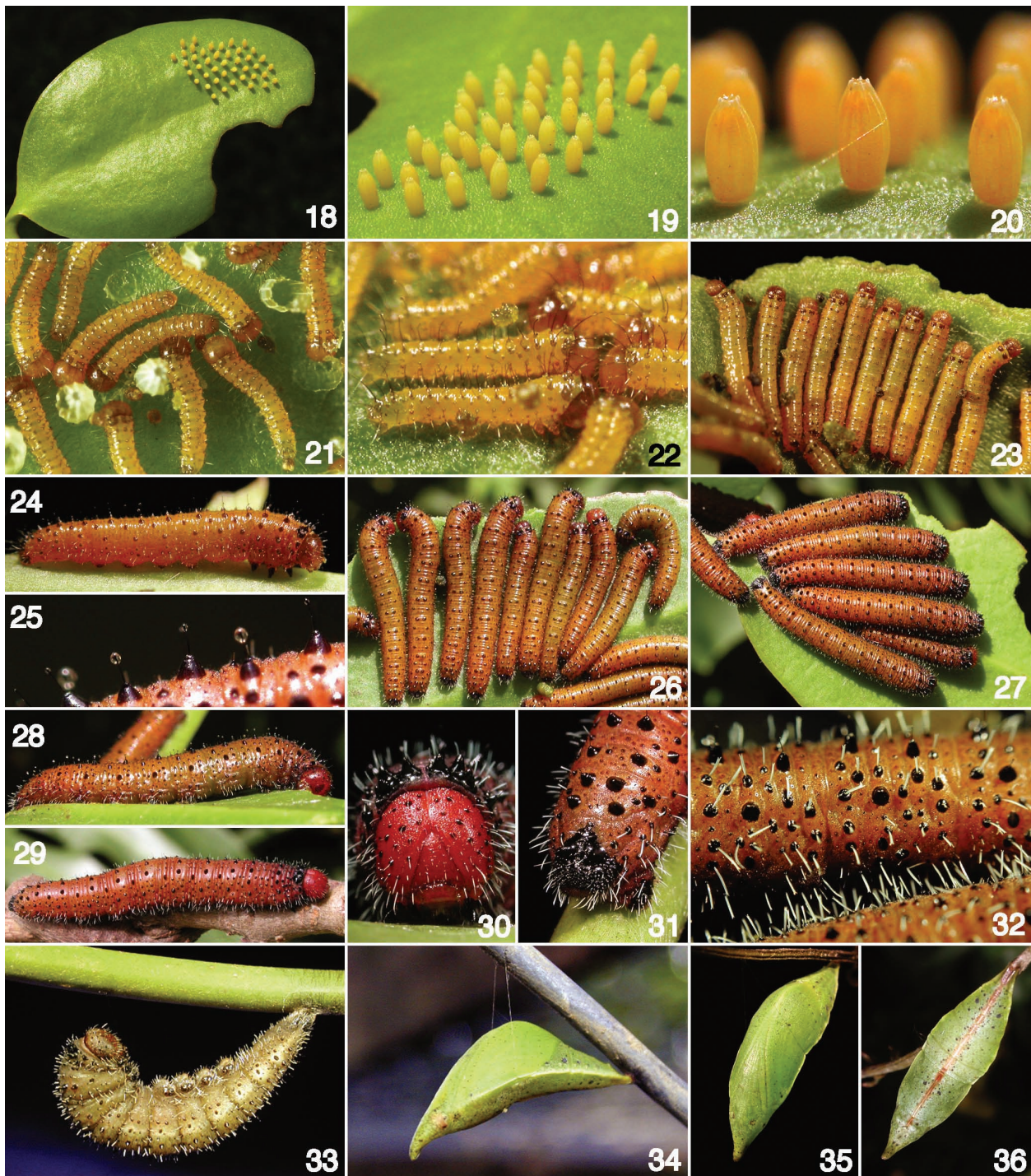
This Neotropical genus ranges from central and southern Mexico to Argentina, and includes 11 described species (Lamas 2004) with greatest diversity in South America. In Colombia, the species generally occur in montane forest up to 2–600 m, but others occur in warmer biomes of the Amazon Basin (Salazar 2004). Larval food plants have been reported for six species, but little reliable information has been published on the morphology and biology of the immature stages. Recorded food plants all belong to the Loranthaceae and Viscaceae, and include the genera *Psittacanthus* (R.L. Murillo pers. comm.), *Struthanthus* (DeVries 1986, 1987), *Tripodanthus* (Biezanko *et al.* 1957; Biezanko 1958, 1959; Biezanko *et al.* 1974; Silva *et al.* 1968) and *Phoradendron* (Beccaloni *et al.* 2008) (Table 1). Historical records from the Brassicaceae, Tropaeolaceae (Brassicales) and Fabaceae (Fabales) for *Hesperocharis marchali* (Guérin-Ménéville, [1844]) (Ronna 1923; Wille 1925; D'Almeida 1928; Biezanko 1938; Silva *et al.* 1968; Hayward 1969) and from the Brassicaceae for *H. anguitia* (Godart, 1819) (Wille 1925) are considered to be in error (Salazar 2004; Beccaloni *et al.* 2008), and most likely represent plants or mistletoe host trees on which the larvae pupate. DeVries' (1987: 87) comment that the “...early stages [of *H. crocea* H.W. Bates, 1866] resemble those of *Catantia*.” is in error as this finding is incongruent with our observations for this taxon, which we provide in detail below. Salazar (2004) noted that males of one species (*H. marchali*) exhibit territorial behavior by patrolling the canopy of trees around midday.

