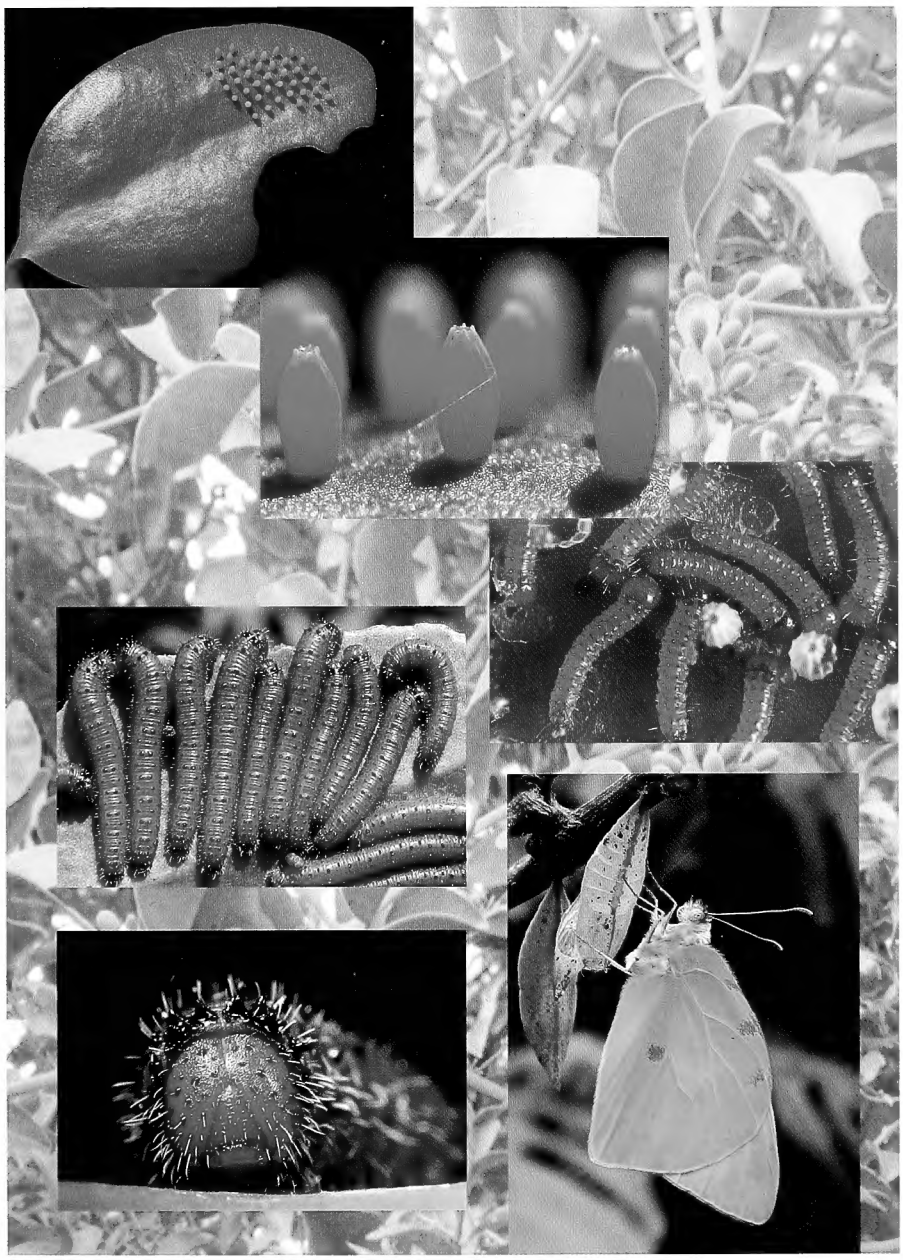
Volume 61 Number 4
14 December 2007
ISSN 0024-0966

Journal of the Lepidopterists' Society



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Journal of The Lepidopterists' Society (ISSN 0024-0966) is published quarterly by The Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007-4057. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057.

Cover Illustration: Life history of *Hesperocharis crocea* from San Pedro de Montes de Oca, San José, Costa Rica showing egg cluster on larval food plant *Struthanthus orbicularis* 4 June 2004 (upper left), eggs 29 May 2004 (upper center), first instar larvae feeding on chorion 2 June 2004 (middle right), third instar larvae feeding on *S. orbicularis* 12 June 2004 (middle left), fifth instar larval head 21 June 2004 (lower left), pupa and freshly emerged adult on its pupal exuvia 19 August 2000 (lower right); photographed by Kenji Nishida, Apdo. 12041002, Paseo Los Estudiantes, San José, Costa Rica, kenji.nishida@gmail.com .

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 61 2007 Number 4

Journal of the Lepidopterists' Society
61(4), 2007, 181-195

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-1α, 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 × 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:

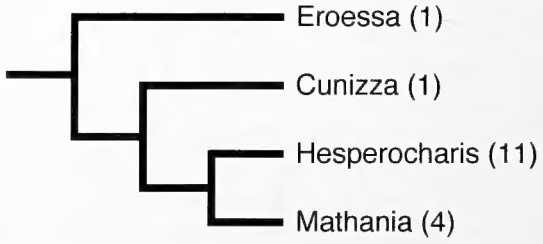
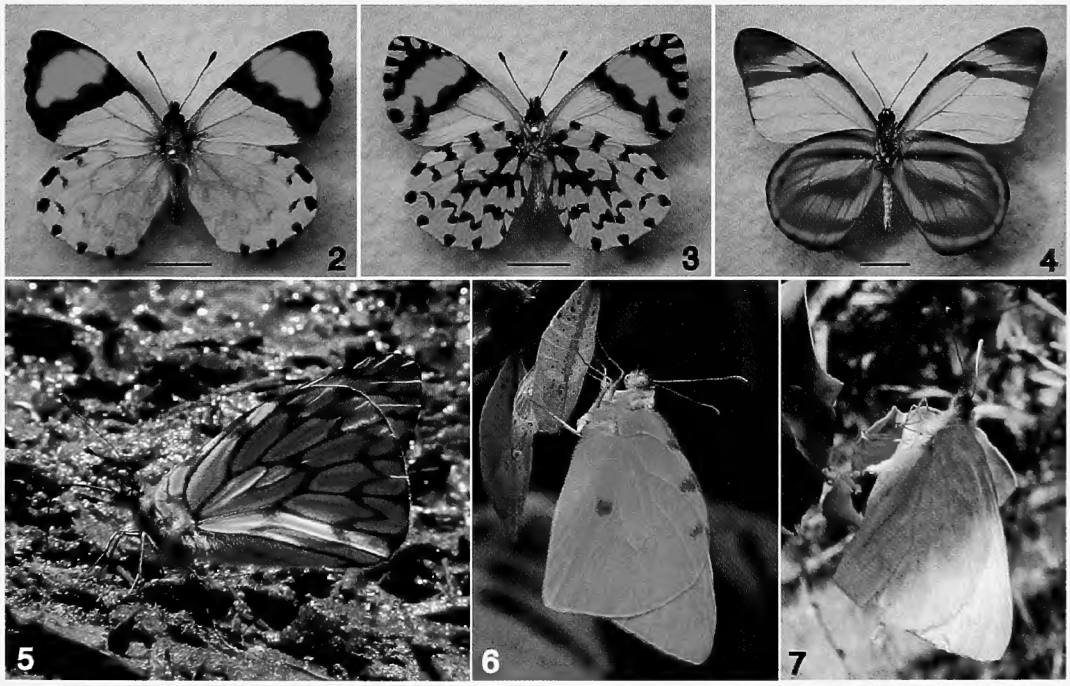


Fig. 1. Phylogeny of the *Hesperocharis* group, showing systematic relationships at the generic level. Phylogenetic hypothesis is based on combined analysis of four genes (*EF-1α, wingless, COI, 28S*) (3675 bp, 1091 parsimony informative characters, consistency index 0.265) for the family Pieridae (Braby *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 (Echeverria *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 magallanica* 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 magallanica*, *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

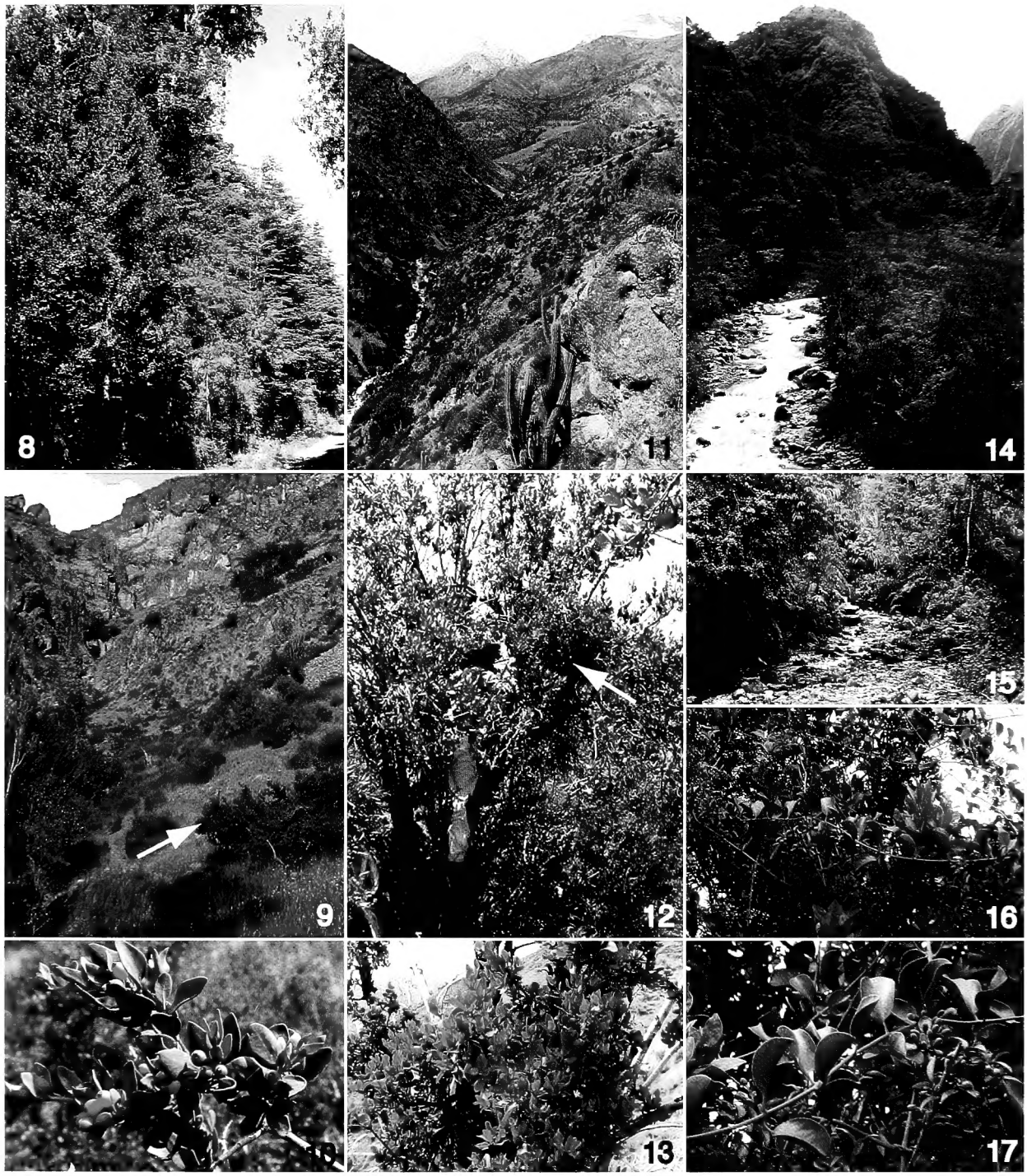
Cunizza is monobasic, containing the single polytypic species *C. hirlanda* (Stoll, 1790) (Fig. 4). The genus occurs in Ecuador, Colombia, Peru, Bolivia, Venezuela, Guyana, Surinam, and Brazil (Lamas 2004). It has also been collected from Bocas del Toro and Darién, Panama, by G. Small (G. Lamas, pers. 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

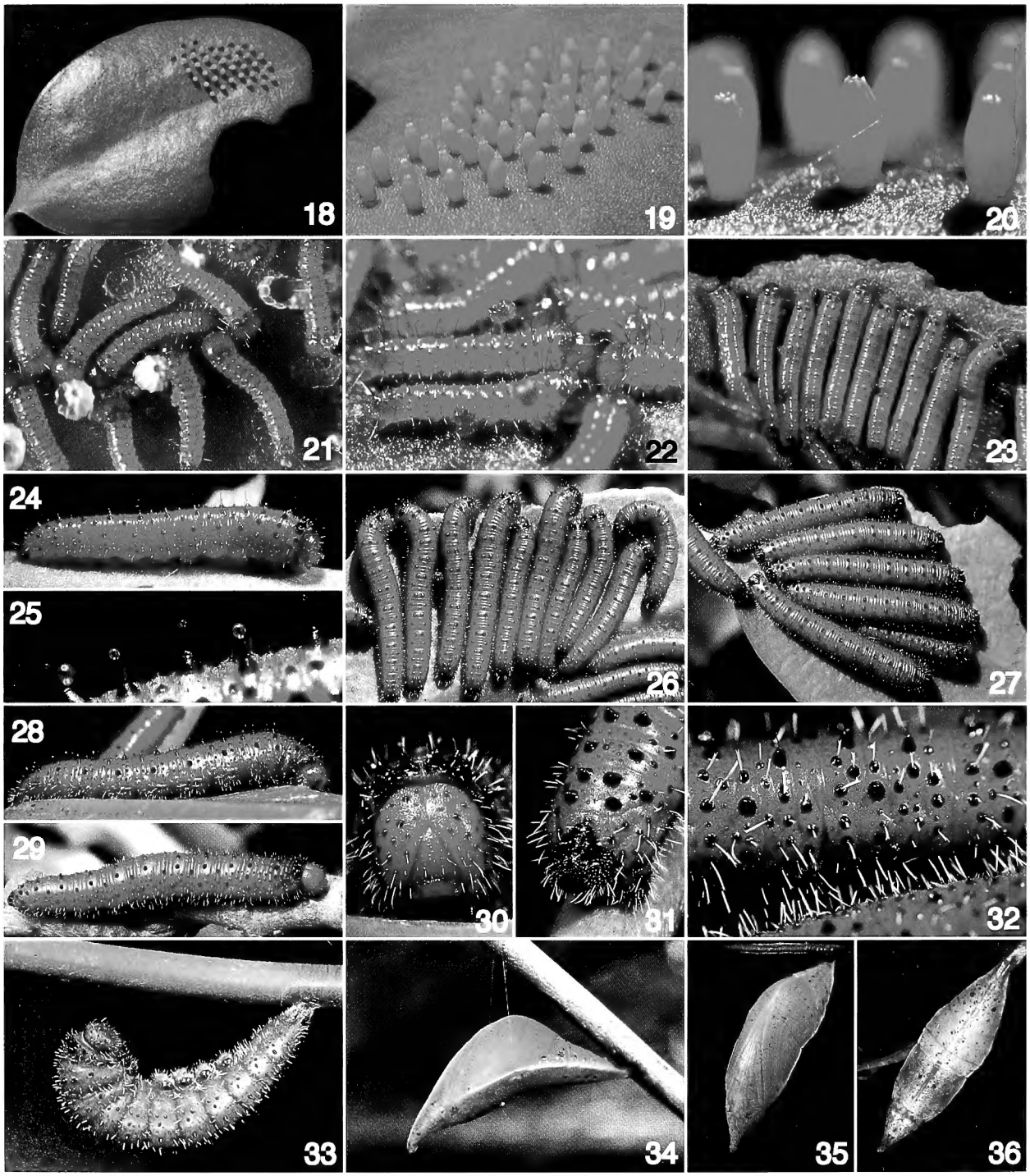
This Neotropical genus ranges from central and southern Mexico to Argentina, and includes 11 described species (Lamas 2004) with greatest diversity in South America. In Colombia, the species generally occur in montane forest up to 2–600 m, but others occur in warmer biomes of the Amazon Basin (Salazar 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-Méneville, [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 *Catasticta*." 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

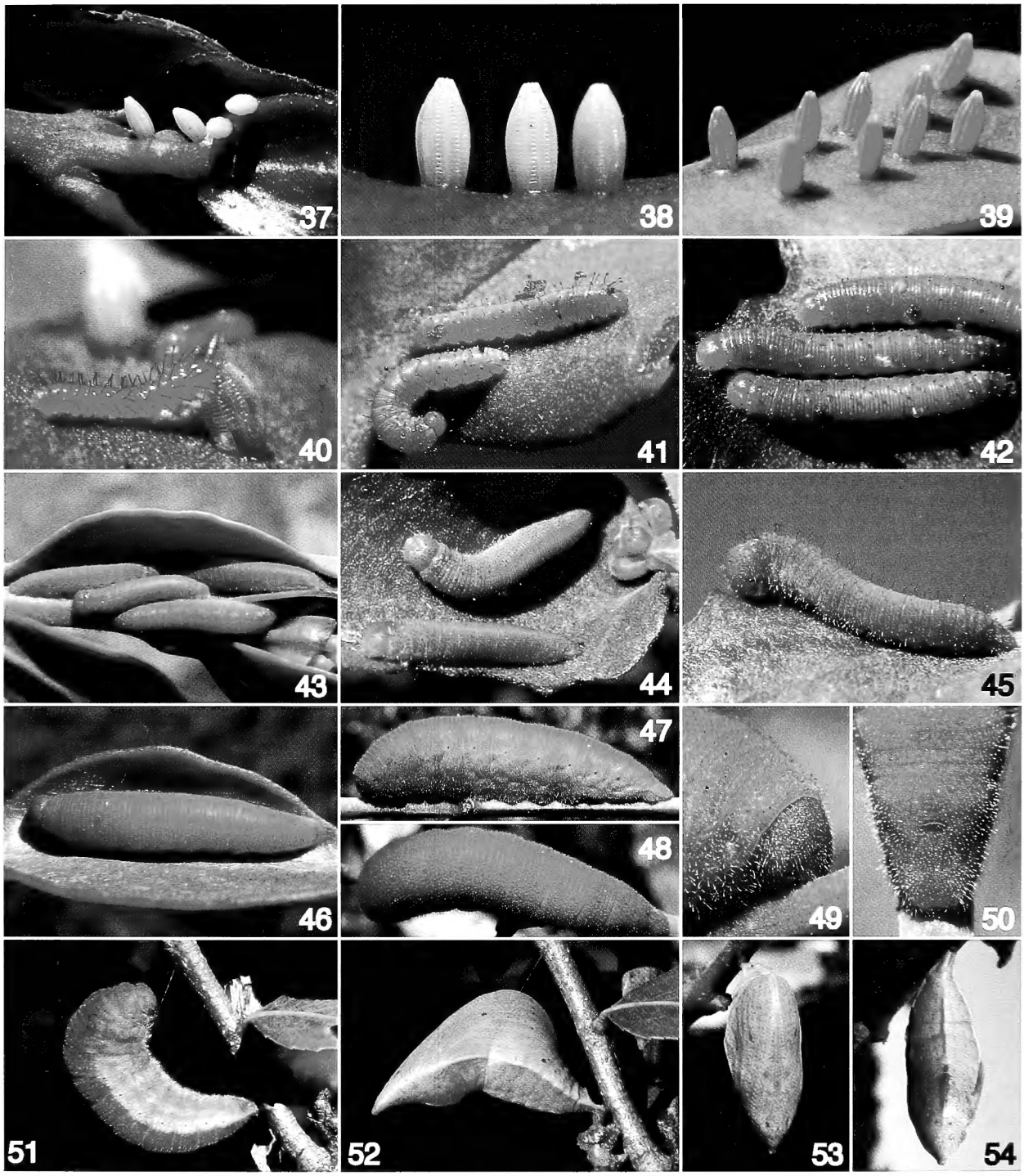
H. crocea (Fig. 6) occurs widely in the tropical latitudes of Central and South America, from southern



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

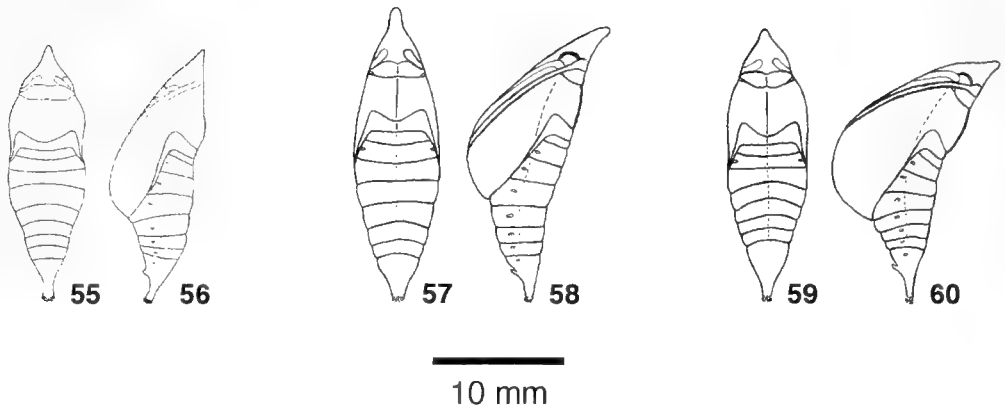
Fifth instar larva (Figs 47–50). 34 mm long; head dull olive-green, densely covered with very short pale brown secondary setae; body various shades of green, from bright green to dull olive-green, with a faint darker green middorsal line, densely covered with short pale reddish-brown secondary setae, 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 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*.