***Hesperocharis crocea* H.W. Bates, 1866**

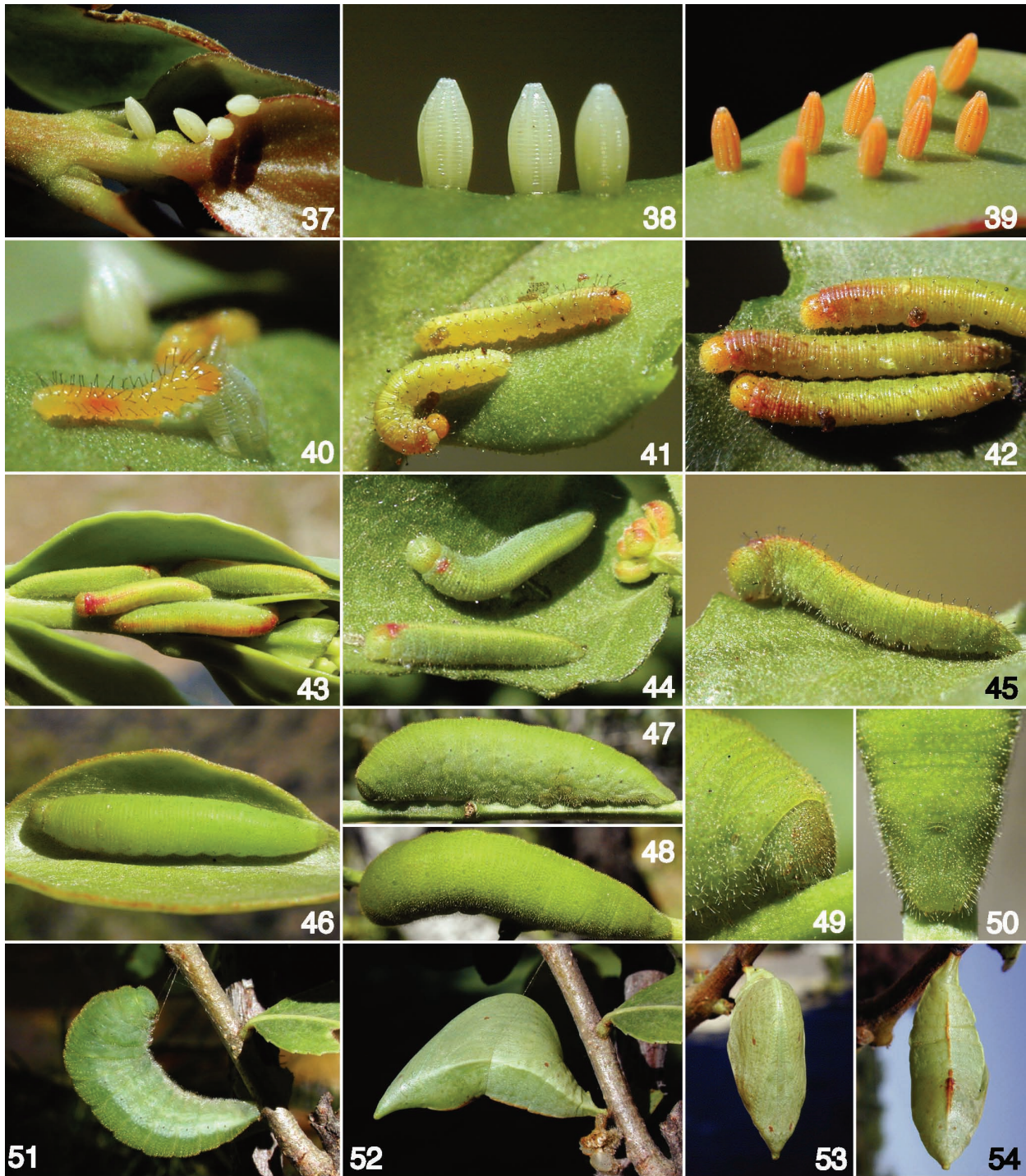
H. crocea (Fig. 6) occurs widely in the tropical latitudes of Central and South America, from southern



Figs. 8–17. Habitats and larval food plants of the *Hesperocharis* group. **8**, *Eroessa chiliensis* habitat, Parque Nacional Puyehue (600 m), Región de Los Lagos, Chile. **9**, *Mathania leucothea* breeding habitat, arrow shows larval food plant *Tristerix verticillatus*, Farellones (1850 m), Región Metropolitana, Chile. **10**, *T. verticillatus*, Farellones (1850 m), Chile. **11**, *Mathania leucothea* habitat, Farellones (1650 m), Chile. **12**, *Mathania leucothea* breeding habitat, arrow shows larval food plant *Tristerix corymbosus* parasitizing host tree *Kageneckia oblonga*, Farellones (1650 m), Chile. **13**, *T. corymbosus*, Farellones (1650 m), Chile. **14**, *Hesperocharis* habitat, San Ramón, (1400 m), Chanchamayo district, Peru. **15**, *Hesperocharis* male puddling habitat, San Ramón (1300 m), Peru. **16**, **17**, *Struthanthus orbicularis*, a larval food plant of *Hesperocharis crocea*, San Pedro de Montes de Oca (1200 m), San José Province, Costa Rica.



Figs. 18–36. *Hesperocharis crocea* immature stages on *Struthanthus orbicularis*, San Pedro de Montes de Oca (1200 m), Costa Rica. 18–20, eggs, showing cohort (18, 19) and lateral view (20). 21, 22, instar I. 23–25, instar II, showing cohort (23), lateral view (24) and primary setae with terminal fluid droplets (25). 26, instar III. 27, instar IV. 28–32, instar V, showing lateral view (28), dorsolateral view (29), anterior view of head capsule (30), posterior view (31) and secondary setae on abdominal segments (32). 33, prepupa, lateral view. 34–36, pupa, showing lateral view (34), ventral view (35) and dorsal view (36).



Figs. 37–54. *Mathania leucothea* immature stages on *Tristerix corymbosus* and *T. verticillatus*, Farellones (1650–1850 m), Región Metropolitana, Chile. 37–39, eggs, showing cohort immediately after oviposition (37), lateral view (38), and cohort two days after oviposition (39). 40, 41, instar I, showing newly emerged larva devouring chorion (40), and after feeding on food plant (41). 42, instar II. 43–45, instar III, showing variation in color pattern (43, 44) and lateral view, note primary setae with terminal fluid droplets (45). 46, instar IV, molting. 47–50, instar V, showing lateral view (47), dorsal view (48), anterolateral view of head capsule (49) and posterior view (50). 51, prepupa, lateral view. 52–54, pupa, showing lateral view (52), ventral view (53) and dorsal view (54).

Table 1. Larval food plants recorded for the *Hesperocharis* group from Central and South America. Plants not determined with certainty to level of genus or family are listed as Santalales

Plant genus	Plant species	Butterfly genus	Butterfly species	Country	Reference
LORANTHACEAE					
<i>Ligaria</i>	<i>cuneifolia</i> (Ruiz & Pav.) Tiegh.	<i>Mathania</i>	<i>carrizoi</i> Giacomelli	Argentina	Jørgensen (1916); Hayward (1960, 1969)
<i>Psittacanthus</i>	<i>schiedeanus</i> (Schlecht. & Cham.) Blume	<i>Hesperocharis</i>	<i>graphites</i> H.W. Bates	Costa Rica	L.R. Murillo (pers. comm.)
<i>Struthanthus</i>		<i>Hesperocharis</i>	<i>crocea</i> H.W. Bates	Costa Rica	DeVries (1986, 1987)
<i>Struthanthus</i>	<i>orbicularis</i> (Kunth) Blume	<i>Hesperocharis</i>	<i>crocea</i>	Costa Rica	Braby and Nishida (this study)
<i>Tripodanthus</i>	<i>acutifolius</i> (Ruiz & Pav.) Tiegh.	<i>Hesperocharis</i>	<i>anguitia</i> (Godart)	Uruguay	Biezanko <i>et al.</i> (1974)
<i>Tripodanthus</i>	<i>acutifolius</i>	<i>Mathania</i>	<i>carrizoi</i>	Argentina	Jørgensen (1916); Hayward (1960, 1969)
<i>Tripodanthus</i>	<i>acutifolius</i>	<i>Hesperocharis</i>	<i>erota</i> (Lucas)	Uruguay	Biezanko <i>et al.</i> (1974)
<i>Tripodanthus</i>	<i>acutifolius</i>	<i>Hesperocharis</i>	<i>leucania</i> (Boisduval)	Brazil; Uruguay	Silva <i>et al.</i> (1968); Biezanko <i>et al.</i> (1974)
<i>Tripodanthus</i>	<i>acutifolius</i>	<i>Hesperocharis</i>	<i>paranensis</i> Schaus	Brazil; Uruguay	Biezanko <i>et al.</i> (1957); Biezanko (1958, 1959)
<i>Tristerix</i>		<i>Mathania</i>	<i>leucothea</i> (Molina)	Chile	Calvert (1900)
<i>Tristerix</i>	<i>corymbosus</i> (L.) Kuijt	<i>Mathania</i>	<i>leucothea</i>	Chile; Argentina	Izquierdo (1895); Ureta (1940); Hayward (1969); Peña (1975); Courtney (1986); Shapiro (1991b); Peña and Ugarte (1996); Braby and Nishida (this study)
<i>Tristerix</i>	<i>verticillatus</i> (Ruiz & Pav.) Barlow & Wiens	<i>Mathania</i>	<i>leucothea</i>	Chile	Braby and Nishida (this study)
VISCACEAE					
<i>Phoradendron</i>	<i>piperoides</i> (Kunth) Trel.	<i>Hesperocharis</i>	<i>crocea</i>	El Salvador	Beccaloni <i>et al.</i> (2008)
<i>Phoradendron</i>	<i>piperoides</i>	<i>Hesperocharis</i>	<i>graphites</i>	El Salvador	Beccaloni <i>et al.</i> (2008)
SANTALALES					
'Loranthus'		<i>Hesperocharis</i>	<i>anguitia</i>	Brazil	Beccaloni <i>et al.</i> (2008)
		<i>Mathania</i>	<i>carrizoi</i>	Argentina	Jørgensen (1916); Hayward (1960, 1969)

Mexico (de la Maza 1987) to northwestern Peru, and includes three named subspecies (Lamas 2004). The nominate subspecies ranges from Mexico to Panama. DeVries (1986, 1987) noted in Costa Rica that it occurs in disturbed habitats (between 700–1200 m) and listed the larval food plant as *Struthanthus* (Loranthaceae). *Phoradendron piperoides* (Kunth) Trel. (Viscaceae) has also been listed as a larval food plant in El Salvador (Beccaloni *et al.* 2008). DeVries (1987: 88) provided brief notes on the immature stages; however, the description and habits of the pupa, viz. "...may pupate in clusters on the trunk of the tree upon which the hostplant grows. Pupa mottled green, white and brown, resembling a bird dropping. In color and shape very similar to *Catastica*," are in error as these observations do not accord with our findings. The following descriptions and illustrations of the immature stages and biological notes are based on material reared from Costa Rica during 2000 and 2004–05. Voucher material is lodged in USNM and MCZ. In addition, we have examined two larval skins and one pupal exuvia preserved in the BMNH. The material was reared from Loranthaceae from Mexico, sometime around the turn of the twentieth century. The specimens each have five labels, as follows: "BMNH DES No. Rh. 2880 *Hesperocharis crocea*. Roths. Coll. | Misantla, Veracruz (E. Gugelmann) | *Hesperocharis crocea* | Misantla VII. N°138 | Rothschild Bequest B.M. 1939–1.". The second larva is similarly labeled except with "Rh. 2881" on first label and "*Hesperocharis crocea* (on Loranthaceae)" on third label. The pupa is similarly labeled except with "Rh. 2882" on first label and the fourth label is missing, although "N°138" is marked on the card bearing the pupal skin.