ACKNOWLEDGEMENTS

We are very grateful to G. Lamas, A.M. Shapiro and R.K. Robbins for comments on the manuscript, G.A. Beccaloni for considerable help with literature on larval food plants of Neotropical Lepidoptera, Jorge Llorente Bousquets for literature, and K. Pullen and A. Sequeira for translations of historical Spanish literature. We thank G. Lamas,, P. DeVries and L.R. Murillo for biological information, L.J. Aitchison for field assistance in Costa Rica, and I. Chacón and J. Montero for access to material lodged at INBio. C.O. Morales and A. Ugarte assisted with plant identifications; P. Hanson and M. Wood identified the trichogrammatid and tachinid parasites, respectively. A. Ugarte kindly provided much hospitality, biological information and assistance with field locations in Chile, and L. Rodríguez helped with access to mistletoes in Costa Rica. Material from Costa Rica was collected under permit PI-045-ACCVC (Ministerio del Ambiente y Energía) and from Chile under CONAF permit 11/2000 (Ministerio de Agricultura). This research was supported by an Australian Research Council Fellowship (grant number F19906650) and a Fulbright Postdoctoral Fellow Award funded through the auspices of the Australian-American Fulbright Commission to MFB. The Putnam Expeditionary Fund of the Museum of Comparative Zoology also provided generous support for field work in South America.

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Received for publication 22 November 2006; revised and accepted 10 August 2007

Journal of the Lepidopterists' Society
61(4), 2007, 196-198

A NEW SPECIES OF *BRYOLYMNIA* HAMPSON FROM SOUTHEASTERN ARIZONA (NOCTUIDAE)

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ABSTRACT. ***Bryolymnia anthracitaria***, new species, is described from southeastern Arizona. Adults and male and female genitalia are illustrated, and comparison is made with the other two North American species.

Additional key words: ***Bryolymnia anthracitaria***, *Bryolymnia semifascia*, *Bryolymnia viridimedia*, Arizona, Noctuidae, taxonomy, Xyleninae

According to the most recent catalog of the World Noctuidae (Poole, 1989), there are seventeen currently described species of *Bryolymnia*, two of which occur in the United States and the remainder range from Mexico to Argentina. *Bryolymnia semifascia* (Smith, 1900), (Fig. 1), was described from Garfield Co., Colorado with the holotype placed in the National Museum of Natural History [USNM], Smithsonian Institution, Washington, DC. *Bryolymnia viridimedia* (Smith, 1905), (Fig. 2), was described from Cochise Co., Arizona with the holotype placed in the American Museum of Natural History [AMNH], New York, NY.

To date, *B. viridimedia* and the new species have been recorded only from southeastern Arizona with very few records for the former. On the other hand, *B. semifascia* is a relatively common species that ranges from Colorado southward to western Texas, southern New Mexico and southeastern Arizona.

Specimens of the new species have resided undescribed in museum and personal collections for sixty years. The earliest records that we found are four specimens in the Los Angeles County Museum of Natural History collected in July, 1947 by J. A. Comstock and L. M. Martin in Madera Canyon, Santa Rita Mts., Arizona. Additional specimens were collected in southeastern Arizona in 1959–60 by J. G. Franclemont and placed in the collection at Cornell University, Ithaca, NY. McFarland first collected specimens in the Huachuca Mts., in 1986. Since then, additional material was obtained by several other collectors. Genitalic examination of the moth places it in the genus *Bryolymnia* (subfamily Xyleninae, tribe Elaphriini). The genitalia of *B. semifascia* are illustrated for comparison (Figs. 3–5). A male specimen of *B. viridimedia* was not available for dissection.

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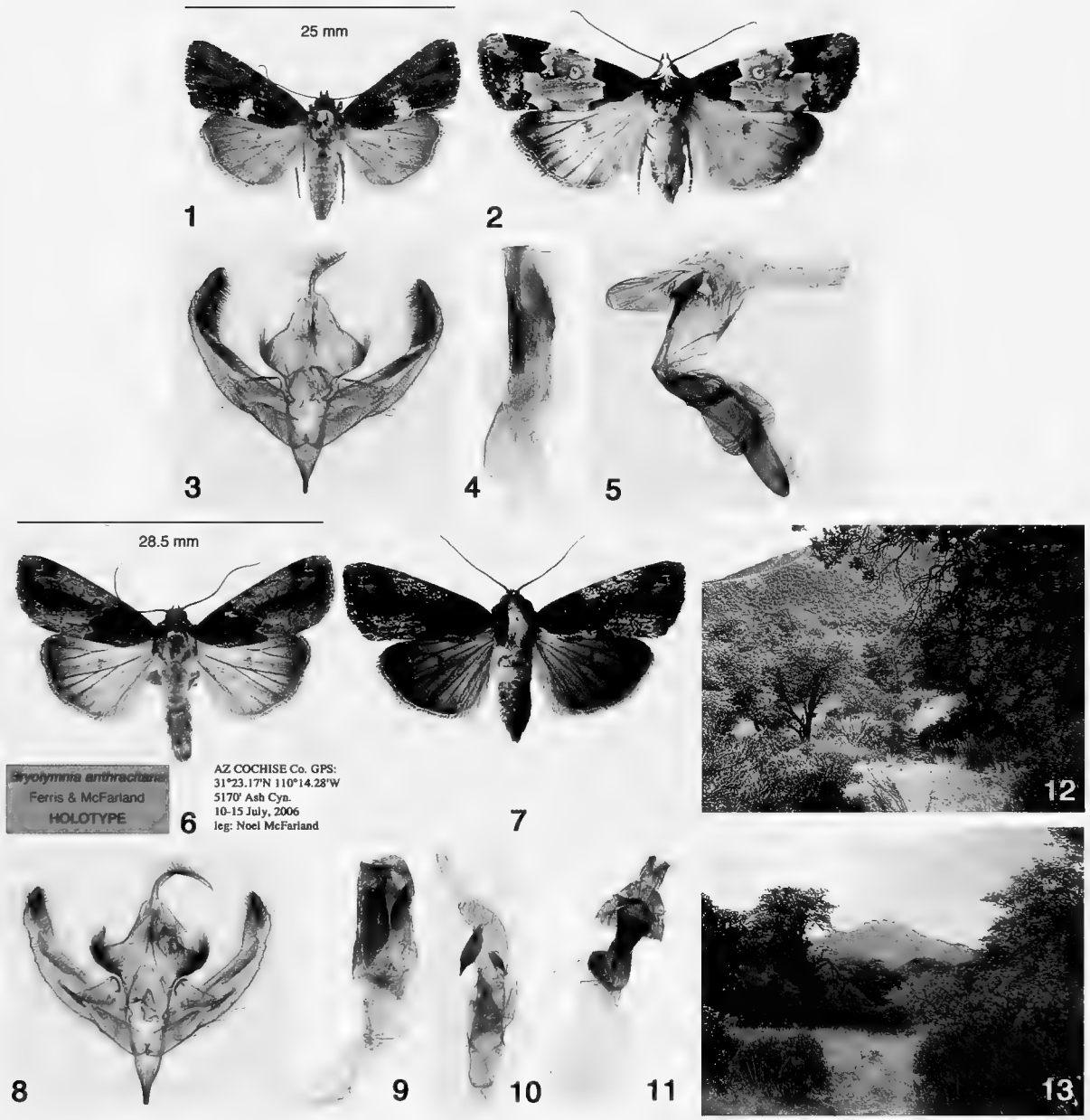
Bryolymnia anthracitaria Ferris and McFarland, **new species**
(Figs. 6–11)

Diagnosis. *B. anthracitaria* is immediately separated from all other members of the genus by the broad jet black basal patch covering almost half of the dorsal forewing (DFW), and the additional horizontal oblong black patch covering the middle of the outer half of the wing. *B. semifascia* has a broad blackish area across the lower half of the DFW interrupted by a white spot; *B. viridimedia* has a broad greenish DFW median band.

Description. MALE (Figs. 6, 8–10). *Head:* Vestiture rough, scales moderately narrow; frons slightly rounded, gray with central patch of darker scales; no frontal protuberance. Labial palpus robust, covered with dark brown scales flecked with gray scales, upturned and nearly appressed to front; middle segment elongate, more than 3 times length of basal segment; apical segment slightly shorter than basal segment. Well-developed eye with ocellus. Vertex scales slender and a mixture of dark brown and gray. Antenna brown, filiform, ventrally setose; scape mottled dark brown dorsad, tuft of white scales ventrad. Proboscis well developed. *Thorax:* Centrally divided rough collar of pale-tipped dark brownish-black scales; thick tegulae nearly black; central area covered with slender whitish scales and edged with brown scales. Forelegs and midlegs covered with brown scales, white-ringed at tarsal joints; hindlegs with long hairlike paler brown and whitish scales, white-ringed at tarsal joints. Ventral thorax clothed in long hairlike whitish scales. *Abdomen:* Covered with long hairlike pale brown and whitish scales, darker dorsad; dorsal tuft of pale-tipped dark brown scales projects from segment I. *Forewing:* Length (base to apex, n = 20): 12.0–14.5 mm, ave. 13.5 mm. Basal area black extending to irregular thin pale edge of diagonal antemedial band; antemedial band narrow and brown with scattered lighter and darker scales. Median line very poorly defined, broken and essentially absent. Orbicular and reniform spots each very weakly defined by a very narrow nearly circular black ring; claviform spot a short and narrow black dash. Postmedial area with mottled blackish, brown, and paler scales; narrow irregular black postmedian band terminating in a black spot at the costa. A broad horizontal black dash extends across the middle of the wing from the outer edge of the antemedian band to the



FIGS. 1–2. **1,** *Bryolymnia semifascia*, AZ, Cochise Co., Huachuca Mts., Ash Canyon, 5170' (1577m), 25.vi.2005; **2,** B. *viridimedia*, same locality, 6.vii.1982.

FIGS. 3–5. B. *semifascia* male genitalia: **3,** genitalia with aedeagus removed; **4,** aedeagus; **5,** aedeagus with vesica everted.

FIGS. 6–7. B. *anthracitaria*: **6,** male holotype and pin labels, AZ, Cochise Co., Huachuca Mts., Ash Canyon, 5170' (1577m), 10–15 July, 2006; **7,** female paratype, same locality, 1.vii.1992.

FIGS. 8–11. B. *anthracitaria* genitalia: **8,** male genitalia with aedeagus removed; **9,** aedeagus; **10,** aedeagus with vesica everted; **11,** female genitalia.

FIGS. 12–13. Habitat photos: **12,** Type locality; **13,** Ash Canyon with Miller Peak in center distance, looking west. *Arctostaphylos pungens* Humboldt, Bonpland, Knuth (Manzanita) is in the foreground; the larger trees are *Quercus emoryi* Torrey (Emory oak).

subterminal line. The subterminal line is narrow, even and brown; the broad adterminal line is segmented with alternating black and whitish patches merging with the terminal line; the fringe is brown. There is a narrow irregular black apical patch. Ventrally the ground color is brownish-fuscous with a central horizontal long dash; the apical patch is weakly repeated. *Hindwing*: Fuscous basad and centrad shading to brown at the margin; fringe scales pale-tipped, brown basally; discal spot poorly defined and postmedial line absent. Ventrally the ground color is fuscous, paler than in the forewing; the discal spot is weakly defined and a partially-defined postmedian line extends from the costa to about mid-wing. *Genitalia* (Figs. 8–10) [2 dissections]: Costa of valve widely sclerotized, terminating in a broad pointed tip; corona absent; sacculus moderately sclerotized with slender elongate extension appressed to valve; clasper a broad wedge-shaped plate, rounded distally; saccus produced and narrowing to a rounded pointed tip; juxta trapezoidal and deeply incised; uncus narrow at base, expanding slightly in mid-region, then tapering to a sharply pointed tip, only slightly flattened laterally; prominent blunted triangular socii. Aedeagus sheath with elongated triangular sclerotized patch extending from about mid-length to apex; vesica broadly tubular then tapering beyond second cornutus; two unequal heavily sclerotized nearly flat broad cornuti each tapering to a sharp point, the larger distal cornutus about 4X the area of the smaller basal one. FEMALE. (Figs. 7, 11). Basically like the male in most respects except: antenna filiform; dorsal scale tuft on abdominal segment I reduced relative to male; forewing length (base to apex, n = 5): 14.0 –16.0 mm, ave. 15.2 mm.; hindwing color brownish-fuscous, darker than in male. *Genitalia* (Fig. 11) [1 dissection]: Ovipositor lobes bluntly pointed, moderately setose; anterior and posterior apophyses of approximately equal length; ostium bursae conical with wide mouth, heavily sclerotized; ductus bursae heavily sclerotized, relatively short, expanding at junction with corpus bursae; corpus bursae long, oval, signum absent; very short appendix bursae arising from left posterior portion on corpus bursae, from which vary narrow ductus seminalis originates.

Holotype. Male: ARIZONA, Cochise Co., Huachuca Mts., Ash Canyon, 31° 23.27'N 110° 14.28'W, 5170' (1577m), 10–15 July, 2006, N. McFarland, deposited in National Museum of Natural History [USNM], Smithsonian Institution, Washington, DC.

Paratypes. (45m, 15f): ARIZONA. Cochise Co., same locality as Holotype, 23 June–4 August, C. D. Ferris, P. M. Jump, N. McFarland, R. Robertson (22m, 5f); Copper Canyon, 6000' (1830m), B. M. Walsh (1f); Pima/Santa Cruz cos., Madera Canyon, Santa Rita Mts., 4880–5880' (1488–1769m), 9–30 July, J. A. Comstock and L. M. Martin, J. G. Franclemont, B. M. Walsh (4m, 5f); Santa Cruz Co., Peña Blanca Canyon, 3950–4000' (1205–1220m), 14 July–23 August, J. G. Franclemont, B. M. Walsh (15m, 3f); Patagonia Mts., Harshaw Creek, 5000' (1525m), 12–22 July, B. M. Walsh (4m); Atascosa Mts., Sycamore Canyon, 4 August, 1966, R. and J. Robertson (1f). Paratype depositories: Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada [CNC]; Essig Museum of Entomology, Univ. of California, Berkeley, CA [UCB]; Los Angeles County Musuem of Natural History [LACM]; Cornell University, Ithaca, NY [CUIC]; private collections of C. D. Ferris, N. McFarland, B. M. Walsh.

Etymology. The specific epithet *anthracitaria* is derived from the Latin noun (*anthracites*) with the nominal adjective suffix *–aria* (like coal) to describe the jet black maculation of the moth's dorsal forewing and thorax.

Biology. Unknown. The habitat is desert mountain canyons in the ecotonal zone between the grassland and oak woodland (Figs. 12–13).

Distribution and Flight Period. To date, the moth is known only from Cochise, extreme southern Pima, and Santa Cruz counties in southeastern Arizona. In most years, adults first appear and reach a peak from late June to early July during the last of the very hot and dry period before the onset of the monsoonal rains, but a few have also been collected well into August. Flight records span from 22 June to 23 August.

Discussion. Sixty-one specimens were examined, some by photograph. Collection years span from 1947 to 2006.

As noted from the forewing length measurements above, adults vary in size to some degree. In a few females, the dorsal hindwing color is very pale rather than brownish-fuscous. A few specimens manifest a rather pale postmedian ground color. In some individuals, the black horizontal dash extends basad and merges with the black basal patch.

Recently, specimens of a green *Bryolymnia* have been taken in Arizona (Mt. Graham, July, 2007) by B. M. Walsh and in New Mexico (Manzano Mts., late May–early July, 2006–2007) by R. Holland. These moths are considerably smaller than *B. viridimedia* with slightly different maculation. They resemble to some degree the Mexican *B. bicon* (Druce). Until specimens can be dissected and compared, it remains unclear if one or more species is involved, and if the moths are *B. bicon* or an undescribed species.

ACKNOWLEDGEMENTS

We express our appreciation to the following for supplying data, photographs, and loan material: J. D. Lafontaine, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada, and who also kindly reviewed the manuscript prior to submission; B. M. Walsh, Univ. of Arizona, Tucson, AZ; J. A. Powell, Essig Museum of Entomology, Univ. of California, Berkeley, CA; M. G. Pogue, Smithsonian Institution, Washington, DC.; L. Prevett, Bisbee, AZ. Two anonymous reviewers provided helpful suggestions.

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Received for publication 21 May 2007; revised and accepted 29 June 2007

Journal of the Lepidopterists' Society
61(4), 2007, 199-212

DID A MEMBER OF THE *VANESSA INDICA* COMPLEX (NYMPHALIDAE) FORMERLY OCCUR IN NORTH AMERICA?

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ABSTRACT. The North American Oligocene fossil *Vanessa amerindica* is thought to be most like *V. indica*. Based on an 18th century painting made by the English naturalist Henry Seymer Jr., the possible existence of a member of the *indica* complex that occurred in North America as late as circa 1770 is demonstrated. New information on the classification of the nine extant species currently included in *Vanessa sensu stricto* strongly suggests that this apparently undescribed species is most closely related to the Atlantic Islands endemic, *V. vulcania*. Three competing scenarios that attempt to explain the highly disjunct distribution of the species that make up the *V. indica* complex are discussed, and it is concluded that the genus *Vanessa* most probably originated in North America, and that *V. vulcania* represents a separate, Atlantic colonisation event, separate from the Pacific colonisation event that gave rise to the Asiatic *V. indica*-group. This implies that, contrary to earlier hypotheses that sought to explain the distributional gap between the Canaries and India, the *indica* complex may never have been established on the western Palaearctic mainland, or in the Eremic Zone (Morocco to Somalia and Tien Shan). An African species formerly placed in *Antanartia* is formally transferred to the genus *Vanessa* (*Vanessa abyssinica*, **comb. nov.**).

Additional key words: Tertiary, relict, introduction, biogeography, Newfoundland, Macaronesia, Henry Seymer.

According to Art Shapiro (1992a), "The most peculiar Palearctic butterfly distribution is that of the Indian Red Admiral, *Vanessa indica* (Herbst)." Although the taxonomy of this member of the Nymphalidae has since changed — *V. indica* (Herbst, 1794), in Shapiro's sense, is now divided into three allopatric species — the enigma to which he referred remains: how can the 7000 km gap in distribution between the Indian red admirals found on Madeira and the Canary Islands, and those occupying the rest of the range, in the Oriental region and far eastern Palaearctic, be explained? No extant member of the species complex to which these butterflies belong is known from the rest of the western Palaearctic, North Africa, or North America.

Fresh interest in this problem has come from the recent discovery of an 18th century painting of a member of the *Vanessa indica* complex, supposedly based on a specimen collected in Newfoundland *circa* 1770. This illustration is one of some 300 surviving images of exotic butterflies and moths made by the little-known British naturalist Henry Seymer (1714–1785), together with his son, Henry Seymer Jr. The Seymers obtained their natural history specimens, notably of molluscs and insects, through dealers, travellers, military personnel and other contacts. Based on an extensive analysis of all the known Seymer Lepidoptera paintings, and their notes and records, it has been demonstrated that the vast bulk of their exotic material came from China, Java, India, West Africa, South Africa, South America, Jamaica, and the early British colonies in North America (Vane-Wright & Hughes, 2005: table 1, p. 254). Their Lepidoptera collection apparently totalled some 20,000 specimens, but it was dispersed immediately after Henry Sr.'s death, and nothing is yet known to have survived (Vane-Wright & Hughes, 2005; Barker & Vane-Wright, 2007).

The Seymer paintings, made during the period 1755–1783, appear to have been intended as a virtual record of the collection. If so, it is fortunate they had such foresight. The level of accuracy achieved ranges from good to outstanding. Minute detail is often finely rendered, and the coloring remains authentic in all but a few instances (Vane-Wright & Hughes, 2005). The lack of degradation of tint that might be expected in such old watercolors is no doubt a consequence of the fact that, through the intervening years, the pictures were rarely on show, and were evidently preserved in library conditions.

The idea that a member of the *V. indica* complex recently occurred in North America is so surprising that, without a specimen and independent verification, considerable doubt must be accepted—although we

believe the case for authenticity (presented below) is good. However, *whatever the final conclusion regarding the painting*, it has stimulated us to review the "*Vanessa indica* problem" and, in turn, challenge two previous hypotheses regarding the biogeography of these butterflies, and support instead an alternative hypothesis in which North America plays a key role.

Phylogenetic Relationships of the Red Admiral Butterflies

The type species of *Vanessa* Fabricius, 1807, *Papilio atalanta* Linnaeus, 1758, is the familiar Red Admiral butterfly. In his major revision, Field (1971) placed five species of red admirals in the genus: *V. atalanta* (L., 1758), *V. tameamea* Eschscholtz, 1821, *V. indica* (Herbst, 1794), *V. dejeanii* Godart, 1824, and *V. samani* (Hagen, 1895), but more species are now recognized (see below). The two other main species groups usually included within the genus are the painted ladies (placed by Field in the genus *Cynthia*; type species *Papilio cardui*) and the antipodal admirals (placed by Field in *Bassaris*; type species *Papilio itea*).

DNA sequence data (Wahlberg *et al.*, 2005) suggest that within *Vanessa* and contrary to earlier phylogenetic work based solely on morphology (e.g. Craw, 1989, Holloway & Nielsen, 1999), the red admirals (*Vanessa sensu stricto*) have a sister-group relationship with *Vanessa abyssinica* (Felder & Felder, 1867), a montane butterfly from East Africa. Previously *V. abyssinica* was treated as a member of the endemic Afrotropical genus *Antanartia* Rothschild & Jordan, 1903 (e.g. Howarth, 1966; Ackery *et al.*, 1995).