Immature stages. *Egg* (Figs 18–20). 1.3 mm high, 0.6 mm wide; yellow to yellow-orange; bottle-shaped, with base flattened and narrower in width than middle; chorion with about 12 coarse longitudinal ribs, each terminating at micropylar end where they form a small protuberance or nodule, a series of finer transverse striae between longitudinal ribs.

First instar larva (Figs 21, 22). 3.5 mm to 4.8 mm long; head pale red or dark reddish-black; body orange with numerous long dark reddish-brown primary setae; prothorax with a prominent reddish-brown subdorsal patch bearing three long setae, and a lateral seta; meso- and metathorax each with a pair of long dorsal setae, a subdorsal seta and a lateral seta, all forming a transverse row anteriorly; abdominal segments 1–9 each with a pair of long dorsal setae and a lateral seta, both forming a transverse row anteriorly, and a subdorsal seta posteriorly; abdominal segment 10 with two long dorsal setae and a series of 4–6 colorless setae posteriorly.

Second instar larva (Figs 23, 24). 4.5 mm to 7.6 mm long; similar to first instar, but primary setae smaller and arising from black conical protuberances, a few white secondary setae on each segment.

Third instar larva (Fig. 26). 14 mm long (max); similar to final instar, but white secondary setae shorter and less conspicuous.

Fourth instar larva (Fig. 27). 23 mm long (max); similar to final instar larva.

Fifth instar larva (Figs 28–32). 36–38 mm long (max); head red or black, with numerous small black protuberances from which arise

short, somewhat flattened, white secondary setae bifurcated at apex; body dull orange-brown, with a paler middorsal line, numerous small black protuberances on each segment from which arise short, somewhat flattened, white secondary setae bifurcated at apex, and a series of larger, black conical protuberances from which arise short, spine-like black primary setae clubbed at apex; prothorax with a prominent black dorsal patch subdivided in half by middorsal line, each half bearing three prominent protuberances, from which arise spine-like black setae, and three smaller raised areas from which arise flattened white setae; abdominal segment 10 with a broad black dorsal patch bearing two protuberances; spiracles black. Number and arrangement of large conical, black protuberances on segments as follows: prothorax with one laterally; meso- and metathorax each with a pair dorsally, one subdorsally and two laterally, all forming a transverse row anteriorly; abdominal segments 1–9 each with a pair dorsally, one subdorsally and one laterally, the subdorsal protuberance being posterior to the dorsal and lateral protuberances. Body changes to pale greenish-brown during prepupal stage (Fig. 33).

Pupa (Figs 34–36). 23 mm long, 7 mm wide; dull green or pale brown, speckled with small black spots and a few larger black spots, particularly on mesothorax (including wing case) and abdominal segments 4–8; head with eye pinkish-orange, anterior end produced to a prominent point or projection, which is rounded, slightly upturned and beak-like; wings convex ventrally, cases of forewing with a transverse row of five small black spots near posterior margin; a pale, prominent lateral ridge extending from mesothorax to abdominal segment 10; a broad reddish middorsal line extending from prothorax to abdominal segment 10 (including cremaster). Attached by cremaster, to small pad of silk spun over substrate, and a weak central silken girdle which passes over abdominal segment 1. Prior to adult emergence the wing cases change to yellow.

Larval food plants. In Costa Rica, eight different cohorts of the immature stages were recorded on *Struthanthus orbicularis* (Kunth) Blume (Loranthaceae) (Figs 16, 17) growing at several locations in the central valley at altitudes between 950 and 1200 m. Localities included Alajuela (Parque on Avenida 7 and Calle Central in Alajuela Centro, Alajuela Province), San José (Barrio La Paulina, and Universidad de Costa Rica in San Pedro de Montes de Oca, San José Province), and San Pedro (San José Province). In most locations the larval food plant grew commonly in suburban areas parasitizing various non-indigenous host trees, including *Bauhinia purpurea* L. (Fabaceae), *Ligustrum lucidum* W.T. Aiton (Oleaceae), *Citrus limon* (L.) Burm. f. (Rutaceae) and *Casuarina cunninghamiana* Miq. (Casuarinaceae). In addition, a cohort of second instar larvae on *S. orbicularis* collected from CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) campus in Turrialba (Cartago Province) at 550 m, were successfully reared in captivity on *S. marginatus* (Desr.) Blume.

Biology. Eggs were laid in large compact clusters (Fig. 18), ranging from 26–68 eggs per cluster (\bar{x} = 43.2; n = 5 cohorts), on a new leaf of the larval food plant. After hatching, the newly emerged larvae devoured most of the chorion. The larvae fed gregariously on the new leaves, and sometimes flowers. Prior to eating they spun considerable quantities of silk over the leaf surface, including the petiole. Whilst feeding, they

typically aligned themselves in compact rows, starting from the leaf apex or outer margin and working back towards the petiole (Figs 23, 26, 27). Instars I–IV were observed to produce clear fluid droplets from the tips of the black spine-like setae (Fig. 25). Instars II–IV readily regurgitated green fluid from the mouth when molested or disturbed, whereas final instar larvae were reluctant to exhibit this behavior when harassed. Larvae, when close to pupation, apparently leave the food plant to pupate elsewhere. For example, at San Pedro, five pupae were found attached to a metal fence immediately beneath the larval food plant (Fig. 34). These pupae, and those larvae reared in captivity, pupated singly, and were usually suspended horizontally or sometimes vertically with head directed downwards, with the ventral surface facing uppermost (Fig. 34). The pupae were polymorphic, with two color forms (green, brown) recorded. In both forms, the dorsal surface resembled a small leaf (Fig. 36), with the anterior projection of the head mimicking the apex, the reddish middorsal line the midrib, abdominal segments 9 and 10 the petiole, and the scattered black spots dead leaf tissue. Adults (Fig. 6) emerged around dawn in captivity but were rarely observed in the field. On a few occasions we observed adults flying rapidly near the larval food plant during periods of sunlight or females were seen ovipositing; at the Universidad de Costa Rica a male was recorded feeding on flowers of *Acnistus arborescens* (L.) Schltld. (Solanaceae) on 18 June 2005 (Nishida *et al.* 2008). In contrast, DeVries (1987) noted that adults are often seen in suburban areas of San José, but as singletons, their flight reminiscent of orange nymphalids.

At constant rearing temperature (23–24°C, a few degrees above the average yearly temperature for San José) the life cycle from egg to adult was completed in approximately six weeks (egg 6 days; larva 20 days; prepupal stage 1–2 days; pupa 15–18 days). In the vicinity of San José, the immature stages were recorded during the months of January–March (dry season) and, more frequently, June–August (mid wet season). It is not known if the species breeds during the other months of the year, particularly the period September–December (late wet season), and if it undergoes pupal diapause. Our field observations suggest the species is multivoltine and probably breeds continuously throughout the year.

A parasite, *Hyphantrophaga virilis* (A & W) (Diptera: Tachinidae), was reared from a pupa (specimen deposited in UCR).

Our observations on clutch size and larval behavior for *H. crocea* contrast with those recorded for *H. graphites* H.W. Bates in Costa Rica (at Volcan Barva,

2400 m) in which the yellow eggs are laid singly on the larval food plant *Psittacanthus schiedeana* (Schlecht. & Cham.) Blume and the larvae feed solitarily (L.R. Murillo pers. comm.).

Mathania Oberthür, 1890

This small genus includes four species, plus another that is presently undescribed (Lamas 2004). *Mathania* is restricted to South America, ranging from Ecuador to Chile and Argentina. Larval food plants have been reported only for the two temperate species in Chile and Argentina, and include the genera *Ligaria*, *Tripodanthus* (Jørgensen 1916; Hayward 1960, 1969) and *Tristerix* (Izquierdo 1895; Ureta 1940; Peña 1975; Courtney 1986; Peña & Ugarte 1996) (all Loranthaceae). Izquierdo (1895) and Ureta (1940) provided brief descriptions and biological notes of the immature stages of the Chilean species, *M. leucothea* (Molina, 1782). For comparison with other members of the *Hesperocharis* group we provide a more detailed account of the morphology and biology of this taxon below.

***Mathania leucothea* (Molina, 1782)**

This species (Fig. 7) is restricted to the temperate areas of central Chile and central western Argentina: in Chile, it is recorded from the Provinces of Coquimbo to Valdivia (Peña & Ugarte 1996) and, in Argentina, the Provinces of Río Negro and Chubut of Patagonia (Shapiro 1991b). In Chile, *M. leucothea* breeds predominantly in the dry mid-elevation slopes (1400–1900 m) of the Andes supporting xerophytic open-woodland scrubs and thickets (matorral desert) (Figs 9, 11), although adults occasionally disperse into the higher altitudes at Farellones (2500 m) (Courtney 1986) and the lower altitudes of Santiago (*ca.* 600 m) where it may be seen in suburban gardens (Ureta 1940; A. Ugarte pers. comm.). The immature stages have been reported from *Tristerix corymbosus* (L.) Kuijt (Loranthaceae) (Izquierdo 1895; Ureta 1940; Hayward 1969; Peña 1975; Courtney 1986; Peña & Ugarte 1996) which, east of Santiago, commonly parasitizes the host trees *Kageneckia oblonga* Ruiz & Pav. and *K. angustifolia* D. Don. (Rosaceae) (Courtney 1986). Izquierdo (1895) first documented the morphology of the immature stages, together with brief notes on their behavior. A crude illustration of the pupa was provided but the other stages were not depicted. Courtney (1986) made a detailed study of oviposition behavior and aspects of clutch size. A more comprehensive description of the immature stages, together with a

summary of the general biology of the species, is given below. Our observations were made in the vicinity of Farellones on the western slopes of the Andes east of Santiago during 1–3, 11 December 2000. We sampled two areas: curva 14 to ranger station at 1600–1700 m, and curva 18 at 1850 m. Voucher material is lodged in USNM and MCZ.

Immature stages. *Egg* (Figs 37–39). 1.3 mm high, 0.6 mm wide; white when newly laid, later changing to orange; bottle-shaped, with base flattened and narrower in width (0.4 mm) than middle; chorion with 12–14 coarse longitudinal ribs, each terminating at micropylar end where they form a small protuberance or nodule, a series of about 25 finer transverse striae between longitudinal ribs.

First instar larva (Figs 40, 41). 3 mm long at eclosion, 5 mm long prior to molting; head pale orange; body orange-yellow after eclosion, about two days later changes to pale green after consuming food, with numerous long black primary setae bifurcated at apex; prothorax with a prominent subdorsal patch bearing three long setae, and a lateral seta; meso- and metathorax each with a pair of long dorsal setae, a subdorsal seta and a lateral seta, all forming a transverse row anteriorly; abdominal segments 1–9 each with a pair of long dorsal setae and a lateral seta, all forming a transverse row anteriorly, and a subdorsal seta posteriorly; abdominal segment 10 with two long dorsal setae and a series of 4–6 colorless setae posteriorly.

Second instar larva (Fig. 42). 8 mm long; similar to first instar larva, but with a paler green dorsal line, a variable red middorsal patch on thorax (more pronounced on prothorax), primary setae smaller, a few pale brown secondary setae on each segment.

Third instar larva (Figs 43–45). 12 mm long; similar to final instar larva, but with a variable red middorsal band on thorax, sometimes extending to final abdominal segment, band more pronounced on prothorax and mesothorax.