Superficial comparison indicates that this new arrangement is credible: all five remaining *Antanartia*, including the type species, *Papilio delius* Drury, 1782, have distinct hindwing tails at vein M3, whereas *V. abyssinica* does not, looking instead rather like a small and drab red admiral (Fig. 1a). The work of Nakanishi (1989) on the early stages of *abyssinica* is consistent with this placement, as it has a peculiar setal arrangement in the first larval instar otherwise known only from *Vanessa*, and it shares the habit, in later instars, of making a nest by tying both edges of a leaf together with silk. Nakinishi recorded that neither *Antanartia schaenia* nor *A. hippomene* exhibit these *Vanessa* characters.

However, as also pointed out to us by Thomas Dimock, adult *abyssinica* are highly distinctive compared with all other *Vanessa s.s.* Notably, at least two of the hindwing ocelli always have blue pupils (invariably black in other *Vanessa s.s.*); the hindwing marginal band widens at cell M_1, lacks any black submarginal spots (as seen in an aberration of *V. atalanta*: Frohawk, 1938: p. 86), and continues anteriorly into cell R_5 (unlike other *Vanessa s.s.*); and hindwing vein $Sc+R_1$ is relatively elongate, giving the wing a unique, almost square aspect. All of these differences can be seen as autapomorphies, except the first, which may be a symplesiomorphy (e.g. this condition is frequent in subgenus *Cynthia*, in *V. (C.) cardui*, for example, being referred to as form

Fig. 1. (on facing page) The species of the genus *Vanessa sensu stricto*. Left halves show upperside, right halves corresponding underside. All figures (with exception of **b**) have been brought to the same forewing length to facilitate comparison; information on actual size is included with each separate legend. With the exception of **b** and **h**, all images are based on specimens in the Natural History Museum, London (BMNH); fw-l. = forewing length. **a**, *V.* (*Vanessa*) *abyssinica abyssinica* (Felder & Felder, 1867), male [Ethiopia: Mt Zuquála, over 9000 ft, 25–27.x.1926, H. Scott; BM1927-127; fw-l. 21 mm.] [Howarth, 1966: 31, indicates a range of 17–22 mm for male *V. abyssinica*, and 20–24 mm for female]; **b**, *V.* (*Vanessa*) sp. nov. (*V. vulcania*-group), female? [Newfoundland, *ca* 1770; from 'profile' image made by Henry Seymer Jr., *ca* 1773; Vane-Wright & Hughes, 2005: 164/5; fw-l. estimated at 35 mm — see text]; **c**, *V.* (*Vanessa*) *vulcania* Godart, 1819, female [Spain: Canary [Islands], iv.1885; Leech Collection, BM1901-173; fw-l. 34 mm] [Field, 1971: 24, gives male 26–32 mm, female 29–33 mm, but there are larger and smaller examples in the BMNH collection — see text]; **d**, *V.* (*Vanessa*) *indica indica* (Herbst, 1794), male [China: Siao-Lou, 1900; Oberthür Collection, BM1927-3; fw-l. 33 mm] [Field, 1971: 21, gives male 25–34 mm, female 27–37 mm]; **e**, *V.* (*Vanessa*) *indica pholoe* (Fruhstorfer, 1912), male [SW India: Anamully Hills, 3000–4000 ft., *Davison*; Godman-Salvin Collection, BM1903-4; fw-l. 30 mm] [Field, 1971: 22, gives male 27–29 mm, female 28–30 mm]; **f**, *V.* (*Vanessa*) *indica nubicola* (Fruhstorfer, 1898), male [Sri Lanka: Newara Eliya, vi.1921, *W. Ormiston*; BM1922-315; fw-l. 27 mm] [Field, 1971: 22, gives male 26–31 mm, female 30–33 mm]; **g**, *V.* (*Vanessa*) *buana* Fruhstorfer, 1898, male [Indonesia: S Sulawesi, Bonthain, 5–7000 ft., x.1895, *A. Everett*; Rothschild Bequest, BM1939-1; fw-l. 24 mm] [Field, 1971: 23, gives male 27.5 mm; assuming figures in Tsukada, 1985: 82, are life-size, females are *ca* 25–27 mm]; **h**, *V.* (*Vanessa*) *dilecta* Hanafusa, 1992, male [Indonesia: W Timor, Mt Mutis, v.1992; Hanafusa Collection] [Hanafusa, 1992, gives male fw-l. 27.5–30.5 mm, female 30–31 mm.]; **i**, *V.* (*Vanessa*) *samani* (Hagen, 1895), male [Indonesia: SW Sumatra, Danan Bento Morass, Ft. of Korintji Peak, 5000 ft., viii.1921, *C.F. & J. Pratt*, 7.22; Joicey Bequest, BM1934-120; fw-l. 23 mm] [Field, 1971: 27, gives male 25 mm, female 23 mm]; **j**, *V.* (*Vanessa*) *dejeanii dejeanii* Godart, 1824, male [Indonesia: E Java, *H. Fruhstorfer*; Fruhstorfer Collection, BM1937-285; fw-l. 24 mm] [Field, 1971: 26, gives male 23–26 mm, female 23–27 mm]; **k**, *V.* (*Vanessa*) *dejeanii sambaluna* (Frushtorfer, 1898), male [Indonesia: Lombok, Sambalun, 4000 ft., 1896, *H. Fruhstorfer*; Oberthür Collection, BM1927-3; fw-l. 25 mm] [Field, 1971: 26, gives same size as *d. dejeanii*, including *sambaluna* as a subjective synonym]; **l**, *V.* (*Vanessa*) *dejeanii mounseyi* (Talbot, 1936), male [Philippines: [Mindanao]; W. Dannatt Collection, BM1940-130; fw-l. 24 mm] [Field, 1971: 27, gives a value of 26 mm for a male]; **m**, *V.* (*Vanessa*) *atalanta atalanta* (Linnaeus, 1758), male [Germany: Berlin; Leech Collection, BM1901-173; fw-l. 30 mm] [Field, 1971: 14, gives male 27–31.5 mm, female 27–34 mm]; **n**, *V.* (*Vanessa*) *atalanta rubria* (Fruhstorfer, 1909), male [Canada: Newfoundland, W.c. St. John. 39.9.26. 65 655™; fw-l. 29 mm] [Field, 1971: 16, gives male 25–34 mm, female 25–35 mm]; **o**, *V.* (*Vanessa*) *tameamea* Eschscholtz, 1821, female [USA: Hawaii, Kauai, Mt Waimea, 3000 ft., vi.1894, *Perkins*; BM1899-227; fw-l. 34 mm] [Field, 1971: 18/19, gives male 31–37, female 32–40 mm].

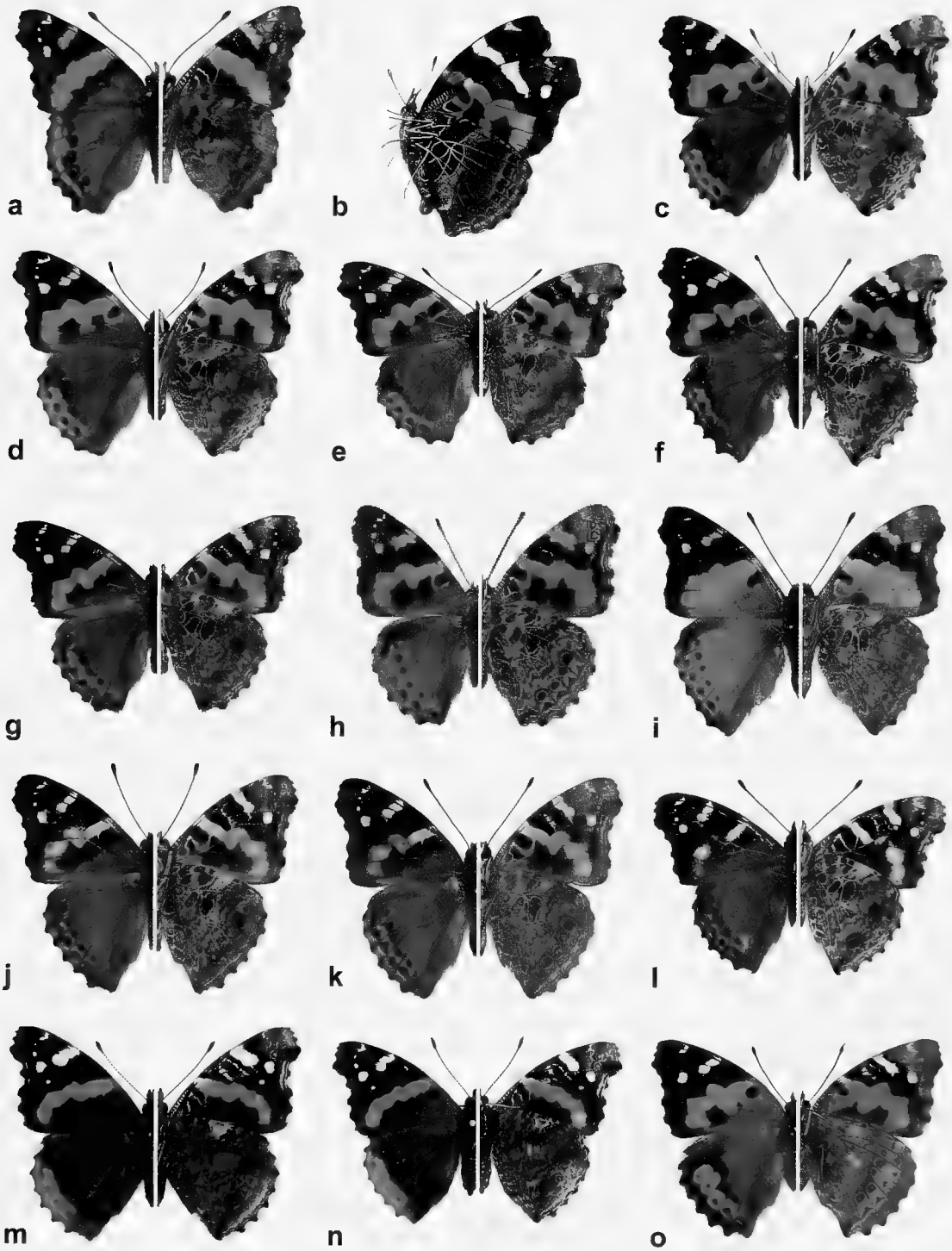

Figure 1

'ocellata'). All of this would be consistent with *V. abyssinica* being the most basal member of *Vanessa s.s.*

According to the molecular findings, within the Nymphalini, true *Antanartia* (comprising the *delius* species group of Howarth, 1966) is relatively remote from *Vanessa*. The sister group of the red admirals, including *V. abyssinica*, is shown by Wahlberg *et al.* (2005) to be the painted lady species group, and the antipodal admirals (but see also Otaki *et al.*, 2006a,b, who found less convincing evidence for these patterns of relationship). According to Wahlberg *et al.* (2005), a single remaining *Vanessa* species, the North American *V. annabella* (Field, 1971), represents a stem lineage for the whole of *Vanessa sensu lato* — suggestive of an American origin for the entire clade. This idea is strengthened by the results of Wahlberg *et al.* also showing that the entire *Vanessa* group, including *V. annabella*, has a sister-group relationship with *Hypanartia* Hübner, 1821 — an entirely tropical American genus (Willmott *et al.*, 2001). Another American butterfly that could belong to this group is *Pycina zamba* Doubleday, 1849. This relatively rare species, found from Mexico to Peru, looks reminiscent of a large *Vanessa*, feeds on Urticacae (*Urera*), and has early stages similar to other members of the Nymphalini, including *Vanessa*, *Historis* and *Smyrna* (Muyshondt & Muyshondt, 1979; DeVries, 1987: 136).

The Species of *Vanessa sensu stricto* and their Distribution

V. abyssinica (Felder & Felder, 1867) is the smallest species in the group, comprising three races restricted to mountainous regions of East Africa (Ackery *et al.*, 1995). As foreshadowed by Nakanishi (1989) and demonstrated by Wahlberg *et al.* (2005: 238), *abyssinica* belongs to *Vanessa sensu stricto*, but this has not been signalled as a formal recombination, now done here for the sake of clarity (Appendix I).

V. atalanta (Linnaeus, 1758) is widespread throughout North America south to Guatemala, Cuba, Hispaniola, the Atlantic Islands, North Africa, and Europe through Pakistan, Kashmir and north of the Himalayas to the Amur River (Field, 1971). The American and Old World populations are divisible as separate subspecies, but are very similar.

V. tameamea Eschscholtz, 1821, the largest species of the group, is endemic to the Hawaiian Islands (Field, 1971).

V. indica (Herbst, 1794), the third species of the red admiral group as dealt with by Field (1971), and accepted by Shapiro (1992a), has since been subdivided. As currently recognized, the very widely distributed nominotypical race is found in central and eastern Asia (Leestmans, 1978: fig.1), occurring from northern India through Nepal and Bhutan to China, Korea, Japan, Siberia (migrants reaching the region of Lake Baikal) and far eastern Russia (migrants reaching Kamchatka: Korshunov & Gorbunov, 1995), and south to Myanmar, Thailand, Laos, Vietnam, Taiwan and northern Philippines (Luzon, Mindoro and Palawan: Treadaway, 1995: 27). The two populations named as *V. i. pholoe* (southern India) and *V. i. nubicola* (Sri Lanka) are virtually indistinguishable on the basis of their male genitalia (Leestmans, 1978) and, given their minor differences in wing pattern, this provides justification for continuing to regard these three taxa as no more than subspecies. Tsukada (1985: 303) treated the populations from southern India and Sri Lanka as the same, under the senior name *V. indica nubicola*.

V. samani (Hagen, 1895) is restricted to west Sumatra, in western Indonesia (Field, 1971).

V. dejeanii Godart, 1824 occurs as three races, one on Java, a second (very doubtfully distinct) on Bali, Lombok and Sumbawa in central Indonesia, and the third on Mindanao and Samar in the southern Philippines (Field, 1971; Treadaway, 1995). Conceivably this last taxon, *V. dejeanii mounseyi*, will prove to be a separate species.

V. buana (Fruhstorfer, 1898) is restricted to the mountains of extreme southern Sulawesi, Indonesia (Vane-Wright & de Jong, 2003). Treated by Field (1971) as one of the subspecies of *V. indica*, the male genitalia of *buana* are very distinct from those of *indica s.s.*, sufficient to justify species-level status (Leestmans, 1978).

V. dilecta Hanafusa, 1992, was described as a separate species from Mt Mutis (2427 m), the highest mountain in Indonesian West Timor. The molecular results of Otaki *et al.* (2006a) suggest that this taxon is very closely related to *V. buana*, and they conclude that *dilecta* should either be treated as a subspecies of *V. buana*, or that the whole *indica* group be regarded as a superspecies. With respect to the former, the occurrence of a species on southern Sulawesi and Timor only would be a unique biogeographical pattern among the butterflies (Vane-Wright & de Jong, 2003). Our examination of the male genitalia of a specimen of *V. dilecta* (made available to us by Dr Otaki) confirms that it is almost identical to that of *V. buana*, as illustrated by Leestmans (1978: pl. 5, fig. 4). However, it also demonstrates that, as observed by Leestmans (1978) and noted by Otaki *et al.* (2006a: 365), the male genitalia of *V. nubicola*, *V. dejeanii*, *V. buana* and *V. dilecta* are all very similar, and both morphology and molecules indicate that this group forms a terminal group within

the *V. indica* complex. This clade has a distribution pattern "(2+5+6)", which is also virtually unique: only the doubtful collective danaine taxon *Tirumala ishmoides* has a comparable range (Vane-Wright & de Jong, 2003: 219), and even this does not include Timor or Sumatra. Our knowledge of these relatively rare montane *Vanessa* taxa may still be incomplete. We suggest that, for the present at least, *V. dilecta* should continue to be regarded as a separate species.

V. vulcania Godart, 1819, is native to the Canary Islands and Madeira in the Atlantic Ocean. Treated by Field (1971) as a subspecies of *V. indica*, in his major papers addressing the question its origin, Shapiro (1990, 1992a; but see also 1992b) overlooked the important work of Leestmans (1978) demonstrating the clear separation between *V. vulcania* and *V. indica*. Despite comments to the contrary by Shapiro (1992a), *V. vulcania* is also found occasionally on the western European mainland (e.g. Opheim, 1960; Gerisch 1975, 1978; Reinhardt & Gerisch, 1982; Fernández-Vidal, 1989). However, there seems nothing to suggest that these mainland records represent anything other than occasional strays or individuals accidentally imported from the Atlantic Islands (Leestmans, 1978).

A Re-assessment of Taxonomic Affinities within *Vanessa sensu stricto*

Field (1971), Leestmans (1978) and Wahlberg *et al.* (2005; and pers. comm.) all agree that the red admirals (*Vanessa s.s.*) form a monophyletic group. However, in their independent molecular analysis, Otaki *et al.* (2006a) did not get consistent support for such a clade. Based on morphological evidence (Leestmans, 1978), *V. atalanta* + *V. tameamea* could form a sister species pair, and this has been corroborated by some molecular data (Niklas Wahlberg and Dan Rubinoff, pers. comm.) although, again, Otaki *et al.* (2006a,b) report only weak support for this pairing.

According to Field (1971: 20), the five subspecies of *V. indica* that he recognized "display no differences in the male genitalia." However, Leestmans (1978) pointed to genital characters that link *V. buana* with the other taxa found in the Malay Archipelago: *V. nubicola* (Sumatra) and *V. dejeanii* (Java to Sumbawa and Mindanao) — to which assemblage the recently described *V. dilecta* (Timor) certainly belongs (Otaki *et al.*, 2006a,b; morphological evidence reported above).

As again clearly demonstrated by Leestmans (1978), although *V. vulcania* is similar to *V. indica*, it can be separated reliably on a number of small features of the male genitalia, as well as aspects of coloration. On this basis, together with its persistently red rather than more fugitive red-orange color, Leestmans (1978) justified recognition of *V. vulcania* as another, separate species.

Niklas Wahlberg (pers. comm.) has as yet unpublished molecular data regarding interrelationships of five of the six members of the *indica* complex: *V. vulcania*, *V. indica*, *V. nubicola*, *V. buana* and *V. dejeanii* (to which *V. dilecta* must be added). The new work confirms this complex as the sister group of the *atalanta*-group. Furthermore, within the complex, *V. vulcania* appears as sister to all the Asiatic taxa. Throughout this paper we refer to (*vulcania*-group + *indica*-group) as the *V. indica* complex. Within the *indica*-group, Otaki *et al.* (2006a,b) found evidence that *dilecta* is sister to *buana*, these two together are sister to *dejeanii*, these three are sister to *samani*, and that these four altogether form a distinctive group sister to *V. indica*.

Thus the relationships of the species of *Vanessa s.s.*, based on the information outlined above, can best be summarized by the following indented table, although evidence for monophyly of the group as a whole, and the *V. atalanta* + *V. tameamea* pairing, may not be very robust:

abyssinica-group [Africa]
  atalanta-group (*atalanta* + *tameamea*) [northern hemisphere]
    vulcania-group (*vulcania*)[Atlantic Islands]
    indica-group (*indica* (*samani*(*dejeanii* +(*buana* + *dilecta*))))
    [Nepal east to Japan and south to Timor]

Possible Origins of the *V. indica* Complex in Macaronesia

As indicated, there is no record for any *indica*-like taxon in the vast area between northern India and the Canary Islands, except occasional strays in western Europe (*V. vulcania* in the Iberian Peninsula, Germany and elsewhere; remarkably, *V. indica indica* has also been recorded from central England: Bretherton, 1989). Field (1971: 24) suggested that what he treated as the disjunct Atlantic Ocean race, *V. indica vulcania*, "may have evolved from specimens accidentally introduced from India by early Portuguese traders" — but on the basis of his morphological findings, Leestmans (1978) dismissed this idea as implausible. As suggested to us by Thomas Dimock, this is also very unlikely in terms of *Vanessa* biology and its ability to remain alive on board ship for several months. Shapiro (1992a), at that point unaware of Leestmans' work, drew attention to an earlier, alternative explanation. Kostrowicki (1969: 282) had suggested that the various

disjunct populations, notably those on the Atlantic Islands, could be relicts of a former, much wider Tertiary range. Shapiro (1992a) commented that molecular genetics could surely distinguish between two such extreme hypotheses, one requiring these Macaronesian populations of *V. indica* to be only hundreds of years old and to have gone through an initial 'bottleneck', the other implying that *V. vulcania* must be hundreds of thousands or even millions of years old. We call the first of these ideas "Field's Introduction Hypothesis" (FIH), and the second "Kostrowicki's Tertiary Relict Hypothesis (KTRH).

While KTRH appeals as a more interesting explanation, the absence of the *indica* complex anywhere in northern Europe, North Africa and North America seems surprising. However, as pointed out to us by Thomas Dimock, it would not be necessary to have continuous suitable habitat from India across the whole of Iran and Africa to Macaronesia. Indeed, large areas of unsuitable land between marginal habitats in the Mediterranean region might have made it more likely that migratory butterflies would reach distant localities, such as the Canary Islands, as they would be obliged to continue their search.

Shapiro (1992a) noted that in Macaronesia the butterfly is tied to *laurisilva* forest, considered to be a relict of former Tertiary broadleaved forests (Kostrowicki, 1969: 285; "nemoral forests": Pielou, 1979: 204–210; Miller & Miller, 1990). However, in the far east the *V. indica*-group does not seem to be confined to such habitats, ranging widely from montane areas in the tropics to a variety of cool temperate zones in the north, in the summer migrating as far as southern Siberia and Kamchatka (Korshunov & Gorbunov, 1995). If the Macaronesian populations of *V. vulcania* are genuine relicts (which must, at least, have island-hopped: Shapiro, 1992b), given the rich and varied forest habitats of North America in particular, it seems curious that no member of the *V. indica* complex has ever been found there.

If *V. vulcania* is a Relict, from Where has the *V. indica* Complex Disappeared?

As already indicated, *V. indica sensu* Field (1971) has largely been dismembered. The remaining populations now assigned to *V. indica* are divisible into just two or at most three subspecies: *V. indica indica* in the main Russian-Indo-Chinese range, including Japan, *V. i. pholoe* (Fruhstorfer, 1912) in southern India, and the very similar *V. i. nubicola* (Fruhstorfer, 1898) in Sri Lanka. As noted above, *V. vulcania* and *V. buana* were separated by Leestmans (1978) as distinct species. These taxonomic changes were made on the basis of small differences in wing patterns and male genitalia. If correct, they offer support for KTRH rather than FIH, insofar as we generally think of species evolving over many thousands if not millions of years, rather than a few hundred generations as implied by FIH. For example, based on extensive allozyme data, Shapiro & Geiger (1989) calculated that the very similar-looking *Vanessa annabella* (North America south to Guatemala) and *V. carye* (Hübner, 1812; South America) diverged about 3 million years ago.

While according to FIH the 7000 km gap from the Atlantic islands to NE India requires no other explanation, KTRH raises the question from where else have populations of the *Vanessa indica* complex disappeared? Given the known distribution of *V. indica sensu lato*, there is little reason to suppose that the *indica* complex ever occurred in South America. On the other hand, it might seem self-evident that it must have been lost from the whole region extending from the Mediterranean to northern India, including the Alps, Balkans, Turkey, Iraq, Iran and Afghanistan (notwithstanding Dimock's suggestion above regarding migration between marginal habitat patches). However, many biotopes in these areas appear suitable for the butterflies. If so, why would they have died out in this region?

Leestmans (1978) made the interesting suggestion that during glacial maxima the *V. indica* complex could have been represented throughout what is now the so-called eremic zone, the vast region of deserts and semi-deserts that runs across almost the whole of North Africa east to Somalia and the Arabian Peninsula, and from there to the Iran Plateau, Thar Desert and Tien Shan (Leestmans, 1978: fig. 1). From southern Morocco it would have been easy for a red admiral to reach both the Canaries and Madeira. With a return to interglacial conditions, the *indica* complex populations would have died out across this huge tract as it became desertified. In contrast, the *laurisilva* forests survived on the well-watered Atlantic islands, until largely destroyed by human activity in the past few hundred years.

A possible objection to such a scheme is that, as the ice retreated northwards, what would prevent the butterflies entering the Mediterranean region? Kostrowicki (1969: 280) discussed the idea that North African mountains played an important role as refugia for butterflies, noting in particular that a number of "typical African subspecies penetrated the Iberian Peninsula." Retreating higher and higher into the mountains, perhaps the *Vanessa* populations became trapped and died out *in situ*, unable to escape northwards. However, if we set this doubt aside, under

Leestman's scenario we might expect that *V. vulcania* and *V. indica indica* would prove to be sister taxa. Leestmans further suggested that the time since *V. vulcania* became separated from the main range of what is now *V. indica* would be about 1 million years. This variant of KTRH we can call "Leestmans' Eremic Zone Hypothesis" (LEZH). A similar scenario is also entertained by Pittaway (1993: 35–36) in an effort to understand the distribution of western Palaearctic hawkmoths, and he notes inter alia that "by the end of the Tertiary ... most eastern Asiatic species [of plants] had vanished from Europe (*c.* 1 million years BP)."

There is, however, a major alternative possibility: a North American origin (Vane-Wright, in Shapiro, 1990: 222) and subsequent loss ("American Origin Hypothesis": AOH). Given the likelihood that the genus *Vanessa* is fundamentally American (stem group position of *V. annabella*; sister group relationship with *Hypanartia*), and given that *V. atalanta* occurs as two subspecies, one in the New World and one in the Old, we should consider the idea that ur-*indica* originated in the Nearctic. Could the *indica* complex, in the form of *V. vulcania*, have reached the Atlantic Islands from eastern North America, rather than North Africa, while the Asian *indica*-group species reached Asia from western North America via Beringia? *V. indica* actually occurs in Beringia during the summer months, reaching to more than 50°N in Kamchatka.

Under AOH, one might expect *V. vulcania* to be the (relatively ancient) sister group of a clade comprising all the eastern *indica*-group taxa, and this is supported by the most recent molecular findings, as summarized in the indented table above. As already noted, under LEZH we might expect *vulcania* and *indica indica* to be (more recent) sister taxa. Under FIH, if Portuguese traders were responsible, perhaps a Goanese population (*V. i. pholoe*) would be the most likely sister to *vulcania*, with a separation time of only a few hundred years. These alternatives are not supported by the current systematic arrangement (see table above).

While AOH would explain away the 7000 km gap between Macaronesia and India (under this scheme there is no compelling reason to suppose the *indica* complex ever occurred in this intervening region), it does so by substituting an even larger 10,000 km gap between Kamchatka and Madeira. Thus a choice between these two scenarios could be affected by any evidence of former presence of the *Vanessa indica* complex in either North America or the western Palaearctic/North Africa. Before turning to this issue, it is worth noting that there appears to be virtually no evidence of exclusive biogeographical connections between Macaronesia and the Indo-Australian region. Increasing knowledge of the phylogenetic relationships of Macaronesian plants reveals that the great majority have their closest relatives in Europe and North Africa, although there do appear to be some links to East Africa, South Africa and, most notably in this context, the Americas (Carine *et al.*, 2004).

A Fossil Member of the *Vanessa indica* Complex

There is one known fossil clearly relevant to this debate, the early Oligocene butterfly *Vanessa amerindica* Miller & Brown, 1989. This was described from the Florissant formation of Colorado (dated at *ca* 35 million years BP), and the authors considered it to be most like *Vanessa indica* amongst the recent fauna (Miller & Brown, 1989). Taken at face value this is consistent with AOH, and could be another example of marked stasis coupled with local extinction that may be emerging as characteristic of butterfly evolution during the middle to late Tertiary (e.g. Hall *et al.*, 2004; Vane-Wright, 2004). Even so, this is not evidence enough to suggest that the modern distribution of *Vanessa* is somehow directly linked to the tectonic break up of the North Atlantic. This would only be plausible if the *V. indica* complex could be demonstrated to be at least 70 million years old (cf. Miller & Miller, 1990). Given the great rarity of butterfly fossils, the existence of *V. amerindica* dated at 35 mya is, however, both suggestive and challenging.

An 18th Century Record of an Apparently New Member of the *V. indica* Complex from North America

As indicated in the introduction, while researching a set of previously unpublished 18th century paintings of world Lepidoptera made by the British naturalists Henry Seymer (1714–1785) and Henry Seymer Jr, (1745–1800), we came across an image of what is undoubtedly a member of the *Vanessa indica* complex (Fig. 1b; Vane-Wright & Hughes, 2005: 165). The Seymers indicated that their painting was based on a specimen sent to them from Newfoundland, but gave no further details of date or collector. What credibility can be given to this seemingly very unlikely record?

Among hundreds of images of Lepidoptera made from the Americas, Europe, Africa, Asia and even Australia, the Seymers illustrated just three other species purportedly from Newfoundland. The island is an entirely plausible source for all three of them (details below). Moreover, their image of *Vanessa* (Fig. 1b) cannot be matched precisely to any of the known living taxa currently included within the *V. indica* complex (cf. Figs 1c–l). Neither can it be matched to *V. amerindica*,

as the fossil does not permit detailed evaluation based on wing patterns.

The other species the Seymers illustrated from Newfoundland were two swallowtails and a ghost moth: *Papilio brevicauda brevicauda* Saunders, 1869; *Papilio canadensis* Rothschild & Jordan, 1906; and *Sthenopis purpurascens* (Packard, 1863) (Vane-Wright & Hughes, 2005). *P. brevicauda* is quite narrowly restricted to parts of Quebec and the Maritime provinces of eastern Canada, where it is "widespread and commonly encountered in Newfoundland" (Layberry *et al.*, 1998: 83). *P. canadensis* is well-known from almost all parts of Canada, including Newfoundland (Layberry *et al.*, 1998: 87–88).

S. purpurascens (Hepialidae) is one of four species belonging to the exclusively North American genus *Sthenopis* Packard, 1865, known from USA and Canada (Nielsen *et al.*, 2000: 850). Newfoundland records for *Sthenopis purpurascens* (Packard, 1863) are based on material housed in collections of the Canadian Forest Service (Corner Brook, NL; and Edmonton, Alberta), and Agriculture Canada Research Station (St. John's, NL). The identifications of this material (under the synonymous name *Sthenopis quadriguttatus* (Grote, 1864)) were made by Canada Agriculture personnel in Ottawa (David Larson, pers. comm., September 2007; see also Bowers & Pardy, 1996). Currently, this is the only *Sthenopis* known from Newfoundland.

The dates for the four paintings on which these images appear are: *V. indica* complex ca 1773, *P. brevicauda* February 1776, *P. canadensis* 1772, and *S. purpurascens ca* 1773. The reason for uncertainty over the date for the *Vanessa* image is that the Seymer paintings were cropped at some point in the past to fit into a binding, and in some cases the dates have been cut off, in part or whole (Vane-Wright & Hughes, 2005: 53). In most cases other clues are available to give approximate dates, and we think that 1773 (not earlier than 1772, and unlikely to be later than 1776) is a good estimate for the date of the painting on which the *Vanessa* appears.

The Seymers misidentified the two swallowtails, but were aware that the other two insects represented undescribed species: the ghost moth they compared to *Hepialus humuli* (L.), and the *Vanessa* they noted as "Simillima *Atalanta* nostrae." These illustrations are probably the first known for all four taxa. However, at the same time Pieter Cramer (1775: 132, Pl. 84, figs E,F) presented images of a "vulcain" (Red Admiral) from China, under the name *Papilio atalanta*. His discussion indicates that he was aware of differences between his specimen and the familiar European insect. The paintings in Cramer clearly show true *Vanessa indica*, and demonstrate that by the 1770s Chinese material of this species was already reaching European collectors.

The Seymers had a great deal of material from China, and therefore it is conceivable they accidentally mislabelled a Chinese specimen of *V. indica*, and then made a slightly inaccurate picture of it. While not error-free, the Seymer paintings are, in general, precise (Vane-Wright & Hughes, 2005: 268). In several ways the Seymer image fits *V. vulcania* far better than true *V. indica* (see below). So an alternative possibility might be that the Seymers obtained a specimen of *V. vulcania* from the Canaries or Madeira, and then made a slightly inaccurate picture of that. Plants used in horticulture were certainly available from the Canary Islands by the mid 18th century, and probably much earlier (e.g. the endemic *Isoplexis canariensis*, named by Linnaeus in 1753; Vane-Wright & Hughes, 2005: 212). However, *V. vulcania* was not described until 1819, and very few other endemic Atlantic island Lepidoptera were named before that time: *Pararge xiphia* (Fabricius, 1775), endemic to Madeira, is a rare example (Weingartner *et al.*, 2006). There is absolutely nothing to suggest that the Seymers ever received any insect material from the Atlantic Islands (Vane-Wright & Hughes, 2005: 254, table 1), whereas they undoubtedly did obtain a considerable number of insects from Newfoundland and China.

If we assume that all four taxa stated by the Seymers to have come from Newfoundland originated from a single source, then these specimens must have been collected before 1772. We found no further information concerning their possible origin (Vane-Wright & Hughes, 2005: 260), although we speculated that Joseph Banks might have collected this material during his visit to the island in 1766 (see Lysaght, 1971). By about 1775 the Seymers were also receiving specimens from Newfoundland collected by a Mr Top, an island resident. There is nothing to suggest that Banks visited China during this period, nor Top either.

As there is no reason to doubt the provenance of the other Lepidoptera reported by the Seymers from Newfoundland, this putative record for the *Vanessa indica* complex in Canada should be given credence. The evidence of *Papilio brevicauda* is significant, as it is a narrowly distributed species found only in north-eastern Canada. We are thus confident that the *Vanessa* image must be based on one or more specimens that came into the Seymers' possession *ca* 1770, and we see no particular reason to doubt the given provenance of Newfoundland, and some reasons to accept it. This includes our conviction that the image (Fig. 1b), which is detailed, cannot be matched precisely to any of the

old world taxa that make up the *V. indica*-group, including *V. indica indica*, or to *V. vulcania* (Figs 1c–l).

However, Thomas Dimock (in litt., 2007) has pointed out six peculiarities of the Seymer image which do give rise to questions regarding its accuracy—were it to be assumed that it is based on either *V. indica* or *V. vulcania* with incorrect provenance. We comment on each of these points, in turn:

1. "First is the extent and intensity of the blue markings on the HW underside, much bluer than any known *Vanessa* today." As reproduced there is a blue cast. The original paintings are no longer readily available to us for re-examination. They were photographed as large format transparencies in 1992, scanned in 2004, and the resultant "tif" file was transformed in Adobe Photoshop to make the images presented here, in 2006. If you take a flash photograph of the underside of a *V. vulcania* specimen you will not see a blue cast, but you will see a very strong blue area at the end of the forewing discal cell, and a complete series of post-ocellar blue marks in cells R_1–CuA_2, as in the Seymer image.

2. "No living species of *Vanessa* has such a gigantic white costal bar extending into cell M_3 . . . when measured along its greatest length, [it] reaches 7/15 (46.7%), or nearly half of the way to the wing margin near the tornus ... The white bar in *V. vulcania* (Fig. 1c) reaches only 4/15 (26.7%), of the distance to the tornus." Using the large white submarginal spot in cell M_2 as a marker, we suggest that the Seymer image does not show this bar extending into cell M_3, but crossing cell M_2 to end at vein M_3. Measured on a full-size photograph of the Seymer image, we make the extent 42.5%, not 46.7%. The extent of this mark in *V. indica* and *V. vulcania* can often exceed 30%, but undoubtedly this does represent a major difference to these species. Is such an extent impossible? Frohawk (1938: plate 20, p. 86) illustrates an aberration ('albo-punctura') of *V. atalanta* from Erith, England (now preserved in the BMNH), in which the outer half of forewing cells M_2 and M_3 are largely filled with white. In cell M_2 it appears to consist of an extension of the white bar that has fused with the main submarginal white spot. Measuring on the underside from the costa, where the bar elements commence, to the margin of white area at vein M_3, gives a value of 41% for the ratio in this *atalanta*. Making these measurements to vein M_3 in *V. vulcania* and *V. indica* typically gives 38–40%. In subgenus *Cynthia* the white bar often extends back to vein M_3. Field (1971: fig. 158) illustrates a specimen of *V. (C.) annabella* in which this is so; it has a value of 38.5%. We conclude that the Seymer figure is not so extreme as Dimock suggests, and is not implausible.

3. "No living species has the small posterior extension of this bar extending from the distal side of the bar, as the painting has." It is certainly true that in the great majority of *Vanessa* (*Vanessa*) specimens that have this small extension (not all do), it arises from the proximal side of the bar. However, in such cases this extension occurs in the anterior half of cell M_2, whereas the Seymer image shows this area filled with white and contiguous with the element of the bar in cell M_1. The extension in the Seymer image occurs in the posterior half of cell M_2, reaching vein M_3 as already discussed. So in this case we are not comparing like with like. We have searched for *Vanessa* (*Vanessa*) with the posterior half of cell M_2 filled with white but, apart from the Frohawk example described above, which is too extreme, we have not found anything really comparable. However, in *Vanessa* (*Cynthia*), the bar often crosses the whole of M_2, and where it does so, the extension into the posterior half of the cell can be distal. Field (1971: figs 133,134) illustrates a specimen on *V. (C.) terpsichore* in which the configuration of the whole bar approaches that of the Seymer image. We conclude that if the Seymer image does represent a *Vanessa* in which the bar reaches across the whole of cell M_2, the distal extension is entirely plausible.

4. "In the painting, the hindwing ocelli are all longitudinally flattened, equal in size, and the anterior four are in a very straight line, unlike all other *Vanessa*." We agree that this configuration looks odd. The most complete ocellus on the hindwing underside in most *V. indica* and *V. vulcania* is the most posterior one, in cell CuA_1, and the Seymer image conforms in this regard. In *V. indica* and *V. vulcania*, however, as in other *Vanessa*, the more anterior border ocelli vary in size and shape, but have their centers located on a smooth arc, parallel to the curve of the wing margin.

5. "The painting shows a total of six ocelli or ocelli without pupils. *Vanessa* have only five, never a sixth ocellus in cell Sc + R_1." We also agree that all *Vanessa* we have examined have only five border ocelli on the hindwing, occurring in cells R_5 to CuA_1 inclusive. We have not seen any *Vanessa* with a clear ocellus in cell R_1, although this is part of the nymphalid groundplan, and can be seen very clearly in some species (e.g. *Charaxes analava*: Nijhout & Wray, 1986). According to Beldade & Brakefield (2003: 176), all marginal wing cells appear to have the potential to produce eyespots, and laboratory selection experiments rapidly reveal the capacity of species to produce ocelli in cells that do not normally exhibit them. "Eyespot number is not a very fixed trait even within a species" (Antónia Monteiro, in litt., July 2007). In conclusion on this point, we agree that the configuration of the hindwing ocelli in the

Seymer image are uncharacteristic of known *Vanessa* species, and could either reflect the fact that, as we suggest, this is a new species, or that the Seymer image is inaccurate in this respect. The hindwing underside pattern of *Vanessa* is very complex, and is a considerable challenge for any artist. Another possibility is that the Seymers' specimen had the apex of the hindwing missing, and Henry Jr. simply interpolated what he thought it should look like. There is ample evidence that the Seymers 'perfected' incomplete specimens based on their general knowledge of similar species.

6. "Finally, look at the hindwing on the painting and notice how far distally from the dark discal spot that vein M_3 branches from Cu_1. It should arise from the posterior end of the discal spot, not 3mm distally. Differences this great have been used to distinguish genera." There seems no doubt that the hindwing venation has been misinterpreted in the Seymer image—and the forewing venation is also incorrect. Very few illustrators at this date produced accurate images of Lepidoptera wing venation. It was not until William Jones (1794) published his ground-breaking comparative work, some 20 years later, that lepidopterists regularly started to render accurate wing-vein schemes.

In conclusion, Dimock comments "Of course, all of these "inaccuracies" support the authors' the hypothesis [see below] that the painting is of an extinct species." With respect to points 1–6 raised by Dimock above, on reflection we consider that 1–3 are consistent with our view that the Seymer image does represent an extinct species, while 4–6 probably do reflect genuine inaccuracies.

Shapiro says that *V. vulcania* is more like far-eastern *V. indica* than SE Asian, and that it also varies in the direction of Holarctic *atalanta*. However, as pointed out by Bascombe *et al.* (1999), *V. indica indica* is a migrant, and it hardly varies over its extensive range. John Tennent (2005, and pers. comm.) has related how he remembers "seeing *indica* occasionally in Hong Kong ... it's a small pale shadow of the brilliant, whopping thing that occurs on Madeira and the Canaries." The Seymer paintings were executed life size (Vane-Wright & Hughes, 2005), and the forewing length of the supposed Newfoundland specimen, as figured, measures 35 mm — quite large for any red admiral except *V. tameamea*. While examination of a long series of *V. indica* from China and a considerable number of *V. vulcania* in the Rothschild Collection (at the Natural History Museum, London) confirms that the latter is undoubtedly "redder" in some sense than the more orange eastern taxon, any impression of larger size must be an illusion or a sampling artefact. A few female specimens from China equal or slightly exceed a forewing length of 35 mm, which is also about the maximum found among material from the Canaries. In this context it is notable that the forewing lengths of the two original specimens of *V. amerindica* are given as 24 mm and 27 mm (Miller & Brown, 1989: 1). Some individuals of both *V. indica* and *V. vulcania* have a forewing length as short as 25 mm, or even less.

The persistent red coloration of *V. vulcania* appears to be a specific feature (fresh *V. indica* may be almost as red, but invariably fade to orange during life, or post-mortem). From this it would seem that, on the basis of its more orange color, Seymer's image (Fig. 1b) does not represent *V. vulcania* (Fig. 3), but this cannot be given much weight. Assuming the postdiscal white patterning of the forewing has been rendered accurately (see discussion if Dimock's points 2 and 3, above), it is not *V. indica* either (Figs 1d–f). As Higgins & Riley (1980: 102) point out, in the Canary Red Admiral "the short band of three white spots runs from the costa at a right angle", whereas in *V. indica* this band is oblique. This reliable difference is most readily appreciated by extending an imaginary line along the distal margin of this short band. In *V. indica* this imaginary line will always enter (at the very least touch) the large white submarginal spot in cell M_2, whereas in *V. vulcania* such a line is always proximal to the smaller M_2 white spot, and never runs through it.