Fourth instar larva (Fig. 46). 18 mm long; similar to final instar larva, but some larvae may possess a small red dorsal patch on prothorax or even a red middorsal band.

Fifth instar larva (Figs 47–50). 34 mm long; head dull olive-green, densely covered with very short pale brown secondary setae; body various shades of green, from bright green to dull olive-green, with a faint darker green middorsal line, densely covered with short pale reddish-brown secondary setae, each segment with a few short, obscure black primary setae bifurcated at apex; spiracles pale brown to black. Number and arrangement of primary setae on segments as follows: prothorax with three subdorsal setae and a lateral seta; meso- and metathorax each with a pair of dorsal setae, a subdorsal seta and a lateral seta, all forming a transverse row anteriorly; abdominal segments 1–9 each with a pair of dorsal setae and a lateral seta, all forming a transverse row anteriorly, and a subdorsal seta posteriorly. Body remains green during prepupal stage (Fig. 51).

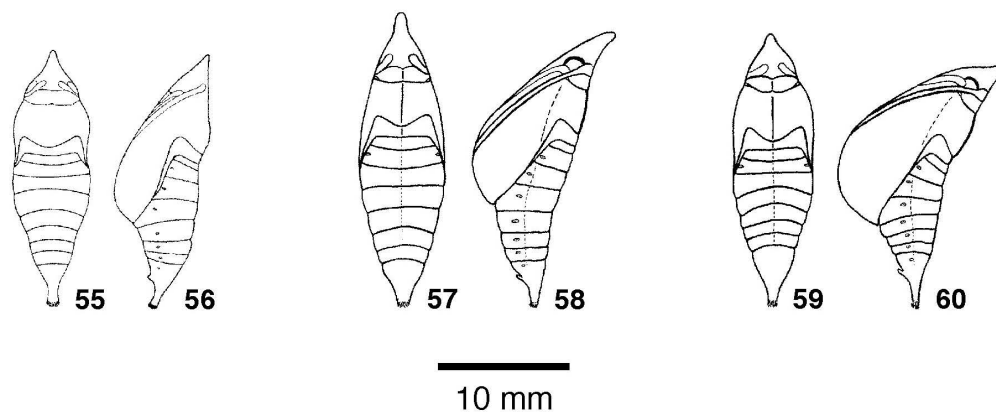
Pupa (Figs 52–54). 21 mm long, 10 mm wide; pale green or pale brown, with a few small reddish spots, particularly on head ventrally, prothorax (including wing case) and abdominal segments 4–6, and some smaller obscure dark reddish spots on wing case; head with anterior end produced to a rounded, beak-like point; wings strongly convex ventrally, cases of forewing with a transverse row of five small obscure black spots near posterior margin; a pale, prominent lateral ridge extending from mesothorax to abdominal segment 10; a broad reddish middorsal line extending from prothorax to abdominal segment 10; dorsal surface concave in region of abdominal segment 1; ventral surface with a few obscure reddish spots, including a pair at anterior end. Attached by cremaster, to small pad of silk spun over substrate, and a central silken girdle which passes over abdominal segment 1.

Larval food plants. Besides *Tristerix corymbosus* (Figs 12, 13) we also recorded the immature stages on *T. verticillatus* (Ruiz & Pav.) Barlow & Wiens (Fig. 10) parasitizing *Lithraea* (Anacardiaceae) and *Quillaja*

saponaria Molina (Rosaceae) near Farellones. This additional food plant was recorded only at the higher elevations (1850 m), whereas at altitudes below 1700 m only *T. corymbosus* was used. However, where the two species occurred in sympatry, *T. verticillatus* appeared to be the preferred larval food plant. For example, on one host tree that supported four clumps of *T. corymbosus* and single small clump of *T. verticillatus*, no immature stages were found on the former species but numerous cohorts (19 egg clusters, more than 30 early instar larvae) were present on the clump of *T. verticillatus*, despite the fact that this species grew in close proximity to the more abundant *T. corymbosus*.

Biology. We summarize below the life cycle and behavior based primarily on our observations near Farellones, supplemented with the earlier observations made by Izquierdo (1895) and Courtney (1986).

Eggs were laid mainly on the upperside of new soft leaves of the mistletoe food plants; only rarely were they found on the petiole and stems subtending new growth (Fig. 37). The eggs were laid either solitary (9% of all cohorts, $n = 54$) or, more usually, in small loose clusters ranging from 2–9 eggs per cluster. The majority of clusters (66% of all cohorts, $n = 54$) comprised 3–4 eggs per cluster, a finding in agreement with previous studies on the frequency distribution of clutch size (Courtney 1986). When freshly laid, eggs were initially white (Fig. 38) but after 22 hrs changed to cream or pale orange; subsequently they changed to dark orange (Fig. 39), but never red as indicated by Courtney (1986). Courtney (1986) found that females preferentially oviposited on clumps without flowers and, in the case of *T. corymbosus*, those parasitizing *K. oblonga*; he also recorded a greater proportion of eggs on new leaves and stems less than 10 cm from the apex of the terminal shoots. The first instar larva emerged from near the apex of the egg and then either partly or completely devoured the chorion (Fig. 40) before proceeding to graze the leaf surface. Izquierdo (1895) noted that the early instar larvae are usually covered in their own excrement (Fig. 42), and we observed in instars I–III that this is due to the presence of numerous clear fluid droplets, to which the feces adhere, at the tips of the black forked setae (Fig. 45). These fluid droplets were absent in the later instars (IV, V). The early instar larvae (I–III) were semi-gregarious (Figs 42, 43), feeding singly or in small groups of two or three. In contrast, the late instar larvae (IV, V) (Figs 47, 48) fed solitary on the leaves (or sometimes the soft new stems) of the larval food plant. In contrast to *Hesperocharis*, the larvae did not spin much silk over the leaf substrate before feeding. All larval instars were well camouflaged on the larval food plant. Instars II and III closely resembled