As examination of Field (1971: figs 33–80), Tsukada (1985: plate 49) and Figs 1a–o will confirm, the condition of this character in *V. indica* is shared with all other known *Vanessa s.s.*, including *V. abyssinica* — *V. vulcania* being the only exception. This feature thus represents an apomorphy for the *V. vulcania*-group, and on this basis we suggest that the Seymer image, which shows exactly the same configuration (despite the very large submarginal spot shown in cell M_2), represents an undescribed and recently extinct member of the *V. vulcania* species group from North America. This previously unknown species differs from *V. vulcania* in having the principal forewing band orange rather than bright red; in having the short preapical forewing band composed of four elements (in cells C, R, M_1 and M_2) in which the white element in the anterior half of M_2 is the same width as in M_1, with a small distal extension into the posterior half of M_2, instead of small proximal extension to the white mark in M_1 that is confined to the anterior half of M_2; and in having the submarginal white spot in forewing cell M_2 large (*ca* 2 mm diameter), not small as in *V. vulcania* (usually about 1 mm diameter, although it can be larger).

Finally, regarding the plausibility of this apparent record, it is necessary to consider environmental

conditions in Newfoundland. Being unable to survive harsh winters, *Vanessa* species only occur in far northern areas, such as Lake Baikal (*V. indica*) and Newfoundland (*V. atalanta*), by annual remigration from the south. If, as pointed out to us by as Thomas Dimock, we accept the Seymer record as genuine, then his material must have been collected in the summer or autumn months, and been derived, directly or indirectly, from spring or early summer migrants from the far south. In which case one would expect that early collectors would have obtained this species from source colonies in the USA — as in the case of *Vanessa* (*Cynthia*) *virginiensis* (Drury, 1773), first discovered in the USA, and which only reaches Newfoundland during the summer months (Layberry *et al.*, 1998). If it is assumed that such a butterfly would have been common and abundant, like most familiar *Vanessa* species, then this is puzzling and must add to the uncertainties regarding the Seymer record. On the other hand, most genera do include genuinely rare species, often including some that appear close to extinction.

Given the various doubts indicated above, and that this insect is known only from a painting which could be inaccurate in details of pattern and provenance, we do not propose to give it a formal name. However, should the existence of such a *Vanessa* in North America ever be independently confirmed, we urge that it be named in honor of Henry Seymer.

CONCLUSIONS

While Wahlberg *et al.* (2005) conclude that the Palaearctic region and subsequent dispersal played a crucial role in the diversification of the *Nymphalis*-group *sensu lato*, we suggest here that North America could have been the origin for *Vanessa*, including not only the painted ladies, but also the red admirals. Were this to be the case, it would be plausible that offshoots of the group reached the Old World on several occasions, giving rise to *V. abyssinica* in Africa, *V. atalanta atalanta* in the Palaearctic, *V. tameamea* in the Pacific, and *V. vulcania* in the Atlantic. Under this model the *V. indica*-group was established from the same American stem-lineage as *V. vulcania*, reaching Asia via Beringia or the Pacific rather than across the Atlantic and through the Mediterranean and North Africa.

If the *indica* complex did evolve in North America 35 million or more years ago (Miller & Miller, 1990), then the distance over which the postulated Atlantic colonisation event took place would have been less than current geography implies. According to the reconstructions of Owen (1983: e.g. map 22), at 180–200 mya, the crust that is now Newfoundland held a position relative to north-western Africa more or less identical to where Madeira lies today. While this neat correspondence makes the point, it is undoubtedly misleading. Moreover, the Atlantic islands are oceanic, and have never been connected to any mainland area. According to current estimates, Madeira is little more than 5 million years old, although the origin of nearby Santo Porto may be as old as 14 mya, and the oldest island in the Canaries (Fuerteventura) probably exceeds 20 my (Hughes & Malmqvist, 2005: 292). The presence of the endemic *Vanessa tameamea* on Hawaii surely gives convincing evidence of the ability of the red admirals to colonize remote oceanic islands. *V. indica* and *V. atalanta* readily travel long distances and, as their annual re-colonisation of boreal areas each spring demonstrates, they can occur in almost any suitable habitat if weather conditions permit.

In final conclusion, we suggest that, even as recently as 1770, an extinct member of the *Vanessa indica* complex may have occurred in North America, and was able to reach Newfoundland during summer months. While not substantiated, this suggestion cannot be discounted on the basis of the extant distribution of the *V. indica* complex. Molecular investigations already appear decisive regarding rejection of an introduction hypothesis (FIH) in favor of some form of tertiary relict hypothesis (KTRH) for the existence of the Atlantic Islands endemic, *V. vulcania*. Molecular systematics could also be used to evaluate the plausibility of the former occurrence of the *indica* complex in North America, based on the different phylogenetic implications of extinction in Old World eremic zone, coupled with divergence about one million years ago (LEZH, with *V. vulcania* and *V. indica indica* as putative sisters), vs. extinction in North America, coupled with divergence several millions of years ago (AOH, with *V. vulcania* and the whole Asiatic *indica*-group as putative sisters). Current evidence already favors the latter interpretation. We urge molecular systematists to try to obtain multiple samples of all *Vanessa* taxa (subspecies as well as species) and, by using data from numerous genes, attempt to give a truly robust answer to what remains a fascinating biogeographical question: how did this most peculiar distribution come about?

ACKNOWLEDGEMENTS

The authors are much indebted to John Tennent for valuable information, gentle correction and constructive comment, Kim Goodger and the NHM photo studio for originating most of the color images (as digital files), and Professor Michael Boppré for assembling the final color plate. Joji Otaki (University of the Ryukyus) presented reprints, and generously sent us a pair of *V. dilecta* for dissection. We are grateful to David Larson (Biological Survey of Canada, Terrestrial Arthropods of Newfoundland and Labrador project) kindly made available information about

Newfoundland Hepialidae. Arthur Rydon kindly answered our queries regarding the biology of *Pycina*, and James Hogan gave us access to the Oxford University Museum *Vanessa* collection. Roger Vila (MCZ) and Niklas Wahlberg (Stockholm) offered constructive criticism of an earlier version of the MS, and NW together with Dan Rubinoff (Hawaii) also generously shared new, unpublished information. Thomas Dimock and Art Shapiro provided detailed criticisms of our first submitted draft, and we have revised the final version in light of their most valuable comments. The first author also wishes to thank Art Shapiro for engaging discussions on these insects in the past, and to acknowledge the National Endowment for Science, Technology and the Arts (NESTA), and the Natural History Museum (NHM), London, for continuing support.

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Received for publication 2 September 2006; revised and accepted 2 October 2007

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APPENDIX I

Checklist of the nine extant species of the subgenus *Vanessa* (*Vanessa*) currently recognized, and their accepted subspecies. *Pyrameis abyssinica* Felder & Felder, 1867, is here formally transferred to *Vanessa*, based on the results of Nakanishi (1989) and Wahlberg *et al.* (2005), and the discussion presented above. In addition, we include the fossil taxon *V. amerindica* Miller & Brown, and note the unnamed *indica*-complex taxon reported ca 1773 by Henry Seymer and Henry Seymer Jr. (see text). Among recently described *Vanessa* taxa, *V. pulchra* Chou, Yuan, Yin, Zhang &Chen, 2002, appears to be an aberration of *V.* (*Cynthia*) *cardui* (L.), and is not included here.

VANESSA (*VANESSA*) Fabricius, 1807 (type species: *Papilio atalanta* Linnaeus, 1758)
(Lepidoptera: Papilionoidea: Nymphalidae: Nymphalinae: Nymphalini: Nymphalina)

†*V.* (*Vanessa*) *amerindica* Miller & Brown, 1989 [USA (Florissant formation, Colorado; Oligocene fossil)], incertae sedis

†*V.* (*Vanessa*) sp. nov. [North America, Newfoundland, circa 1770; apparently extinct; see text], *vulcania*-group

1 *V.* (*Vanessa*) *abyssinica* (Felder & Felder, 1867), **comb. nov.**

abyssinica abyssinica (Felder & Felder, 1867) [Ethiopia]

abyssinica jacksoni (Howarth, 1966) [Kenya, northern Tanzania], **comb. nov.**

abyssinica vansomereni (Howarth, 1966) [western Uganda, Rwanda, Democratic Republic of the Congo (Kivu, Ituri)], **comb. nov.**

2 *V.* (*Vanessa*) *vulcania* Godart, 1819 [Spain (Canary Islands), Portugal (Madeira), occasional records from mainland of western Europe] [Higgins & Riley, 1980, considered *vulcania* to be a synonym of *V. calliroe* (Hübner, 1808); we follow Aguiar & Karsholt, 2006, in continuing to employ Godart's name]

3 *V.* (*Vanessa*) *indica* (Herbst, 1794)

indica indica (Herbst, 1794) [northern India, Nepal, Myanmar, Thailand, Laos, Cambodia, Vietnam, China, Korea, Russia (Siberia, Kamchatka, Sakhalin), Japan (including Ryukyu Islands), Taiwan, Philippines (Luzon, Mindoro, Palawan)]

indica pholoe (Fruhstorfer, 1912) [southern India (western Ghats)]

indica nubicola (Fruhstorfer, 1898) [Sri Lanka]

4 *V.* (*Vanessa*) *samani* (Hagen, 1895) [Indonesia (Sumatra)]

5 *V.* (*Vanessa*) *dejeanii* Godart, 1824

dejeanii dejeanii Godart, 1824 [Indonesia (Java)]

dejeanii sambaluna (Frushtorfer, 1898) [Indonesia (Bali, Lombok, Sumbawa)] [synonymized with *dejeanii dejeanii* by Field, 1971, but maintained as distinct by Tsukada, 1985]

dejeanii mounseyi (Talbot, 1936) [Philippines (Mindanao, Samar)] [possibly a distinct species]

6 *V.* (*Vanessa*) *buana* Fruhstorfer, 1898 [Indonesia (southern Sulawesi)]

7 *V.* (*Vanessa*) *dilecta* Hanafusa, 1992 [Timor] [Otaki *et al.*, 2006a, suggest that this may be a subspecies of *buana*, but provisionally maintained here as a full species—see text]

8 *V.* (*Vanessa*) *atalanta* (Linnaeus, 1758)

atalanta atalanta (Linnaeus, 1758) [Atlantic islands, North Africa (south to northern Chad), Europe and temperate Eurasia eastwards to Pakistan, Kashmir, northern Himalayas and the Amur River]

atalanta rubria (Fruhstorfer, 1909) [Canada, USA, Mexico, Guatemala, Cuba, Haiti, Dominican Republic]

9 *V.* (*Vanessa*) *tameamea* Eschscholtz, 1821 [USA (Hawaii)]

Journal of the Lepidopterists' Society
61(4), 2007, 213–221

PARASITISM OF BARRENS BUCK MOTH *HEMILEUCA MAIA* DRURY IN EARLY AND LATE SUCCESSIONAL PINE BARRENS HABITATS

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ABSTRACT. Barrens buck moth, *Hemileuca maia*, is predominantly associated with early successional pine barrens dominated by scrub oak, *Quercus ilicifolia*. To determine if *H. maia*'s association with these open habitats within pine barrens on Cape Cod is due to reduced rates of parasitism, we compared mortality of *H. maia* larvae on scrub oak in early successional right-of-way habitat and climax pitch pine communities. We established experimental populations of *H. maia* in both habitats and assessed parasitism in two consecutive years. Contrary to our hypothesis, parasitism by the introduced generalist tachinid *Compsilura concinnata* did not vary among habitats in either year, nor did it cause significant mortality to *H. maia* larvae in either year. In 2002, mortality from the native hymenopteran *Hyposoter fugitivus* was significantly reduced in forest plots and in 2003 parasitism by the native tachinid *Leschenaultia fulvipes* was significantly higher in power line right-of-way plots. Parasitism rates in both years did not appear high enough to underlie the documented differences in habitat selection by buck moth.

Additional key words: Habitat heterogeneity, *Compsilura concinnata*, enemy-free space, natural enemies, Cape Cod, *Quercus ilicifolia*.

The distribution of many insect herbivores is at least partially a function of the threat imposed by natural enemies, either through direct attacks or by causing herbivores to seek out niches that act as refuges (Schultz 1983, Jeffries & Lawton 1984, Price 1987, Bernays & Graham 1988, Stamp 2001, Williams *et al.* 2001). Life history strategies that avoid peak periods of natural enemy abundance are likely to be favored by natural selection (Schultz 1983, Jeffries and Lawton 1984, Tauber *et al.* 1986, Lill 2001). These include changes to life history attributes such as development and phenology, which minimize exposure to natural enemies (Bernays & Graham 1988, Mira & Bernays 2002), chemical defenses (Denno *et al.* 1990, Stamp 2001), or utilization of specific positions within a habitat where pressure from natural enemies is reduced (Stamp & Bowers 1988, Stamp & Bowers 1991). Habitat structure may also play an important role in providing enemy-free space for many insects (Ohsaki & Sato 1990).

Barrens buck moth (*Hemileuca maia* Drury, Saturniidae), is a univoltine, diurnal species with special concern status in the state of Massachusetts (Nelson 2002, NHESP 2007) and is considered to be rare throughout most of northern New England (Boettner *et al.* 2000). It appears to be restricted to isolated, remnant pitch pine (*Pinus rigida* Mill.) – scrub oak (*Quercus ilicifolia* Wangenh.) barrens in the northeastern United States, a habitat threatened by multiple anthropogenic factors (Tuskes *et al.* 1996, Wagner *et al.* 2003, Barbour *et al.* 1998). Furthermore, the distribution of *H. maia* within pine barrens is concentrated in only a few habitats (Schweitzer 1983, Tuskes *et al.* 1996, Nelson 2002) despite the occurrence of its primary host plant, scrub oak, across a much larger geographic range. Northeastern populations of *H. maia* appear to be particularly abundant in anthropogenically-created, early-successional habitats including road margins and power line rights-of-way (Schweitzer 1991, Nelson 2002, S. Haggerty, pers. com.). The occurrence of *H. maia* in early successional habitats and its apparent absence in later successional forests has not previously been explained. One possible factor is the effect of natural enemies, which is thought to increase with habitat complexity (Langellotto & Denno 2004). The sparse vegetation and lack of stratification in early successional areas may offer enemy-free or at least enemy-reduced space for *H. maia*.

Numerous parasitoids attack the larvae of *H. maia* (Schaffner & Griswold 1934, Arnaud 1978, Krombein *et al.* 1979, Piegler 1994, Boettner *et al.* 2000). Common species include *Hyposoter fugitivus* (Say) (Ichneumonidae) and *Meteorus autographae* (Muesebeck) (Braconidae) and the tachinid *Leschenaultia fulvipes* (Bigot) (Schaffner & Griswold 1934, Boettner *et al.* 2000). The non-native tachinid

Compsilura concinnata (Meigen), an important threat to saturniids (Boettner *et al.* 2000, Kellogg *et al.* 2003) also parasitizes *H. maia* and the congener *H. lucina* (Stamp 1990, Boettner *et al.* 2000).

Although the diversity of parasitoids attacking *H. maia* has been documented, little effort has been made to quantify stage-specific mortality, which is instrumental in understanding population dynamics. When stage-specific mortality has been determined, it has focused only on early-instars (Boettner *et al.* 2000). Thus, the impact of parasitoids on later instars and pupae is unknown.

Our study quantified mortality sources for *H. maia* larvae and pupae in two distinct habitats within pitch pine - scrub oak barrens on Cape Cod, MA. Research focused on three separate but related hypotheses: (1) the spatial distribution of *H. maia* is influenced by parasitoids, (2) habitat structure alters the species composition of the parasitoid fauna, and (3) habitat structure influences the level of mortality caused by parasitoids. Based on these hypotheses, we tested two predictions: (i) the community of parasitoids attacking *H. maia* will be richer in late successional (closed-canopy forest) habitat as opposed to early successional (open-area) habitat, and (ii) *H. maia* mortality from parasitoids will be reduced in early-successional habitat.

MATERIALS AND METHODS

Site description. Our study site was located on the peninsula of Cape Cod in Massachusetts, USA. The study area was located within Cape Cod National Seashore in Barnstable County, and consisted of a 9 km area running north-south throughout a portion of the outer Cape. The area included a 40 m wide power line right-of-way bounded by a mature closed-canopy pitch pine forest to the east, and a paved bike trail to the west. The power line right-of-way was mechanically cut every 3–4 years, perpetually maintaining an early successional habitat. A buffer corridor of pitch pine, scrub oak, black oak (*Quercus velutina* Lam.), black cherry (*Prunus serotina* Ehrh.), and beach plum (*Prunus maritima* Marsh) was left intact parallel to the bike trail. The vegetation within the power line right-of-way was cut to a height of <10 cm in 2002. By the summer of 2003, scrub oak, black oak, pitch pine, cherry and beach plum had re-sprouted from the stumps or roots. Pitch pine was the dominant tree in the closed canopy forest. Black, scarlet (*Q. coccinea* Muenchh.) and scrub oak were also present as canopy and subcanopy trees. Temperature and light intensity were significantly higher in the power line corridor than in the closed-canopy forest (JAS unpublished).

Larval mortality. 2002 – Baseline data on parasitism were collected in 2002 in a 1.5 km portion of the main 2003 study area. First instar *H. maia* larvae were deployed in the field for 12 days on scrub oaks within three distinct habitats. Each plot consisted of one scrub oak. Three plots were located within closed canopy forest (FOREST), three were located along the forest / power line border (EDGE), and three were within the power line / bike trail buffer (BUFFER). The central portion of the power line corridor was not useable, as it had been mowed the previous winter. Sixty-five first instar larvae were released at each plot. Larvae were monitored and counted on a daily basis, and were retrieved after 12 days to prevent dispersal losses which increase in late instars. Larvae were retrieved as late second and early third instars, then reared indoors until pupation or until parasitoids issued. A control population was reared entirely in the lab. The control group was collected as late first instars and thus a small proportion were parasitized. To account for the base level of parasitism within the control group, Henderson-Tilton's formula for unequal populations was employed prior to analysis (Henderson 1955).

In addition, five naturally occurring larval clusters were collected from the buffer area. Most of these aggregations consisted of third and fourth instars. All larvae were collected and reared under the same conditions as experimental larvae.

For indoor rearing, groups of 25–30 larvae were placed in 31 cm x 23 cm x 10 1/2 cm ventilated plastic boxes and maintained indoors at room temperature. Larvae were provided with fresh scrub oak foliage every 2–3 days. Florists' aqua-picks were used to keep foliage fresh. Fifth and sixth instar larvae were transferred to disposable 0.47 L plastic cups (4–6 larvae / cup) with 5 cm of potting soil for pupation, and were fed as above. Pupae were transferred to a 0.75 m^2 wooden frame rearing box covered with 2.5 mm wire mesh. The box was filled with 5 cm of soil and kept at room temperature until adult emergence in September and October. Adults mated within the box, and red oak (*Q. rubra* L.) branches were placed inside to provide females with oviposition surfaces. Eggs were kept outdoors in aerated plastic containers throughout the winter.

2003 – In early May, overwintered egg masses were moved indoors and kept refrigerated at a temperature of ~3°C until ready for use in field experiments. Hatching commenced on 31 May, with the majority of the egg masses hatching by 6 June, coinciding with bud break and egg hatch in natural populations. All larvae were hatched by 14 June.

Twelve plots were selected throughout the 9 km study area in locations where naturally-occurring clusters of

H. maia were observed in 2002. The area was divided into six 1.5 km sections with two plots in each section. All sections contained one plot along the power line corridor and one plot within the closed canopy forest. This was done to ensure equal dispersion of treatments (Hurlbert 1984). The location of each plot was randomly selected within the habitat, with two restrictions: (i) plots were at least 50 m from one another, and (ii) forest plots were at least 40 m from the eastern edge of the power line corridor. Each plot consisted of one scrub oak tree. Small (< 3 m tall) scrub oaks similar to those chosen by females in natural populations were selected (Sferra & Dunwiddie 1990, Schweitzer 1991). In instances where an appropriate tree could not be located at the randomly selected distance, the nearest tree located due south of that location was chosen.

Approximately 50 first instar *H. maia* larvae were deployed on each tree; this number is at the low end of aggregations in natural populations but is within the range of naturally occurring egg masses (Nelson 2002). To prevent dispersal losses, wandering larvae were confined to the immediate vicinity of scrub oak trees with 25 cm high aluminum flashing ground barriers (*H. maia* can not ascend aluminum flashing) placed around each tree outside the drip-line, approximately 1.75 m in diameter. Flashing was countersunk approximately 10 cm into the ground so that larvae could not go underneath it. Tall vegetation, sticks, leaves, and other debris were cleared from the inner perimeter to prevent larvae from climbing on other materials to reach the top of the flashing. When necessary, oak branches were trimmed or tied together so that the drip-line remained within the flashing perimeter. Small-scale experiments conducted in 2002 indicated that the ground barrier method causes minimal short-term disturbance to the habitat yet was completely successful in preventing larvae from wandering.

Mesh bird exclosures were placed around each tree on which larvae were deployed, enclosing both the tree and the aluminum flashing barrier. Exclosures were constructed using sections of 1.9 cm PVC pipes covered with 2.5cm netting (after Campbell *et al.* 1984). The exclosures eliminated bird predation but still allowed unfettered access by parasitoids. Comparison of plots with and without this type of exclosure indicated that neither diversity nor abundance of parasitoids attacking *H. maia* in New York was affected (DP unpublished).

Larvae were counted at least every other day. After a period of 7–10 days (approximately the length of an instar) the larvae were retrieved and replaced with 50 laboratory-reared larvae of the next instar. This time period varied based on weather conditions, as larvae developed more quickly during periods of warm, dry weather. This sequential deploy, collect, and replace technique (Boettner *et al.* 2000) was continued until the fifth instar, and was used to quantify mortality of *H. maia* throughout each of its larval stages. To limit the already large number of larvae required for this method, fifth and sixth instars were considered together, and were deployed for a period of 11 days. Retrieved larvae were reared in the laboratory until adults emerged or parasitoids issued.