Figs. 55–60. Pupae of the *Hesperocharis* group. **55, 56**, *Eroessa chiliensis* from Chile (modified from Angulo and Weigert 1974), showing dorsal (**55**) and lateral (**56**) views. **57, 58**, *Hesperocharis crocea* from Costa Rica, showing dorsal (**57**) and lateral (**58**) views. **59, 60**, *Mathania leucothea* from Chile, showing dorsal (**59**) and lateral (**60**) views. All figures are twice natural size.

developing flower buds due to presence of the pinkish-red dorsal patch or band behind the head (Figs 43, 42); when not feeding the larvae typically rested on a leaf petiole, along the leaf midrib or a stem. Instars IV and V closely matched the new leaf growth and, since the body color varied slightly according to the color of foliage being consumed, were exceedingly difficult to detect. The mid instar larvae (III, IV) were noticed to spin a silken platform on the upperside of a leaf, to which they attached prior to molting. When attacked by parasitoids or molested, the larvae wriggled the head and anterior part of body backwards and thrashed with violent rapid movements, but did not regurgitate fluid. In the field, five empty pupal exuviae from the previous season were recorded, all from the larval food plants (4 on *T. tetrandus*, 1 on *T. verticillatus*). In each case, the pupae were solitary and well concealed, being situated beneath dense clumps of mistletoes. These pupae were attached either to the haustorium or to thin branches of the mistletoe, being suspended horizontally with the head directed downwards and the ventral surface facing uppermost (see also Fig. 52). Pupal color was polymorphic. Those reared from larvae in captivity were initially bright green but after about five days a proportion (35%, $n = 14$) changed to pale greenish-brown, pale brown or pale yellowish-brown; the others remained bright green or changed only slightly to dull dark green or pale green. The dorsal surface of the pupa resembled a small leaf (Fig. 54), with the head mimicking the leaf apex, the middorsal line the midrib, abdominal segments 9 and 10 (including the cremaster) the petiole, and the black spots dead leaf tissue. Adults, in early December, were observed flying throughout the

day, with flight continuing to about 1915 h. Both sexes flew rapidly and frequently around the host trees supporting the larval food plants, occasionally pausing to feed from flowers of vines. A female was observed at 1315 h ovipositing on a leaf of the food plant (Fig. 7). Courtney (1986) noted that during oviposition, duration of egg-laying is brief and the wings remain closed; he suggested that suitable oviposition sites may involve chemical cues once the host tree is located visually.

The seasonality of *M. leucothea* is not clearly understood. Adults are on the wing from November to late February (Courtney 1986) or early autumn, depending upon the season. The flight period is asynchronous with, and temporally separated from, the reproductive phenology of *Tristerix corymbosus*, which flowers mainly during the winter months, from early autumn (March) to late spring (November) (Aizen 2005). Izquierdo (1895) observed that in summer and autumn several generations are completed and that winter is passed in the pupal stage. Adults were relatively abundant near Farellones, but those encountered in early December 2000 were all in 'worn' to 'very worn' condition, indicating that they had been on the wing for some time. The immature stages at this time comprised predominantly eggs and early instar larvae (I–III); only three late instar larvae were found (at lower altitudes) but no live pupae were present. The life cycle, from egg to pupa, was completed in about four weeks when the various stages were reared under ambient conditions during December: egg 8 days, larva 25 days (duration of instars as follows: I 5 d, II 3 d, III 4 d, IV 5 d, V 8 d), prepupa 1 day ($n = 3–11$). The pupal stage was more variable, but the duration was not

correlated with pupal color. A few developed directly and emerged in late December/early January after a pupal duration of 18 days, but the majority entered diapause and the adults did not emerge until the following season, in late November 2001 (A. Ugarte, pers. comm.). Four pupae transported to Boston, USA (Northern Hemisphere), in December remained dormant for varying lengths of time, with the adults emerging 115, 184, 205 and 365 days after pupation. These field and captive rearing observations suggest the species is predominantly univoltine with the main adult emergence in late spring, followed by a facultative pupal diapause in which one or more partial generations are completed during summer. Pupal diapause during the cooler months would ensure survival in winter when snow regularly falls above 1700 m at Farellones.

A series of parasitoids, *Trichogramma* (Hymenoptera: Trichogrammatidae), were reared from eggs.

DISCUSSION

The Anthocharidini *sensu stricto* comprises a well-supported monophyletic group of seven genera. Recent systematic studies based on molecular data indicate that these genera fall into two reciprocally monophyletic groups: the *Anthocharis* group, containing the genera *Euchloe*, *Anthocharis* and *Zegris* in an unresolved trichotomy; and the *Hesperocharis* group, containing the genera *Eroessa*, *Cunizza*, *Hesperocharis* and *Mathania* (Braby *et al.* 2006). The *Anthocharis* group specializes on crucifers in the families Brassicaceae and Resedaceae (Brassicales) (Braby & Trueman 2006) and occurs widely in the Holarctic of the Northern Hemisphere; in the Nearctic Region it reaches its southernmost limit in northern Mexico (de la Maza 1987). In contrast, the *Hesperocharis* group is biogeographically separated from the *Anthocharis* group, being restricted to the Neotropical Region, from southern Mexico to Patagonia of central southern Argentina and Chile.