Late stage *H. maia* lose their gregariousness and complete their development as solitary larvae (Tuskes *et al.* 1996, Nelson 2002). To account for this behavioral change, fewer fifth instar larvae were deployed on each tree but the number of trees they were deployed on was increased. Three trees in each habitat, including the original plot tree, were selected in every 1.5 km section. These additional trees were selected due north and due south of each original plot tree at a minimum distance of 20 m from the original. Ten larvae were placed on each tree. As these trees were in relatively close proximity to one another, and because the additional trees were chosen based on the location of the original plot tree, they were considered together as one plot in all analyses.

Pupal mortality. In 2003, we deployed a total of 120 *H. maia* pupae in marked locations in both forest and power line habitats. At each of the 12 plots, ten pupae were buried approximately 5 cm beneath the soil, approximating natural depths (Nelson 2002). Pupae were buried in two rows of five in a north-south direction, each a distance of 0.5 m from one another. The sex of each pupa was recorded. The location of each pupa was marked with a discrete 40 cm steel rod so it could be relocated in the future. The sex of pupae was determined prior to being buried on August 4 and 5. Half of the pupae buried at each plot were enclosed in small cylindrical cages made from 6 cm^2 sections of 0.64 cm galvanized hardware cloth. One pupa was enclosed in each cage. This design eliminated small mammal predation but allowed access to invertebrate predators. All plots contained three caged and three uncaged males, and two caged and two uncaged females. Pupae were retrieved on Sept. 21. A pupa was considered to have been depredated if it was not retrieved from the marked release location, or if it was damaged.

Statistical Analysis. 2002 Larval mortality: Each different mortality source was analyzed separately using the Kruskal-Wallis nonparametric test. Only larvae that were retrieved from the field were included in the analysis, since we could not determine causes of mortality for missing larvae. Two plots, one edge plot

Table 1. Mortality of *H. maia* larvae collected from naturally-occurring populations on Cape Cod, MA in 2002. Values indicate the percentage of parasitized larvae from the different parasitoid species. CoCo = *Compsilura concinnata*, HyFu = *Hyposoter fugitivus*, MeAu = Meteorus autographae, and LeFu = *Leschenaultia fulvipes*.

Site	Date	N	Instar	CoCo	HyFu	MeAu	LeFu	Survival*
NP1	20 June	13	3	0	7.7	0	0	92.3
NP2	20 June	24	3/4	0	4.2	0	0	79.2
NP3	21 June	15	4	6.7	13.3	0	0	80.0
NP4	21 June	15	3/4	13.3	0	0	0	86.7
NP5	21 June	20	4	35.0	0	5.0	10.0	55.0

*Value reflects total survival and includes mortality from non-parasitoid sources.

and one buffer plot, were excluded from the analysis because no larvae were recovered. Only descriptive statistics are presented for the parasitism occurring in natural populations.

2003 Larval mortality: Analysis was conducted using a series of t-tests. All instars and mortality sources were analyzed separately. Cumulative mortality was calculated using the equation described in Elkinton *et al.* (2006):

Cumulative Mortality = $1-(1-m_1)(1-m_2)(1-m_3)...(1-m_i)$
where m_i *is the fraction of larvae dying during instar i.*

2003 Pupal mortality: Pupal mortality data were analyzed as a split-split plot to examine the interactions among habitat, sex, and treatment (cage vs. no cage) for parasitism and predation.

RESULTS

Larval Mortality. In 2002, three species of parasitoids were recorded from experimental populations of *H. maia* larvae: *Meteorus autographae*, *Hyposoter fugitivus*, and the exotic *Compsilura concinnata*. In addition to parasitism, several larvae succumbed to a *Beauvaria sp.* fungus, and others died of unknown causes. Parasitism by *H. fugitivus* was significantly higher in buffer plots (df = 2, p=0.009). There were no other differences in the parasitoid fauna among the three different habitat types (Figure 1).

The 'control' population experienced parasitism from three of the parasitoids, albeit in very low numbers. Control larvae succumbed to 1.7% mortality from *C. concinnata*, 5.0% mortality from *M. autographae*, and 5.0% mortality from *H. fugitivus*, all of which emerged during or prior to the third instar. This indicates that all three parasitoids are capable of attacking first instar *H. maia* larvae.

Naturally occurring *H. maia* larvae were collected primarily as late third and fourth instars, and were consequently exposed to parasitism for a greater period of time than the experimental populations. These larvae had moderate levels of *C. concinnata* parasitism and were also parasitized by a fourth species not found in the experimental populations, the native tachinid *Leschenaultia fulvipes* (Table 1). There was little parasitism by *M. autographae* and *H. fugitivus* in natural populations, although it is likely that these species parasitized and killed early instar *H. maia* larvae before they were collected.

Parasitism was markedly lower in 2003 than in the previous year (Table 2). The three species of parasitoids recovered from the 2002 experimental populations were present again in 2003, though in much lower numbers. In addition, *L. fulvipes* was recovered from late-instar experimental *H. maia* larvae in 2003. As many as eight individual *L. fulvipes* puparia were obtained from a single *H. maia* host. Additional sources of larval mortality included a *Beauvaria sp.* fungus, a virus and unknown factors.

With the exception of *L. fulvipes* parasitism of fifth and sixth instar *H. maia* larvae, where parasitism was significantly higher in power line plots (t_5=2.60, p=0.048), all other comparisons for all instars were not significant. If a correction for multiple tests is conducted (adjusted alpha=0.0024), then even the difference in *L. fulvipes* parasitism of fifth and sixth instars becomes insignificant. While some advocate the use of corrections for multiple tests (Peres-Neto 1999), others maintain strong arguments against adjusting the alpha level (Gotelli & Ellison 2004), and we leave the final determination to the reader's discretion. None of the parasitoids, either acting alone or taken as a whole, caused high levels of mortality to *H. maia* larvae, which had uniformly high survival.

Comparisons of cumulative mortality rates also indicated that parasitism by *L. fulvipes* in power line plots was significantly higher than in forest plots (t_6=2.49, p=0.047). Mortality inflicted by the other parasitoid species did not differ between the different habitats (Figure 2).

Pupal mortality. The test for interactions between habitat, sex, and treatment (cage vs. no cage) and all combinations of these was not significant. The test for

Table 2. Two-tailed test results for 2003 *H. maia* larval mortality study on Cape Cod, MA, comparing power line populations to forest populations. Values indicate the percentage of parasitized larvae from power line (POW) and forest (FOR) populations. Where mortality sources are marked (°), there was insufficient information to conduct statistical analyses, as only 1 of 12 sites showed evidence of mortality from that source. CoCo = *Compsilura concinnata*, HyFu = *Hyposoter fugitivus*, MeAu = *Meteorus autographae*, LeFu = *Leschenaultia fulvipes*.

Mortality	Instar	POW	FOR	DF	T	P
CoCo	1	0	0	-	-	-
HyFu	1	0	0	-	-	-
MeAu	1	0	1.55 ± 0.98	5	-1.58	0.175
LeFu	1	0	0	-	-	-
Fungus°	1	0	0.68 ± 0.68	-	-	-
Virus	1	6.02 ± 2.2	8.47 ± 2.6	9	-0.71	0.495
Unknown	1	8.25 ± 3.5	8.75 ± 2.2	8	-0.12	0.906
Survival	1	85.79 ± 4.8	80.6 ± 2.8	8	0.94	0.376
CoCo°	2	0.35 ± 0.35	0	-	-	-
HyFu°	2	0	0.33 ± 0.33	-	-	-
MeAu°	2	0	0.38 ± 0.38	-	-	-
LeFu	2	0	0	-	-	-
Fungus	2	0.68 ± 0.43	0.33 ± 0.33	9	0.64	0.537
Virus	2	5.72 ± 3.1	5.48 ± 2.8	9	0.06	0.957
Unknown	2	6.75 ± 1.2	7.18 ± 1.1	9	-0.27	0.796
Survival	2	86.52 ± 3.2	86.3 ± 3.4	9	0.05	0.958
CoCo°	3	0	4.25 ± 4.25	-	-	-
HyFu	3	0	0	-	-	-
MeAu	3	0	0	-	-	-
LeFu	3	0	0	-	-	-
Fungus°	3	0	1.07 ± 1.07	-	-	-
Virus	3	0.8 ± 0.51	1.4 ± 0.68	9	-0.70	0.500
Unknown	3	3.6 ± 0.59	5.67 ± 0.73	9	-2.20	0.055
Survival	3	95.61 ± 1.0	87.62 ± 4.8	5	1.62	0.166
CoCo°	4	0	4.87 ± 4.87	-	-	-
HyFu	4	0	0	-	-	-
MeAu	4	0	0	-	-	-
LeFu	4	1.15 ± 0.51	0.67 ± 0.67	9	0.57	0.580
Fungus	4	3.67 ± 1.7	1.03 ± 0.71	6	1.40	0.210
Virus	4	1.9 ± 1.1	2.33 ± 1.5	9	-0.23	0.821
Unknown	4	4.37 ± 2.0	6.78 ± 2.3	9	-0.80	0.443
Survival	4	88.92 ± 3.8	84.33 ± 7.0	7	0.58	0.581
CoCo	5/6	0	3.58 ± 2.4	5	-1.49	0.196
HyFu	5/6	0	0	-	-	-
MeAu	5/6	0	0	-	-	-
LeFu	5/6	19.2 ± 6.0	2.98 ± 1.6	5	2.60	0.048
Fungus	5/6	3.33 ± 2.27	0	5	1.47	0.203
Virus°	5/6	0	0.55 ± 0.55	-	-	-
Unknown	5/6	2.87 ± 1.6	3.65 ± 1.3	9	-0.39	0.709
Survival	5/6	74.65 ± 7.5	89.27 ± 4.1	7	-1.72	0.129

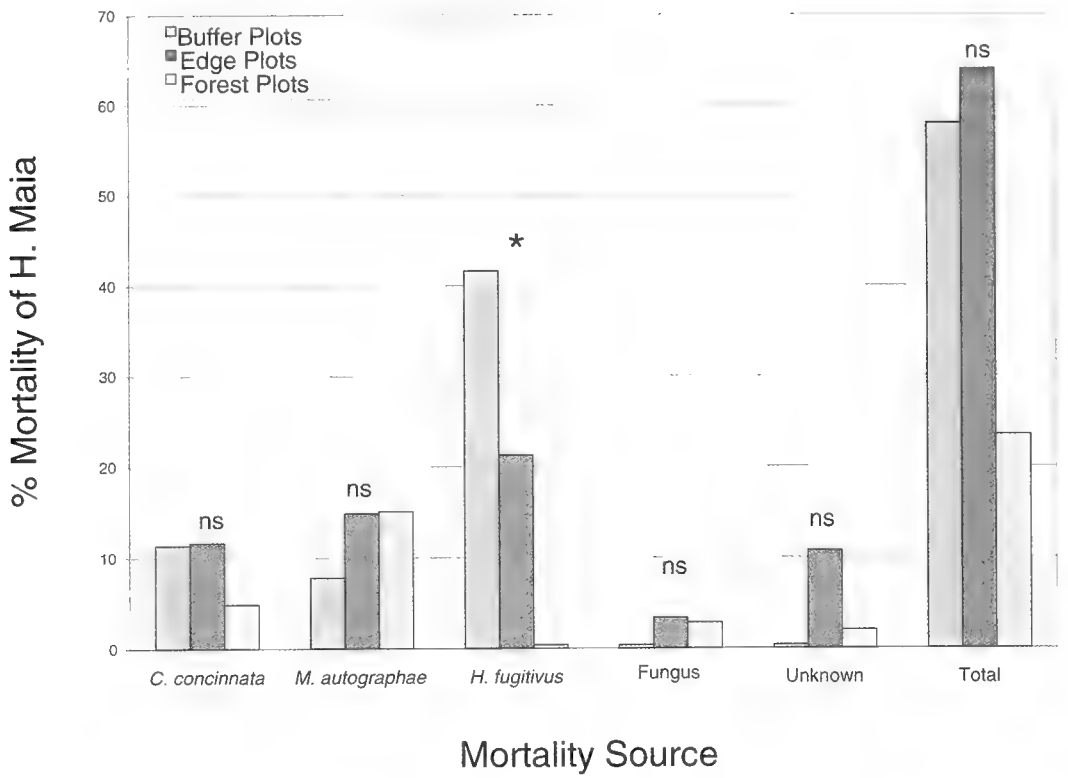

Fig. 1. Mortality of *H. maia* larvae on Cape Cod, MA in 2002. Mortality was calculated using Kruskal-Wallis nonparametric tests. A notation of 'ns' indicates that the comparison is not statistically significant at alpha 0.05. An asterisk (*) indicates a statistically significant comparison at alpha 0.05.

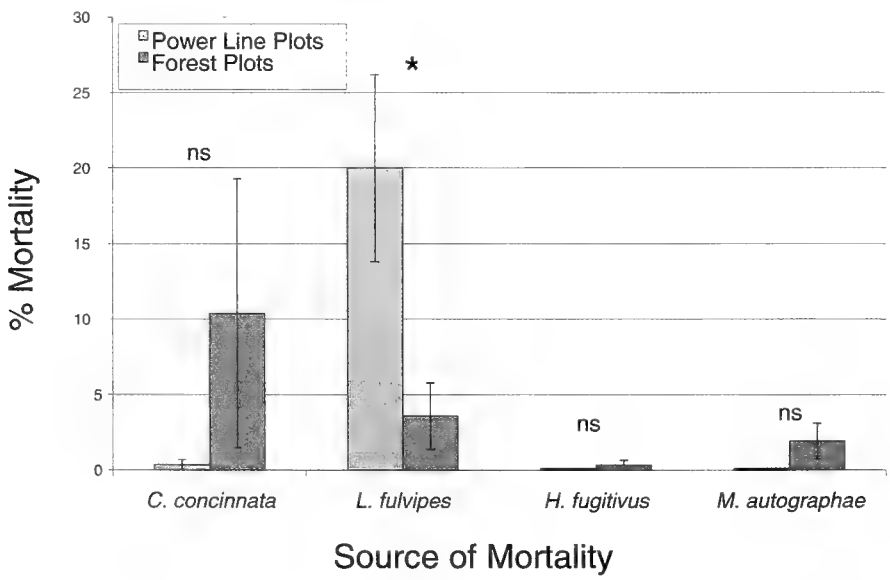

Fig. 2. Mean cumulative mortality (±SE) of *H. maia* larvae by parasitoids in 2003 on Cape Cod, MA. A notation of 'ns' indicates that the comparison is not statistically significant at alpha 0.05. An asterisk (*) indicates a statistically significant comparison at alpha 0.05.

differences between habitat and sex was also not significant. There was a significant difference between the predation of caged and uncaged pupae (t_1=24.21, p=<.0001), with 5.8 ± 8.8% (mean ± SE) of caged pupae and 38.4 ± 21.5 (mean ± SE) of uncaged pupae depredated. With one exception, all predated pupae were simply missing. In only one instance was a caged pupa eaten, presumably by an insect predator. We found no parasitism of either caged or uncaged pupae.

DISCUSSION

Four species of parasitoids were reared from *H. maia* on Cape Cod during the two-year study. *Meteorus autographae* and *H. fugitivus* were primarily associated with early instar *H. maia* larvae. *Leschenaultia fulvipes* was not recovered from the experimental populations in 2002, which spanned only the first three instars. *Leschenaultia fulvipes* did occur in wild populations of late instar *H. maia* larvae in 2002, and again in late-instar experimental *H. maia* larvae in 2003, suggesting that *L. fulvipes* is predominantly associated with later instar *H. maia*. However, extensive parasitism by *L. fulvipes* in early instar larvae has been frequently observed in other *Hemileuca* populations (J. Tuttle, pers. com.). While it is possible that *L. fulvipes* parasitized and killed their early instar hosts before they were collected as 3rd and 4th instars, it should be noted that *L. fulvipes* was not represented in the control population.

The recovery of *Meteorus autographae* from *H. maia* is a new host record. Several previously collected specimens identified as *M. hyphantriae* from Plymouth and Brewster Counties in Massachusetts also were identified as *M. autographae*. We suggest that *M. hyphantriae* records from *H. maia* in old collections be reexamined for possible misidentifications, because many historic records appear to be from the same region (S. Shaw, pers. com.).

The tachinid *Compsilura concinnata* was also more prevalent in late-instar *H. maia*, consistent with prior observations with other Lepidoptera (Webber & Schaffner 1926, Burgess & Crossman 1929, Boettner *et al.* 2000, Kellogg *et al.* 2003). However, in 2002, *C. concinnata* was reared from second and third instars, and on one occasion even attacked a first instar larva. Although most *C. concinnata* larvae successfully emerged from smaller *H. maia* hosts and formed puparia, 14% of these puparia died, and adults that did emerge were half the size or less of adults emerging from puparia reared from late instars. Significant fitness costs may be incurred by flies attacking smaller individuals (e.g., Raupp & Denno 1983, Reavey 1993). Further, only one *C. concinnata* puparium was produced from each parasitized early instar larva in 2002, while in 2003 multiple emergence occurred in 38.5% of larvae, with as many as five *C. concinnata* produced from a single host.

The 2003 study was designed to specifically assess parasitism of late-instar larvae. While our observations accurately reflect the mortality inflicted on *H. maia* larvae in 2003, this may not be representative of all years. In other years, our study (2002) and those of others (Boettner *et al.* 2000) have shown higher rates of parasitism. However, a similar study in New York's Albany Pine Bush in 2005 found no parasitism by *C. concinnata* and very low parasitism by hymenopterans (DP and B. Hoven, unpublished data). In that study, only *L. fulvipes* was common.

The apparent greater abundance of *H. maia* in open, early successional habitats like powerline right-of-ways does not appear to be a function of changes in parasitoid pressure. There was some evidence that parasitoid species varied spatially among habitats based on the high percentage of *H. fugitivus* recovered from larvae in buffer plots in 2002 and the decreased rate of parasitism by *L. fulvipes* in power line plots in 2003, but all other comparisons were not significant. However, parasitism is but one of several biotic factors that may influence *H. maia* distribution. The abundance of predators, the distribution and quality of host plants, fire management, and microclimate conditions are all factors that may act alone or in combination to affect the oviposition choices made by *H. maia* adult females. Microclimate may be of major importance and should not be overlooked. Increases in temperature and light intensity may enhance behavioral thermoregulation through the absorption of solar energy (Seymour 1974, Cornell *et al.* 1987, Klok and Chown 1999, Hunter 2000). This may be particularly important for *H. maia* larvae on Cape Cod, as these populations are at the extreme northern limit of their geographic range.

We recorded modest levels of mortality in the pupal stage, although it is unclear what effect, if any, this has on its overall distribution. While pupal mortality is common in many other insect species (e.g., Weseloh 1985, Gould *et al.* 1990, Fuester & Taylor 1996, Tanhuanpää *et al.* 1999, Hastings *et al.* 2002), we are unaware of additional studies that examine pupal mortality of *H. maia*. Thus, we cannot competently assess whether the mortality levels that we observed constitute significant losses for this species. There was no evidence of pupal parasitism in either habitat. There was also no evidence that predators prefer the larger female pupae to the smaller male pupae. A significantly greater number of uncaged pupae were depredated as compared to those in cages. This suggests that

predation was caused by birds, mammals, and/or large insect predators, as the mesh cages were accessible to smaller invertebrates. In only one instance was there clear evidence that a small invertebrate predator consumed a caged *H. maia* pupa.

The lack of significant mortality from the introduced *C. concinnata* offers some hope for future management of *H. maia* because it suggests that populations can be enhanced through habitat protection and management. In contrast, management of several other species of threatened saturniids in the northeast may be thwarted by the dominance of this tachinid as a mortality factor. Our data do suggest that the well-documented decline in populations of many saturniids in the northeast may be due to more than one factor, and the role of *C. concinnata*, which has been proposed as a major contributor to the decline, will depend on the species in question.

ACKNOWLEDGEMENTS

We would like to thank Scott Shaw and Nina Zitani for identifying parasitoids and Ann Hajek for identifying pathogens and fungi. We thank Dillon Finan, Colleen O'Connell and Jenny Smith for their enormous efforts both in field and in the lab. For guidance on various aspects of the project, we thank Mike Nelson, Dale Schweitzer, Paul Goldstein and Eric Quinter. Many thanks to Nancy Finley and the Cape Cod National Seashore for providing both housing and field sites. We also thank Jim Tuttle and an anonymous reviewer for providing helpful comments on the manuscript. This research was supported in part by a National Science Foundation grant DEB-089699 to J.S. Elkinton and D. Parry, a Simeone Graduate Fellowship (SUNY – ESF) to J.A. Selfridge, and the Edna Bailey Sussman Fund.

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Received for publication 2 November 2006; revised and accepted 2 November 2007

Journal of the Lepidopterists' Society
61(4), 2007, 222–227

POTENTILLA FRUTICOSA (ROSACEAE) AS A NECTAR PLANT FOR BUTTERFLIES

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ABSTRACT. Despite its wide distribution, little documentation exists to confirm that butterflies use the woody shrub *Potentilla fruticosa* (Linnaeus) (Rosaceae) as a nectar plant. During the summer of 2004, we observed 36 individual butterflies belonging to 10 species nectaring on *P. fruticosa* in the Jemez Mountains, New Mexico. Butterflies spent 56% of total observed nectaring time on *P. fruticosa*, where it composed 26% of total blooming forb availability (out of 17 plant species). We used the anthrone method for carbohydrate analysis of *P. fruticosa* nectar samples and found significantly more ($\chi \pm^{SE}$ µg/2ml) carbohydrates (i.e., nectar) in flowers (n=68) excluded from nectivores (26.83±1.35 µg/2ml) than available (n=63) to nectivores (6.71+1.40 µg/2ml). Carbohydrate levels were also significantly higher in nectar later in the sampling season (Two-way ANOVA with repeated measures, $p<0.05$). Although anecdotal observations suggest that *P. fruticosa* is not a preferred nectar source for butterflies in the northern Rocky Mountains and in others areas of its range, our results indicate that *P. fruticosa* is an important nectar resource for adult butterflies in the Jemez Mountains, New Mexico.

Additional key words: *Pentaphylloides floribunda*, flower visitation, Lepidoptera, nectar, nectaring

The wide distribution and blooming phenology of shrubby cinquefoil *Potentilla fruticosa* (Linneaus) (Rosaceae) [syn: *Pentaphylloides floribunda* (Pursh) A. Löve] make it a potential nectar source for many insect species. The life history and ecological characteristics of this shrub are well documented (Elkington & Woodell 1963, NRCS 2006, USGS 2005). In North America, ornamental and wild cultivars bloom from May to September with two main flowering periods in May and August. The latter is more vigorous and produces larger flowers (Elkington & Woodell 1963). *P. fruticosa* is intolerant of shade, and the wild North American form produces yellow flowers, while some horticultural varieties originating from Asia produce white, pink, orange, or red flowers (Elkington & Woodell 1963, NRCS 2006). Inflorescences are terminal and appear solitary or in small clusters. Flowers have five petals, triangular ovate sepals, and open nectaries (Elkington & Woodell 1963, USGS 2005). In North America, *P. fruticosa* ranges from the Arctic slope of northern Alaska to Newfoundland, south to the Sierra Nevada and Rocky Mountains, and east through the Great Lakes to New England and Labrador (Elkington & Woodell 1963, NRCS 2006, USGS 2005). North American individuals appear to be uniformly diploid, but populations are tetraploid in Europe and diploid or hexaploid in Asia (Elkington & Woodell 1963).

Little documentation exists on the use of *P. fruticosa* as a nectar source by insects, other than a limited number of species belonging to the orders Diptera, Coleoptera, Hymenoptera (Elkington & Woodell 1963) and Lepidoptera (Voss 1954, Emmel 1964, Emmel *et al.* 1992, Opler & Krizek 1984). The Brooklyn Botanic Garden (2007) lists *P. fruticosa* as a bee-pollinated species, and several gardening and horticultural websites recommend *P. fruticosa* for butterfly gardens.

Voss (1954) observed five species of butterflies nectaring on *P. fruticosa* in Michigan. These were *Danaus plexippus* (Linnaeus), *Nymphalis milberti* (Godart), *Satyrium titus*, (Fabricius) (Nymphalidae), *Lycaena dorcas* (Kirby) (Lycaenidae) and *Erynnis lucilius* (Scudder & Burgess) (Hesperiidae). In the central Rocky Mountains of Colorado, Emmel (1964) and Emmel *et al.* (1992) observed five species of butterflies nectaring on *P. fruticosa*; *Euphydryas anicia eurytion* (Mead), *Polygonia zephyrus* (Edwards) (Also known as *Polygonia gracilis* (Grote & Robinson), *Satyrium titus titus*, *Euphydryas anicia capella* (Barnes) (Nymphalidae), and *Lycaena rubidus* (Behr) (Lycaenidae). The Wisconsin Department of Natural Resources (2006) listed *P. fruticosa* as a nectar source for the endangered *Calephelis mutica* (McAlpine)

(Riodinidae) and Opler and Krizek (1984) listed *P. fruticosa* as the larval host plant for *L. dorcas*. Webster & deMaynadier (2005) listed *P. fruticosa* as the host and principle nectar plant for *L. dorcas claytoni* (Brower) in Maine.

We have been studying butterfly abundance and species richness in Bandelier National Monument and the Valles Caldera National Preserve, New Mexico, 1999–2004 (Kleintjes Neff *et al.* 2007, USGS 2005). In an experiment evaluating the impact of ungulate browsing upon butterflies and their host plants, we found butterfly richness and abundance to be greatest in areas containing *P. fruticosa* (unpubl. data). We additionally found butterflies nectaring on *P. fruticosa*, yet in the literature we found little documentation to confirm its use as a nectar source in the wild. Moreover, peer review of our initial qualitative observations was met with skepticism by reviewers. As a result, the objective of our study was to quantify the use (e.g., species visitation rates, nectar carbohydrate content) of *P. fruticosa* flowers by adult butterflies in the Jemez Mountains, New Mexico.

MATERIALS AND METHODS

Study Area. During the summer of 2004 (9 July–9 August), we worked within four study plots in the Jemez Mountains, New Mexico. Two were located in Bandelier National Monument (mixed conifer-MC4, meadow-MD) and one each in the adjacent Santa Fe National Forest (ski basin-SB) and Valles Caldera National Preserve (Valles Caldera-VC). We chose sites that had ~25% total available blooming forb cover of *P. fruticosa* due to little or no elk browsing (inside exclosures and near human traffic). All sites were located within openings surrounded by mixed conifer-aspen forest between 2700m and 2830m in elevation. Sites were approximately 1200 m^2 in size except for SB, which was approximately 576 m^2 in size. Sites were considered independent (>2 km from each other). We collected butterfly foraging observations and estimated nectar plant availability in the MC4, MD, and SB sites. We sampled nectar availability for analysis at all four sites.

Adult butterfly foraging behavior. We compiled butterfly foraging observations (1000–1500hr) from 10 July–4 August. Once an individual was sighted, we noted the species and then waited 5 sec. before initiating a 5 min. observation period. Butterflies were identified to species by sight and if necessary compared with voucher specimens or photographs (Glassberg 2001). For each butterfly, we collected detailed foraging time budgets which included recording the percent total observation time (sec) spent flying, basking, nectaring, mating, and in combat. We also recorded the percent time each individual spent nectaring per plant species and basking per substrate.

Floral abundance and phenology. We estimated flower availability for eleven randomly selected plants in each site. We categorized the availability of open *P. fruticosa* flowers/plant by intervals of 50 flowers (1–50, 51–100, 101–150, 151–200 flowers). In three sites (MD, MC4, SB) we randomly selected five flowers for phenology studies (bud-to-bloom-to-closing) to determine the average time an individual flower was open (i.e., nectar was available). We marked individual flowers with flagging and noted the stage (bud, bloom, closing, closed) of development every day until they senesced.

Nectar Plant Availability. We conducted a rapid assessment of blooming forb availability in each butterfly foraging observation site using Foxx and Hoard (1995) for plant species identification. We walked three (20-m) transect lines through each site. At every four meters along each transect we noted the closest blooming forb in a 2-m radius from the observer. We computed frequency of occurrence for available forb species by dividing the occurrence of each species closest to the observer from the total number of observations. Data were collected on 13 July and 6 August.

Nectar availability and analysis. We measured the greatest height and width of each randomly selected *P. fruticosa* shrub per site (n=11). On each plant, we randomly selected 12 freshly opened flowers for nectar analysis. We bagged [treated] six flowers per plant and left six unbagged [untreated]. Bags excluded nectivores 24 hr prior to sampling. Bag material consisted of soft window screening, which excluded nectivores yet allowed air circulation. We extracted nectar from three flowers per treatment with micro-pipettes (10 µl; 1 µl increments) and paper wicks of ©Whatman's filter paper (2x8 mm paper insect "points") (Kearns & Inouye, 1993). We removed flower stamens with forceps prior to nectar sampling to decrease potential contamination by pollen and to make nectaries more accessible. We used the pipette samples to quantify nectar volume in the field and the wicks to analyze total carbohydrate content and type in the lab. We took samples between 0930–1440 hrs within two sampling periods (16–27 July, 29 July–5 August) to correspond with early- and late-season nectar availability. Samples were stored at room temperature and analyzed in lab at the University of Wisconsin-Eau Claire during September–November. We used a Spectronic 20D+ spectrophotometer to estimate the absorbance of total carbohydrate in solution as done by McKenna and Thomson (1988). We pooled individual nectar samples

per plant and averaged the absorbance to estimate mean nectar production per flower. We used a Two-way ANOVA with repeated measurements to test for significant differences ($p<0.05$) between treatments, periods and the interaction of treatment*period. Proportional data received a squareroot arcsin transformation.

RESULTS

Floral abundance and phenology. We found that 57% of all observed plants (n=44) contained 1–50 flowers, 32% contained 51–100 flowers, 9% contained 101–150 flowers and 2% contained 151–200 flowers in full bloom. Mean blooming period length of individual flowers (n=14) was 4.91 (± 0.61SE) days. Although individual flowers bloomed for a short time, new flowers were continuously produced on each shrub.

Nectar Plant Occurrence. Similar percentages (24%, 23%, 30%) of *P. fruticosa*, compared to the availability of other blooming forbs, were available to butterflies in all three sites. Only *Achillea lanulosa* (Nutt) (Asteraceae) had greater (51%) availability than *P. fruticosa* in one site (MD). Overall, *P. fruticosa* was the most available nectar source, with *A. lanulosa* availability a close second (Table 1).

Adult butterfly foraging behavior. We collected foraging observations from a total of 59 individual butterflies. Butterflies spent significantly more observation time (76%) nectaring than any other activity (8% flying, 16% other (basking/mating/combating)) (Univariate ANOVA, df=2, F=80.4, $p<0.01$). Butterflies that nectared (n=54) spent more (56%) time nectaring on *P. fruticosa* than any other plant species (Table 1). *A. lanulosa* was the second most available species of blooming forb (25%), but butterflies nectared on it for only 3.5% of the total observation time. *Helenium hoopesii* ((Gray) Bierner) (Asteraceae), however, comprised less than 1% of total forb availability, yet was the second most preferred species. It received 15% of the total observed nectaring time (Table 1).

Of the 59 total observations, we observed 36 individuals from ten species of butterflies nectaring on *P. fruticosa* (Fig. 1). These species were *Speyeria hesperis hesperis* (Edwards), *Cercyonis oetus* (Boisduval), *Vanessa cardui* (Linnaeus), *Vanessa annabella* (Field) (Nymphalidae), *P. gracilis*, *Hemiargus isola* (Reakirt), *Lycaena arota* (Boisduval), *Plebejus icarioides* (Boisduval), *Leptotes marina* (Reakirt) (Lycaenidae), and an unknown *Colias* species (Fabricius) (Pieridae).

Nectar availability and analysis. We found that *P. fruticosa* produces nectar, although the quantity of nectar produced per flower was minute (<1 µl). Nectar was occasionally noted to enter the micropipettes, but it was not enough to quantify to µl. Analysis of nectar samples indicated the presence of carbohydrates. There was a significantly higher carbohydrate content for bagged than unbagged flowers and carbohydrate levels

Table 1. (A) Total percentage of blooming shrub and forb availability and (B) percentage of total observed time butterflies spent nectaring on blooming forbs in the Jemez Mountains, New Mexico, July–August 2004.

Blooming Forb Species	(A) Percentage of total blooming shrub and forb availability	(B) Percentage of total observation time butterflies nectared on the shrub or forb
Potentilla fruticosa (Linnaeus) (Rosaceae)	25.80	56.17
Achillea lanulosa (Nutt) (Asteraceae)	24.82	3.50
Potentilla pulcherrima (Lehm) (Rosaceae)	10.25	2.23
Galium spp. (Rubiaceae)	9.75	1.85
Potentilla hippiana (Lehm) (Rosaceae)	6.30	0.09
Erigeron spp. (Asteraceae)	4.44	10.18
Campanula rotundifolia (Linnaeus) (Campanulaceae)	3.95	0.00
Geranium richardsonii (Fisch & Trautv) (Geraniaceae)	3.58	0.00
Pseudocymopterus montanus ((Gray) Coult & Rose) (Apiaceae)	2.59	0.00
No blooming shrub or forb	2.59	-
Cirsium undulatum ((Nutt) Spreng) (Asteraceae)	1.85	1.85
Tragopogon dubius (Scop) (Asteraceae)	1.11	0.00
Helenium hoopesii ((Gray) Bierner) (Asteraceae)	0.74	14.81
Helianthella quinquenervis ((Hook) Gray) (Asteraceae)	0.62	7.38
Monarda menthifolia ((Graham) Fern) (Lamiaceae)	0.62	0.00
Unk. Composite	0.62	0.00
Allium spp. (Liliaceae)	0.37	1.94

were also significantly higher later in the sampling season (Two-way ANOVA with repeated measures, df=1 for each; treatment F=106.6, period F=52.2, treatment*period F=17.3, all p<0.01) (Table 2).

DISCUSSION

Our study documented the use of *P. fruticosa* as a nectar source by ten species of butterflies in the Jemez Mountains, New Mexico. This is a new nectar plant host record for nine species of butterflies, other than for *P. gracilis ssp. zephyrus*.

Our results suggest that butterflies preferred *P. fruticosa* nectar more than that provided by other species of available blooming forbs. Although our observations suggest a higher preference for *H. hoopesii* than *P. fruticosa* due to relative plant abundance and foraging studies, it is not known whether this was due to nectar quality, quantity, or foraging energy expenditure. Since *H. hoopesii* is a composite, this behavior may be a result of spending more time on one plant with multiple flowers in one inflorescence instead of expending energy to forage on the multiple single flowers of *P. fruticosa*.

The filter paper wicking technique proved suitable for the amount of nectar collected from *P. fruticosa*. It worked well, as the flowers have shallow nectaries easily accessible by pointed paper wicks. Using micro-capillary pipettes for quantification in the field proved inadequate for the amount of nectar produced by *P. fruticosa*.

It is well documented that the availability of sugar in the adult diet can significantly increase longevity and fecundity (Hill & Pierce 1989, Hill 1989, Norris 1935, David & Gardiner 1962). Since this was a baseline study, we calculated only total carbohydrate content of *P. fruticosa* nectar samples. However, studies have shown that nectars fed on by Lepidoptera are generally sucrose-rich and contain relatively high concentrations of amino acids (Baker & Baker 1977, 1982, 1983, 1990) and that some butterflies detect and select for amino acids in their diet (Erhardt & Rusterholz 1998, Alm *et al.* 1990, Hill & Pierce 1989). Amino acids present in *P. fruticosa* nectar may have affected butterfly preference as a nectar source, but this was not addressed by our study. We suggest that future research quantify both the relative amounts of sugars (i.e., sucrose, fructose, glucose) as well as amino acids in *P. fruticosa* nectar.

Results from our carbohydrate analysis indicate that greater amounts of nectar were removed from flowers available to large (>2.0mm) nectivores compared to

Fig. 1. Butterflies photographed nectaring on *Potentilla fruticosa* in North Central New Mexico. **A.** *Plebejus icarioides*, Jemez Mountains, Los Alamos Co. **B.** *Agriades glandon*, Sangre de Cristo Mountains, Taos Co. **C.** *Leptotes marina*, Jemez Mountains, Los Alamos Co. **D.** *Vanessa cardui*, Jemez Mountains, Los Alamos Co. **E.** *Polygonia gracilis ssp. zephyrus*, Jemez Mountains, Los Alamos Co. **F.** *Lycaena arota*, Jemez Mountains, Los Alamos Co. **G.** *Cercyonis oetus*, Jemez Mountains, Los Alamos Co.

Table 2. Mean (+SE) carbohydrate content for sample treatments and periods in the Jemez Mountains, New Mexico, July–August 2004.

Sample Period	Bagged	Unbagged
1st period	17.42 µg/2ml	4.18 µg/2ml
2nd period	36.24 µg/2ml	9.24 µg/2ml
Mean (+SE)	26.83 ± 1.35 µg/2ml	6.71 ± 1.40 µg/2ml

Two-way ANOVA with repeated measures; treatment (bagged vs. unbagged), sample period, treatment*sample period, all significant at $p<0.01$.

those flowers excluded from foragers. Greater amounts of nectar were also produced later in the sampling season. We do not know whether the seasonality was an artifact of sampling pre and post rainy season or was associated with the phenology of the early and late blooming flush of *P. fruticosa*.

Outside of our study area, we compiled additional observations, both anecdotally and intentionally, on *P. fruticosa* in areas known to experience the impacts of elk browsing. Anecdotally, we noted an *Agriades glandon* (de Prunner) (Lycaenidae) nectaring on *P. fruticosa* near Williams Lake in the Sangre de Christo Mountains. At the National Elk Refuge in Jackson Hole, WY, we quantified butterfly foraging observations and blooming forb availability for 3 days (31 July– 2 August) in 2004. Our intent was to document whether butterflies (and which species) nectared on *P. fruticosa* in the northern Rocky Mountains and whether elk browsing levels were comparable to that in the Jemez Mountains. In two open, mesic meadow plots, blooming *P. fruticosa* accounted for 35% and 15% of flowering plant availability in comparison to *Solidago* spp. (Asteraceae) (25% and 15% respectively) and *Aster* spp. (Asteraceae) (20% and 10% respectively). As a result of 6.5 hours of total observation time (~1000–1200hrs/day) we observed a limited number (<40) of butterflies belonging to 14 species, 5 of which were observed nectaring on flowers and only two of which, *Phyciodes pascoensis* (W. G. Wright) (Nymphalidae), and *L. rubidus*, were nectaring on *P. fruticosa*. We also collected nectar samples, but they were stolen and thus unavailable for analysis. Our limited evidence from the refuge suggested that *P. fruticosa* was not a preferred nectar source for butterflies, but more data are needed to validate this assumption.

Our research confirms that *P. fruticosa* is a preferred nectar source for butterflies in the Jemez Mountains, New Mexico. We speculate that this is due to a limited number of shrub and forb nectar sources later in the summer and during periods of drought. This supports the importance of the availability of this widely distributed and "weedy" shrub for nectaring insects, especially in areas where the species suffers from overbrowsing by cattle and ungulates, which can reduce flower availability.

ACKNOWLEDGEMENTS

We thank Steve Cary and Paul Opler for species confirmation and encouragement to pursue the study, Dorothy Hoard for field assistance, Julie Anderson for technical assistance and Jodi Swanson and anonymous reviewers for manuscript review. We thank David Dobkin and Eric Cole for assistance in using the National Elk Refuge, Jackson, WY. The project was funded in part by grants from the Council for Undergraduate Research Summer Research Opportunity Fund, the University of Wisconsin-Eau Claire Office of Research and Sponsored Projects and the National Park Service-Bandelier National Monument.

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Received for publication April 30 2006; revised and accepted 2 November 2007

Journal of the Lepidopterists' Society
61(4), 2007, 228-232

BUTTERFLY DRAWINGS BY JOHN ABBOT IN THE HOUGHTON LIBRARY, HARVARD UNIVERSITY, THAT ARE WRONGLY ATTRIBUTED TO AN "INFERIOR COPYIST"

Additional key words: Coleoptera, Edward Doubleday, Thaddeus W. Harris, Lepidoptera.

On 4 June 1839, the English lepidopterist Edward Doubleday (1810–1849) related an interesting discovery to his good friend, American entomologist Thaddeus W. Harris (1795–1856). Doubleday wrote, "A few days since I found at a Booksellers 84 drawings by Abbot containing 150 figures of Georgian Coleoptera & about 350 of Lepidoptera. They are bound in a small folio volume, & did belong to Swainson. As many of the things figured are new to me I thought that they might not be known to you either, & so gave £7..7..0 for them and brought them away determining to send them as a trifling present to you in my next parcel. I hope they may contain something new to you" (T. W. Harris correspondence, Ernst Mayr Library, MCZ, Harvard University). Doubleday attributed these drawings to the English–born naturalist John Abbot (1751–*ca.*1840), who had been living in Georgia since 1776. On 15 September 1839, Harris expressed his gratitude for the "costly present of Abbot's drawings" (T. W. Harris correspondence, Mayr Library).

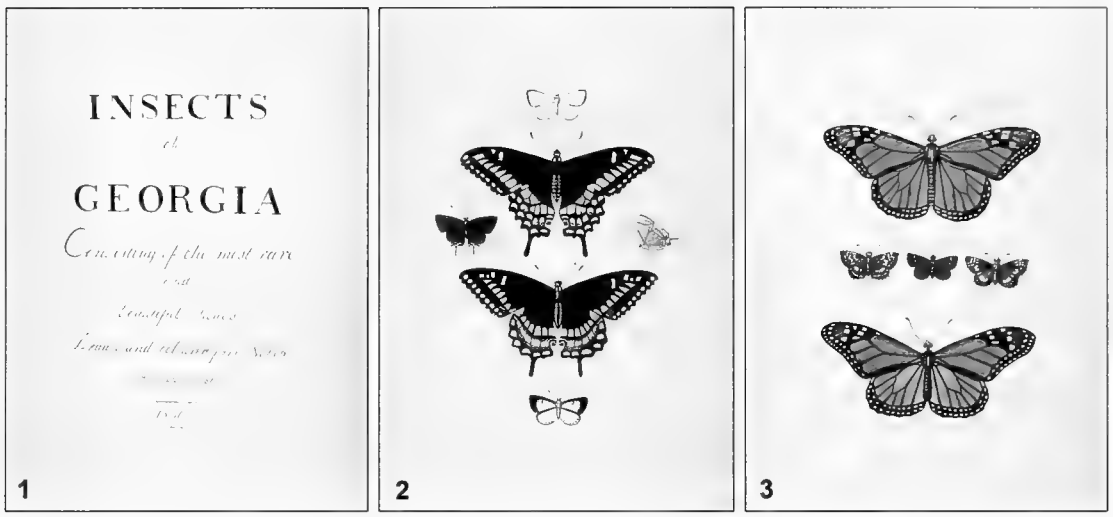
Scudder (1869) transcribed Doubleday's letter, but altered some of the details. He misquoted the letter to say that the drawings "did not belong to Swainson," when the opposite was indicated. The English naturalist William Swainson (1789–1855) received many drawings from John Abbot between 1818 and 1835 (Calhoun 2007). Swainson may have sold this volume prior to his relocation to New Zealand in 1840. He offered various drawings and specimens for sale in 1839 (Parkinson 1984, Natusch & Swainson 1987). Doubleday probably purchased the volume not long after the bookseller had obtained it, possibly from Swainson himself.