The pupae of the *Hesperocharis* group (Figs 55–60) share a number of features in common with that of the *Anthocharis* group, as well as those of the Pseudopontiinae, Dismorphiinae, Coliadinae, *Colotis* group and *Leptosia* in possessing ‘type I’ morphology, but differ fundamentally from that of the Pierini, which have ‘type II’ morphology (Braby *et al.* 2006). Within the *Hesperocharis* group, the morphology of the egg, first instar larva and pupa of *Hesperocharis* and *Mathania* show a close relationship, supporting the systematic conclusions of Klots (1933) and Braby *et al.* (2006) based on adult morphological and molecular characters, respectively, for these taxa. The two genera

diverge markedly in the larval stage, particularly in the late instars. These differences are probably related to differences in behavior: the larvae of *Hesperocharis* are gregarious and have longer and more densely covered setae and conspicuous protuberances on the body, while those of *Mathania* are semi-gregarious or solitary, particularly in the late instars, and have less conspicuous setae over a smoother surface. The morphology of the pupa of *Hesperocharis* (Figs 57, 58) and *Mathania* (Figs 59, 60) is very similar in profile to that of *Eroessa* (Figs 55, 56), indicating a close relationship among these three genera. In *Eroessa*, the head has a long anterior projection which tapers to a rounded point, the ventral surface of the prothorax (wings) is strongly convex, and abdominal segments 8–10 bearing the cremaster is long and slender. The ventral surface of the pupa of *Eroessa*, like *Hesperocharis* and *Mathania*, is broadly oval-shaped (except for the extremities); however, unlike the two other genera, the dorsal surface is relatively straight and not arched or concave. However, in profile, the shape of the dorsal surface of *Eroessa* more closely resembles that of *Mathania* than *Hesperocharis*. Additional morphological structures, particularly the egg and larva of *Eroessa* and the immature stages of *Cunizza*, would provide further data for comparison, and an independent character set to support or refute the topology of Figure 1. *Eroessa* appears to have retained a number of plesiomorphic traits in the adult, including a relatively long labial palpus, a well-developed valva of the male genitalia, presence of all five radial veins in the forewing, and the origin of vein M_1 arising from the cell (instead of stalked with the radial stem vein) in the forewing (Klots 1933). These characteristics, together with its small geographical area of distribution, occupation in temperate relict Tertiary valdivian forest, monotypic status and phylogenetic position, suggest it is probably a relictual taxon from southern Gondwana.

A list of the known larval food plants of the *Hesperocharis* group is summarized in Table 1. Reliable data has been recorded only for *Hesperocharis* and *Mathania*. The limited data show that two families of Santalales (Loranthaceae, Viscaceae) have been recorded, with most records for the Loranthaceae. Only the genus *Phoradendron* is recorded for Viscaceae, whereas four genera are recorded for Loranthaceae. *Ligaria*, *Tripodanthus* and *Tristerix* comprise small, putatively relictual Gondwanan genera (Barlow 1983), whereas *Struthanthus* is more widely distributed in Central and South America. The use of *Phoradendron* strongly suggests the larval food plant range of the *Hesperocharis* group may be considerably wider than present records indicate since, within the Santalales, the

Viscaceae are somewhat distantly related phylogenetically to the Loranthaceae (Nickrent *et al.* 1998). Nevertheless, available data suggests the ancestral feeding state for the clade *Hesperocharis* + *Mathania* is Loranthaceae (Table 1), implying an independent colonization of Viscaceae. The sister group relationship between *Cunizza* and *Hesperocharis* + *Mathania* (Fig. 1) implies that the larvae of *Cunizza* probably also specialize on mistletoes in the Loranthaceae or Viscaceae. Moreover, adults of *Cunizza* have the hindwing underside aposematic (Fig. 4), a trait that is characteristic of mistletoe feeding pierids in general (Braby & Trueman 2006).

Confirmation of the larval food plant of *Eroessa* is needed to reconstruct the ancestral food plant of the *Hesperocharis* group, which was equivocal in the analysis of Braby and Trueman (2006). The most parsimonious reconstruction for the ancestral food plant of the Anthocharidini is Brassicales, but the evolutionary pathway of host use within the clade *Anthocharis* group + *Hesperocharis* group remains unclear. If *Dasyphyllum* (Asterales: Asteraceae) proves to be the larval food plant of *Eroessa*, then there are at least two equally plausible hypotheses, each involving two major host shifts given the topology of Figure 1: (1) Brassicales → Asterales → Santalales; or (2) Brassicales → Santalales → Asterales. The first scenario implies that mistletoe feeding evolved in the clade *Cunizza* + (*Hesperocharis* + *Mathania*) from an Asterales-feeding ancestor of the *Hesperocharis* group. The second scenario implies that mistletoe feeding evolved in the clade *Eroessa* + (*Cunizza* + (*Hesperocharis* + *Mathania*)) from a Brassicales-feeding ancestor of the Anthocharidini; Asterales-feeding in *Eroessa* subsequently evolved due to a host shift from Santalales. From an evolutionary perspective the crucial question remains as to whether the larval food plant of *Eroessa* represents an ancestral (hypothesis 1) or derived (hypothesis 2) state within the *Hesperocharis* group. On the other hand, if the larval food plant of *Eroessa* proves to belong in the Brassicales, as would be predicted based on food plant usage in the *Anthocharis* group (i.e. the sister lineage of the *Hesperocharis* group), this would simplify the number and complexity of host shifts within the Anthocharidini. In either case, it is highly probable that the larval food plant of *Eroessa* will prove to be a rainforest host tree parasitized by mistletoes, otherwise the mechanism for such radical shifts between phylogenetically distantly related plant orders remains problematic. In the Aporiina, Braby and Trueman (2006) concluded that evolutionary shifts from mistletoes to mistletoe host trees occurred multiple times (and more frequently than the reverse pathway

from host trees to mistletoes), resulting in exploitation of novel food plants outside the conventional three orders of Fabales, Brassicales and Santalales. If such a pathway occurred in the *Hesperocharis* group (i.e. hypothesis 2) this would readily explain the apparent exceptional use of Asterales, a larval food plant otherwise unique within the Pierinae. Despite substantial gaps in basic field knowledge, exploitation of mistletoes by *Hesperocharis* + *Mathania* appears to have facilitated adaptive radiation within this clade, resulting in 15 species compared to its species-poor sister lineage *Eroessa*.

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