After the death of T. W. Harris in 1856, his library was purchased for the Boston Society of Natural History by John P. Cushing (1786–1862) (Anonymous 1860). Cushing, a philanthropist from Watertown, Massachusetts, also contributed to the purchase of Harris' insect collection for the BSNH. Higginson (1906) recalled that Cushing was "the only man in Boston, or its vicinity, who was suspected of being a millionaire." Cushing amassed a fortune in China and became a "wealthy, benevolent citizen." He established a magnificent conservatory and actively participated in public enterprises and charities (Drake 1880).

When the volume of insect illustrations was received by the BSNH, it was described as containing "all the originals of the drawings in 'Abbot and Smith's rarer Lepidopterous Insects of Georgia,' beside many others yet unpublished" (Anonymous 1860, Higginson 1869). Various sets of Abbot's drawings have been misidentified as the originals for Smith & Abbot (1797), which are currently deposited in the John Work Garrett Library of the Johns Hopkins University (Calhoun 2006). In 1946, all of Abbot's illustrations in the possession of the BSNH were purchased for $800 by Harvard University (accession record, Houghton Library, Harvard University). These drawings, including the volume presented to T. W. Harris in 1839, are now preserved in the Houghton Library.

Thirty years after the volume was acquired by the BSNH, Scudder (1888b) denounced its association with Abbot. Kirby (1888) wondered why Scudder (1888a) had overlooked it in his biography of Abbot. In response, Scudder retorted, "The small volume of paintings referred to by Mr. Kirby is in the library of the Boston Society of Natural History, and was not mentioned by me because the less said about it the better. It was picked up at a book shop, bears the date 1830, and though Doubleday paid seven guineas for it, it is certainly not the work of Abbot, but of a very inferior copyist—some of the paintings being the merest daubs. It is scarcely the least value" (Scudder 1888b). Following Scudder, Faxon (1896) ignored this volume when discussing Abbot's insect drawings at the BSNH. Dow (1914) reiterated the opinion of Scudder, considering them to be the work of "a pupil or imitator." Lacking additional information, the Houghton Library continues to catalog the volume as the work of an inferior copyist. However, this notion was proposed when details of Abbot's life and artistic methods were poorly understood. A comparison of this volume with other drawings and manuscripts indicates that it is unquestionably the work of Abbot.

Analysis. I examined these illustrations at the Houghton Library in November 2005. They are bound in a small volume measuring approximately 20 x 33 cm (8 x 13 in), with mottled brown boards and a brown leather spine that lacks a title. Inside the volume is the bookplate of Edward Doubleday. Placed below this is another bookplate that reads, "Boston Society of Natural History/From the Library of/Thaddeus William



Figs. 1–3. Pages from John Abbot's 1830 insect volume (Department of Printing and Graphic Arts, Houghton Library, Harvard College Library, Harvard University; MS Typ 426.5). **1,** title page. **2,** drawing no. 29 of *Celastrina neglecta* (W. H. Edwards), *Papilio polyxenes* Fabricius, and *Strymon melinus* (Hübner). **3,** drawing no. 32 of *Danaus plexippus* (L.), *Pyrgus communis* (Grote), and *Amblyscirtes vialis* (W. H. Edwards).

Harris, M.D./Presented by J. P. Cushing, Esq." On the first page, handwritten in ink, is a dedication from Doubleday: "To Dr. T. W. Harris (Entomologorum Americanum Princeps), This volume of Drawings by Abbot is presented as a small token of esteem and affectionate remembrance by his much obliged friend, Edward Doubleday." There is no evidence that William Swainson owned the volume, thus Doubleday must have been informed of this fact by the bookseller. A small blue card, bearing a typed quote from Scudder (1888b) that questions their provenance, was inserted into the volume in 1935. The title page of the volume, dated 1830, is written in John Abbot's distinctive hand (Fig. 1).

Unbeknownst to S. H. Scudder, Abbot also produced two very similar volumes of insect drawings that are now preserved in the Robert W. Woodruff Library (Emory University), and the Kenan Research Center (Atlanta History Center). These volumes, completed in 1827 and 1828, are roughly the same size as the 1830 volume and include the same type of title page (Baker 1959, Rogers 1978). Analogous title pages are also included with two volumes of Abbot's bird drawings, dated 1823 and 1827 (Sewell 1972, Simpson 1984). Abbot obviously produced multiple sets of drawings with similar title pages between 1820 and 1830. These title pages are characterized by large block letters that read "BIRDS of GEORGIA" and "INSECTS of GEORGIA" (Fig. 1). Script subtitles read "Consisting of the most rare kinds Drawn and coloured from Nature by John Abbot." Abbot replaced the word "rare" with "remarkable" for his 1827 insect volume.

Dow (1914) mentioned that T. W. Harris' son, Edward Doubleday Harris, recalled, "as a lad, circa 1851–2, he watched his father devote an afternoon to engrossing a neat title page to a volume of drawings of John Abbot." Dow supposed this was for the 1830 insect volume, but he did not realize that the title page for these drawings is written in Abbot's hand. Instead, Harris undoubtedly created his title page for a group of unbound drawings that he borrowed in 1851 from Abbot's friend, Augustus G. Oemler (letter from Oemler, dated 14 March 1851, Mayr Library). These drawings were purchased from Oemler for the BSNH in 1873 and transferred to Harvard University in 1946. The fate of Harris' title page is unknown, as it is no longer included with Oemler's collection of drawings in the Houghton Library.

The 1830 volume contains 84 drawings. They are rendered in watercolor and graphite on wove paper without watermarks. Sixty drawings depict butterflies and moths, while the remaining 24 are beetles. Many of the illustrations bear penciled numbers and identifications in the hand of T. W. Harris. Additional notations are probably by S. H. Scudder and include references to other Abbot drawings that were owned by the BSNH (e.g. the Oemler set). The figures are arranged into geometric patterns that usually feature one or two large species with two or more smaller species (Figs. 2, 3). They are not placed into taxonomic

Table 1. Butterfly species depicted in John Abbot's 1830 volume of insect drawings in the Houghton Library, Harvard University. Figures: D=dorsal, V=ventral, m=male, f=female. Figures are listed top to bottom, left to right. Nomenclature follows Opler & Warren (2006).

Drawing no.	Species depicted	Figures
25	a. *Ancyloxypha numitor* (Fabricius)	Dm, Vf
	b. *Amblyscirtes aesculapias* (Fabricius)	Dm
	c. *Papilio glaucus* L. (dark form)	Df
	d. *Amblyscirtes alternata* (Grote & Robinson)	Df
	e. *Atrytone arogos* (Boisduval & Le Conte)	Df
	f. *Anatrytone logan* (W. H. Edwards)	Dm
26	a. *Papilio glaucus* L.	Dm, Vm
	b. *Poanes yehl* (Skinner)	Dm, Df
27	a. *Papilio palamedes* Drury	Dm
	b. *Polites vibex* (Geyer)	Dm, Df
	c. *Papilio cresphontes* Cramer	Dm
28	a. *Papilio troilus* L.	Dm, Df
	b. *Erynnis juvenalis* (Fabricius) or *E. horatius* (Scudder & Burgess)	Dm, Df
29	a. *Celastrina neglecta* (W. H. Edwards)	Dm, Df
See Fig. 2	b. *Papilio polyxenes* Fabricius	Dm, Df
	c. *Strymon melinus* (Hübner)	Dm, Vm
30	a. *Eurytides marcellus* (Cramer) (summer form)	Dm
	b. *Eurytides marcellus* (Cramer) (spring form)	Dm
	c. *Hemiargus ceraunus* (Fabricius)	Dm, Df
31	a. *Battus philenor* (Linnaeus)	Dm, Df, Vf
	b. *Hermeuptychia sosybius* (Fabricius)	Df, Vm
	c. *Neonympha areolatus* (J. E. Smith)	Df, Vf
32	a. *Danaus plexippus* (L.)	Dm, Df
See Fig. 3	b. *Pyrgus communis* (Grote)	Dm, Df
	c. *Amblyscirtes vialis* (W. H. Edwards)	Df
33	a. ?*Oligoria maculata* (W. H. Edwards)	Dm
	b. *Panoquina ocola* (W. H. Edwards)	Df
	c. ?*Euphyes vestris* (Boisduval)	Df, Vm
	d. *Danaus gilippus* (Cramer)	Dm
	e. *Erynnis brizo* (Boisduval & Le Conte)	Df
	f. ?*Erynnis zarucco* (Lucas)	Df
34	a. *Vanessa atalanta* (L.)	Df, Vf
	b. *Phyciodes tharos* (Drury)	Dm, Df
	c. *Erynnis martialis* (Scudder)	Df
	d. *Limenitis archippus* (Cramer)	Dm, Vm

Table 1. Continued

Drawing no.	Species Depicted	Figures
35	a. *Agraulis vanillae* (L.)	Dm, Df, Vf
	b. *Nastra lherminier* (Latreille)	Dm, Df
	c. *Lerema accius* (J. E. Smith)	Dm, Df
36	a. *Cercyonis pegala* (Fabricius)	Dm, Df
	b. *Thorybes pylades* (Scudder)	Dm, Vm
	c. *Megisto cymela* (Cramer)	Df
	d. *Hesperia attalus* (W. H. Edwards)	Dm
37	a. *Asterocampa clyton* (Boisduval & Le Conte)	Dm
	b. *Ascia monuste* (L.)	Dm
	c. *Euptoieta claudia* (Cramer)	Dm
38	a. *Asterocampa celtis* (Boisduval & Le Conte)	Dm, Vm
	b. *Anatrytone logan* (W. H. Edwards)	Df, Vf
	c. *Hylephila phyleus* (Drury)	Dm, Df
	d. *Atrytone arogos* (Boisduval & Le Conte)	Df, Vf
	e. *Junonia coenia* Hübner	Df
39	a. *Atlides halesus* (Cramer)	Dm, Df
	b. *Feniseca tarquinius* (Fabricius)	Dm, Df
	c. *Calephelis virginiensis* (Guérin-Méneville)	Df
40	a. *Polygonia interrogationis* (Fabricius)	Dm, Vm
	b. *Calycopis cecrops* (Fabricius)	Dm, Df
	c. *Cupido comyntas* (Godart)	Dm
41	a. *Autochton cellus* (Boisduval & Le Conte)	Dm
	b. *Achalarus lyciades* (Geyer)	Dm
	c. *Thorybes bathyllus* (J. E. Smith)	Dm
	d. *Thorybes* sp.	Dm, Df (2)
	e. *Erynnis zarucco* (Lucas)	Dm
	f. *Epargyreus clarus* (Cramer)	Dm
	g. *Urbanus proteus* (L.)	Dm
42	a. *Zerene cesonia* (Stoll)	Dm, Df, Vm
	b. *Satyrium calanus* (Hübner)	Dm, Df, Vm
	c. *Enodia portlandia* (Fabricius)	Df, Vf
43	a. *Phoebis sennae* (L.)	Dm, Df
	b. *Vanessa virginiensis* (Drury)	-Dm, Vf
44	a. *Eurema daira* (Godart)	Dm, Df
	b. *Abaeis nicippe* (Cramer)	Dm
	c. *Abaeis nicippe* (Cramer) (yellow form 'flava' Strecker)	Df
	d. *Pyrisitia lisa* (Boisduval & Le Conte)	Dm, Df

order, but simply grouped into visually pleasing compositions. Abbot employed this same format for his 1827 and 1828 insect volumes.

At least 64 species of butterflies are portrayed (Table 1), including some that Abbot rarely figured, such as *Panoquina ocola* (W. H. Edwards), *Poanes yehl* (Skinner), *Hemiargus ceraunus* (Fabricius), and *Calephelis virginiensis* (Guérin-Méneville). The single figure of *Amblyscirtes vialis* (W. H. Edwards) (Fig. 3) is his only known representation of this species. Characteristic of Abbot's methods, duplicate figures are shared among the 1827, 1828, and 1830 volumes. As expected, the 1828 and 1830 volumes are most alike. The 1828 volume portrays 54 of the same butterfly species as the 1830 volume, and three compositions are exact duplicates. The 1827 volume contains only 43 of the same butterfly species as the 1830 volume, and no compositions are duplicated.

Abbot was 79 years old in 1830. The insect drawings that he prepared during this period are generally less precise than his earlier watercolors. Some of the figures are feebly rendered and difficult to identify, but this relaxed style is not unusual among Abbot's insect illustrations (Calhoun 2007). It has recently been shown that the quality of his artwork varied considerably during the six decades that he lived in America (e.g. Rogers-Price 1983, Simpson 1984, Calhoun 2006, 2007). Abbot is not known to have produced any more insect drawings of this type after 1830. He seems to have ceased working about five years later at the age of 84.

The 1830 insect watercolors were created by a remarkable artist in the twilight of his career. They journeyed from America to England, then back again. In the process they passed through the hands of three legendary nineteenth century naturalists, bridging the scientific divide between the Old and New Worlds. No longer can these illustrations be regarded as "scarcely the least value."

ACKNOWLEDGEMENTS

I would like to thank the librarians of the Houghton Library (Harvard University), especially Hope Mayo and Caroline Duroselle-Melish, for assistance during my visit and the permission to reproduce Abbot's artwork. Thomas Ford arranged for photography. Robert Young and Dana Fisher (Ernst Mayr Library, MCZ, Harvard University) kindly provided access to manuscripts in their care and granted permission to quote from them. David Faulds (Woodruff Library, Emory University) and Michael Rose (Kenan Research Center, Atlanta History Center) accommodated my visits and answered many questions. Finally, I offer my gratitude to James K. Adams (Dalton College) and an anonymous review for their valuable comments.

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Received for publication 20 May, revised and accepted 10 August 2007

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THE GENUS *PARIDES*. BUTTERFLIES OF THE WORLD, SUPPLEMENT 13, by Tommaso Racheli. Supplement 13: 116 pages, 82 figures; 24 × 34 cm; ISBN 3-937783-24-5; EUR 70.00. Antiquariat Goecke & Evers, Keltern. Publication date: 15 December 2006. Additional information of the "Butterflies of the World" series can be obtained at www.insecta.de/shop/openstore.htm.

Tommaso Racheli's "The Genus *Parides*" is Supplement 13 of Bauer & Frankenbach's series "Butterflies of the World". Racheli's monograph is matched with a pictorial catalogue in the same series, "Papilionidae XIII. *Parides*. Butterflies of the World. Part 26." by Edwin Möhn, also published in 2006. The "Butterflies of the World" series has been published since 1998, and by now covers most major groups of butterflies. Most volumes are published both in German and English editions, and usually their text component is very short. Some parts, however, have a more detailed text which is published as a Supplement, and this is the case for Racheli's volume.

Over the years, Dr. Racheli has published many important studies about the New World Troidini butterflies of genera *Battus* and *Parides*. At present, he is mainly pursuing research in Ecuador and Laos. His supplement 13 on *Parides* summarizes and updates its taxonomic treatment, which has not undergone extensive revision since the 1994 book by Tyler, Brown and Wilson.

Racheli's monograph begins with a review of the importance of Papilionidae swallowtail butterflies in many fields, from genetics to population dynamics studies, and introduces the genus *Parides* as "an unended quest". In "The enigma of *Parides*", the author addresses the geographical variation of this Central and South American group of species, with the informal style of a professor telling an interesting story about the huge taxonomic complexity of this genus. Avoiding additional discussion of this controversial field, Racheli follows the nomenclatural treatment of Tyler *et al.* (1994), while his systematic arrangement follows the cladistic hypothesis proposed by Racheli & Olmisani (1998).

In addition to a monographic taxonomic treatment, Tommaso Racheli's book covers several other aspects of *Parides*, such as synonymies, general range, range maps for each nominate subspecies, descriptions of the adults, illustrations and descriptions of the genitalia (mainly the male), pre-imaginal stages, and general observations. Even if there were nothing else of interest in the Supplement, which is not the case at all, the "Historical Notes" would be worth reading. The author does an excellent and critical job of revising the historical and taxonomic changes applied to the Papilionidae since Haases's 1893 study, the first to divide *Papilio* into three main categories. The classification of *Parides* is carefully reviewed, contrasting the results obtained from different character sources, and discussing the inherent problems of individual analyses.

To address the natural history of the Troidini, the author discusses the available data for every developmental phase of these butterflies – eggs, larvae, pupae and adults. An abridged table containing the *Aristolochia* host plants used by each *Parides* species is presented, with some modifications and additions since Tyler *et al.* (1994)'s book. Focusing on the adults, a series of morphological structures containing important taxonomic characters is discussed. There is also an impressively detailed table featuring the male genitalia traits of each and every species of *Parides*, addressing the variation of this character along the geographical distribution of some species. For those interested in the morphological study of this group, this is an outstanding resource. Other important information on *Parides* is also made available in the Supplement: habitats, eco-ethology, phenology, and aposematic coloring.

Racheli also recovers the refuge theory in order to propose a biogeographical hypothesis for the New World Troidini. Though this theory has received much criticism, Racheli's discussion on Troidini shows that this issue still deserves further investigation.

In the "Systematic account" section, the author thoroughly characterizes the distribution of each species using detailed, clear and comprehensive maps. Racheli's book provides each taxon with a careful description of its type and distribution, as well as commentaries, with details on each subspecies of each species. Upon reading this section, one will notice the care with which the reader is offered full information towards best identifying this complex Papilionidae group. The species presentation follows the clade sequence put forth in the phylogenetic hypothesis of Racheli & Olmisani (1998), and differs from the order followed by Möhn (2006) in the second part of the *Parides* treatment in the series. This makes simultaneous searching of text and figures a bit confusing. For this reason, it would have been helpful if both authors had followed the same order in their presentation of the *Parides* species. Also, the two authors are not always in accordance in their division of

species into subspecies, as is the case of *P. sesostris zischrai* – considered a distinct subspecies by Möhn and synonymous with *P. sesostris sesostris* by Racheli.

As Möhn's volume features a brief abstract about each one of the species and subspecies, this volume, by itself, can be considered an extraordinary field guide to *Parides* identification. It is important to acknowledge the careful work that was performed in order to catalogue the figures of *Parides* species and subspecies. Möhn's illustrations are pleasant, yet remain faithful to scientific accuracy, and the care with which small wing pattern differences along the geographical distribution of each entity is shown is impressive. The pictures make it possible to understand how difficult it is to identify *Parides* species and subspecies, due both to their intraspecific variability and their interspecific similarity.

Racheli's monograph on *Parides* is amusing reading for both Lepidopteran academic scientists and butterfly enthusiasts. The Supplement alone is a worthwhile purchase and the concurrent acquisition of the Möhn's volume is recommended, but not mandatory, to be fully updated on this butterfly group.

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Received 15 October 2007; revised and accepted 30 October 2007

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BUTTERFLIES OF WEST AFRICA, 2 volume set, by Torben B. Larsen. 865 pages, 125 plates; 11.3 × 8.4 in; ISBN 10: 8788757439 and 13: 978-8788757439; USD $229. Apollo Books; Publication date: October 2005.

This impressive two-volume work illustrates and guides the reader through the extraordinary butterfly fauna of fifteen countries comprising tropical West Africa. From savannah to rain forest, each of the roughly 1500 species is described in detail with notes on identification, habits, early stages and distribution. The author's enjoyable writing style, and first hand accounts through his extensive field work takes the reader into the tropics for a unique perspective on the lives of these fascinating and diverse creatures.

The first volume contains introductory chapters covering evolution, historical accounts of past researchers, a global perspective of the region's fauna, the biogeographical regions of West Africa, ecology, migration, extinction and conservation. A color map of the vegetation zones and current political boundaries of Africa is included. The bulk of the text is devoted to species accounts in a well-organized structure. Distinguishing features of tribes and genera are discussed followed by species accounts. Numerous line drawings and black and white photographs punctuate the text. The author has gone to great lengths to allow the reader to identify even difficult groups through the use of illustrations conveniently located within the text.

The second volume contains 130 stunning plates depicting approximately 3800 specimens in full color. Upper- and undersides are depicted for most species. Specimens are clearly identified by scientific name and a species number corresponding with the species accounts. Country of origin for each of the specimens illustrated is included. The volumes are well indexed by genera and species.

Several impressive regional volumes have been published in recent years, including Parson's "Butterflies of Papua New Guinea" and Mayberry's "Butterflies of Australia". Larsen's "Butterflies of West Africa" continues the trend of excellence and gives the reader a comprehensive identification guide and in-depth understanding of life histories, habits, and a historical account of the butterfly fauna of West Africa. Considering the number of species treated, this work is truly monumental.

"Butterflies of West Africa" is a must for anyone interested in the butterfly fauna of Africa and perhaps sets a new standard for any regional identification guide. Readers interested in butterflies, especially tropical butterflies, ecology or conservation will find this work fascinating.

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Received 27 February 2007; revised and accepted 30 October 2007

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Date of Issue (Vol. 61, No. 4): 14 December 2007

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